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Special issue: Invited Expert Review

Received Dec. 16, 2019 Accepted Dec. 23, 2019

Edited by: Zhizhong Gong, China Agricultural University, China

Running title: Epigenetic codes of plant abiotic stress

## **Epigenetic regulation in plant abiotic stress responses**

Ya-Nan Chang<sup>1,2</sup>, Chen Zhu<sup>1</sup>, Jing Jiang<sup>3</sup>, Huiming Zhang<sup>1,3</sup>, Jian-Kang Zhu<sup>1,4</sup>  
and Cheng-Guo Duan<sup>1,3\*</sup>

<sup>1</sup>Shanghai Center for Plant Stress Biology and Center of Excellence in Molecular Plant Sciences, Chinese Academy of Sciences, Shanghai 2001602, China

<sup>2</sup>University of Chinese Academy of Sciences, Beijing 100049, China

<sup>3</sup>State Key Laboratory of Crop Stress Adaptation and Improvement, School of Life Sciences, Henan University, Kaifeng 475004, China

<sup>4</sup>Department of Horticulture and Landscape Architecture, Purdue University, West Lafayette, IN 47907, USA

\*Correspondence: Cheng-Guo Duan (cgduan@sibs.ac.cn)

### **ABSTRACT**

In eukaryotic cells, the expression of protein-coding genes is greatly influenced by the dynamic chromatin environment. Epigenetic mechanisms, including covalent modifications to DNA and histone tails and the accessibility of chromatin, create various chromatin situations for stress-responsive gene

This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the Version of Record. Please cite this article as doi: 10.1111/jipb.12901.

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expression for adaptation to formidable conditions in nature. Most epigenetic modifications are reversible. For example, DNA and histone methylation can be catalyzed by methyltransferases and can be undone by demethylases. Recent studies have revealed that many epigenetic factors participate in abiotic stress responses, and many specific modifications are inducible and changeable in stressful environments. In this review, we summarize recent progresses on the cross-talk between epigenetic mechanisms and abiotic stress responses in plants. Our review focuses on extreme-temperature stress, drought stress, salt stress, abscisic acid (ABA)-mediated stresses, nutrient stress, ultraviolet (UV) stress and stress memory.

## INTRODUCTION

Plants live in constantly changing environments that are usually unfavorable or stressful for growth and development. The environmental conditions can be approximately classified into either biotic or abiotic stress. Abiotic stresses mainly include drought, high salinity, osmotic stress, extreme temperature, heavy metal stress and ultraviolet radiation (Zhu 2016). All these negative environmental elements counteract efforts to improve agricultural productivity and environmental sustainability. Thus, increasing plant stress resistance is critical and is also a fundamental biological problem in agricultural production. The core stress signaling pathways have been gradually unraveled during the past decade (Zhu 2016). Recently, in addition to the elucidation of the signal transduction mechanism underlying abiotic stress responses, increased numbers of studies have shown important participation of epigenetic mechanisms in the response to abiotic stresses (Sahu et al. 2013; Kim et al. 2015). A typical example is the extensive involvements of low temperature-mediated vernalization in flowering (Zhao et al. 2018; Luo and He 2019). Epigenetic mechanisms not only participate in the regulation of stress-responsive genes at the transcriptional and posttranscriptional levels by altering their chromatin status but also can be affected by stress treatments (Kim et al. 2015; Lamke and Baurle 2017; Luo and He 2019). Moreover, epigenetic mechanisms play vital roles in the formation of stress memory, which can be inherited by offspring (Friedrich et al. 2019). Therefore, deciphering the epigenetic codes of plant stress responses is of great significance for the cultivation of stress-tolerant crops.

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## PROFILE OF PLANT EPIGENETIC MECHANISMS

Epigenetics is a rapidly evolving discipline that refers to the study of heritable phenotypic changes that do not involve alteration of the genetic code itself within organisms. Epigenetic mechanisms play critical roles during the life cycle of both plants and animals (Duan et al. 2018). Epigenetic codes, including mainly DNA methylation, histone modifications, histone variants and some non-coding RNA (ncRNA) changes, influence the structure and accessibility of chromatin, which in turn alter the activity of gene expression (Duan et al. 2018). The effects of epigenetic mechanism-based regulation on gene expression depend on not only the types of epigenetic marks but also their position on genes. Heterochromatic marks such as DNA methylation and H3K9me2, for example, usually display repressive effects on downstream gene expression by inhibiting transcription when they are present within the promoter region. Intragenic heterochromatic elements are required for the proper processing of full-length transcripts (Wang et al. 2013b; Lei et al. 2014; Duan et al. 2017b). Considering the universality of transposable element (TE) insertion within genes in plant genomes (Makarevitch et al. 2015), particularly within stress-responsive genes, such a mechanism is of great significance to the dynamic regulation of stress responses. DNA methylation at the 5' position of cytosine (5mC) is one of the hallmarks of epigenetic mechanisms. In plants, DNA methylation occurs in all kinds of cytosine contexts, including CG, CHG and CHH (where H represents A, T or C), which are catalyzed by METHYLTRANSFERASE 1 (MET1), CHROMOMETHYLASE 3 (CMT3) and DOMAINS REARRANGED METHYLTRANSFERASE 2 (DRM2), respectively, in the model plant species *Arabidopsis* (Law and Jacobsen 2010; Duan et al. 2018; Zhang et al. 2018). Among them, the 24 nt siRNA-dependent RNA-directed DNA methylation (RdDM) pathway contributes to asymmetric CHH methylation, which is a plant-specific de novo DNA methylation mechanism (Law and Jacobsen 2010; Zhang et al. 2018). Epigenetic codes, including DNA methylation, are dynamically regulated by different catalytic enzymes. DNA methylation can be erased by members of the DNA glycosylase family of demethylases, including DEMETER (DME), Reprssor of Transcriptional Silencing 1 (ROS1) /DEMETER-LIKE 1 (DML1), DML2 and DML3 in *Arabidopsis* (Zhang et al. 2018; Liu and Lang 2019). Recent studies have indicated that ROS1 demethylase finds its target DNA via two complexes: the Increased DNA methylation (IDM)

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histone acetyltransferase complex and the SWI2/SNF2-Related 1 (SWR1) chromatin remodeling complex (Duan et al. 2017a; Nie et al. 2019).

In addition to DNA methylation modification, covalent modifications to histone tails, such as methylation, acetylation, phosphorylation, ubiquitination, sumoylation, glycosylation and ADP-ribosylation, constitute the other conserved epigenetic code across different kingdoms (Liu et al. 2010). Similar to those of DNA methylation, the levels of histone modifications are dynamically determined by different catalytic enzymes. The variety of histone modification types determines the complexity of functionality. Moreover, the molecular function of histone modification depends on not only the type but also the extent of certain modifications (Liu et al. 2010; Duan et al. 2018). For example, histone H3 lysine tri-methylation (H3K27me<sub>3</sub>) is usually associated with euchromatin, whereas H3K27me<sub>1</sub> is a heterochromatic marker (Liu et al. 2010). A high deposition of H3K4me<sub>3</sub> and H3K36me<sub>3</sub> marks is often observed on actively expressed genes, whereas H3K9me<sub>2</sub> marks are present within heterochromatic regions (Liu et al. 2010). These histone marks are catalyzed and removed by specific enzymes or a complex of them, which are referred to as the writer and eraser proteins/complex, and are recognized by reader proteins (Liu et al. 2010). For example, H3K27me<sub>3</sub>, which is a representative repressive marker that exhibits high deposition on stress-responsive genes, is catalyzed by the polycomb repressive complex 2 (PRC2) via the histone methyltransferases CURLY LEAF (CLF), SWINGER (SWN), and MEDEA (MEA) and their cofactors and is recognized by the PRC1 complex via the H3K27me<sub>3</sub> reader proteins LIKE HETEROCHROMATIN PROTEIN 1 (LHP1), EARLY BOLTING IN SHORT DAY (EBS), and SHORT LIFE (SHL) and their cofactors in *Arabidopsis* (Mozgova and Hennig 2015; Li et al. 2018; Yang et al. 2018b). As an active marker, H3K4me<sub>3</sub> is also present on a large number of stress-responsive genes. The COMPASS complex is responsible for the genome-wide deposition of H3K4me<sub>3</sub>, which is catalyzed by the methyltransferases ARABIDOPSIS TRITHORAX-LIKE PROTEIN 1 (ATX1) and ATX2 and regulates the transcription of various stress response genes (Saleh et al. 2008; Fromm and Avramova 2014). Both H3K4 and H3K27 methylation is undone by the jumonji (JMJ) family of histone demethylases (Liu et al. 2010). In addition to histone methylation, other histone marks, such as acetylation, phosphorylation and ubiquitination, have also been reported to participate in the regulation of multiple stress responses (Kim et al. 2015). The dynamic shift in

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different epigenetic codes is of great significance to biological processes, particularly in response to environmental stimuli (Zhang et al. 2018). For example, a large number of heat stress-responsive genes are dynamically regulated by RdDM pathway-mediated DNA methylation (Popova et al. 2013). Salt-induced expression of the AtMYB74 transcription factor is silenced by RdDM in normal conditions but is activated upon salt treatment (Popova et al. 2013; Xu et al. 2015).

## **EPIGENETIC REGULATION DURING THE EXTREME-TEMPERATURE STRESS RESPONSE**

Ambient temperature is essential for normal plant growth and development. Along with a changing climate, heat/cold stresses caused by abnormally high/low temperatures have become a major challenge for crop productivity. Cold stress has a great influence on plant metabolism and the transcriptome, including the direct inhibition of key metabolic enzymes and the reprogramming of gene expression (Zhu 2016). During the past few decades, many studies have elucidated the mechanisms of heat and cold stress responses (Driedonks et al. 2015; Guo et al. 2018; Liu et al. 2018b; Ding et al. 2019).

### **Cold stress**

The C REPEAT BINDING FACTOR (CBF)-COLD RESPONSIVE (COR) signaling pathway is one of the well-characterized mechanisms during the plant cold stress response. In this mechanism, cold stress induces the expression of transcription factors such as CBF family proteins, and these TFs bind to the promoters to activate the expression of downstream *COR* genes (Chinnusamy et al. 2007; Zhu 2016). A recent study indicated that the chromatin remodeler PICKLE (PKL) participates in the CBF-dependent cold stress response in *Arabidopsis*. Yang et al. revealed that the *pk1* mutant is hypersensitive to chilling and cold stress treatments (Yang et al. 2019). The expression of the transcription factor gene *CBF3* and of downstream *COR* family genes such as *COR15B* and *RESPONSIVE TO DEHYDRATION 29A (RD29A)* was downregulated in the *pk1* mutant after 3 h of cold treatment compared to that in wild-type plants. PKL participates in the regulation of the RdDM pathway and is also required for the deposition of H3K27me3 via cooperation with PHOTOPERIOD INDEPENDENT EARLY FLOWERING 1 (PIE1) in the SWR1 chromatin remodeling complex and

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with the H3K27me3 methyltransferase CLF in the PRC2 complex (Carter et al. 2018). H3K27me3 deposition occurs in a number of COR genes (Kwon et al. 2009). Therefore, it is possible that PKL responds to cold stress by affecting the H3K27me3-dependent chromatin status of COR genes.

In addition to histone methylation, other histone modifications also play important roles in the cold stress response. Histone acetylation is enriched in the bodies of a large number of cold-responsive genes (Zhu et al. 2008; Park et al. 2018). This process is dynamically regulated by histone acetyltransferases (HATs) and histone deacetylases (HDACs). Overexpression of *Arabidopsis* Histone Deacetylase 2D (HD2D) resulted in a slow increase in malondialdehyde (MDA) content upon cold stress treatment; thus, the transgenic plants were more tolerant to cold treatment, which could inhibit cell metabolism and lead to cell death (Han et al. 2016), suggesting that the dynamic regulation of histone acetylation is an important aspect of the regulation of the cold stress response. Histone acetylation is induced upon cold treatment in the promoter regions of some COR genes, such as *COR15A* and *COR47* (Pavangadkar et al. 2010), implying that these genes are potential targets of histone deacetylases/acetyltransferases. Moreover, recent studies have indicated that another HD2 family deacetylase, HD2C, in *Arabidopsis* is a target of HIGH EXPRESSION OF OSMOTICALLY RESPONSIVE GENES 15 (HOS15)-mediated degradation upon cold treatment (Park et al. 2018). HOS15 is a component of the CULLIN 4 (CUL4)-based E3 ubiquitin ligase complex (Zhu et al. 2008). As such, mutation of *HD2C* increases the acetylation level in the promoter region of COR genes, making those plants more tolerant to cold treatment (Pavangadkar et al. 2010; Park et al. 2018). In contrast to histone acetylation, H3K27me3 deposition in the *COR15A* and *GALACTINOL SYNTHASE 3* (*GOLS3*) genes decreased after cold treatment (Kwon et al. 2009). These results indicated that a large number of genes involved in cold responses are under the control of histone modification-dependent epigenetic regulation.

It is known the transposon domestication plays essential role in the evolution of plant genomes (Bennetzen and Wang 2014). In a previous report, the anthocyanins level-dependent diversity of fruit color in blood orange is closely related with cold-induced transcription activation of a retrotransposon (Butelli et al. 2012). In this study, the authors demonstrated that the expression of *Ruby* gene,

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which is required for the biosynthesis of anthocyanins, varies greatly among different varieties. In the varieties of *Ruby*-expression, a retrotransposon is localized in the upstream region of *Ruby* transcription start site, and cold-induced retrotransposon transcription also activated the transcription of *Ruby*, and this induction was fruit-specific, suggesting that cold-induced activation of transposon participates in the formation of agronomic traits in plants possibly through epigenetic mechanisms.

### Heat stress

The transcriptional regulatory network of the heat stress response in plants has been thoroughly reviewed (Ohama et al. 2017). HEAT SHOCK TRANSCRIPTION FACTOR A1s (HSFA1s) are the core TFs involved in the heat stress response. The multilevel regulation of HsfA1s determines the complexity of the heat stress response. On the one hand, HSFA1s are partly controlled by phosphorylation/dephosphorylation, SUMOylation and protein-protein interactions; on the other hand, HSFA1s are predicted to directly regulate the expression of heat-induced TFs such as DEHYDRATION-RESPONSIVE ELEMENT BINDING PROTEIN 2A (DREB2A), HSFA2, HSF7s, HSFs and MULTIPROTEIN BRIDGING FACTOR 1C (MBF1C) (Ohama et al. 2017). Last, downstream responsive genes are activated by those TFs. Previous studies have revealed that histone dynamics and the RdDM pathway are involved in the heat stress response (Popova et al. 2013; Lamke et al. 2016; Yang et al. 2018a). When plants are exposed to high temperature, the production of heat shock proteins (HSPs) protects proteins or other components from denaturing and misfolding (Wang et al. 2004). Heat stress induces the sustained accumulation of H3K9Ac and H3K4me3 in HSP18, HSP22.0, APX2 and HSP70. Among these genes, the accumulation of H3K9Ac and H3K4me3 in HSP18, HSP22.0 and APX2 but not HSP70 is HSFA2 dependent (Lamke et al. 2016). The Arabidopsis SUPPRESSOR OF DRM1 DRM2 CMT3 (SDC) protein, an F-BOX family protein that mediates protein degradation, can transcriptionally regulate the expression of a subset of genes that response to long-term heat stress (Sanchez and Paszkowski 2014). The SDC gene is a target of the RdDM pathway and can be epigenetically silenced in normal conditions but activated by heat stress; thus, the activity of this gene contributes to



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the recovery from stress (Popova et al. 2013), suggesting that the transcriptional response of heat stress at least partly depends on the RdDM pathway.

## **EPIGENETIC REGULATION OF THE SALT STRESS RESPONSE**

High salinity, which causes ion toxicity (mainly that of Na<sup>+</sup>), hyperosmotic stress and secondary stresses such as oxidative damage, is an enormous challenge hindering normal plant growth and development (Zhu 2016). In plants, cellular ion homeostasis is controlled by the Ca<sup>2+</sup>-CALCINEURIN B-LIKE PROTEIN (CBL)-CBL INTERACTING PROTEIN KINASE (CIPK) module. High Na<sup>+</sup>, low K<sup>+</sup>, excess Mg<sup>2+</sup> and high/low pH cause a rapid shift in Ca<sup>2+</sup>, which activates the SALT OVERLY SENSITIVE3(SOS3)-SOS2-SOS1, CBL1/9-CIPK23-*Arabidopsis* K<sup>+</sup> TRANSPORTER (AKT1), CBL2/3-CIPK3/9/23/26-putative Mg<sup>2+</sup> transporter and CBL2-CIPK11/14-H<sup>+</sup> ATPase signaling pathways, respectively (Zhu 2016). HIGH-AFFINITY K<sup>+</sup> CHANNEL 1 (HKT1), which mediates Na<sup>+</sup> influx in plants, is an important transporter involved in the SOS pathway (Rus et al. 2001). Mutation of *HKT1* could suppress the hypersensitive phenotype of *sos3* plants to NaCl (Rus et al. 2001). The putative 2.6 kb tandem repeat region of the *HKT1* promoter from the ATG start codon is heavily methylated (Baek et al. 2011). In the RdDM pathway, RNA-dependent RNA polymerase 2 (RDR2) is required for the biogenesis of 24-nt siRNAs (Xie et al. 2004), thus regulating non-CG methylation in *Arabidopsis*. Baek et al. revealed that the mutation of *RDR2* led to high transcription of the *AtHKT1* gene and that depleting the predicted RdDM target region and tandem repeat sequence of *AtHKT1* resulted in a NaCl-sensitive phenotype (Baek et al. 2011), indicating that *AtHKT1* is a target of RdDM-mediated DNA methylation. Similar regulatory activity was also observed in wheat (Kumar et al. 2017). The R2R3-MYB family transcription factor MYB74 is a salt-induced TF. Similar to *AtHKT1*, the *MYB74* promoter is heavily methylated by the 24-nt siRNA-mediated RdDM pathway under normal conditions; thus, *MYB74* maintains a low transcription level. Interestingly, in the case of salt stress, methylation and 24-nt siRNA levels were nearly undetectable, accompanied by the expression of *MYB74* (Xu et al. 2015).

In addition to DNA methylation, the roles of histone modification have gained increased amounts of attention in plant responses to high-salinity stress (Kim et al. 2015). The fine-tuning regulation of acetylation by HATs and HDACs



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makes plants better adaptable to changing environmental conditions. It has been confirmed that HISTONE DEACETYLASE 6 (HDA6) interacts with HD2C to control plant responses to salt stress. High-salinity treatment often induces the deposition of active histone marks such as H3K9/K14Ac and H3K4me3 and decreases the deposition of repressive marks such as H3K9me2 and H3K27me3 on abiotic stress-responsive genes (Sokol et al. 2007; Chen et al. 2010; Yolcu et al. 2016). Both the induction of H3K9/K14Ac and the removal of H3K9me2 upon salt treatment contributed to higher expression of *ABI1* and *ABI2* in *hda6/hd2c* mutants (Luo et al. 2012). The expression of HKT1, a representative gene that mediates high Na<sup>+</sup> influx and that is highly enriched in H3K27me3, is activated by salt treatment due to the removal of H3K27me3, at least in part (Sani et al. 2013). H3 Ser-10 phosphorylation, which is usually related to chromatin density, is another histone marker that can be induced by salinity treatment. In tobacco BY-2 cells and Arabidopsis T87 culture cells, the increase in H3 Ser-10 phosphorylation, H3 phosphorylation/acetylation and H4 acetylation display a time course pattern (Sokol et al. 2007). Surprisingly, the changes in these three types of modification are not completely consistent in response to cold and high-salinity stresses, suggesting that the regulatory mechanism varies in the response to different stresses (Sokol et al. 2007; Kim et al. 2015).

## **EPIGENETIC REGULATION OF DROUGHT STRESS RESPONSES**

The regulatory network involved in the drought stress response and tolerance in plants has been increasingly elucidated (Osakabe et al. 2014). Drought stress usually induces the synthesis of the phytohormone ABA in organisms, and in turn, ABA promotes drought tolerance (Shinozaki and Yamaguchi-Shinozaki 2007). An early study in 2007 indicated that the Arabidopsis SNF2/Brahma-type chromatin remodeling protein CHROMATIN REMODELING 12 (CHR12) mediates temporary growth arrest upon perceiving stresses, including drought and heat stresses (Mlynarova et al. 2007). NINE CIS-EPOXYCAROTENOID DIOXYGENASE 3 (NCED3) is one of the key enzymes involved in ABA synthesis (Nambara and Marion-Poll 2003). Deposition of H3K4me3 within the *NCED3* gene body region increases after drought stress, thus activating the transcription of the *NCED3* gene (Ding et al. 2011). In addition to the effect on the core ABA signaling pathway, Kim et al revealed that the expression of drought stress-induced genes is closely related to the alteration of histone

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dynamics (Matsui et al. 2008; Kim et al. 2012; To and Kim 2014; Kim et al. 2015). Expression of the drought-responsive genes *RD29A*, *RD29B*, *RD22* and *RAP2.4* is induced under drought stress (Okamoto et al. 1997; Takahashi et al. 2000), and the longer the drought persisted, the more the gene was expressed (Kim et al. 2008). The expression patterns of these genes are dependent on different histone modifications, at least partly. Under drought stress conditions, increasing H3K4me3 and H3K9Ac in the promoter regions of *RD29A*, *RD29B*, *RD22* and *RELATED TO AP2.4 (RAP2.4)* contributes to the active expression of these genes. Moreover, the abundance of histone marks within drought stress response genes varies with the degree of drought. The increase in H3K4me3 and H3K9Ac modifications was much higher under strong drought stress conditions than under moderate drought stress conditions (Kim et al. 2012; Matsui et al. 2008). After recovery from dehydration, H3K4me3 and H3K9Ac are removed from these gene regions, and the removal of H3K9Ac is more rapid than is that of H3K4me3 (Kim et al. 2012), which possibly occurs because H3K4me3 plays a role in drought stress memory. A recent study showed that the decrease in H3K27me3 deposition within the gene body region of drought stress-responsive TFs contributed to drought stress tolerance of *Arabidopsis* (Ramirez-Prado et al. 2019). LHP1 is one of the H3K27me3 reader proteins within the PRC1 complex (Mozgova and Hennig 2015). It has been known that ANAC019 and ANAC055, which are two *Arabidopsis* NAC (ANAC) family TFs involved in plant development and the response to environmental stimuli, can be induced by ABA treatment (Jiang et al. 2009). A recent publication showed that ANAC019 and ANAC055 are target genes of PRC1-LHP1-mediated transcriptional repression. Mutation of *LHP1* increased ABA sensitivity and drought tolerance, and the deposition of H3K27me3 on these two genes was lower in the *lhp1* plants than in the wild-type plants. Therefore, drought stress-induced expression of *ANAC019* and *ANAC055* increased in the *lhp1* mutant compared with the wild-type plants. Some target genes of ANAC019 and ANAC055, such as *VEGETATIVE STORAGE PROTEIN 1 (VSP1)*, were consistently upregulated in *lhp1* plants (Ramirez-Prado et al. 2019). This finding suggests that the PRC complex negatively regulates ABA-dependent drought tolerance via transcriptional repression of the ANAC019 and ANAC055 transcription factors. As summarized above, both H3K4me3 and H3K9Ac increased in drought stress-responsive genes, and H3K27me3 decreased, thus promoting the transcription of these genes under drought stress conditions.

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In addition to different histone modifications, several studies also revealed the involvements of DNA methylation in drought stress response. A study in *Populus trichocarpa* found that drought stress treatment could induce alterations in the DNA methylation level and thereby alter the expression patterns of many drought stress-responsive genes (Liang et al. 2014), although the molecular mechanism underlying this induction remains unclear. Using genome-wide association study analysis in maize, Mao et al. identified that a miniature inverted-repeat transposable element (MITE) inserts in the promoter of a *NAC* gene (*ZmNAC111*) to repress its expression through RdDM-mediated DNA methylation and H3K9me2 deposition (Mao et al. 2015). In summary, the findings above suggest that the chromatin status shaped by histone modifications and DNA methylation plays essential roles in the drought stress response, and *NAC* genes are the major integrator of multiple epigenetic mechanisms.

## **EPIGENETIC REGULATION OF ABA-MEDIATED STRESS RESPONSES**

ABA plays a crucial role in the regulation of stress responses in plants. Multiple environmental stresses, such as cold, drought, and high salinity, induce the biogenesis of ABA, which controls seed germination, stomatal closure, transcription of stress-responsive genes, etc. The core regulatory pathway of ABA signaling has been gradually identified (Zhu 2016). Under stress conditions, ABA binds to PYRABACTIN RESISTANCE1 (PYR1)/PYR1-LIKE (PYL)/REGULATORY COMPONENTS OF ABA RECEPTORS (RCAR) ABA receptors, which then bind to and inhibit clade A PHYTOCHROME-ASSOCIATED PROTEIN PHOSPHATASE TYPE 2C (PP2Cs), resulting in the release of SNF1-RELATED PROTEIN KINASE 2 (SnRK2s), which are key kinases involved in ABA signaling (Zhu 2016). The activated SnRK2s subsequently phosphorylate downstream effectors to regulate multiple biological processes, such as transcription, RNA processing, chloroplast regulation, epigenetic modification, miRNA regulation and even flowering time regulation (Wang et al. 2013a).

During the past decade, extensive efforts have been made to elucidate the epigenetic mechanisms involved in ABA-mediated stress responses (Liu et al. 2007; Chen and Wu 2010; Luo et al. 2012; Mehdi et al. 2016; Zhu et al. 2018). A recent study indicated that the transcription of the ABA receptors PYL4, PYL5

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and *PYL6* is controlled by histone acetylation. *PYL4* and *PYL5* are involved in ABA-mediated inhibition of germination, stomatal closure and activation of ABA-responsive genes (Gonzalez-Guzman et al. 2012). *PYL6* has been shown to interact with *AtMYC2*, a regulator of both ABA and jasmonic acid (JA) signaling pathways (Abe et al. 2003; Kazan and Manners 2013), and ABA treatment can enhance this interaction, serving as a putative link between the ABA and JA signaling pathways (Aleman et al. 2016). The ARABIDOPSIS MULTICOPY SUPPRESSOR OF IRA1 (*MSI1*)-HDA19-SWI-INDEPENDENT3-LIKE (*SNL*) histone deacetylation complex has been shown to target the promoters of *PYL4*, *PYL5* and *PYL6*, thus repressing the expression of those genes (Mehdi et al. 2016). In addition to being deposited on ABA receptor genes, H3Ac is also involved in the transcriptional regulation of PP2C family proteins, such as ABA INSENSITIVE 1 (*ABI1*) and *ABI2*, which were mentioned above (Luo et al. 2012).

In conjunction with *FUSCA3* (*FUS3*) and *LEAFY COTYLEDON1* and 2 (*LEC1* and *LEC2*), the *ABI3* TF has been reported to participate in early seed development (Santos-Mendoza et al. 2008). Histone dynamics are related to ABA signaling output (mainly concerning the inhibition of germination) in early seedling development (Ryu et al. 2014). It is known that the *BRI1-EMS-SUPPRESSOR 1* (*BES1*)-*TOPLESS* (*TPL*)-HDA19 histone deacetylation complex represses the expression of *ABI3* (Ryu et al. 2014). *BES1* can directly bind to the promoter region of *ABI3* and then recruit histone deacetylase HDA19 to deacetylate H3Ac. Additionally, histone dynamics are also involved in the fine-tuning regulation of *SnRK2.8* via *ABI3* (Wu et al. 2019). ABA treatment can induce the expression of *ABI3*, and subsequently, *ABI3* binds to the RY motif of histone demethylase *JMJ30* to activate its expression. *JMJ30* can remove the repressive marker H3K27me3 from the promoter region of *SnRK2.8*; *SnRK2.8* kinase, in turn, activates the expression of *ABI3* (Wu et al. 2019).

Histone H2B monoubiquitination catalyzed by *HISTONE MONOUBIQUITINATION 1* (*HUB1*) and/or *HUB2* is usually associated with gene activation, whereas H2B deubiquitination catalyzed by *UBIQUITIN-SPECIFIC PROTEASE 26* (*UBP26*) is required for heterochromatic silencing (Sridhar et al. 2007). The absence of *HUB1* or *HUB2* reduced seed

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dormancy by repressing the expression of dormancy-related genes, including *DELAY OF GERMINATION 1 (DOG1)*, *ABI4*, *NCED9*, *PEROXIREDOXIN ANTIOXIDANT (PER1)*, *CYTOCHROME P450 707A2 (CYP707A2)* and *ACYLTRANSFERASE 2 (ATS2)* (Liu et al. 2007; Chinnusamy et al. 2008), suggesting that histone ubiquitination plays a role in seed dormancy. In summary, the expression patterns of many ABA-responsive genes are dynamically regulated by multiple kinds of histone modifications.

In addition to histone modification, it has been reported that the expression of a subset of ABA-inducible genes are regulated by ROS1-dependent DNA demethylation (Kim et al. 2019). Upon ABA treatment, expression of some ABA-inducible genes was decreased in *ros1* mutant, and more than 60% of their proximal regions became hypermethylated. *NICOTINAMIDASE 3 (NIC3)* encodes an enzyme that converts nicotinamide to nicotinic acid in the NAD<sup>+</sup> salvage pathway and is linked to ABA responsiveness. NIC3 is reported to be one of targets of ROS1, and ABA treatment induced the activation of it (Kim et al. 2019). There are other ABA-inducible genes under ROS1 regulation which are also potential links between DNA methylation and ABA response. DNA methylation not only alters the expression of ABA stress responsive genes in transcriptional level but also mediates the proper subcellular location of their proteins (Khan et al. 2014). The mutants of two DEAD-box RNA helicases, *STRESS RESPONSE SUPPRESSOR1 (STRS1)* and *STRS2*, have been shown to display tolerance to abiotic stresses. Khan et al. showed that both ABA treatment and the malfunctions of RdDM-mediated DNA methylation and HD2C-mediated histone deacetylation led to a mis-localization of *STRS2* and/or *STRS1*. Using an genetic screen based on ABA inhibition of seed germination and seedling growth, Dr. Gong's laboratory identified a mutant of *Arabidopsis thaliana* *POL2a/TILTED1 (TIL1)*, which encodes a catalytic subunit of DNA polymerase  $\epsilon$  (Yin et al. 2009). The *til1/abo4* mutant not only displayed ABA hypersensitivity but also released transgene silencing in the *ros1* mutant without changing DNA methylation.

Additionally, several studies have revealed an important involvement of chromatin remodeling complex in the regulation of ABA-mediated stress responses (Figure 4) (Saez et al. 2008; Han et al. 2012; Peirats-Llobet et al. 2016). As early as 2008, Saez et al. demonstrated that SWITCH/SUCROSE

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NONFERMENTING 3B (SWI3B), an Arabidopsis homolog of the yeast SWI3 subunit of SWITCH/SUCROSE NONFERMENTING (SWI/SNF) chromatin-remodeling complex, participated in ABA stress responses (Saez et al. 2008). The *swi3b* mutant showed a reduced sensitivity to ABA and reduced expression of *RD29B* and *RAB18*. The authors revealed that SWI3B directly interacts with HYPERSENSITIVE TO ABA1 (HAB1), a PP2C protein that negatively regulates ABA signaling. Interestingly, the same group further revealed that the chromatin remodeling ATPase BRAHMA (BRM), the other subunit of SWI/SNF complex, represses ABA response in the absence of the stress stimulus in Arabidopsis (Han et al. 2012). They found that BRM binds to *ABI5* promoter to repress its expression by affecting the stability of a nucleosome. Moreover, the developmental defects of *brm* mutant could be partially overcome by reduction of ABA response, suggesting a role of BRM in the balance between growth and stress responses. Recently, this group expanded their understanding on BRM-mediated ABA stress responses (Peirats-Llobet et al. 2016). Peirats-Llobet et al. demonstrated that SnRK2.2/2.3/2.6 kinases in core ABA signaling pathway could directly interact with and phosphorylate BRM. The phosphomimetic BRM displayed ABA hypersensitivity. They found that the SnRK2-dependent phosphorylation of BRM led to the inhibition of its activity, whereas PP2CA-mediated dephosphorylation of BRM restored its ability to repress ABA response. Therefore, we can conclude from this report that ABA core signaling pathway can directly control BRM-mediated chromatin status through a rapid phosphorylation-based switch, which in turn affects ABA stress response.

## **EPIGENETIC REGULATION IN THE RESPONSES OF NUTRIENT STRESS AND UV STRESS**

### **Nutrient stress**

Proper uptake of nutrients is critical for plants growth and development. Plants have evolved sophisticated mechanisms for adaptation to fluctuating availability of nutrients in soil (Gojon et al. 2009; Davidian and Kopriva 2010). To date, most of the studies of epigenetic regulation in plant response to nutrient stresses have focused on histone methylation, histone variants and DNA methylation. In the response to high N supply, high nitrogen treatment represses the expression of root nitrogen transporter (*NRT2.1*), in which the HIGH NITROGEN INSENSITIVE 9 (*HNI9*) participates in the deposition of



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H3K27me3 on *NRT2.1* gene (Widiez et al. 2011). Histone H4R3 symmetric demethylation (H4R3sme2), which is catalyzed by PRMT5, was involved in iron homeostasis (Fan et al. 2014). Mutation in PRMT5 also affected the expression of iron uptake- and homeostasis-related genes. The histone acetyltransferase GENERAL CONTROL NON-REPRESSIBLE 5 (GCN5) participates in iron response by regulating FRD3-mediated iron homeostasis (Xing et al. 2015). GCN5 could directly bind to the promoters of iron-related genes, including FERRIC REDUCTASE DEFECTIVE 3 (FRD3), to modulate the acetylation levels of H3K6Ac and H3K14Ac. In *gcn5*, iron translocation from the root to the shoot was impaired and iron was detained in root compared with in WT in *Arabidopsis*. Over-expression of FRD3, a citrate efflux protein and the direct target of GCN5, could rescue the phenotype of *gcn5* (Xing et al. 2015).

In the response to phosphate (Pi) stress, H3K4me3, histone acetylation and histone variant H2A.Z have been shown playing important roles. The PHD protein ALFIN-LIKE 6 (AL6) could bind to H3K4me3 mark and affect transcript maturation and stability of critical genes involved in root hair elongation. The *al6* mutant displayed pleiotropic phenotype in response to Pi starvation stress. *Arabidopsis* histone deacetylase HDA19 was shown to control root cell elongation in both Pi starvation and sufficient conditions (Chen et al. 2015). Chen et al. demonstrated that the mutation of HDA19 resulted in fewer root hairs upon low Pi treatment through targeting SPX(SYG1/Pho81/XPR) domain-containing proteins and genes involved in membrane lipid remodeling (Chen et al. 2015). Moreover, the SWR1-mediated H2A.Z deposition were also involved in Pi homeostasis. H2A.Z deposition has been observed in the Pi starvation-induced genes, such as *SPX1* and *SRG3*. These genes could be activated by the loss of H2A.Z in Pi high supply condition, for example, in the mutant of ARP6 which is a key component of SWR1 complex (Smith et al. 2010). Another example is that mutation of IPK1-mediated activation of many Pi starvation-induced genes was related with a reduction of H2A.Z deposition in these genes. IPK is the inositol pentakisphosphate 2-kinase which is required for the biosynthesis of phytic acid, one source of P in the seed (Kuo et al. 2014). In addition to the changes on histone modifications, Pi starvation could result in an extensive remodeling of global DNA methylation in *Arabidopsis* and rice, which often associated with changes in gene expression (Secco et al. 2015; Yong-Villalobos et al. 2015). Meanwhile, some DNA methylases, such as MET1, DRM1 and DRM2 were induced after low



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Pi availability treatment. In sulphate response, some key sulphate responsive genes, such as sulphate transporter genes *SULPHATE TRANSPORTER 1.1* (*SULTRI.1*) and *SULTRI.2*, were subjected to DNA methylation-dependent regulation (Huang et al. 2016). Mutation in MORE SULPHUR ACCUMULATION1 (*MSA1*), which is required for the biosynthesis of a universal methyl donor S-adenosylmethionine (SAM), resulted in a global reduction of DNA methylation levels, including *SULTRI.1* and *SULTRI.2* (Huang et al. 2016). More recently, Chen et al. identified the genome-wide DNA methylation change upon prolonged Zn deficiency and demonstrated that differential DNA methylation in the CpG and CHG, but not in the CHH context, was related to the up-regulation of a few Zn-deficiency genes (Chen et al. 2018). Interestingly, the *ddc* (*drm1/drm2/cmt3*) mutant, which lacking non-CG methylation, displayed severer developmental defects under Zn deficiency (Chen et al. 2018). These results indicated a connection between the response of Zn deficiency and DNA methylation dynamics.

#### UV stress

Lang-Mladek et al. demonstrated that UV-B stress could release transgene silencing through immediate and heritable changes in H3Ac but not in DNA methylation (Lang-Mladek et al. 2010). While, this doesn't mean that DNA methylation is completely excluded in UV-radiation stress response. Pandey and Pandey-Rai evaluated the DNA methylation dynamics in response to UV-B radiation in *Artemisia annua* which could produces artemisinin, a sesquiterpene that is required for the frontline treatment of malaria (Pandey and Pandey-Rai 2015). *DOUBLE BOND REDUCTASE 2* (*DBR2*) is a key regulatory gene of artemisinin biosynthesis. In this study, UV-B treatment activated the expression of *DBR2* gene through inducing DNA demethylation in *DBR2* promoter regions which contains additional WRKY transcription factor binding sites (Pandey and Pandey-Rai 2015). More recently, Pandey et al. showed that DNA methylation was involved in UV-B-induced flavonoid biosynthesis in *Artemisia annua L* (Pandey et al. 2019). They demonstrated that UV-B treatment caused the hypomethylation in whole genome of *Artemisia annua L*. In particular, UV-B irradiation promoted the demethylation of *AaPAL1* promoter region, which release the binding sites of several transcription factor and thereby increased the

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expression of MYB transcription factors, including MYB1, MYC and WRKY (Pandey et al. 2019).

## **EPIGENETIC MEMORY OF ABIOTIC STRESS RESPONSES**

Under natural conditions, it is usually inevitable for plants to experience repeated stress. To some extent, plants can retain the response information for at least some specific responsive genes after prior stress for some time to ensure that they can adapt to the same adversity more rapidly. This kind of action employed by plants facing recurring stress was named stress priming (Ding et al. 2012). According to recent studies, the establishment of stress memory is closely associated with epigenetic regulation (Lamke and Baurle 2017; Friedrich et al. 2019). During the past decade, deciphering the epigenetic memory of plant stress responses has become a fascinating topic in the field of stress biology research. Many publications have shown that stress treatment can induce alterations in the chromatin status of stress-responsive genes, and these epigenetic alterations are still present during the short-term performance or even within progeny (Ding et al. 2012; Sani et al. 2013; Sanchez and Paszkowski 2014; Virilouvet et al. 2014; Avramova 2015; Hilker et al. 2016; Yang et al. 2017). In *Arabidopsis*, priming is a phenomenon through which a transient abiotic stress cue leads to modified (typically faster or stronger) defense responses upon exposure to a recurring stress (Lamke and Baurle 2017). Ding et al. demonstrated that H3K4me3 deposition in trainable genes increased to higher level than that in non-trainable genes after multiple exposures to drought stress (Ding et al. 2012), suggesting that H3K4me3 may act as a persistent epigenetic mark associated with the transcriptional memory. The same group further showed that H3K4me3, but not H3K27me3, may be an epigenetic memory mark for the examined dehydration stress responding genes (Liu et al. 2014). Interestingly, Sani et al revealed that salt treatment priming led to a decrease in H3K27me3 at the edges of H3K27me3-enriched islands in the whole genome, resulting in the shortening and fractioning of these islands (Sani et al. 2013). However, H3K4me2, H3K4me3 and H3K9me2 islands did not show any changes between primed and nonprimed plants. The salt treatment-induced genes bearing H3K27me3 deposition showed alterations in response to a second treatment. However, this does not mean that H3K4me2 and H3K4me3 are excluded in the stress memory of plants. Another study revealed that the heat stress-induced gene *HSP22.0* is involved in heat stress

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memory (Lamke et al. 2016). Upon heat stress treatment, the expression of *HSP22.0* increased, and the increased expression could last for a longer time than could that of *HSP70*. The authors found that heat stress could induce the deposition of active histone marks, such as H3K4me3, H3K4me2 and H3K9Ac, in both the *HSP22.0* and *HSP70* genes. However, after the plants were subjected to the normal condition again, the levels of these three marks in *HSP70* gradually decreased to the baseline levels. In contrast, the high levels of H3K4me3 and H3K4me2 but not H3K9Ac were maintained in *HSP22.0* (Lamke et al. 2016). Although many studies have focused on the transcriptional memory mediated by different histone modifications (Berger 2007; Heard and Martienssen 2014; Zheng et al. 2017), how epigenetic enzymes sense adverse conditions and how the chromatin status is maintained in the offspring remain unknown.

In addition to priming memory, increasing evidence indicated that nonsequence-based epigenetic modification could transmit from one generation to next generation (Lang-Mladek et al. 2010; Iwasaki and Paszkowski 2014; Zheng et al. 2017; Cong et al. 2019), which is named as “transgenerational memory” (Heard and Martienssen 2014). The formation of stress-induced transgenerational memory in advanced generations is helpful for plants to achieve a better balance between survival and reproduction (Molinier et al. 2006). A recent study revealed that drought stress induced the epimutations (DNA methylation status) change and a high percentage (>40%) of drought-induced epimutations maintained the changed status in advanced generations. Meanwhile, the advanced generations showed decreasing effective tiller numbers (reducing water consumption) and increasing seeds setting rate (maintaining the yield). Thus, one possible reason is that the maintenance of drought-induced DNA methylation status in progeny participates in the drought stress response and in the long-term adaptation to the drought conditions (Zheng et al. 2017). More recently, another study indicated that DNA methylation participated in the transgenerational memory of the response to heavy metal stress in rice (Cong et al. 2019). Cong et al. demonstrated that Heavy Metal-transporting P-type ATPase genes (HMAs) was upregulated in response to heavy metal stress and the transgenerational memory of gene expression was observed after the removal of heavy metals (Cong et al. 2019). They further revealed that the DNA methylation state of a *Tos17* retrotransposon was altered in response to the heavy metal stress and displayed transgenerational inheritance within three generations. Similarly, Ito et al. demonstrated that heat

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stress treatment could transcriptionally activate a retrotransposon *ONSEN*, and heat-induced *ONSEN* activation and transposon was promoted in the mutants of small interfering RNAs (siRNAs) biogenesis (Ito et al. 2011). Although both *ONSEN* transcripts and extrachromosomal DNA gradually decayed, new *ONSEN* insertions were observed in the progeny of stressed plants deficient in siRNAs. Therefore, the author deduced that stress memory could be maintained in plants with compromised siRNA biogenesis. In brief, as summarized in a review, although these studies have showed the involvements of epigenetic mechanisms in the formation of transgenerational stress memory (Weinhold 2018), the underlying epigenetic mechanisms have been rarely investigated.

### CONCLUSIONS AND PERSPECTIVES

Being exposed to continuously changing conditions in nature, plants have to make a variety of changes to better adapt to their environment. As summarized in Figure 5, numerous efforts have been made to explore the epigenetic code involved in plant abiotic stress response (Popova et al. 2013; Kim et al. 2015; Lamke and Baurle 2017). These reports support the conclusion that epigenetic mechanisms are widely involved in the plant abiotic stress response. As summarized above, a large number of components involved in the abiotic stress response have been shown to be the targets of epigenetic machinery, and the expression of epigenetic marks is activated/repressed after abiotic stress treatments. In addition to DNA methylation, histone modifications, chromatin remodeling complex and histone variants, some long non-coding RNAs (lncRNAs) may also participate in multiple stress responses (Zhao et al. 2018). Moreover, small RNA-mediated RNA silencing, which was not included in this review, is another regulatory mechanism of abiotic stress response. It has been shown that *Arabidopsis* ARGONAUTE 1 (AGO1) could associate with SWI/SNF chromatin remodeling complex and small RNAs to bind to a number of stress-responsive genes and regulate their expression (Liu et al. 2018a), suggesting a cross-talk of different epigenetic mechanisms in response to abiotic stresses. The dynamic changes in epigenetic marks on stress-responsive genes make their chromatin status accessible or inaccessible, which in turn regulates the expression of stress-responsive genes at the transcriptional or posttranscriptional level. However, the entire understanding of the plant epigenetic mechanisms in response to abiotic stress remains elusive. How stresses activate epigenetic mechanisms and the subsequent transcriptional

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reprogramming is rarely reported. It is also unclear how epigenetic signals are inherited by the offspring in stress memory. Undoubtedly, deciphering the epigenetic codes of plant abiotic stress responses deserves more attention in future studies. With the development of high-throughput sequencing, the epigenomes of increasing numbers of crop plants are being annotated, which will greatly increase the number of studies on the epigenetic mechanisms of crop stress adaptation.

## ACKNOWLEDGMENTS

The work of Dr. C.G.D. was supported by Chinese Academy of Sciences and the Strategic Priority Research Program of the Chinese Academy of Sciences (XDB27040203).

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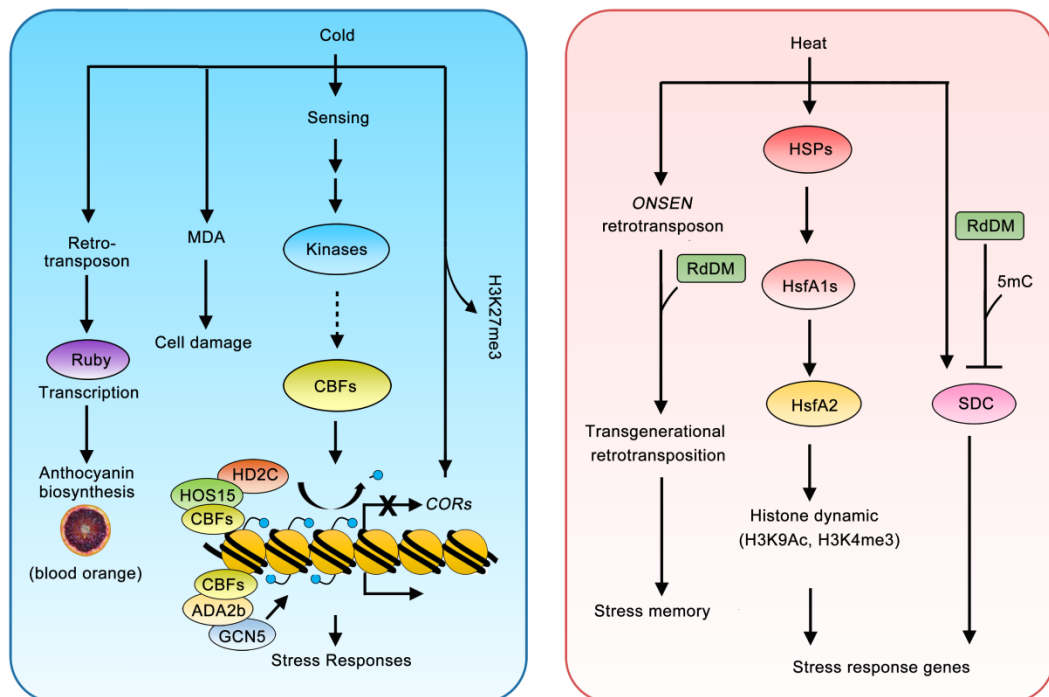
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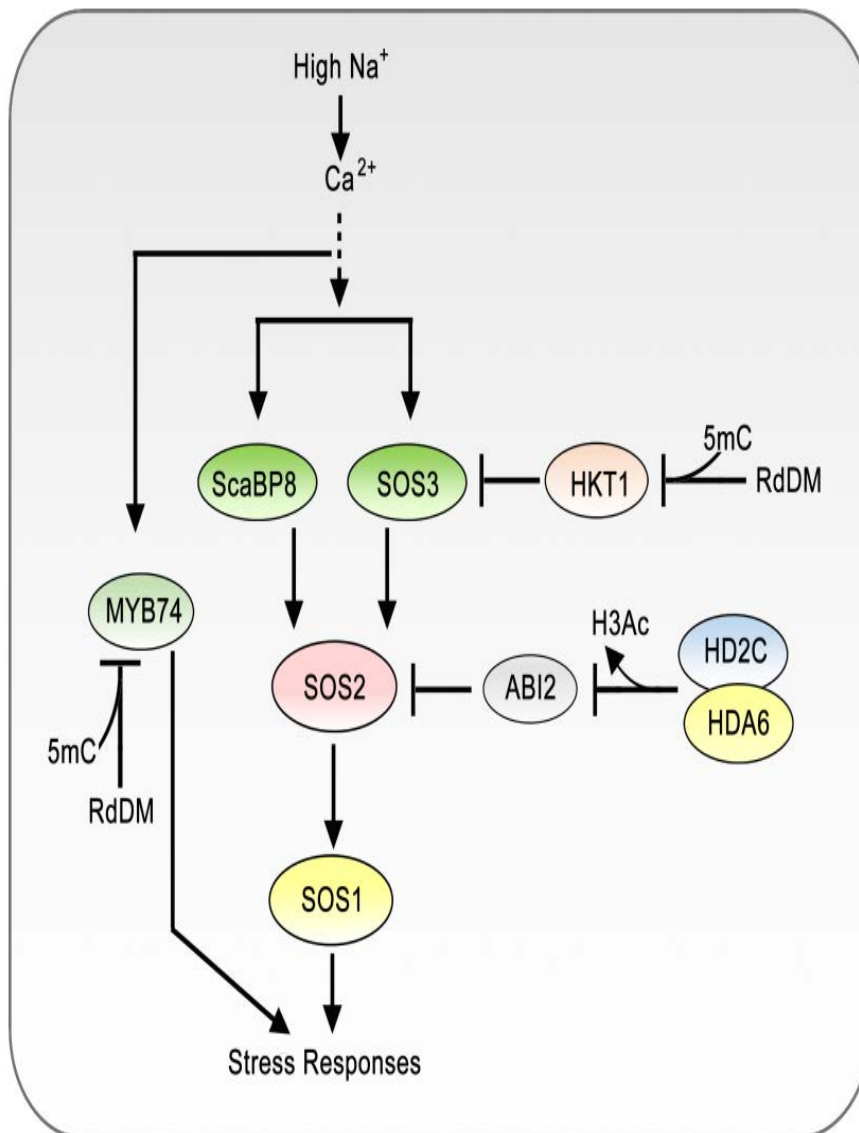
**Figure 1. Epigenetic regulation of cold and heat stress responses**

Left panel: HD2D negatively regulates the synthesis of MDA upon cold treatment, thus decreases cell damage caused by low temperature; In normal condition, HD2C is recruited by HOS15-CBFs and deacetylates the promoter regions of cold-responsive COR genes; Cold treatment induces the removal of H3K27me3 in COR genes, such as *COR15A* and *ATGOLS3*; ADA2b-GCN5 promotes the expression of COR genes through enhancing CBF1 binding to COR genes and increasing H3Ac in the promoter region of COR genes. In blood orange, cold stress can induce the activation of retrotransposon, which leads to the transcription of the downstream *Ruby* gene and the subsequent biosynthesis of anthocyanins specifically in fruit (Butelli et al. 2012). Right panel: HSFA1s are core TFs in heat stress; HSFA2 is one of direct targets of HSFA1s; HSPs are heat-induced proteins. Upon heat stress treatment, both H3K9Ac and H3K4me3 are increased in some members of HSPs family; SDC is one target of RdDM pathway, which is also induced by heat stress. Heat stress also activates the transcription of ONSEN retrotransposon and the retrotransposition, and RdDM pathway is required for the transgenerational retrotransposition memory.



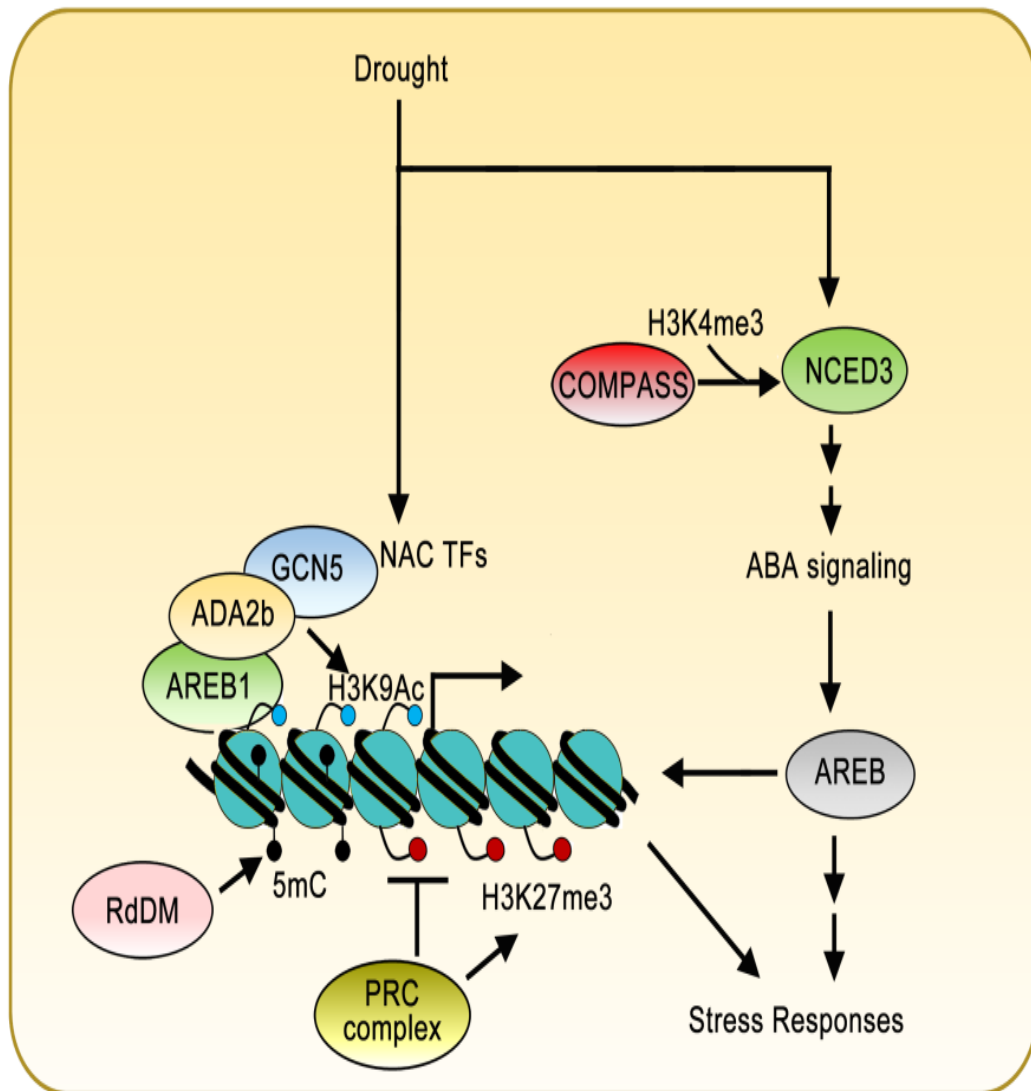
## Figure 2. Epigenetic regulation of salt stress response

MYB74 and HKT1 are induced by high salinity; Both HKT1 and MYB74 are silenced by 24-nt siRNAs-dependent RdDM pathway in normal condition; Upon high salinity treatment, H3Ac and H3K4me3 are increased in *ABI2* while H3K9me2 decreased, and the alteration of H3Ac is partially regulated by HDA6-HD2C complex.



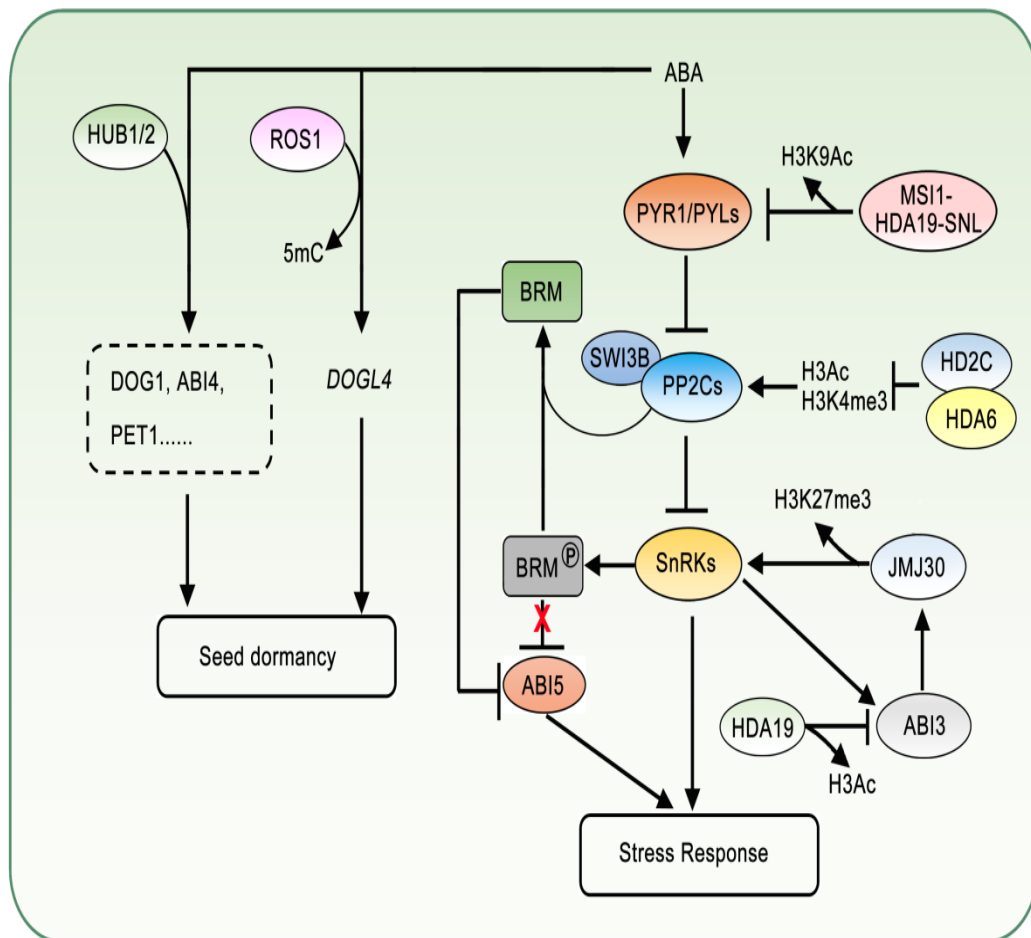
### Figure 3. Epigenetic regulation of drought stress response

Drought stress induces the synthesis of ABA; H3K4me3 deposition by COMPASS complex promotes the expression of *NCED3*; Several members of NAC family TFs can be induced by drought stress; PRC complex-mediated deposition of H3K27me3 represses the expression of NAC TFs; The induction of H3K4me3, H3K9Ac deposition and the removal of H3K27me3 in *RD29A*, *RAB18*, *RD29B* and *RD22* promote the expression of these drought stress-responsive genes; ADA2b-GCN5 promotes the expression of *PtrNAC006*, *PtrNAC007* and *PtrNAC120* through enhancing AREB1 binding to those genes and increasing H3Ac in the promoter regions of these NAC TFs. In maize, the *NAC* TF gene is a target of RdDM-mediated transcriptional gene silencing.



#### Figure 4. Epigenetic regulation of ABA-mediated stress response

*PYL4*, *PYL5* and *PYL6* are repressed by MS11-HDA19-SNL co-repressor complex through removing H3K9Ac of these genes; Upon ABA treatment, both H3Ac and H3K4me3 are increased in *ABI1*, *ABI2* and *HAI1* which are mediated by HD2C-HDA6 module; JMJ30 can remove the H3K27me3 in *SnRK2.8* and contribute to the activation of *ABI3*, which enhances the activation of *SnRK2.8* in turn; HDA19 promotes the removal of H3Ac in *ABI3*; In seed dormancy, DOG1, ABI4, NCED9 and PER1 are positively regulated by HUB1 and HUB2; ROS1-mediated DNA demethylation negatively regulates the imprinting of *DOGL4* gene in seed dormancy process; The chromatin remodeling protein BRM can be phosphorylated/dephosphorylated by SnRK2 kinases/PP2Cs and the dephosphorylated BRM bears capacity of repressing *ABI5* transcription. SWI3B, the other subunit of SWI/SNF chromatin remodeling complex, could directly interact with PP2C protein HAB1 to regulate ABA response.



**Figure 5. A summary of the cross-talks between epigenetic mechanisms and abiotic stress responses**

