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Regulatory Function of Histone Modifications in Controlling Rice Gene Expression and Plant Growth

Dao-Xiu Zhou · Yongfeng Hu

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Abstract Histone modifications play pivotal roles in chromatin remodeling and gene regulation. Rice genome possesses multiple genes encoding different classes of histone modification enzymes. Specific histone modification patterns in rice are associated with either heterochromatic or euchromatic regions or related to gene expression. Functional studies of several rice genes encoding histone deacetylases and histone methyltransferases and demethylases reveal specific regulators involved in transposon repression, development regulation, and responses to environmental conditions. Functional interplay between rice histone modification regulators in gene regulation and transposon silencing and their implication in rice epigenetic variation are discussed.

Keywords Chromatin · Histone acetylation · Methylation · Histone deacetylase · Histone methyltransferase · Histone demethylase · jmjC · SUVH · SIR2 · Epigenetic regulation · Stress inducible

In eukaryotes, the genomic DNA is tightly compacted into a complex structure known as chromatin. To control genome activities, the accessibility of chromatin is dynamically regulated during growth and development. The massive changes in gene expression that occur during developmental transitions rely at least in part on epigenetic processes such as chromatin remodeling to establish specific states for gene expression. In addition, plants are sessile organisms that have to adapt to their living environments. It is therefore essential for plants to develop rapid responses to changes in environmental conditions for their adaptation and survival. Rapid changes of chromatin structure play a central role in regulating gene expression in response to environmental cues. During the last decade, many plant DNA-binding transcription factors involved in developmental and inducible gene regulations have been identified. However, how these factors activate or repress transcription in a specific chromatin context is not clearly known. Chromatin structure and remodeling are basic components of genetic and epigenetic regulations of genome expression (Horn and Peterson 2002). Nucleosome is the basic structure of chromatin and is composed of 4 types of core histones. Covalent modifications of the N-terminal tails of the core histones play pivotal roles in chromatin remodeling and in gene regulation (Millar and Grunstein 2006). Histone modifications include acetylation, methylation, phosphorylation, ubiquitinylation, and others. Most of the modifications are on the lysine, arginine, or serine residues of H3 or H4. Specific patterns of histone modifications determine active or repressed states of the cognate chromatin (Berger 2007). Different chromatin structures define distinct epigenomes which is reflected by specific gene expression pattern of different cell types and responses to different environmental conditions. Histone modification and recognition genes are found to play important roles in many different aspects of developmental, cellular and genetic processes in *Arabidopsis*. Functional study of rice histone modification and recognition is emerging. Here, we review recent data of rice histone modification regulation and its function in rice gene expression and plant growth and development. Since there is no much information on histone phosphorylation and ubiquitination in rice, the review will focus on the regulatory mechanism of histone acetylation and methylation.

D.-X. Zhou (✉) · Y. Hu
Institute de Biologie des Plantes, UMR8618, Université Paris-sud 11,
91405 Orsay, France
e-mail: dao-xiu.zhou@u-psud.fr

Histone acetylation in the regulation of rice gene expression

Among histone modifications, histone lysine acetylation appears to be a dynamic reversible switch for interconversion between permissive and repressive transcriptional states of chromatin domains. Strong acetylation of histones induces relaxation of chromatin structure and is associated with transcriptional activation, whereas weak acetylation leads to chromatin compaction and gene repression (Berger 2007). N-terminal lysine residues of histone H3 (K9, K14, K18 and K23) and H4 (K5, K8, K12, K16 and K20) are found to be acetylation/deacetylation targets in *Arabidopsis* (Earley et al. 2007; Zhang et al. 2007a). The dynamic modulation of histone acetylation in plants is shown to be important for plants to adapt their growth and development to environment changes such as light, temperature, biotic, and abiotic stresses (Chen and Tian 2007; Servet et al. 2010). In rice, acetylation of H3K9 and H4K12 is elevated in genes located in euchromatic regions (Yin et al. 2008), suggesting that these markers may be associated with active genes. Dynamic and reversible changes in histone H3 acetylation and H3K4 methylation occur at submergence-inducible genes in rice (Tsuji et al. 2006). When submerged, the rice ADH1 (alcohol dehydrogenase 1) and PDC1 (pyruvate decarboxylase 1) genes are activated in two phases: the first activation occurs after 2 h of submergence, the second after 12 h. The first induction seems to be associated with tri-methylation of histone H3K4 on the 5′- and 3′-coding regions, while the second induction is correlated with increased histone H3 acetylation throughout ADH1 and PDC1 genes. The methylation and acetylation levels return to the initial levels after re-aeration. These data nicely demonstrate the dynamic and reversible changes of histone H3K4 methylation and H3 acetylation in responses to environmental changes in rice. In addition, histone H3K9 acetylation is required for the expression of *RICE FLOWERING LOCUS T 1* (*RFT1*/*FT-L3*) that is the closest homologue of *Heading date 3a* (*Hd3a*) encoding a mobile flowering signal and promote floral transition under short-day conditions (Komiya et al. 2008), showing a role of histone acetylation in the regulation of rice developmental transitions.

Function of histone deacetylases genes in rice

The homeostatic balance of nucleosomal histone acetylation is maintained by actions of histone acetyltransferases and histone deacetylases (HDAC). Plant HDAC can be grouped into three classes. Among them, two have primary homology to yeast HDAC groups: reduce potassium dependency 3 (RPD3), and silent mating-type information regulation-2 (SIR2; Fig. 1; Pandey et al. 2002). The other group known as the HD2 class is found in plants only (Lusser et al. 1997). During the last years, HDAC function has been most studied in *Arabidopsis*. One of the *Arabidopsis* RPD3 type genes, *AtHD1* (*HDA19*) seems to be a polyvalent HDAC involved in many developmental and stimulus-responsive pathways. Down-regulation of the gene induces pleiotropic developmental abnormalities (Tian and Chen 2001). Other *Arabidopsis* RPD3-like genes are involved in the control of flowering time, root hair production, RNAi-dependent DNA methylation, and nucleolar dominance in allopolyploid hybrids (Wu et al. 2000; Xu et al. 2005; Aufsatz et al. 2002; Pontes et al. 2007). Rice genome contains at least 19 HDAC genes (Hu et al. 2009; Fig. 1). Expression and functional studies suggest that individual rice HDAC genes have specific development functions that may be divergent from the *Arabidopsis* homologues. Expression of rice HDAC genes shows tissue/organ specificity. For instance, *HDA710* was more expressed in germinating and young seedlings as well as in stamens, whereas *HDA703* was highly expressed in callus and in imbibed seeds. *HDA714* and *HDA706* were found to be mainly expressed in shoots and leaves, whereas *HDA716* showed a strong expression in developing endosperm and germinating seeds. Most of the HDAC genes are responsive to drought or salt stresses. For instance, two genes (*HDA703* and *HDA710*) are induced, while nine others (i.e., *HDA701*, *HDA702*, *HDA704*, *HDA705*, *HDA706*, *HDA712*, *HDA714*, *HDA716*, *HDT701*, and *HDT702*) are clearly repressed by drought and salt (Hu et al. 2009). Down-regulation of most of HDAC genes may be important for stress-inducible gene expression in rice. These HDACs may repress stress-responsive gene expression in the absence of stress signals. Therefore, histone acetylation/deacetylation switch is suggested to be an important mechanism of short-term gene regulation in plants (Zhou 2009), may be largely involved in stress responses in rice. While most of the HDAC proteins are localized in nucleus, a few of them are localized in the chloroplast (e.g., HDA714) and/or mitochondrion (e.g., HDA714, SRT702; Chung et al. 2009b), suggesting that these HDACs may have specific functions in rice cells, which remain to be determined.

It has been shown that over-expression of *OsHDAC1* (*HDA702*) leads to increased growth rate and altered architecture in transgenic rice (Jang et al. 2003). It is recently shown that OsHDAC1 epigenetically represses the *OsNAC6* gene that controls rice seedling root growth (Chung et al. 2009a). OsHDAC1 interacts with the *OsNAC6* gene promoter and deacetylates histone H3K9, K14 and K18 and H4K5, K12 and K16. However, over-expression of several other rice HDAC genes does not produce any visible

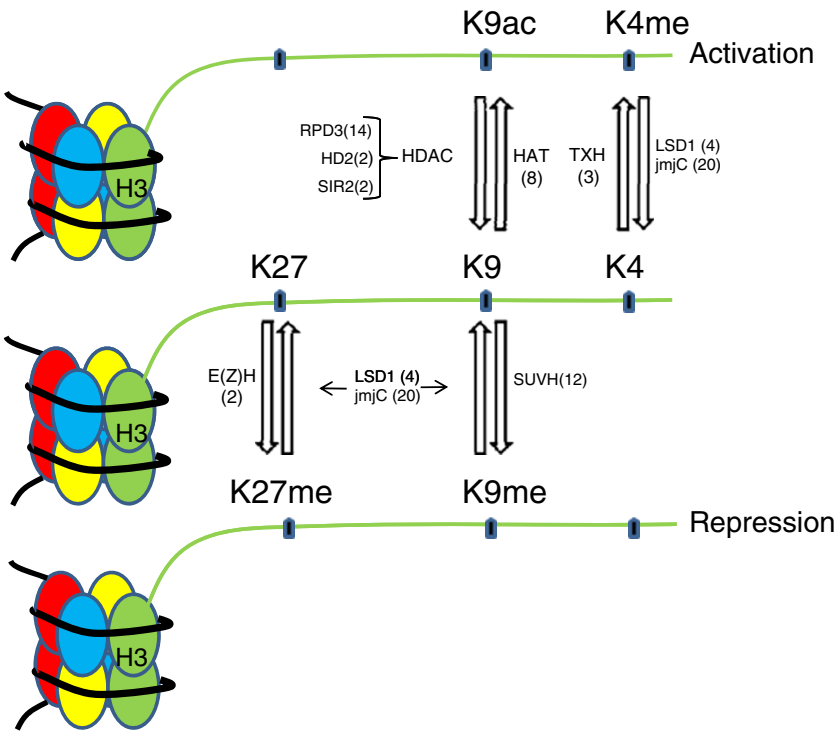

Fig. 1 Schematic representation of reversible modifications of histone H3K4, K9, and K27. Histone H3K9 acetylation and H3K4 methylation are markers for gene activation. Histone H3K9 acetylation/deacetylation is catalyzed by histone acetyltransferases (HAT) and deacetylases (HDAC) that has three groups (RPD3, HD2 and SIR2). H3K9 methylation is mediated by Su(var) 3-9 homologues (SUVH) , while that of histone H3K4 and H3K27 is suggested to be mediated by Tritorax homologues (TXH) and E(Z) homologues, respectively. Histone lysine demethylases LSD1 and jmjC proteins are suggested to be involved in the reversion of methylated H3K4, K9, and K27. *Numerals in parentheses* are numbers of genes found in rice genome.

phenotype. In contrast, down-regulation of a few HDAC genes affects different developmental aspects (Hu et al. 2009). Although the mechanism by which *HDAC* are involved in rice development regulation is unclear, those rice genes seem to have divergent developmental functions compared to closely related homologues in *Arabidopsis*.

SIR2 proteins are NAD^+-dependent HDACs, some of which have been found to be involved in increasing lifespan in yeast and animals (reviewed in Finkel et al. 2009). Plant genomes seem to contain relatively fewer *SIR2* homologues than other eukaryotes. In rice or *Arabidopsis*, only two *SIR2* family genes have been identified (Pandey et al. 2002). Phylogenetic analysis of identified plant *SIR2* homologues shows that they belong only to two of the four classes of the family, which have only plant and animal members (Huang et al. 2007). As there are fewer *SIR2*-related genes found in plant genomes, important questions arise such as whether plant SIR2-related proteins conserve the similar functions as yeast and animal SIR2 proteins. The expression patterns of the two rice genes (*SRT701* and *SRT702*) are different (Hu et al. 2009). The two proteins are likely to have distinct functions. In addition, SRT701 (also called OsSRT1) is a nuclear protein, while SRT702 seems to be localized in the mitochondria (Huang et al. 2007; Chung et al. 2009b). SRT701 is widely expressed but with higher levels in rapidly dividing tissues. *SRT701* RNAi leads to an increase of histone H3K9 acetylation and a decrease of H3K9 dimethylation. *SRT701* RNAi induces H_2O_2 production, DNA fragmentation, cell death, and lesions mimicking plant hypersensitive responses induced by pathogen attacks, whereas over-expression of the gene enhanced tolerance to oxidative stress (Huang et al. 2007). Many transposons and retrotransposons in addition to genes related to hypersensitive response and/or programmed cell death are activated in the RNAi plants. Histone H3K9 acetylation on transposable elements and some of the hypersensitive response-related genes is increased in the RNAi plants, indicating that transposons and cell death-related genes might be amongst the primary targets of SRT701 for histone deacetylation. Therefore, SRT701 may be required for genome stability to ensure plant cell growth, but likely implicating different molecular mechanisms from yeast and animal homologues. These results suggest that histone acetylation is an important component for transposon repression in rice (Fig. 2; see below).

Histone methylation and histone lysine methyltransferases in rice

Histone lysine methylation is an important epigenetic modification with both activating and repressive roles in gene expression. Histone lysine residues can be mono-, di-, or trimethylated, where each distinct methyl state may have different biological functions (Bannister and Kouzarides 2004). For instance, di- and trimethylation of H3K9 (H3K9me2, H3K9me3) and trimethylation of H3K27 (H3K27me3) negatively correlate with gene expression,

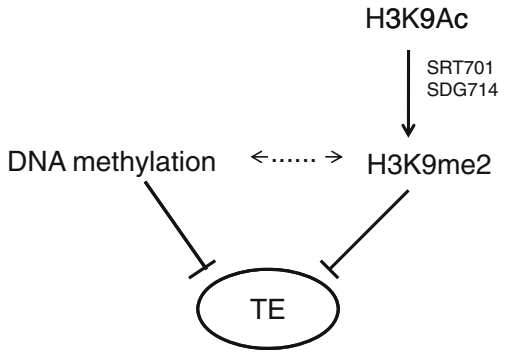

Fig. 2 A model of epigenetic repression of transposable elements (TE) in rice. Both DNA methylation and histone modifications are important components of transposon silencing. Three rice genes are shown to be involved histone H3K9 deacetylation (SRT701) and methylation (SDG714) in transposon repression.

whereas trimethylation of H3K4 (H3K4me3), as mentioned above, positively correlate with the expression of target genes (Pfluger and Wagner 2007; Fig. 1). These differently methylated histone lysine residues are recognized by different chromatin protein modules that induce distinct chromatin structures. For instance, H3K9me2 is shown to be associated with Heterchromatin Protein1 in animal cells (reviewed in Vermaak and Malik 2009), while H3K27me3 is associated with Polycomb group (PcG) repressive complexes in both plant and animal cells (reviewed in Hennig and Derkacheva 2009).

Results from immunostaining and chromatin immunoprecipitation (ChIP) coupled with DNA microarray (chip) (ChIP-chip) analysis in *Arabidopsis* suggest that methylation of H3K9 and H3K27 is important for chromatin structure and gene regulation. H3K9me2 is found to be enriched in heterochromatic repetitive sequence regions, while H3K9me3 and H3K27me3 are distributed in the 5′ ends of genes in euchromatic regions (Lippman et al. 2004; Turck et al. 2007; Zhang et al. 2007b). The distribution of H3K9me3 and H3K27me3 does not overlap, suggesting that they may respond to different cellular signals or be involved in distinct regulatory pathways. Analysis of H3K4 methylation of two entire chromosomes in rice revealed that half of protein-coding genes have di- and/or trimethylated H3K4 (Li et al. 2008). Rice genes with predominantly H3K4me3 are actively transcribed, whereas genes with predominantly H3K4me2 were transcribed at moderate levels (Li et al. 2008).

Enzymes involved in histone methylation usually contain a motif called SET domain, which is named after three *Drosophila* genes: Su(var)3-9, Enhancer of zeste (E(Z)) and Trithorax, the mutation of which either enhance or suppress epigenetic mutations. A large number of SET-domain genes are identified in rice and *Arabidopsis* genomes (Fig. 3). Su (var) 3-9 homologues (SUVH) are found to be mostly involved in H3K9 methylation (Fig. 1). *Arabidopsis* SUVH protein KYPTONITE (KYP) was discovered in a screen for suppressor of an epigenetic mutation due to hypermethylation of cytosine on the locus of *SUPERMAN*. Both *Arabidopsis* and rice SUVH proteins are found to have H3K9 mono- and di-methylation activities. This raises a question whether H3K9me3 exists in plants. E(Z) homologues which are components of PcG complexes are responsible for H3K27me3 (Fig. 1). Several homologues of E(Z) in *Arabidopsis* (i.e., CURLY LEAF (CLF), SWINGER (SWN), MEDEA (MEA)) which are components of PcG-related complexes (PRC2), are shown to behave as essential regulators of plant developmental transitions (Pien and Grossniklaus 2007). The homologues of E(Z) and other PRC2 components are also identified in rice and some of them are characterized to have functions in rice development, which seem not be the same as found in *Arabidopsis* (Luo et al. 2009; Fig. 3). This suggests that rice PcG proteins may have functional specificities. Whether the rice E(Z) homologues have the H3K27 methyltransferase activity remains to be determined. Trithorax proteins are a group of methyltransferases for H3K4 methylation (Fig. 1). *Arabidopsis* TRITHORAX-RELATED1, 2 (ATX1, 2) and ATX-Related7 (ATXR7) are shown to be involved in the H3K4 methylation required for the expression of *FLOWERING LOCUS* C (*FLC*), a flowering repressor (Pien et al. 2008; Saleh et al. 2008; Tamada et al. 2009). In contrast, two other ATX-Related genes, ATXR5 and ATXR6, are H3K27 monomethyltransferases required for chromatin structure and gene silencing (Jacob et al. 2009). In the rice genome, three thithorax homologues (TXH) are found and their function has not been studied yet (Fig. 3).

Drosophila Su(var)3-9 protein was the first identified histone lysine methyltransferase specific for H3K9 (Rea et al. 2000). Multiple Su(var)3-9 methyltransferases have been identified in mammals and are shown to play an important role in chromatin function and development (Sims et al. 2003). In line with the genomic characteristics, plant genome encodes many SUVH genes (Baumbusch et al. 2001; Fig. 3). This may be because a large fraction of the genome is repetitive sequences and extensive heterochromatic silencing processes require different SUVH functions. For instance, *Arabidopsis* genome contains ten *SUVH* genes, of which *KYP* (also known as *SUVH4*), *SUVH5* and *SUVH6* are shown to undergo H3K9 methylation in a locus-specific manner (Ebbs et al. 2005; Ebbs and Bender 2006; Jackson et al. 2004). The three *Arabidopsis* SUVH proteins display mono- or dimethyltransferase activity of histone H3K9 (Ebbs and Bender 2006; Jackson et al. 2004). Rice genome encodes 12 SUVH genes (Fig. 3). One of rice SUVH genes, namely *SDG714*, is found to be involved in H3K9me2 and DNA methylation of *Tos17*, a *copia*-like retrotransposon (Ding et al. 2007). A systematic study of rice SUVH genes revealed that different members display distinct function in histone H3K9 methylation, DNA

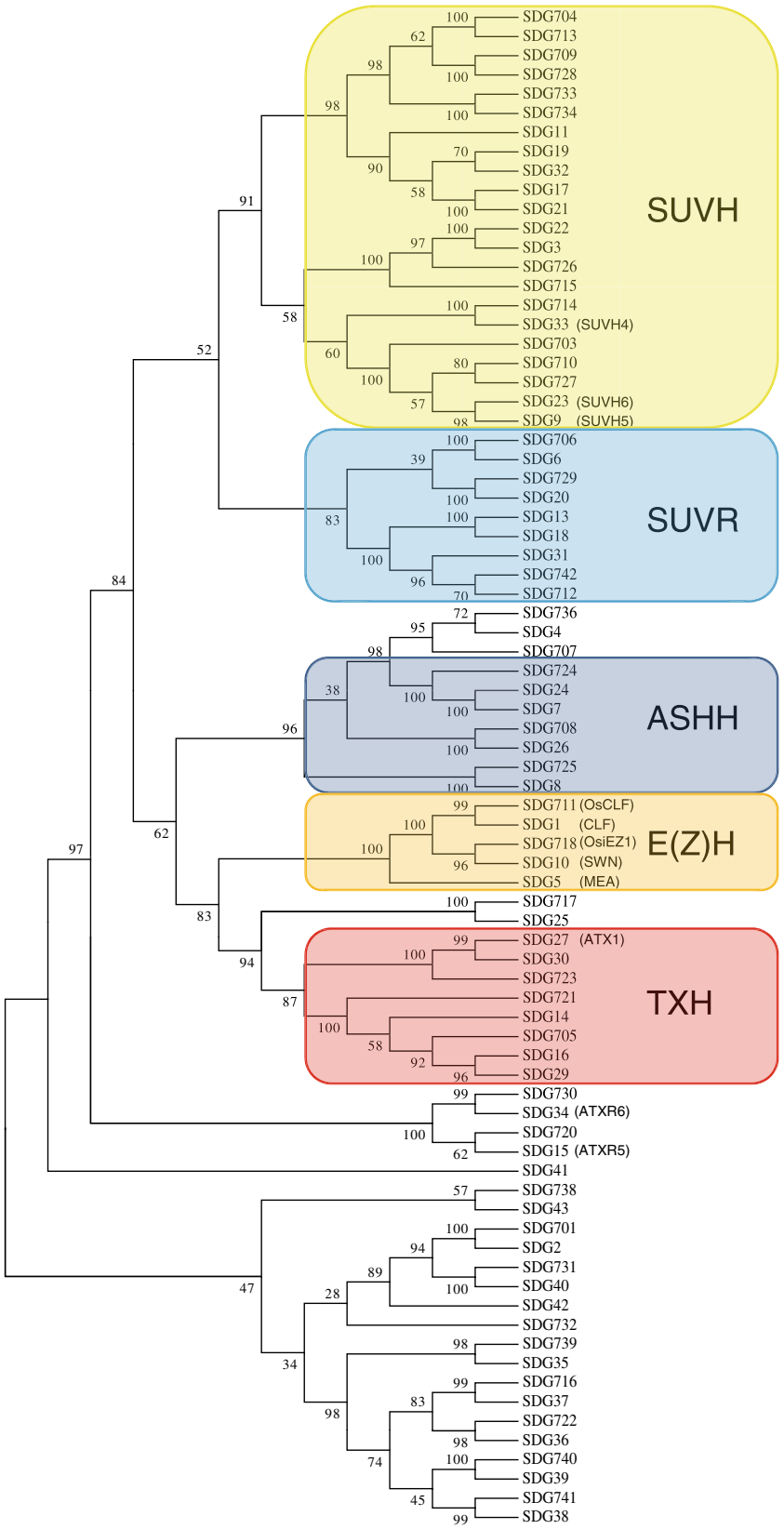

Fig. 3 Phylogenetic relationship of SET domain-containing proteins in *Oryza sativa* (SDG numbers with three numerals starting with 7) and *A. thaliana* (SDG numbers with 1 or 2 numerals). All the sequences of SET domain-containing proteins were obtained from ChromDB database (www.chromdb.org). The alignment of these sequences was conducted by the ClustalX program. The SET domain sequences were selected to construct the phylogenetic tree by using MEGA3.1. Only the tree topology is shown. The classification of SET domain proteins was in accordance with that described in Baumbusch et al. (2001). *SUVH* SU(VAR)3-9 homolog, *SUVR* SUVH-related, *ASHH* ASH1 homolog, *E(Z)H* E(Z) homolog, *TXH* tritorax homolog. The TXR (TXH-related) and ASHR (ASH1-Related) groups were not noted because of their truncated SET domains. For the proteins that had been published, there designations in the papers were annotated in the parenthesis behind the ChromDB name (SDG7^{+} or SDG^{+}).

methylation, and transposon silencing (Qin et al. 2010). For instance, down-regulation of most of the rice SUVH members does not induce obvious morphological phenotype, while *SDG728* RNAi plants produce deformed seed shape. In addition, both H3K9me2 and H3K9me3 are decreased in the *SDG728* RNAi plants, while down-regulation of other rice SUVH genes (e.g., *SDG713*) only affects H3K9me2. The expression of *Tos17* and a *Ty1-copia* element is activated in RNAi plants of a few SUVH genes (e.g., SDG703, SDG713 and SDG728), but not affected by down-regulation of other SUVH. The activation of *Tos17* is correlated with a clear decrease of H3K9me3 on *Tos17* in *SDG728* RNAi plants, suggesting that H3K9me3 may be an important component of retrotransposon silencing.

As described above, down-regulation of the rice HDAC gene *SRT701* leads to transcriptional activation of many transposons (Huang et al. 2007). Down-regulation of *SRT701* not only augments H3K9ac but also decreases H3K9me2. As acetylated H3K9 needs to be deacetylated by HDAC before methylation, these data suggest that *SRT701* and SUVH genes function within a similar pathway to regulate transposon silencing in rice. Therefore, in addition to DNA methylation that is known to be an important component of transposon and retrotransposnon silencing in plants, histone modification seems to also play a primary role in retrotransposon repression in rice (Fig. 2). Furthermore, SUVH genes (i.e., *SDG714*, *SDG727*, and *SDG710*) are found to have an antagonistic function to the histone H3K9 demethylase gene *JMJ706* in regulating H3K9 methylation and panicle development (Qin et al. 2010).

In addition to the SET domain, plant SUVH proteins contain a plant-specific YDG (named after the three conserved amino acids)/SRA (SET- and Ring Finger-associated) domain. The YDG/SRA domain of KYP/SUVH4 is shown to bind directly to methylated DNA (Johnson et al. 2007), suggesting that DNA methylation and H3K9me2 are correlated in *Arabidopsis* (Soppe et al. 2002; Tariq et al. 2003). Inactivation of rice *SDG714* affected DNA methylation on the *Tos17* locus, suggesting that rice SUVH function may be also linked to DNA methylation involved in retrotransposon silencing.

Histone demethylases

Histone methylation was considered irreversible until recent discovery of histone demethylases (Shi et al. 2004; Cloos et al. 2008). LSD1 was the first histone demethylase to be identified in mammalian cells, and it has been shown to demethylate mono-methylated and di-methylated H3K4 (H3K4me1 and H3K4me2) and H3K9 (H3K9me1 and H3K9me2). In metazoa LSD1 is encoded by a single-copy gene, whereas in rice or *Arabidopsis* four homologues are found (Fig. 4). Three *Arabidopsis LSD1* genes are shown to be involved in

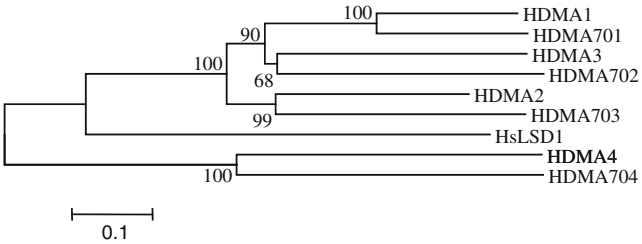

Fig. 4 Phylogenetic relationship of *LSD1* genes from rice (HDM701-704), *Arabidopsis* (HDM1-4) and human LSD1.

flowering regulation, the mutation of which induces H3K4 hyperacetylation and a decrease in H3K27me2 and H3K9me2 on the 5′ region of *FLC* and produce a later flowering phenotype (Jiang et al. 2007). Jumonji C (jmjC) domain-containing proteins have been found to function also as histone demethylases (Trewick et al. 2005). Different classes of jmjC proteins have specific histone lysine targets (Klose et al. 2006). Analysis of plant jmjC domain genes leads to the identification of seven groups of jmjC domain-containing proteins on the basis of the jmjC domain and the overall protein domain architecture (Sun and Zhou 2008). Some of the plant jmjC proteins are conserved with mammalian genes. Others seem not to have close animal homologues. Even in the conserved members, plant proteins have specific modules (Sun and Zhou 2008). Plant jmjC proteins involved specifically in the reversion of di- or trimethylated H3K9 or H3K4 have been identified. Mutations in two *Arabidopsis* jmjC genes, AtJmj4 (also called JMJ14, At4g20400) and EARLY FLOWERING6 (ELF6, JMJ11 or Atjmj1, At5g04240) which are H3K4 demethylases directly repressing the *FLOWERING LOCUS T* (*FT*) and an FT homologue *TWIN SISTER OF FT* (*TSF*) and preventing precocious flowering in *Arabidopsis* (Jeong et al. 2009; Yang et al. 2010). Purified recombinant AtJmj4 protein possesses specific demethylase activity for mono-, di- and trimethylated H3K4. Tagged AtJmj4 and ELF6 proteins associate directly with the *FT* transcription initiation region, a region where the H3K4me3 levels are increased most significantly in the mutants (Jeong et al. 2009). Both jmjC proteins belong to different subclasses of jmjC proteins. It is recently shown that JMJ14 affects mobile RNA silencing in an *Arabidopsis* transgene system. It also enhances asymmetric cytosine (CHH, H=A, T or C) methylation, abundance of transopson transcripts. These results illustrate a link between RNA silencing and histone H3K4me3 demethylation (Searle et al. 2010). Two different subclasses of mammalian jmjC proteins are also found to be H3K4 demethylases. In rice, a jmjC protein (JMJ704) is also identified to have a H3K4 demethylase activity (Peng, J. and Jeong H. J. Functional study of rice jumonji C domain containing gene JMJ704. Abstract P1-53 presented at The Sixth International Rice genetics Symposium, November 16-19, 2009. Manila www.ricegenetics.com).

Arabidopsis INCREASED EXPRESSION OF BONSAI METHYLATION1 (IBM1; also known as AtJmj15 or JMJ25, At3g07610), represses genic cytosine methylation, possibly through demethylation of H3K9 (Saze et al. 2008). *JMJ706*, a rice member of the JMJD2 group of jmjC genes, is shown to encode a heterochromatin-associated protein (Sun and Zhou, 2008). In vitro histone demthylation assays and analysis of T-DNA insertion mutants revealed that JMJ706 is involved in H3K9 demethylation required for the expression of a subset of regulatory genes for rice panicle development. However, the mutation of *JMJ706* seems not to affect DNA methylation in tandem repeats (Sun 2009). Minor changes in DNA methylation on the retrotransposon *Tos17* is observed. Therefore, different plant jmjC proteins involved in H3K9 demethylation may have distinct function in chromatin regulation.

As mentioned above, inactivation of three SUVH genes by amiRNA in the *jmj706* mutant background restore partially the panicle phenotype of *jmj706* and histone H3K9 methylation. This group of SUVH methyltransferase genes and JMJ706 appear to be involved in different regulatory pathways, but simultaneous inactivation could compensate for each other. This indicates that interaction between the two antagonistic families of enzymes is collectively involved to maintain histone H3K9 methylation homeostasis that is important for rice development.

H3K27me3 are found to be distributed in the 5′ ends of genes in euchromatic regions in *Arabidopsis* (Turck et al. 2007; Zhang et al. 2007b). Whether H3K27me3 has a similar distribution on rice genome remains to be determined. The repression of many important plant developmental key genes is mediated by H3K27 methylation involving PcG protein complexes. For instance, SET domain-containing PcG proteins CLF and SWN are required for H3K27me3-mediated silencing of important developmental regulatory genes such as the floral organ homeotic gene *AGAMOUS* during vegetative growth, the meristem regulator *SHOOTMERISTEMLESS* (*STM*) in seedlings and the seed development gene *PHERES* in vegetative tissues (reviewed in Pien and Grossniklaus 2007). The establishment and the maintenance of the repression of the flowering repressor *FLC* is also mediated by H3K27 methylation. This suggests that H3K27me-mediated gene silencing may be mainly involved in developmental decision in plants. However, activities involved in the demethylation of H3K27me3 remain to be identified in plants.

Conclusions and perspectives

Current knowledge on the function of histone modification regulation and recognition suggests that there are both conservation and difference between plants and other eukaryotic systems in chromatin mechanism of gene regulation. The sessile lifestyle of plants requires increased developmental plasticity. Histone modification and recognition are essential for programming and reprogramming of plant developmental processes and for rapid responses to environmental cues. Plant genomes contain a large portion of repetitive sequences, the repression of which involves both DNA methylation and histone modifications. In addition, plants have large families of genes involved in histone modifications. Studying specific functions of the individual family members will be needed to understand the complexity of regulation of histone modification and epigenomic dynamics during plant developmental transitions and in responses to environmental conditions. Identifying functional interaction between histone modification regulators and other chromatin or signaling factors (such as chromatin remodeling factors, DNA-binding transcription factors) will be required to provide a mechanistic view on how histone modification integrates cell signals to regulate chromatin structures. Identifying the mechanism of recognition and reading of different histone modification markers constitutes another challenge of chromatin signaling for gene regulation. Rice as a cereal has specific development and growth specificities. Studying the mechanism of establishment, maintenance, and erasure of specific rice epigenomes will be essential to unravel the epigenetic mechanism of rice gene regulation. Progresses in this field in rice will have a great impact on the understanding of genetic and epigenetic basis of cereal growth and adaptation to environmental conditions such as water, light, temperature, soil, and pathogens. It is suggested that interaction between plant genomes of different origins during crosses may generate specific epigenetic mechanisms of gene regulation such as allelic inactivation and genomic imprinting (Ishikawa and Kinoshita 2009). Epigenomes related to rice hybrid vigor have been recently reported (He et al. 2010). Importantly, it is recently shown that parent plants with little genomic DNA sequence variations, but contrasting epigenetic modification (i.e., DNA methylation) can generate a panel of epigenetic recombinant inbred lines showing variation and high heritability over many generations for several important traits in *Arabidopsis* (Johannes et al. 2009; Reinders et al. 2009). It remains to know whether variations in chromatin modification (both histone modification and DNA methylation) will be useful as a resource to create novel epigenetic variations controlling important agronomical traits that could be exploited for rice breeding.

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