

## Invited Expert Review

Involvement of Histone Modifications in Plant Abiotic Stress Responses<sup>□</sup>Lianyu Yuan<sup>1,2†</sup>, Xuncheng Liu<sup>1†</sup>, Ming Luo<sup>1</sup>, Songguang Yang<sup>1</sup> and Keqiang Wu<sup>3\*</sup><sup>1</sup>Key Laboratory of Plant Resources Conservation and Sustainable Utilization, South China Botanical Garden, the Chinese Academy of Sciences, Guangzhou 510650, China<sup>2</sup>University of Chinese Academy of Sciences, Beijing 100049, China<sup>3</sup>Institute of Plant Biology, College of Life Science, National Taiwan University, Taipei 106<sup>†</sup>These authors contributed equally to this work.<sup>\*</sup>Corresponding authorTel/Fax: +86 20 3708 7810; E-mail: [kewu@ntu.edu.tw](mailto:kewu@ntu.edu.tw)<sup>□</sup> Articles can be viewed online without a subscription.Available online on 2 May 2013 at [www.jipb.net](http://www.jipb.net) and [www.wileyonlinelibrary.com/journal/jipb](http://www.wileyonlinelibrary.com/journal/jipb)

doi: 10.1111/jipb.12060



Keqiang Wu  
(Corresponding author)

## Abstract

As sessile organisms, plants encounter various environmental stimuli including abiotic stresses during their lifecycle. To survive under adverse conditions, plants have evolved intricate mechanisms to perceive external signals and respond accordingly. Responses to various stresses largely depend on the plant capacity to modulate the transcriptome rapidly and specifically. A number of studies have shown that the molecular mechanisms driving the responses of plants to environmental stresses often depend on nucleosome histone post-translational modifications including histone acetylation, methylation, ubiquitination, and phosphorylation. The combined effects of these modifications play an essential role in the regulation of stress responsive gene expression. In this review, we highlight our current

understanding of the epigenetic mechanisms of histone modifications and their roles in plant abiotic stress response.

**Keywords:** Abiotic stresses; gene regulation; histone modifications.

Yuan L, Liu X, Luo M, Yang S, Wu K (2013) Involvement of histone modifications in plant abiotic stress responses. *J. Integr. Plant Biol.* 55(10), 892–901.

## Introduction

In eukaryotes, genomic DNA is packaged with histones to form a complex structure known as chromatin. The fundamental unit of chromatin is the nucleosome, which is composed of approximately 146 base pairs of DNA wrapped on a histone octamer containing two copies of histone H2A, H2B, H3, and H4. Chromatin structure influences the accessibility of transcription factors and cofactor for DNA-templated processes. The structure and function of chromatin are regulated by multiple epigenetic mechanisms, including DNA methylation, histone modifications, adenosine triphosphate (ATP)-dependent

chromatin remodeling, placement of histone variants and regulation by non-coding RNA (Berger 2007). The N-terminal tails of the histone proteins can undergo a variety of posttranslational modifications, including acetylation, methylation, ubiquitination, phosphorylation, and sumoylation. The complement of modification is proposed to store the epigenetic memory inside a cell in the form of a “histone code” that determines the chromatin structure and gene activity (Jenuwein and Allis 2001). Generally, lysine acetylation correlates with transcriptional activation (Kouzarides 2007), whereas lysine methylation leads to either transcriptional activation or repression depending on which residues are modified

and the type of modification present. For example, methylation of lysine 4 and lysine 36 on histone H3 are associated with gene activation, whereas methylation of lysine 9 and lysine 27 are associated with gene silencing (Kouzarides 2007; Liu et al. 2010).

Emerging evidence suggests that histone modifications play important roles in regulating plant responses to abiotic stresses (Chinnusamy et al. 2008; Luo et al. 2012a). In *Arabidopsis*, the drought stress induces an increase of H3K4me3 and H3K9ac in the promoter regions of stress-responsive genes, *RD29A*, *RD29B*, *RD20*, and *RAP2.4* (Kim et al. 2008a; Chinnusamy and Zhu 2009). Drought stress causes dynamic genome-wide changes of histone H3K4me1, H3K4me2 and H3K4me3 in *Arabidopsis* (van Dijk et al. 2010). In rice seedlings, 4,837 genes are differentially H3K4me3 modified under drought stress (Zong et al. 2012). Upon cold exposure, a genome-wide demethylation was observed in root tissues of maize seedlings (Steward et al. 2002). Cold treatment also induces the expression of the genes encoding histone deacetylases (HDACs), leading to global histones H3 and H4 deacetylation in maize (Hu et al. 2011). In *Arabidopsis*, cold exposure decreases H3K27me3 of two cold responsive genes, *COR15A* and *GOLS3* (Kwon et al. 2009). Furthermore, the plant hormone abscisic acid (ABA) was reported to regulate abiotic stress-inducible gene expression by affecting histone H3 acetylation and methylation (Chen and Wu 2010; Chen et al. 2010; Dehesh and Liu 2010; Luo et al. 2012b). Taken together, these studies suggest that posttranslational histone modifications play an important role in modulating the gene activity in plant responses to abiotic stresses.

Activation or repression of the gene activity in responding to abiotic stresses is often associated with multiple epigenetic changes. For example, ABA and salt stresses increase the levels of H3K9K14ac and H3K4me3 of stress-inducible genes (Chen et al. 2010). Salinity stress activates the expression of members of *AP2/EREB*, *bZIP*, *NAC*, and *MYB* transcription factors by decreasing DNA methylation and increasing levels of histone H3K4me3 and H3K9ac in soybean (Song et al. 2012). These studies suggest a combination effect of DNA methylation and histone modifications in the regulation of stress-inducible gene expression. The combined effects of different chromatin remodeling factors may provide sophisticated and effective mechanisms to regulate gene expression in plant responses to environmental stresses. In this review, we discuss the recent findings on the functions and mechanisms of histone modifications involved in plant responses to abiotic stresses.

## Histone Acetylation and Deacetylation

Acetylation modification of the lysine residues at the N terminus of histone proteins plays a crucial role in regulation of eukaryotic gene activities. Acetylation of core histones often produces

an “open” chromatin configuration and is associated with gene activation, whereas deacetylation of histones is correlated with “closed” chromatin structure and gene repression (Shahbazian and Grunstein 2007). Reversible acetylation of histones is catalyzed by histone acetyltransferases (HATs) and HDACs.

## Histone Acetyltransferases

In plants, there are four families of HATs including GNAT (GCN5-related N-terminal acetyltransferase) family, MYST (MOZ, Ybf2/Sas3, Sas2, and Tip60) family, CBP (CREB-binding protein) family, and TAFII250 (TATA-binding protein-associated factors) family (Pandey et al. 2002). Twelve HATs has been identified in *Arabidopsis* (Pandey et al. 2002). The GCN5 protein is the catalytic subunit of several multi-protein HAT complexes. Several GCN5-containing transcriptional coactivator complexes have been identified, including SAGA, ADA, SLIK, and others (Kaldis et al. 2011). Alteration/deficiency in activation 2 (ADA2) adaptor proteins are integral parts of GCN5-containing complexes. Two ADA2 factors, ADA2a and ADA2b, have been identified in *Arabidopsis* (Stockinger et al. 2001). SaGa-associated factor 29 (SGF29) protein is a subunit shared between the SAGA and ATAC complexes (Nagy et al. 2010). The GCN5-containing protein complexes play an essential role in many plant development processes, such as meristem function, cell differentiation, leaf and floral organogenesis (Bertrand et al. 2003; Vlachonassios et al. 2003; Kornet and Scheres 2009; Servet et al. 2010). *Arabidopsis* HAC1 is homologous to the animal p300/CREB (cAMP-responsive element-binding protein)-binding proteins. It was found that *Arabidopsis* HAC1 participates in many physiological processes, including root elongation, fertility, flowering, and de novo shoot regeneration (Deng et al. 2007; Li et al. 2011b). More recently, it was found that IDM1, a variant of histone H3 acetyltransferase, recognizes methylated DNA and unmethylated histone H3K4 and regulates active DNA demethylation in *Arabidopsis* (Qian et al. 2012). Furthermore, another putative HAT ROS4 with high sequence similarity in the acetyltransferase domain to the GNAT family plays a role in anti-silencing of the RNA-directed DNA methylation pathway (Li et al. 2012).

Recent studies suggested the involvement of HATs and HAT-containing complexes in abiotic stress responses. GCN5 was shown to interact specifically with a phosphatase 2C protein (AtPP2C-6-6), and *gcn5* mutants exhibited upregulation of a subset of the stress-inducible genes (Servet et al. 2008). Furthermore, loss of function mutants of *SGF29a* encoding a subunit of GCN5 complex in *Arabidopsis* displayed increased tolerance to salt stress compared to the wild-type (Kaldis et al. 2011). These findings suggest a role of the GCN5-containing complex in stress responses. Mutations of another GCN5-

containing complex component *ADA2b* in *Arabidopsis* showed reduced H3 and H4 acetylation and decreased transcription of *COR6.6*, *RAB18*, and *RD29b* genes under salt stress (Kaldis et al. 2011). Furthermore, the cold-induced transcription factor CBF1 can physically interact with ADA2 and GCN5 (Mao et al. 2006). More recently, it was shown that GCN5 and ADA2 positively regulate the expression of cold-inducible genes during cold accumulation in *Arabidopsis* (Pavangadkar et al. 2010). Taken together, these findings suggest that the GCN5-containing activator complexes might be recruited by the transcription factor CBF1 in activation of cold responsive genes.

Elongator is a histone HAT complex consisting of six subunits, ELP1 to ELP6, and is highly conserved in eukaryotic organisms (Versees et al. 2010). In *Arabidopsis*, the Elongator HAT complex is involved in ABA, drought and oxidative stress responses (Chen et al. 2006; Zhou et al. 2009). ABO1 encodes a homolog of yeast Elongator subunit ELP1. The *abo1* mutant showed a drought and oxidative-resistant phenotype. Furthermore, the *abo1* mutation enhanced ABA-induced stomata closing and increased ABA sensitivity in inhibiting seedling growth, suggesting a role of ABO1 in abiotic stress response and ABA signaling pathways (Chen et al. 2006). Loss-of-function mutants of *ELP2*, *ELP4*, and *ELP6* in *Arabidopsis* also showed ABA-hypersensitive phenotypes. Mutations in *ELP2*, but not *ELP4* and *ELP6*, caused stomatal closing to be hypersensitive to ABA. In addition, *elp2*, *elp4*, and *elp6* mutants were all more resistant to oxidative stress produced by methyl viologen and to CsCl compared to the wild type (Zhou et al. 2009). These findings suggest that the HAT Elongator complex plays an important role in ABA, drought and oxidative stress responses in *Arabidopsis*.

Eight HATs has been identified in rice (Liu et al. 2012a). Transcript levels of *OshAC701*, *OshAC703*, *OshAG702*, *OshAG703*, and *OshAM701* were significantly elevated in response to exogenous ABA application. Furthermore, salt treatment induced the expression of *OshAC701*, *OshAC703*, *OshAC704*, and *OshAG703*, while cold exposure depressed the expression of these genes (Liu et al. 2012a). These findings suggest that HATs may play important roles in response to abiotic stresses in rice.

## Histone Deacetylases

Eukaryotic HDACs are grouped into three major families, RPD3/HDA1 (reduced potassium dependency protein 3) superfamily, SIR2 (silent information regulator protein 2) family and the HD2 (Histone decetylase 2) family (Pandey et al. 2002). In *Arabidopsis*, 18 HDACs were identified and 12 of them belong to the RPD3/HDA1 superfamily, four belong to the HD2 family, and two belong to the SIR2 family (Hollender and Liu 2008; Alinsug et al. 2009). Histone deacetylase 19 (HDA19) has been characterized as a global repressor in *Arabidopsis* (Tian and

Chen 2001). Furthermore, *hda19* mutants exhibited a wide range of developmental abnormalities affecting flowers and siliques, premature death of seedlings, reduced male and female fertility, and embryonic defects (Tian and Chen 2001; Tian et al. 2003; Tanaka et al. 2008; Zhou et al. 2013). Similar to HDA19, HDA6 is a global repressor involved in ethylene (ET) and jasmonic acid (JA) pathway, senescence, flowering, repression of embryonic properties and leaf development (Murfett et al. 2001; Earley et al. 2006a; Tanaka et al. 2008; Wu et al. 2008; Zhu et al. 2011; Luo et al. 2012c). Furthermore, HDA6 was also reported as an essential component in gene silencing including RNA-directed DNA methylation (RdDM) (Aufsatz et al. 2002, 2007) and maintenance of transposon element and rRNA gene silencing (Lippman et al. 2003; Earley et al. 2006b, 2010; Liu et al. 2012b). Another RPD3/HDA1-type HDAC, HDA15, associates with phytochrome interacting factor 3 (PIF3) in repression chlorophyll biosynthesis and photosynthesis genes (Liu et al. 2013). The plant-specific HD2 proteins, HD2A and HD2B, are required to establish leaf polarity of *Arabidopsis* (Ueno et al. 2007).

Histone deacetylase proteins also play crucial roles in plant responses to environmental stresses. *HDA19* is involved in JA and ET signaling of pathogen response in *Arabidopsis*. Over-expression of *HDA19* in *Arabidopsis* resulted in the increased *ERF1* expression and more resistance to the pathogen *Alternaria brassicicola* (Zhou et al. 2005). More recently, it was also reported that HDA19 represses salicylic acid (SA)-mediated defense responses in *Arabidopsis*. Loss-of-function of *HDA19* increased the SA content and the expression of PR genes, resulting in enhanced resistance to the pathogen *Pseudomonas syringae* (Choi et al. 2012). Furthermore, HDA19 can interact with ERF and WRKY transcriptional factors involved in abiotic and biotic stress responses (Song et al. 2005; Kim et al. 2008b). The AP2/EREBP-type transcriptional repressor ERF7 interacts with the *Arabidopsis* homolog of a human global corepressor, SIN3, which in turn interacts with HDA19 in repression of abiotic stress responsive genes (Song et al. 2005). Furthermore, HDA19 also interacts with two type III WRKY transcription factors, WRKY38 and WRKY62, and represses their transcription activities in plant basal defense responses (Kim et al. 2008b). These studies suggest that HDA19 play crucial roles in hormone signaling pathways in response to both abiotic and biotic stresses.

The *Arabidopsis* HDA6 mutant, *axe1-5*, and HDA6 RNA-interfering plants were hypersensitive to ABA and salt stresses (Chen et al. 2010), suggesting a negative role of HDA6 in ABA and salt-stress responses. In *axe1-5* and HDA6-RNAi plants, the expression of the JA responsive genes, *PDF1.2*, *VSP2*, *JIN1*, and *ERF1*, was downregulated, indicating that HDA6 is involved in JA response (Wu et al. 2008). Furthermore, loss-of-function mutants of *HDA6* display reduced freezing tolerance and altered gene expression after cold acclimation, indicating that HDA6 has

a critical role in cold acclimation and freezing tolerance (To et al. 2011). The expression of four *Arabidopsis* HD2 genes, *HD2A*, *HD2B*, *HD2C*, and *HD2D*, was repressed by ABA and salt (Chinnusamy et al. 2008; Luo et al. 2012a). Furthermore, overexpression of *AtHD2* in transgenic *Arabidopsis* plants conferred an ABA insensitive phenotype and enhanced tolerance to salt and drought stresses (Sridha and Wu 2006). These findings suggest that HD2 proteins are involved in plant response to ABA and salt stresses. In addition, the HD2 protein HD2C can interact with HDA6 *in vitro* and *in vivo* (Luo et al. 2012b), implying that HD2 and HDA6 proteins may be functionally associated in plant responses to ABA and salt stresses. More recently, the involvement of *Arabidopsis* SRT2 in basal defense was reported (Wang et al. 2010). The expression of *SRT2* can be induced by *Pst* DC3000 inoculation. Mutation of *SRT2* increases the expression of the SA biosynthesis genes, *PAD4*, *EDS5*, and *SID2*, in *Arabidopsis* plants, suggesting that SRT2 might be a negative regulator of basal defense by suppressing the SA biosynthesis.

Rice genome encodes at least 19 HDAC proteins (Hu et al. 2009). Recent studies suggest that HDACs may play an important role in regulating stress response in rice. The transcripts of *OsHDA705*, *OsHDT701*, and *OsHDT702* are affected by SA, JA, or ABA, whereas the expression of *OsHDA714*, *OsSRT701*, and *OsSRT702* is modulated by abiotic stresses, such as cold, mannitol, and salt (Fu et al. 2007). These findings indicate that the rice HDACs may be involved in multiple signaling pathways in response to environmental stresses. Downregulation of *OsSRT1* in rice induces an increase of histone H3K9ac and a decrease of H3K9me<sub>2</sub>, leading to H<sub>2</sub>O<sub>2</sub> production, DNA fragmentation, cell death, and lesions mimicking plant hypersensitive responses during incompatible interactions with pathogens (Huang et al. 2007). In contrast, overexpression of *OsSRT1* in rice resulted in enhanced tolerance to oxidative stress. Furthermore, overexpression of *OsHDT701* in transgenic rice leads to decreased levels of histone H4 acetylation on flowering repressor genes and defense-related genes, and enhanced susceptibility to the pathogens (Li et al. 2011a; Ding et al. 2012a). Silencing of *OsHDT701* in transgenic rice causes elevated levels of histone H4 acetylation and elevated transcripts of pattern recognition receptors and defense-related genes (Ding et al. 2012a). These studies suggest that the rice HDACs function in both abiotic and biotic stress responses. In barley, the HD2 genes were also found to respond to treatments with plant stress-related hormones such as JA, ABA, and SA, implying an association of these genes with plant resistance to biotic and abiotic stresses (Demetriou et al. 2009).

## Histone Methylation and Demethylation

The steady-state level of a covalent histone modification is controlled by a balance between enzymes that catalyze the

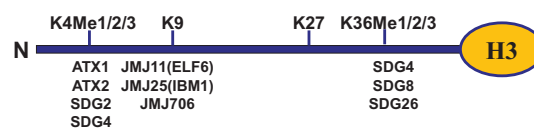
addition and removal of a given modification. The methylation marks are written on lysine or arginine by distinct enzymes, namely, histone lysine methyltransferases (HKMTs) or protein arginine methyltransferases (PRMTs). Methylation marks can be removed by eraser enzymes, the histone demethylases (HDMs; Liu et al. 2010). In *Arabidopsis*, histone lysine methylation occurs mainly at Lys4, Lys9, Lys27, and Lys36 of H3 (Figure 1). Generally, histone H3K9 and H3K27 methylation is associated with transcriptional gene silencing, whereas H3K4 and H3K36 methylation is associated with gene activation.

## Histone Lysine Methyltransferases and Protein Arginine Methyltransferases

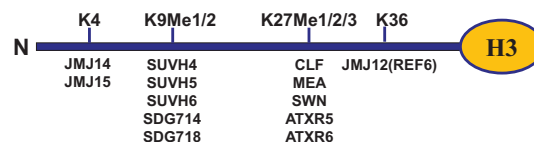
Histone lysine methyltransferases are characterized with a SET domain. Thirty-one and 25 genes encoding putative SET domain-containing proteins have been identified in *Arabidopsis* and rice, respectively (Ng et al. 2007; Lu et al. 2008). Based on the homology of SET domains with proteins in animals and yeast and the characteristics of the conserved domains, SET domain proteins in plants are classified into four categories, SU(VAR) 3–9 groups, E(Z) (enhancer of zeste) groups, TRX (trithorax) groups, and ASH1 (absent, small, or homeotic discs 1) groups (Springer et al. 2003; Zhao and Shen 2004). Members of the plant SET-domain family proteins were shown to play crucial functions in diverse processes including flowering time control, cell fate determination, leaf morphogenesis, floral organogenesis, parental imprinting and seed development (Liu et al. 2010; Berr et al. 2011).

The *Arabidopsis* TRX-like factor ATX1, which tri-methylates histone H3 at lysine 4 (H3K4me<sub>3</sub>), is involved in dehydratation

### Gene activation



### Gene repression



**Figure 1. Histone lysine methyltransferases and demethylases in gene activation and repression.**

Active histone marks (H3K4Me<sub>1/2/3</sub> and K36Me<sub>1/2/3</sub>) and repressive histone marks (H3K9Me<sub>1/2</sub> and H3K27Me<sub>1/2/3</sub>) are written by histone lysine methyltransferases but removed by demethylases.

stress signaling in both ABA-dependent and ABA-independent pathways (Ding et al. 2011). The *atx1* plants exhibit decreased germination rates, larger stomata apertures, more rapid transpiration and decreased tolerance to dehydration stress. Dehydration stress increased ATX1 binding to *NCED3*, and ATX1 was required for the increased level of *NCED3* transcript and nucleosomal H3K4me3 that occurred during dehydration stress. ATX1 can influence the gene expression in both ABA-dependent and ABA-independent pathways, implicating that ATX1 is involved in diverse dehydration stress-response mechanisms in *Arabidopsis* (Ding et al. 2011). ATX1 was also shown to be necessary for the induction of WRKY70, a transcription factor in the SA pathway involved in defense against bacterial pathogens (Alvarez-Venegas et al. 2007). In barley, the transcription of *HvTX1* encoding a TRX-like H3K4 methyltransferase shows a remarkable increase upon drought treatment (Shvarts lu et al. 2010). Taken together, these findings indicate that plant TRX-like factors play an essential role in plant responding to environmental stresses.

The *Arabidopsis* SDG8 (SET DOMAIN GROUP8) protein is a yeast SET2 and *Drosophila* ASH1 homolog (Kim et al. 2005). *Arabidopsis* SDG8 plays a crucial role in plant defense against fungal pathogens by regulation of a subset of genes in the JA and/or ET signaling pathway (Berr et al. 2010). Loss-of-function mutant *sdg8-1* displays reduced resistance to the necrotrophic fungal pathogens *A. brassicicola* and *Botrytis cinerea*. *sdg8-1* impairs dynamic changes of histone H3K36 methylation at defense marker genes, suggesting that SDG8 mediates pathogen responses by regulating histone methylation of defense responsive genes. The WD40 protein, MSI1 (Multicopy Suppressor of IRA1), is a subunit of the Polycomb group (PcG) complex that has an H3K27 methylation activity. Recent work showed that *Arabidopsis* *msi1* mutants displayed increased tolerance to drought stress (Alexandre et al. 2009). The expression of stress and ABA responsive genes was upregulated in *msi1* plants, and MSI1 bind to the chromatin of *FD20*, suggesting that MSI1 suppresses stress responsive genes in an ABA-dependent manner.

Arginine methylation mainly occurs at Arg2, Arg8, Arg17, and Arg26 of histone H3, and Arg3 of histone H4. Arginine methylation is catalyzed by a small group of PRMTs. It was reported that SKB1 (PRMT5) is involved in salt stress response (Zhang et al. 2011). Mutation of *SKB1* results in a salt hypersensitivity phenotype. SKB1 associates with chromatin and thereby increases the H4R3sme2 level to suppress the transcription of a number of stress-responsive genes. During salt stress, the H4R3sme2 level is reduced, as a consequence of SKB1 disassociating from chromatin to induce the expression of the stress-responsive genes (Zhang et al. 2011). These findings indicate that SKB1 mediates salt response by altering the methylation status of H4R3sme2 of stress responsive genes.

## Histone Demethylases

Histone demethylases play important roles in regulation of methylation homeostasis. Jumonji proteins (JMJs) were first identified to be involved in histone mono-, di-, and trimethylation in human and yeast cells (Tsukada et al. 2006). *Arabidopsis* genome encodes 21 JMJs which are grouped into five subfamilies, KDM5/JARID1 group, KDM4/JHDM3 group, KDM3/JHDM2 group, JMJD6 group, and JmjC domain-only group (Liu et al. 2010). Jumonji proteins play an essential role in control of flowering time, floral organ development and brassinosteroid signal transduction. The KDM4/JHDM3 group members, ELF6/JMJ11 (Early Flowering 6) and its close homolog REF6/JMJ12 (Relative of Early Flowering 6) play divergent roles in control of flowering time (Noh et al. 2004). *elf6/jmj11* mutant displays early flowering, while *ref6/jmj12* shows a FLC-dependent late-flowering phenotype (Noh et al. 2004). ELF6/JMJ11 and REF6/JMJ12 physically interact with BES1 and are recruited to BES1 target sites reducing their H3K9me3 levels, suggesting a role of these JMJs in modulating brassinosteroid signaling (Yu et al. 2008). Recently, *Arabidopsis* ELF6/JMJ12 was suggested to be a H3K27 demethylase specifically demethylates H3K27me3 and H3K27me2 (Lu et al. 2011). Rice JHDM2 family protein JMJ706 has been shown to demethylase histone H3K9me3. Loss-of-function mutants of *JMJ706* cause flower organ number variation of spikelets and global elevation of H3K9me2 and H3K9me3 levels (Sun and Zhou 2008). More recently, rice JMJ703 was identified as a histone lysine demethylase that specifically demethylates all three forms of H3K4me in rice (Chen et al. 2013; Cui et al. 2013). Loss-of-function mutation of *JMJ703* affects stem elongation and plant growth and leads to misregulation of the activities of transposons in rice (Chen et al. 2013; Cui et al. 2013). These studies suggest that JMJs play essential roles in plant development and gene silencing.

Lysine-specific demethylase (LSD1) is another family of histone demethylases, which remove only di- and mono-methyl groups from lysine residues (Klose and Zhang 2007). In *Arabidopsis*, there are four LSD1 homologs, FLD (FLOWERING LOCUS D), LDL1 (LSD1-LIKE 1), LDL2 and LDL3. It was reported that FLD, LDL1, and LDL2 are required in the control of flowering (Jiang et al. 2007). LDL1 reduces the levels of H4K4me in chromatin of the floral repressor *FLC* and sporophytically silences the floral repressor *FWA*. LDL1 and LDL2 act in partial redundancy with FLD to repress the *FLC* expression (Jiang et al. 2007). These studies reveal a crucial role of plant LSD1 proteins in regulation of flowering.

Although the involvement of plant HDMs in abiotic stresses has not been reported, recent studies suggest a possible role of histone demethylation in plant stress responses. Abscisic acid increases H3K9K14ac and H3K4me3 while it decreases

H3K9me2 of ABA responsive genes, such as *ABI1*, *ABI2*, and *RD29B* in *Arabidopsis* (Chen et al. 2010), indicating that some HDMs might act to activate the ABA-responsive genes by removal of the methyl groups from histone H3K9me2. Dynamic changes of H3K4 mono-, di-, and tri-methylation were also observed in *Arabidopsis* in response to dehydration stress (van Dijk et al. 2010). Downregulation of stress responsive genes upon dehydration treatment is accompanied with an obvious decrease of H3K4me and H3K4me3, while the H3K4me2 levels were only slightly reduced, indicating that HDMs might modulate the expression of dehydration stress responsive genes. More recent studies also indicate a dynamic change of H3K4me3 in rice under drought stress (van Dijk et al. 2010; Zong et al. 2012). In drought stress, 4 837 genes were differentially H3K4me3-modified, with 3 927 genes with increased H3H4me3 and 910 genes with decreased H3H4me3. The H3K4me3 modification level was mainly increased in genes with low expression and decreased in genes with high expression under drought stress, suggesting that the rice HDMs might act preferentially to the active genes during drought stress.

## ATP-Dependent Chromatin Remodeling

Adenosine triphosphate-dependent chromatin remodeling complexes use the energy of ATP hydrolysis to alter the structure of chromatin, which is an important epigenetic mechanism in the regulation of eukaryotic gene expression (Vignali et al. 2000). Recent studies revealed that ATP-dependent chromatin remodeling factors play important roles in plant responses to abiotic stresses. SWI3B encoded an *Arabidopsis* homolog of the yeast SWI3 subunit of SWI/SNF chromatin-remodeling complexes (Sarnowski et al. 2002, 2005). SWI3B directly interacts with HAB1, a protein phosphatase type 2C, which is a negative regulator of ABA signaling (Saez et al. 2008). The *swi3b* mutants show a reduced sensitivity to ABA-mediated inhibition of seed germination and growth as well as decreased expression of ABA-responsive genes, *RAB18* and *RD29B*. These findings suggest that SWI3B is a negative regulator of ABA signaling and HAB1 modulates the ABA response through the regulation of a putative SWI/SNF chromatin-remodeling complex (Saez et al. 2008).

*Arabidopsis* CHR12, a SNF/Brahma (BRM)-type chromatin remodeling factor, has been implicated as a negative regulator in the temporary growth arrest caused by drought and heat stress in *Arabidopsis* (Mlynarova et al. 2007). Exposing *CHR12* overexpressing mutants to stress conditions leads to growth arrest of normally active primary buds, as well as to reduced growth of the primary stem. *AtCHR12* knockout mutant shows less growth arrest than the wild-type when exposed to moderate stress. Without stress, mutant plants are indistinguishable from

the wild-type, and the growth arrest response seems to be dependent on the severity of the stress applied. These data indicate that CHR12 is involved in the response repertoire of plants that permits flexible modulation of growth in adverse environments (Mlynarova et al. 2007).

More recently, the SWI2/SNF2 chromatin remodeling ATPase BRM (BRAHMA) was shown to play an essential role in response of stresses in *Arabidopsis*. It was found that *brm* mutants display increased drought tolerance (Han et al. 2012). *ABI5* expression was derepressed in *brm* mutants in the absence of exogenous ABA but accumulated to high levels upon ABA sensing. Moreover, loss of BRM activity led to destabilization of nucleosomes, indicating that BRM regulate stress responses through the regulation of nucleosome stability of *ABI5* (Han et al. 2012).

## Concluding Remarks

Recent studies indicate that the histone modifications and chromatin remodeling play essential roles in plant stress response. These findings largely broaden our understanding of the flexibility and accuracy of transcription systems in plant cells responding to environmental stimulus. The combined effects of diverse histone modifications provide sophisticated and effective mechanisms to regulate gene activity in plant stress responses. However, the comprehensive mechanisms of the epigenetic factors involved in stress responses are still unclear. The target genes of the histone modification factors are largely unidentified. In addition, the dynamic assembly and occupancy of histone modifications on the targets under different abiotic stresses need to be examined. More recently, the involvement of histone modifications in the training and inheritance of the defensive capacity of plants was also identified (Paszowski and Grossniklaus 2011; Ding et al. 2012b). Further research about the function of histone modification factors in stress response may help to engineer plants with increased tolerance to multiple stresses.

## Acknowledgements

This work was supported by the National Basic Research Program of China (973 program: 2012CB910900), the National Natural Science Foundation of China (31200965 and 31201106), the Guangdong Natural Science Foundation (S2012040006474), and Start-up foundation of South China Botanical Garden, the Chinese Academy of Sciences.

Received 15 Feb. 2013 Accepted 17 Apr. 2013

## References

- Alexandre C, Moller-Steinbach Y, Schonrock N, Gruissem W, Hennig L (2009) *Arabidopsis* MS1 is required for negative regulation of the response to drought stress. *Mol. Plant* **2**, 675–687.
- Alinsug MV, Yu CW, Wu K (2009) Phylogenetic analysis, subcellular localization, and expression patterns of RPD3/HDA1 family histone deacetylases in plants. *BMC Plant Biol.* **9**, 37.
- Alvarez-Venegas R, Abdallat AA, Guo M, Alfano JR, Avramova Z (2007) Epigenetic control of a transcription factor at the cross section of two antagonistic pathways. *Epigenetics* **2**, 106–113.
- Aufsatz W, Mette MF, van der Winden J, Matzke M, Matzke AJ (2002) HDA6, a putative histone deacetylase needed to enhance DNA methylation induced by double-stranded RNA. *EMBO J.* **21**, 6832–6841.
- Aufsatz W, Stoiber T, Rakic B, Naumann K (2007) *Arabidopsis* histone deacetylase 6: A green link to RNA silencing. *Oncogene* **26**, 5477–5488.
- Berger SL (2007) The complex language of chromatin regulation during transcription. *Nature* **447**, 407–412.
- Berr A, McCallum EJ, Alioua A, Heintz D, Heitz T, Shen WH (2010) *Arabidopsis* histone methyltransferase SET DOMAIN GROUP8 mediates induction of the jasmonate/ethylene pathway genes in plant defense response to necrotrophic fungi. *Plant Physiol.* **154**, 1403–1414.
- Berr A, Shafiq S, Shen WH (2011) Histone modifications in transcriptional activation during plant development. *Biochim. Biophys. Acta* **1809**, 567–576.
- Bertrand C, Bergounioux C, Domenichini S, Delarue M, Zhou DX (2003) *Arabidopsis* histone acetyltransferase AtGCN5 regulates the floral meristem activity through the WUSCHEL/AGAMOUS pathway. *J. Biol. Chem.* **278**, 28246–28251.
- Chen LT, Wu K (2010) Role of histone deacetylases HDA6 and HDA19 in ABA and abiotic stress response. *Plant Signal. Behav.* **5**, 1318–1320.
- Chen Z, Zhang H, Jablonowski D, Zhou X, Ren X, Hong X, Schaffrath R, Zhu JK, Gong Z (2006) Mutations in ABO1/ELO2, a subunit of holo-Elongator, increase abscisic acid sensitivity and drought tolerance in *Arabidopsis thaliana*. *Mol. Cell. Biol.* **26**, 6902–6912.
- Chen LT, Luo M, Wang YY, Wu K (2010) Involvement of *Arabidopsis* histone deacetylase HDA6 in ABA and salt stress response. *J. Exp. Bot.* **61**, 3345–3353.
- Chen Q, Chen X, Wang Q, Zhang F, Lou Z, Zhang Q, Zhou DX (2013) Structural basis of a histone H3 lysine 4 demethylase required for stem elongation in rice. *PLoS Genet.* **9**, e1003239.
- Chinnusamy V, Gong Z, Zhu JK (2008) Abscisic acid-mediated epigenetic processes in plant development and stress responses. *J. Integr. Plant Biol.* **50**, 1187–1195.
- Chinnusamy V, Zhu JK (2009) Epigenetic regulation of stress responses in plants. *Curr. Opin. Plant Biol.* **12**, 133–139.
- Choi SM, Song HR, Han SK, Han M, Kim CY, Park J, Lee YH, Jeon JS, Noh YS, Noh B (2012) HDA19 is required for the repression of salicylic acid biosynthesis and salicylic acid-mediated defense responses in *Arabidopsis*. *Plant J.* **71**, 135–146.
- Cui X, Jin P, Gu L, Lu Z, Xue Y, Wei L, Qi J, Song X, Luo M, An G, Cao X (2013) Control of transposon activity by a histone H3K4 demethylase in rice. *Proc. Natl. Acad. Sci. USA* **110**, 1953–1958.
- Dehesh K, Liu CM (2010) Understanding plant development and stress responses through integrative approaches. *J. Integr. Plant Biol.* **52**, 350–353.
- Demetriou K, Kapazoglou A, Tondelli A, Francia E, Stanca MA, Bladenopoulos K, Tsaftaris AS (2009) Epigenetic chromatin modifiers in barley: I. Cloning, mapping and expression analysis of the plant specific HD2 family of histone deacetylases from barley, during seed development and after hormonal treatment. *Physiol. Plant.* **136**, 358–368.
- Deng W, Liu C, Pei Y, Deng X, Niu L, Cao X (2007) Involvement of the histone acetyltransferase AtHAC1 in the regulation of flowering time via repression of FLOWERING LOCUS C in *Arabidopsis*. *Plant Physiol.* **143**, 1660–1668.
- Ding Y, Avramova Z, Fromm M (2011) The *Arabidopsis* trithorax-like factor ATX1 functions in dehydration stress responses via ABA-dependent and ABA-independent pathways. *Plant J.* **66**, 735–744.
- Ding Y, Fromm M, Avramova Z (2012b) Multiple exposures to drought ‘train’ transcriptional responses in *Arabidopsis*. *Nat. Commun.* **3**, 740.
- Ding B, Bellizzi Mdel R, Ning Y, Meyers BC, Wang GL (2012a) HDT701, a histone H4 deacetylase, negatively regulates plant innate immunity by modulating histone H4 acetylation of defense-related genes in rice. *Plant Cell* **24**, 3783–3794.
- Earley K, Lawrence RJ, Pontes O, Reuther R, Enciso AJ, Silva M, Neves N, Gross M, Viegas W, Pikaard CS (2006a) Erasure of histone acetylation by *Arabidopsis* HDA6 mediates large-scale gene silencing in nucleolar dominance. *Genes Dev.* **20**, 1283–1293.
- Earley K, Lawrence RJ, Pontes O, Reuther R, Enciso AJ, Silva M, Neves N, Gross M, Viegas W, Pikaard CS (2006b) Erasure of histone acetylation by *Arabidopsis* HDA6 mediates large-scale gene silencing in nucleolar dominance. *Genes Dev.* **20**, 1283–1293.
- Earley KW, Pontvianne F, Wierzbicki AT, Blevins T, Tucker S, Costa-Nunes P, Pontes O, Pikaard CS (2010) Mechanisms of HDA6-mediated rRNA gene silencing: Suppression of intergenic Pol II transcription and differential effects on maintenance versus siRNA-directed cytosine methylation. *Genes Dev.* **24**, 1119–1132.
- Fu W, Wu K, Duan J (2007) Sequence and expression analysis of histone deacetylases in rice. *Biochem. Biophys. Res. Commun.* **356**, 843–850.
- Han SK, Sang Y, Rodrigues A, Wu MF, Rodriguez PL, Wagner D (2012) The SWI2/SNF2 chromatin remodeling ATPase BRAHMA represses abscisic acid responses in the absence of the stress stimulus in *Arabidopsis*. *Plant Cell* **24**, 4892–4906.
- Hollender C, Liu Z (2008) Histone deacetylase genes in *Arabidopsis* development. *J. Integr. Plant Biol.* **50**, 875–885.
- Hu Y, Qin F, Huang L, Sun Q, Li C, Zhao Y, Zhou DX (2009) Rice histone deacetylase genes display specific expression patterns and

- developmental functions. *Biochem. Biophys. Res. Commun.* **388**, 266–271.
- Hu Y, Zhang L, Zhao L, Li J, He S, Zhou K, Yang F, Huang M, Jiang L, Li L** (2011) Trichostatin A selectively suppresses the cold-induced transcription of the *ZmDREB1* gene in maize. *PLoS ONE* **6**, e22132.
- Huang L, Sun Q, Qin F, Li C, Zhao Y, Zhou DX** (2007) Down-regulation of a *SILENT INFORMATION REGULATOR*<sub>2</sub>-related histone deacetylase gene, *OsSRT1*, induces DNA fragmentation and cell death in rice. *Plant Physiol.* **144**, 1508–1519.
- Jenuwein T, Allis CD** (2001) Translating the histone code. *Science* **293**, 1074–1080.
- Jiang D, Yang W, He Y, Amasino RM** (2007) *Arabidopsis* relatives of the human lysine-specific demethylase1 repress the expression of *FWA* and *FLOWERING LOCUS C* and thus promote the floral transition. *Plant Cell* **19**, 2975–2987.
- Kaldis A, Tsementzi D, Tanriverdi O, Vlachonasios KE** (2011) *Arabidopsis thaliana* transcriptional co-activators ADA2b and SGF29a are implicated in salt stress responses. *Planta* **233**, 749–762.
- Kim SY, He Y, Jacob Y, Noh YS, Michaels S, Amasino R** (2005) Establishment of the vernalization-responsive, winter-annual habit in *Arabidopsis* requires a putative histone H3 methyl transferase. *Plant Cell* **17**, 3301–3310.
- Kim JM, To TK, Ishida J, Morosawa T, Kawashima M, Matsui A, Toyoda T, Kimura H, Shinozaki K, Seki M** (2008a) Alterations of lysine modifications on the histone H3 N-tail under drought stress conditions in *Arabidopsis thaliana*. *Plant Cell Physiol.* **49**, 1580–1588.
- Kim KC, Lai Z, Fan B, Chen Z** (2008b) *Arabidopsis* WRKY38 and WRKY62 transcription factors interact with histone deacetylase 19 in basal defense. *Plant Cell* **20**, 2357–2371.
- Klose RJ, Zhang Y** (2007) Regulation of histone methylation by demethyliminination and demethylation. *Nat. Rev. Mol. Cell. Biol.* **8**, 307–318.
- Kornet N, Scheres B** (2009) Members of the GCN5 histone acetyltransferase complex regulate PLETHORA-mediated root stem cell niche maintenance and transit amplifying cell proliferation in *Arabidopsis*. *Plant Cell* **21**, 1070–1079.
- Kouzarides T** (2007) Chromatin modifications and their function. *Cell* **128**, 693–705.
- Kwon CS, Lee D, Choi G, Chung WI** (2009) Histone occupancy-dependent and -independent removal of H3K27 trimethylation at cold-responsive genes in *Arabidopsis*. *Plant J.* **60**, 112–121.
- Li C, Huang L, Xu C, Zhao Y, Zhou DX** (2011a) Altered levels of histone deacetylase OsHDT1 affect differential gene expression patterns in hybrid rice. *PLoS ONE* **6**, e21789.
- Li W, Liu H, Cheng ZJ, Su YH, Han HN, Zhang Y, Zhang XS** (2011b) DNA methylation and histone modifications regulate de novo shoot regeneration in *Arabidopsis* by modulating WUSCHEL expression and auxin signaling. *PLoS Genet.* **7**, e1002243.
- Li X, Qian W, Zhao Y, Wang C, Shen J, Zhu JK, Gong Z** (2012) Antisilencing role of the RNA-directed DNA methylation pathway and a histone acetyltransferase in *Arabidopsis*. *Proc. Natl. Acad. Sci. USA* **109**, 11425–11430.
- Lippman Z, May B, Yordan C, Singer T, Martienssen R** (2003) Distinct mechanisms determine transposon inheritance and methylation via small interfering RNA and histone modification. *PLoS Biol.* **1**, 420–428.
- Liu C, Lu F, Cui X, Cao X** (2010) Histone methylation in higher plants. *Annu. Rev. Plant Biol.* **61**, 395–420.
- Liu X, Chen CY, Wang KC, Luo M, Tai R, Yuan L, Zhao M, Yang S, Tian G, Cui Y, Hsieh HL, Wu K** (2013) PHYTOCHROME INTERACTING FACTOR3 associates with the Histone Deacetylase HDA15 in repression of chlorophyll biosynthesis and photosynthesis in etiolated *Arabidopsis* seedlings. *Plant Cell* **25**, 1258–1273.
- Liu X, Luo M, Zhang W, Zhao J, Zhang J, Wu K, Tian L, Duan J** (2012a) Histone acetyltransferases in rice (*Oryza sativa* L.): Phylogenetic analysis, subcellular localization and expression. *BMC Plant Biol.* **12**, 145.
- Liu X, Yu CW, Duan J, Luo M, Wang K, Tian G, Cui Y, Wu K** (2012b) HDA6 directly interacts with DNA methyltransferase MET1 and maintains transposable element silencing in *Arabidopsis*. *Plant Physiol.* **158**, 119–129.
- Lu F, Li G, Cui X, Liu C, Wang XJ, Cao X** (2008) Comparative analysis of JmjC domain-containing proteins reveals the potential histone demethylases in *Arabidopsis* and rice. *J. Integr. Plant Biol.* **50**, 886–896.
- Lu F, Cui X, Zhang S, Jenuwein T, Cao X** (2011) *Arabidopsis* REF6 is a histone H3 lysine 27 demethylase. *Nat. Genet.* **43**, 715–719.
- Luo M, Liu X, Singh P, Cui Y, Zimmerli L, Wu K** (2012a) Chromatin modifications and remodeling in plant abiotic stress responses. *Biochim. Biophys. Acta Gene Regul. Mech.* **1819**, 129–136.
- Luo M, Wang YY, Liu X, Yang S, Lu Q, Cui Y, Wu K** (2012b) HD2C interacts with HDA6 and is involved in ABA and salt stress response in *Arabidopsis*. *J. Exp. Bot.* **63**, 3297–3306.
- Luo M, Yu CW, Chen FF, Zhao L, Tian G, Liu X, Cui Y, Yang JY, Wu K** (2012c) Histone deacetylase HDA6 is functionally associated with AS1 in repression of KNOX genes in *Arabidopsis*. *PLoS Genet.* **8**, e1003114.
- Mao Y, Pavangadkar KA, Thomashow MF, Triezenberg SJ** (2006) Physical and functional interactions of *Arabidopsis* ADA2 transcriptional coactivator proteins with the acetyltransferase GCN5 and with the cold-induced transcription factor CBF1. *Biochim. Biophys. Acta* **1759**, 69–79.
- Mlynarova L, Nap JP, Bisseling T** (2007) The SWI/SNF chromatin-remodeling gene AtCHR12 mediates temporary growth arrest in *Arabidopsis thaliana* upon perceiving environmental stress. *Plant J.* **51**, 874–885.
- Murfett J, Wang XJ, Hagen G, Guilfoyle TJ** (2001) Identification of *Arabidopsis* histone deacetylase HDA6 mutants that affect transgene expression. *Plant Cell* **13**, 1047–1061.
- Nagy Z, Riss A, Fujiyama S, Krebs A, Orpinell M, Jansen P, Cohen A, Stunnenberg HG, Kato S, Tora L** (2010) The metazoan ATAC and

- SAGA coactivator HAT complexes regulate different sets of inducible target genes. *Cell Mol. Life Sci.* **67**, 611–628.
- Ng DW, Wang T, Chandrasekharan MB, Aramayo R, Kertbundit S, Hall TC** (2007) Plant SET domain-containing proteins: Structure, function and regulation. *Biochim. Biophys. Acta* **1769**, 316–329.
- Noh B, Lee SH, Kim HJ, Yi G, Shin EA, Lee M, Jung KJ, Doyle MR, Amasino RM, Noh YS** (2004) Divergent roles of a pair of homologous jumonji/zinc-finger-class transcription factor proteins in the regulation of *Arabidopsis* flowering time. *Plant Cell* **16**, 2601–2613.
- Pandey R, Muller A, Napoli CA, Selinger DA, Pikaard CS, Richards EJ, Bender J, Mount DW, Jorgensen RA** (2002) Analysis of histone acetyltransferase and histone deacetylase families of *Arabidopsis thaliana* suggests functional diversification of chromatin modification among multicellular eukaryotes. *Nucleic Acids Res.* **30**, 5036–5055.
- Paszowski J, Grossniklaus U** (2011) Selected aspects of trans-generational epigenetic inheritance and resetting in plants. *Curr. Opin. Plant Biol.* **14**, 195–203.
- Pavangadkar K, Thomashow MF, Triezenberg SJ** (2010) Histone dynamics and roles of histone acetyltransferases during cold-induced gene regulation in *Arabidopsis*. *Plant Mol. Biol.* **74**, 183–200.
- Qian W, Miki D, Zhang H, Liu Y, Zhang X, Tang K, Kan Y, La H Li X, Li S, Zhu X, Shi X, Zhang K, Pontes O, Chen X, Liu R, Gong Z, Zhu JK** (2012) A histone acetyltransferase regulates active DNA demethylation in *Arabidopsis*. *Science* **336**, 1445–1448.
- Saez A, Rodrigues A, Santiago J, Rubio S, Rodriguez PL** (2008) HAB1-SWI3B interaction reveals a link between abscisic acid signaling and putative SWI/SNF chromatin-remodeling complexes in *Arabidopsis*. *Plant Cell* **20**, 2972–2988.
- Sarnowski TJ, Swiezewski S, Pawlikowska K, Kaczanowski S, Jerzmanowski A** (2002) AtSWI3B, an *Arabidopsis* homolog of SWI3, a core subunit of yeast Swi/Snf chromatin remodeling complex, interacts with FCA, a regulator of flowering time. *Nucleic Acids Res.* **30**, 3412–3421.
- Sarnowski TJ, Rios G, Jasik J, Swiezewski S, Kaczanowski S, Li Y, Kwiatkowska A, Pawlikowska K, Kozbial M, Kozbial P, Koncz C, Jerzmanowski A** (2005) SWI3 subunits of putative SWI/SNF chromatin-remodeling complexes play distinct roles during *Arabidopsis* development. *Plant Cell* **17**, 2454–2472.
- Servet C, Benhamed M, Latrasse D, Kim W, Delarue M, Zhou DX** (2008) Characterization of a phosphatase 2C protein as an interacting partner of the histone acetyltransferase GCN5 in *Arabidopsis*. *Biochim. Biophys. Acta* **1779**, 376–382.
- Servet C, Conde e Silva N, Zhou DX** (2010) Histone acetyltransferase AtGCN5/HAG1 is a versatile regulator of developmental and inducible gene expression in *Arabidopsis*. *Mol. Plant* **3**, 670–677.
- Shahbazian MD, Grunstein M** (2007) Functions of site-specific histone acetylation and deacetylation. *Annu. Rev. Biochem.* **76**, 75–100.
- Shvarts lu B, Kahn TG, Pirrotta V** (2010) Polycomb and trithorax control genome expression by determining the alternative epigenetic states of chromatin for key developmental regulators. *Genetika* **46**, 1413–1416.
- Song CP, Agarwal M, Ohta M, Guo Y, Halfter U, Wang P, Zhu JK** (2005) Role of an *Arabidopsis* AP2/EREBP-type transcriptional repressor in abscisic acid and drought stress responses. *Plant Cell* **17**, 2384–2396.
- Song Y, Ji D, Li S, Wang P, Li Q, Xiang F** (2012) The dynamic changes of DNA methylation and histone modifications of salt responsive transcription factor genes in soybean. *PLoS ONE* **7**, e41274.
- Springer NM, Napoli CA, Selinger DA, Pandey R, Cone KC, Chandler VL, Kaepler HF, Kaepler SM** (2003) Comparative analysis of SET domain proteins in maize and *Arabidopsis* reveals multiple duplications preceding the divergence of monocots and dicots. *Plant Physiol.* **132**, 907–925.
- Sridha S, Wu K** (2006) Identification of ATHD2C as a novel regulator of abscisic acid responses in *Arabidopsis*. *Plant J.* **46**, 124–133.
- Steward N, Ito M, Yamaguchi Y, Koizumi N, Sano H** (2002) Periodic DNA methylation in maize nucleosomes and demethylation by environmental stress. *J. Biol. Chem.* **277**, 37741–37746.
- Stockinger EJ, Mao Y, Regier MK, Triezenberg SJ, Thomashow MF** (2001) Transcriptional adaptor and histone acetyltransferase proteins in *Arabidopsis* and their interactions with CBF1, a transcriptional activator involved in cold-regulated gene expression. *Nucleic Acids Res.* **29**, 1524–1533.
- Sun Q, Zhou DX** (2008) Rice jmjC domain-containing gene JMJ706 encodes H3K9 demethylase required for floral organ development. *Proc. Natl. Acad. Sci. USA* **105**, 13679–13684.
- Tanaka M, Kikuchi A, Kamada H** (2008) The *Arabidopsis* histone deacetylases HDA6 and HDA19 contribute to the repression of embryonic properties after germination. *Plant Physiol.* **146**, 149–161.
- Tian L, Chen ZJ** (2001) Blocking histone deacetylation in *Arabidopsis* induces pleiotropic effects on plant gene regulation and development. *Proc. Natl. Acad. Sci. USA* **98**, 200–205.
- Tian L, Wang J, Fong MP, Chen M, Cao H, Gelvin SB, Chen ZJ** (2003) Genetic control of developmental changes induced by disruption of *Arabidopsis* histone deacetylase 1 (*AtHD1*) expression. *Genetics* **165**, 399–409.
- To TK, Nakaminami K, Kim JM, Morosawa T, Ishida J, Tanaka M, Yokoyama S, Shinozaki K, Seki M** (2011) *Arabidopsis* HDA6 is required for freezing tolerance. *Biochem. Biophys. Res. Commun.* **406**, 414–419.
- Tsukada Y, Fang J, Erdjument-Bromage H, Warren ME, Borchers CH, Tempst P, Zhang Y** (2006) Histone demethylation by a family of JmjC domain-containing proteins. *Nature* **439**, 811–816.
- Ueno Y, Ishikawa T, Watanabe K, Terakura S, Iwakawa H, Okada K, Machida C, Machida Y** (2007) Histone deacetylases and ASYMMETRIC LEAVES2 are involved in the establishment of polarity in leaves of *Arabidopsis*. *Plant Cell* **19**, 445–457.
- van Dijk K, Ding Y, Malkaram S, Riethoven JJ, Liu R, Yang J, Laczko P, Chen H, Xia Y, Ladunga I, Avramova Z, Fromm M** (2010) Dynamic changes in genome-wide histone H3 lysine 4 methylation patterns in response to dehydration stress in *Arabidopsis thaliana*. *BMC Plant Biol.* **10**, 238.

- Versees W, De Groeve S, Van Lijsebettens M** (2010) Elongator, a conserved multitasking complex? *Mol. Microbiol.* **76**, 1065–1069.
- Vignali M, Hassan AH, Neely KE, Workman JL** (2000) ATP-dependent chromatin-remodeling complexes. *Mol. Cell. Biol.* **20**, 1899–1910.
- Vlachonasios KE, Thomashow MF, Triezenberg SJ** (2003) Disruption mutations of *ADA2b* and *GCN5* transcriptional adaptor genes dramatically affect *Arabidopsis* growth, development, and gene expression. *Plant Cell* **15**, 626–638.
- Wang C, Gao F, Wu J, Dai J, Wei C, Li Y** (2010) *Arabidopsis* putative deacetylase AtSRT2 regulates basal defense by suppressing PAD4, EDS5 and SID2 expression. *Plant Cell Physiol.* **51**, 1291–1299.
- Wu K, Zhang L, Zhou C, Yu CW, Chaikam V** (2008) HDA6 is required for jasmonate response, senescence and flowering in *Arabidopsis*. *J. Exp. Bot.* **59**, 225–234.
- Yu X, Li L, Guo M, Chory J, Yin Y** (2008) Modulation of brassinosteroid-regulated gene expression by Jumonji domain-containing proteins ELF6 and REF6 in *Arabidopsis*. *Proc. Natl. Acad. Sci. USA* **105**, 7618–7623.
- Zhang Z, Zhang S, Zhang Y, Wang X, Li D, Li Q, Yue M, Zhang YE, Xu Y, Xue Y, Chong K, Bao S** (2011) *Arabidopsis* floral initiator SKB1 confers high salt tolerance by regulating transcription and pre-mRNA splicing through altering histone H4R3 and small nuclear ribonucleo-protein LSM4 methylation. *Plant Cell* **23**, 396–411.
- Zhao Z, Shen WH** (2004) Plants contain a high number of proteins showing sequence similarity to the animal SUV39H family of histone methyltransferases. *Ann. N. Y. Acad. Sci.* **1030**, 661–669.
- Zhou C, Zhang L, Duan J, Miki B, Wu K** (2005) HISTONE DEACETYLASE19 is involved in jasmonic acid and ethylene signaling of pathogen response in *Arabidopsis*. *Plant Cell* **17**, 1196–1204.
- Zhou X, Hua D, Chen Z, Zhou Z, Gong Z** (2009) Elongator mediates ABA responses, oxidative stress resistance and anthocyanin biosynthesis in *Arabidopsis*. *Plant J.* **60**, 79–90.
- Zhou Y, Tan B, Luo M, Li Y, Liu C, Chen C, Yu CW, Yang S, Dong S, Ruan J, Yuan L, Zhang Z, Zhao L, Li C, Chen H, Cui Y, Wu K, Huang S** (2013) HISTONE DEACETYLASE19 interacts with HSL1 and participates in the repression of seed maturation genes in *Arabidopsis* seedlings. *Plant Cell* **25**, 134–148.
- Zhu Z, An F, Feng Y, Li P, Xue LAM, Jiang Z, Kim JM, To TK, Li W, Zhang X, Yu Q, Dong Z, Chen WQ, Seki M, Zhou JM, Guo H** (2011) Derepression of ethylene-stabilized transcription factors (EIN3/EIL1) mediates jasmonate and ethylene signaling synergy in *Arabidopsis*. *Proc. Natl. Acad. Sci. USA* **108**, 12539–12544.
- Zong W, Zhong X, You J, Xiong L** (2012) Genome-wide profiling of histone H3K4-tri-methylation and gene expression in rice under drought stress. *Plant Mol. Biol.* **81**, 175–188.

(Co-Editor: Zhizhong Gong)