Flower Development and Photoperiodic Control of Flowering in Rice

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Abstract: Floral transition, which is referred to as a plant's transition from vegetative stage to reproductive stage, is considered to be a critical developmental switch in higher plants, for a timely flowering is a major factor of reproductive success. Endogenous and environmental cues, such as photoperiod, light quality, plant hormones concentrations and temperature, provide information to the plants whether the environment is favorable for flowering. These cues promote, or prevent, flowering through a complex genetic network, mediated by a careful orchestration of temporal and spatial gene expression. One of such cues is photoperiod. Rice (Oryza sativa L.) serves as a powerful model species for the understanding of flowering in higher plants, including flower development and photoperiodic control of flowering. In this review, we overviewed and discussed the flower development and its model. We also overviewed the photoperiodic pathways in rice flowering control, and summarized the pathways at molecular level.

Key words: rice; flowering time gene; floral transition; flower development; photoperiod

Higher plants undergo a series of developmental phases during their life cycles (Cockram et al, 2007). In general, plants go through four major phases (Bäurle and Dean, 2006). Germination is the first phase that plants develop from embryonic to post-embryonic state. The second phase known as vegetative phase change, is characterized by a transition from a juvenile state into an adult state. The third phase is floral transition, during which a plant transits from a vegetative stage to a reproductive stage. The last phase is senescence (Bäurle and Dean, 2006). Floral transition is one of the major phase changes during a plant’s life cycle. It is intensively regulated by a range of environmental signals, such as daylength, or photoperiod, light intensity, light quality (spectrum composition) and ambient temperature, as well as endogenous signals mediated by plant hormones (Yong et al, 2000; Albani and Coupland, 2010). In addition, the age of the plant, cold temperature and stress also have effects on the timing and quality of floral transition (Levy and Dean, 1998; Albani and Coupland, 2010). These factors affect floral transition through a carefully-orchestrated signal transduction network (Simpson et al, 1999; Albani and Coupland, 2010; Cui et al, 2010).

Flower development and its model

Flowering process involves the transition of different developmental patterns of floral development, the occurrence and development of flower organs and interaction of inner signals under the control of environmental and endogenous cues (Yong et al, 2000). One of the most important contributions to the understanding of flower development is provided by the classic ABC model for floral organ identity (Theissen and Saedler, 2001). According to the ABC model, a flower is composed of four concentric floral whorls which are determined by the combined functions of three classes of homeotic genes (named functions A, B and C) (Ciaffi et al, 2011). The class A genes specify the organs of whorl 1, class A and B genes jointly specify the organs of whorl 2, class B and C genes specify the organs of whorl 3, and finally class C genes specify the organs of whorl 4. This model has been further extended to the ABCDE model which includes class D and class E genes (Immink et al, 2010; Ciaffi et al, 2011).

The ABCDE model, which explains the specification of floral organ identity in Arabidopsis thaliana,
provides a useful framework for explaining the genetic control of flower development in rice (Fig. 1) (Ferrario et al., 2004; Soltis et al., 2007; Theissen and Melzer, 2007; Thompson and Hake, 2009; Litt and Kramer, 2010). Flower of rice has greatly diverged from that of *A. thaliana*. Rice has a peculiar floral structure called floret (Yoshida and Nagato, 2011). The floret contains carpels, stamens, two lodicules, and a palea and lemma, but lacks petals and sepals. Several genes required for floral development in rice correspond to the class A, B, C, D and E genes of *A. thaliana* (Ciaffi et al., 2011). Both conservation and diversification of the genes included in the ABCDE model of floral development in *A. thaliana* and rice can be observed.

Class A genes in rice include three FRUITFULL (FUL)-like genes *OsMADS14*, *OsMADS15* and *OsMADS18*. *OsMADS14* (rice FUL1-like gene) is expressed only in inflorescence and developing caryopses (Pelucchi et al., 2002). The expression of *OsMADS15* (rice FUL2-like gene) initially occurs throughout the spikelet meristem, and then moves to vegetative organs, including lodicules, palea, lemma and glumes (Kyozuka et al., 2000). Over-expression of *OsMADS18* (rice FUL3-like gene) causes an early flowering phenotype and early initiation of axillary shoot meristems. It indicates that *OsMADS18* acts as a promoter in the differentiation activity of the vegetative shoot (Fornara et al., 2004).

The PI-like genes *OsMADS2* and *OsMADS4*, and the AP3-like gene *MADS16/SWP1 (SUPERWOMAN1)* are class B genes (Ambrose et al., 2000; Nagasawa et al., 2003; Arora et al., 2007; Xu and Kong, 2007). In *osmads16/superwoman1 (spw1)* of rice, stamens are replaced by carpels and lodicules (Ambrose et al., 2000; Nagasawa et al., 2003). It indicates that *OsMADS16/SPW1* is required for the development of stamens. *OsMADS2* is important for the lodicule development and *OsMADS4* specifies the lodicule identity. Furthermore, yeast two-hybrid experiments of *OsMADS2* and *OsMADS4* proteins showed that *OsMADS4* and *OsMADS2* interacted with SPW1. Thus, the unequal redundancy of the class B genes occurred. It is noteworthy that petals are replaced by sepals in class B mutants of *A. thaliana* (Ciaffi et al., 2011). Palea and lemma of rice are homologous to sepals of *A. thaliana*.

Class C genes comprise *OsMADS3* and *OsMADS58*, two rice co-orthologous genes of *GAMOUS* (a floral homeotic gene). *OsMADS3* specifies the stamen identity and plays a more relevant role than *OsMADS58* in controlling the ectopic expression of lodicule formation. *OsMADS58* has a stronger role in regulating carpel

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**Fig. 1.** ABCDE model of flower development in *Arabidopsis thaliana* (a) and rice (b) (Ciaffi et al., 2011). According to the basic ABC model, the class A genes specify the organs of whorl 1, class A and B of whorl 2, class B and C of whorl 3, and class C of whorl 4. The extended ABCDE model includes class D genes promoting ovule identity and class E genes acting as cofactors for the class A, B, C, and D genes and required for the development of all the categories of floral organs. The function domains are indicated by colors: A, red, B, yellow, C, purple, D, green and E, light-blue. The ABCDE schemes include the names of the genes assigned in each species to one of the five functional classes. In the ABCDE models of *Arabidopsis thaliana* (a) and rice (b), the genes involved in the regulation of floral organ identity genes are also indicated. Symbol '?' indicates uncertainty about the A and E functions in rice.
morphogenesis and determines floral meristem determinacy in both whorls 3 and 4 (Ciaffi et al, 2011). Dreni et al (2007) indicated that OsMADS3 and OsMADS58 might have a redundant function in specifying floral organ identity, including the carpel. Both OsMADS3 and OsMADS58 show some typical functions of class C genes, similar to those for AG, although they are functionally diversified, with predominant functions in different whorls (Ciaffi et al, 2011). However, the exact genetic control underlying the functional diversification of these two class C genes still needs further investigation.

OsMADS13 and OsMADS21 are two class D genes (Dreni et al, 2007). The osmads21 mutant displayed a normal phenotype, and the osmads13/osmads21 double mutant showed disordered phenotype. The loss function of OsMADS21 did not alter the osmads13 phenotype (Dreni et al, 2007), which suggest that only OsMADS13 is specifically expressed in the ovule primordia and required for specification of ovule identity (Lopez-Dee et al, 1999; Dreni et al, 2007; Yoshida and Nagato, 2011).

Class E genes have two major type genes, the SEP1/2/4-like genes (LOFSEP) and the SEP3-like genes (Malcomber and Kellogg, 2005; Zahn et al, 2005). SEP1/2/4-like genes include OsMADS1 (also known as LHSI), OsMADS3 and OsMADS34. SEP3-like genes include OsMADS7 (also known as OsMADS45) and OsMADS8 (also known as OsMADS24). OsMADS1 is firstly expressed in the spikelet meristem and OsMADS1 plays a key role in the specification floral organs at later stages of development (Chung et al, 1994; Prasad et al, 2001). Ectopic expression of OsMADS1 results in homeotic transformation of glumes into lemma-like organs (Prasad et al, 2001). Overexpression of OsMADS5 promotes early flowering in rice but does not affect floral morphology (Jeon et al, 2000). Gao et al (2010) showed that OsMADS34 played a crucial role in regulating inflorescence and spikelet architecture. OsMADS7/45 and OsMADS8/24 were expressed only in reproductive organs such as inflorescences (Pelucchi et al, 2002). The SEP-like proteins OsMADS7 and OsMADS8 interact with other proteins, including OsMADS18, OsMADS16 and OsMADS13 (Favaro et al, 2003; Kater et al, 2006). The SEP-like proteins OsMADS7 and OsMADS8 share similar interaction pattern with OsMADS1. These three proteins are able to form homodimers (Cui et al, 2010). Interestingly, simultaneous knockdown of the four rice SEP-like genes OsMADS1, OsMADS5, OsMADS7 and OsMADS8 results in the homeotic transformation of all floral organs except the lemma into leaf-like organs, which mimics the phenotype observed with the sep1 sep2 sep3 sep4 quadruple mutant of A. thaliana (Cui et al, 2010). These findings indicate that the four rice genes cover the full class E floral homeotic function (Ciaffi et al, 2011).

Besides the above five class genes, several genes regulating the flower development and determining floral meristem fate have also been identified in rice (Ciaffi et al, 2011). ABBREVIATED PANTHEON ORGANIZATION 1 (APO1) and OPEN BEAK (OPB) are involved in the regulation of class B and C genes, respectively. APO1 encodes an F-box protein closely related to UNUSUAL FLORAL ORGAN (UFO). APO1 regulates class C genes (OsMADS1) and DROPPING LEAF (DL) or it has some class C functions (Ciaffi et al, 2011). OPB encodes a transcription factor with a zinc-finger motif (Horigome et al, 2009). OPB would be required for the proper expression of SPW1, for the expression of the class B gene SUPERWOMAN1 (SPW1) decreases in the opb mutant due to the overlapped expression domains of OPB and SPW1.

DL, a member of the YABBY gene family, is responsible for the specification of carpel identity and meristem determinacy, and also has antagonistic interaction with class B genes (Ciaffi et al, 2011). The analysis of double mutants indicates that OsMADS6 specifies the palea identity, most likely through repressing the expression of DL in the palea. It also regulates the lodicule development by interacting with SPW1, specifies the stamen, carpel and meristem identities with OsMADS3 and OsMADS58. OsMADS6 defines the carpel/ovule development and the floral meristem determinacy with OsMADS13, and finally acts together with DL in terminating the floral meristem (Li et al, 2011). In addition, RETARDED PALEA1 (REP1) encodes a putative protein belonging to a plant-specific TCP transcription factor family (Yuan et al, 2009). In the rep1 mutant, palea growth is delayed and reduced, and cell differentiation is strongly affected. It suggests that REP1 plays a specific role in the regulation of palea development (Yuan et al, 2009).

Photoperiodic control of flowering in rice

Plants require several environmental cues and internal factors to signal flowering (Komeda, 2004; Albani and Coupland, 2010), and one of such cues is photoperiod. Plants can be categorized according to their flowering response to different photoperiods, though accurately
speaking, the regulatory mechanism is determined by the length of darkness. Short-day plants (SDPs) flower when the night is longer than a critical length. Day-neutral plants flower regardless of the night length, their flowering pattern is not based on photoperiodism. In contrast, long-day plants (LDPs) require a shorter darkness in each 24-hour period to induce flowering (Thomas and Vince-Prue, 1997).

A. thaliana serves as a model plant for understanding of photoperiodic control of flowering in LDPs. In contrast, rice is a facultative short-day plant. The identification of a large range of rice mutants and subsequently the cloning of flowering-related genes (Table 1) have greatly assisted the understanding of the control system for flowering (Sun et al, 2007; Li et al, 2009; Wei et al, 2010). Several evolutionarily conserved genes and uniquely acquired genes are involved in the photoperiodic control of flowering in rice (Matsubara et al, 2008; Komiya et al, 2009; Tsuji et al, 2011). Here we will focus on the known photoperiodic pathways which can also be divided into the activation and suppression pathways in the rice flowering (Fig. 2).

**Table 1. Flowering time control genes cloned in rice.**

<table>
<thead>
<tr>
<th>Gene</th>
<th>Gene symbol</th>
<th>Predicted gene product</th>
<th>Function</th>
<th>Chr*</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>DTH8</td>
<td>Days to heading on chromosome 8</td>
<td>a putative HAP3 subunit of the CCAAT-box-binding transcription factor</td>
<td>a flowering repressor</td>
<td>8</td>
<td>Wei et al, 2010</td>
</tr>
<tr>
<td>Ehd1</td>
<td>Early heading date 1</td>
<td>B-type response regulator</td>
<td>a rice-specific flowering regulator</td>
<td>10</td>
<td>Yassuyuki et al, 2009</td>
</tr>
<tr>
<td>Ehd2/</td>
<td>Early heading date 2/</td>
<td>a Cys2His2-type zinc finger protein</td>
<td>a flowering promoter</td>
<td>10</td>
<td>Wu et al, 2008</td>
</tr>
<tr>
<td>RID1/Osd1</td>
<td>Rice indeterminate 1</td>
<td>a Cys2His2-type zinc finger protein</td>
<td>a flowering promoter</td>
<td>10</td>
<td>Wu et al, 2008</td>
</tr>
<tr>
<td>Ehd3</td>
<td>Early heading date 3</td>
<td>a PHD finger gene</td>
<td>a floral promoter</td>
<td>8</td>
<td>Matsubara et al, 2008, 2011</td>
</tr>
<tr>
<td>Ghd7</td>
<td>Grain number, plant height, and heading date 7</td>
<td>a CCT domain protein</td>
<td>delays heading under LD</td>
<td>3</td>
<td>Xue et al, 2008</td>
</tr>
<tr>
<td>Ghd8</td>
<td>Grain yield, heading date, and plant height 8</td>
<td>encodes OsHAP3 subunit of a CCAAT-box binding protein (HAP complex)</td>
<td>delays flowering under LD, promotes flowering under SD</td>
<td>8</td>
<td>Yan et al, 2011</td>
</tr>
<tr>
<td>Hd1</td>
<td>Heading date 1</td>
<td>B-box, CCT-domain</td>
<td>a flowering repressor</td>
<td>6</td>
<td>Kim et al, 2008</td>
</tr>
<tr>
<td>Hd3a</td>
<td>Heading date 3a</td>
<td>a member of putative kinase inhibitor PEBP family</td>
<td>a flowering repressor</td>
<td>6</td>
<td>Tsuji et al, 2011</td>
</tr>
<tr>
<td>OsCOL4</td>
<td>Oryza sativa CONSTANS-like 4</td>
<td>a member of the CONSTANS-like (COL) family</td>
<td>a flowering repressor</td>
<td>2</td>
<td>Lee et al, 2010</td>
</tr>
<tr>
<td>OsGI</td>
<td>Oryza sativa Gigantea</td>
<td>an orthologue of GI gene</td>
<td>an orthologue of GI gene</td>
<td>1</td>
<td>Kim et al, 2008</td>
</tr>
<tr>
<td>OsLFL1</td>
<td>Oryza sativa LEC2 and FUSCA3 like 1</td>
<td>a B3 domain transcription factor</td>
<td>a flowering repressor</td>
<td>1</td>
<td>Peng et al, 2007</td>
</tr>
<tr>
<td>OsMADS14</td>
<td>rice MADS-box protein gene 14</td>
<td>an ortholog of AP1, MADS box protein</td>
<td>a flowering activator</td>
<td>3</td>
<td>Kim et al, 2007</td>
</tr>
<tr>
<td>OsMADS15</td>
<td>rice MADS-box protein gene 15</td>
<td>MADS box protein</td>
<td>a flowering activator</td>
<td>7</td>
<td>Komiya et al, 2009</td>
</tr>
<tr>
<td>OsMADS51</td>
<td>rice MADS-box protein gene 51</td>
<td>MADS box protein</td>
<td>a flowering activator</td>
<td>1</td>
<td>Kim et al, 2007</td>
</tr>
<tr>
<td>OsMADS50</td>
<td>rice MADS-box protein gene 50</td>
<td>homologous to Arabidopsis SOC1</td>
<td>a positive regulator for flowering</td>
<td>3</td>
<td>Ryu et al, 2009</td>
</tr>
<tr>
<td>OsMADS56</td>
<td>rice MADS-box protein gene 56</td>
<td>an orthologue of SOC1/AGL2 red light/far-red light receptors</td>
<td>delays flowering under LD regulates Hdl-mediated expression of Hda3</td>
<td>10</td>
<td>Ryu et al, 2009</td>
</tr>
<tr>
<td>PHYB</td>
<td>Phytochrome B</td>
<td>an orthologue of SOC1/AGL2 red light/far-red light receptors</td>
<td>delays flowering under LD regulates Hdl-mediated expression of Hda3</td>
<td>3</td>
<td>Ishikawa et al, 2011</td>
</tr>
<tr>
<td>RFT1</td>
<td>RICE FLOWERING LOCUS T1</td>
<td>an orthologue of FT, FT-like family genes</td>
<td>a flowering repressor</td>
<td>6</td>
<td>Komiya et al, 2009</td>
</tr>
</tbody>
</table>

*Chromosome where the gene locates. SD, Short-day; LD, Long-day.

**Activation pathways and flowering-time control in rice**

Under short-day (SD) conditions, flowering is promoted by *Heading date 1* (*Hd1*, an orthologue of CO, and a member of the CONSTANS-like (COL) family) and *Early heading date 1* (*Ehd1*, a B-type response regulator) through the activation of FT-like genes (Matsubara et al, 2011). *OsGI* (an orthologue of Gigantea) up-regulates the expression of *Hd1* which is known to be a key integrator of the photoperiod pathway in rice (Kim et al, 2008) and acts upstream of *Ghd8* (*Grain yield, heading date, and plant height* 8, Yan et al, 2011). *Ghd8* encodes the *OsHAP3* subunit of a CCAAT-box binding protein and up-regulates the expression of *Heading date 3a* (*Hd3a*, a rice ortholog of FT) and major flowering promoter of rice under SD conditions) in *Ghd8*-mediated flowering pathways (Kim et al, 2007; Yan et al, 2011). Moreover, *OsGI* regulates the expression of *OsMADS51* (a rice MADS-box protein gene). Both of *OsMADS51* and *Ghd8* regulate the
expression of Ehd1 which acts on Hd3a and affects flowering in rice. It may indicate that Ghd8 links the Hd1- and Ehd1-dominated pathways to regulate flowering (Yan et al, 2011). Moreover, Ehd1 positively regulates Hd3a and promotes floral transition preferentially even in the absence of functional alleles of Hd1 (Izawa et al, 2003; Doi et al, 2004). Thus, Hd1 and Ehd1 function redundantly. RICE FLOWERING LOCUS T1 (RFT1, an FT-like gene) could promote flowering in the absence of Hd3a for RFT1 becomes activated when Hd3a expression is knocked down by RNAi. Double RFT1-Hd3a RNAi plants can not flower even at 300 d after sowing, which reveals that Hd3a and RFT1 are essential for flowering under SD conditions (Komiya et al, 2009). In addition, Ehd2/RID1/OsID1 (a rice ortholog of maize INDETERMINATE1) and Early heading date 3 [Ehd3, a plant homeodomain (PHD) finger gene], as well as OsMADS51, promotes FT-like genes through the up-regulation of Ehd1 under SD conditions. RID1/OsId1/Ehd2, which encodes a Cys2/His2-type transcription factor with zinc finger motifs, functions as the master switch for the floral transition. Ehd3 encodes a nuclear protein that contains a putative transcriptional regulator with two plant homeodomain PHD finger motifs. Ehd3 plays a central role in the up-regulation of Ehd1 which is considered as a promoter in the photoperiod pathway (Matsubara et al, 2011). It can be derived that OsGI, Hd1, OsMADS51, Ehd2/RID1/OsID1, Ehd1, Ghd8, Hd3a, OsMADS14 and OsMADS15 consist of an activation pathway under SD conditions, and Hd1/Ehd1-RFT1-OsMADS14/OsMADS15 is an alternative activation pathway while Hd3a is absent under SD conditions (Fig. 2).

Under long-day (LD) conditions, OsMADS50 (a close homolog to SOC1 in A. thaliana) acts as a promoter in the floral transition in response to LD by suppressing the expression of OsLFL1 (a B3 domain transcription factor) which is a repressor of Ehd1 (Peng et al, 2007; Komiya et al, 2009). Ehd1 up-regulates the positive regulator RFT1 (Komiya et al, 2009). RFT1 protein is produced in leaves and then moves to the shoot apical meristem where floral transition is induced by the RFT1 protein. After the transition, OsMADS14 and OsMADS15 which are regulated by RFT1, initiate the formation of floral organs. Therefore, OsMADS50-OsLFL1-Ehd1-RFT1-OsMADS14/OsMADS15 constitutes an LD activation pathway (Fig. 2). Ghd7 (Grain number, plant height, and heading date 7) encodes a transcription factor with a CCT motif. It acts as a floral repressor by down-regulating Ehd1 through an independent pathway (Xue et al, 2008). The Ghd7-independent pathway is regulated by Ehd3 which up-regulates Ehd1 under SD conditions. It may indicate that Ehd3-Ghd7-Ehd1-RFT1 is another activation pathway of flowering genetic control under LD conditions (Fig. 2). Ehd2/RID1/OsID1 is a positive regulator of Ehd1, which is independent from OsMADS50 (Komiya et al, 2009). It indicates that Ehd2/RID1/OsID1-Ehd1-RFT1 is also an activation pathway under LD conditions.

**Suppression pathways and flowering-time control in rice**

No suppression pathway for flowering under SD conditions is reported in rice up to now. Under LD conditions, signals from light are received by OsGI which regulates the diurnal expression of Hd1 (Kim et al, 2008). Hd1 represses Hd3a expression as a repressor in response to photoperiod changes. This activity may be affected by phytochrome signaling and CK2α activity. PHYB, which codes for a plant photoreceptor, regulates Hd1-mediated expression of Hd3a (Yano et al, 2000; Hayama et al, 2003; Ishikawa et al, 2011; Matsubara et al, 2011). CK2α activity also involves in...
the Hd1-mediated expression and enhances the repressor function of Hd1, thus causing delayed flowering. It suggests that OsGI-Hd1-Hd3a is a long-day suppression pathway (Doi et al, 2004).

Ehd1 and Hd1 function antagonistically because Hd1 represses the expression of Hd3a whereas Ehd1 promotes it (Izawa et al, 2003; Doi et al, 2004). Ehd1 is negatively regulated by multiple factors including Ehd2/RID1/OsID1, Ghd7, OsCOL4, Days to heading on chromosome 8 (DHT8), PHYB and OsMADS56 under LD conditions (Matsubara et al, 2008; Wu et al, 2008; Xue et al, 2008; Yasuyuki et al, 2009; Tsuji et al, 2011). It indicates that Ehd1 integrates multiple signals in the flowering control. OsCOL4, which is a member of the COL family, is a constitutive suppressor of flowering in rice under LD conditions (Lee et al, 2010). OsCOL4 null mutants flowered early under LD condition while OsCOL4 activation-tagging mutants (OsCOL4-D) flowered late. The expression of Ehd1 and Hd3a were increased in the oscol4 mutants, which indicates that OsCOL functions upstream of Ehd1. In the osphyB mutants, the transcript of OsCOL4 was decreased, indicating OsCOL4 functions downstream of OsPHYB. These results suggest that PHYB acts as a negative regulator of LD-flowering through suppression of Ehd1 expression regulated by OsCOL4. DTH8 probably plays an important role in the signal network of photoperiodic flowering as a novel suppressor by down-regulating the transcriptions of Ehd1 and Hd3a under LD condition (Wei et al, 2008). Ghd7 acts as a floral repressor in a unique pathway by down-regulating Ehd1 (Xue et al, 2008). OsMADS56 inhibits flowering probably by binding OsMADS50 to form a complex (Ryu et al, 2009). Thus, OsMADS56 functions as a repressor through OsLFL1-Ehd1 in flowering control. Together, the results suggest that these suppressors are involved in the down-regulation of Ehd1. Thus, they may converge to another LD suppression pathway through Ehd1-mediated expression of Hd3a and cause delayed flowering (Fig. 2).

**PERSPECTIVE**

The molecular genetic dissection of *A. thaliana* and rice has provided models to explain the control of flowering time in higher plants (Yano et al, 2000; Izawa et al, 2003; Hayama and Coupland, 2004). The ancestor of rice diverged from that of *A. thaliana* around 200 million years ago. Photoperiodic responses in *A. thaliana* and rice are perceived by the leaves. Rice shows several differences in flowering response. Firstly, long daylight exposure represses flowering in rice (Hayama et al, 2003). Secondly, the night break response to the light exposure for a short period (about 10 min) at night suppresses flowering. Night break can significantly delay flowering of SDPs and can cancel the effect of dark period (Ishikawa et al, 2005; Tsuji et al, 2011). The differences in flowering response between rice and *A. thaliana* mainly lie in the distinct regulation of their respective regulator genes and the expression of flowering time genes under SD and LD conditions (Peng, 2006). The diversification between *A. thaliana* and rice for floral identity genes suggests that the regulation of homoeotic gene expression would not be tightly conserved. The current model of flower development still needs refinement. Different species appear to have different adaptation strategies to integrate the environmental cues in the genetic networks that control flowering, which will become one of the focuses in the future research on rice flowering mechanism.

Rice is cultivated in a wide range of geographical regions. The major reason is attributed to the diversification of flowering time (Araki, 2001). With the completion of rice genome sequencing, it is found that the majority of homologs of *A. thaliana* flowering time genes can be found in rice genome. Analysis on the function of homologous genes has been an efficient approach to draw a clear research framework for studying flowering time control in rice. The study of the common and unique characteristics of flower development in different species can not only help to get better understanding of the network system, but also reveal the origin and evolution of flower. Multiple genetic pathways ultimately converge to regulation of the expression of a series of flowering genes. Recent progress in rice has identified key regulators determining the photoperiod in cereals (Matsubara et al, 2008; Wu et al, 2008; Wei et al, 2010; Yan et al, 2011). However, several important problems remain unresolved due to the complexity and multiple genetic regulations of flowering. The molecular mechanism underlying the setting of critical night-length is still a mystery. It is not clarified how Hd1 shows different functions under LD and SD conditions. Few cases about the function of photoreceptors in rice are reported. Function identification of many genes implicated in central clock is also rarely documented (Izawa et al, 2003; Peng, 2006; Harmer, 2009). Scientists have conducted research using forward-
genetic approaches to identify variations in flowering time mutants and flowering time genes. Reverse genetic approaches have also been applied to the establishment of mutants. In addition, research on gene functions is conducted by using the artificial microRNA, antisense RNAi (double-stranded RNA interference) and overexpression technology (Xiao, 2009). Moreover, most of the previous studies have dissected the molecular mechanism of flowering in rice and A. thaliana by using pure lines. Hybrid usually shows huge difference in flowering time with parents. Hybrid rice sometimes cannot flower (usually called as big and green plant, BGP) in middle China and north China, even though both parents can flower normally in those places. The non-flowering BGP results in large proportion of losses in rice production. Study on the genetic mechanisms of flowering in hybrid rice may be another hot spot in future.

ACKNOWLEDGEMENTS

We thank Dr Judy LEE (Chinese Academy of Agricultural Sciences) for her comments on this review. The study was funded by the National High Technology Research and Development Program from the Ministry of Science and Technology of China (Grant No. 2010AA101806), and the Bill & Melinda Gates Foundation (Grant No. OPP51587).

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