JIPB Journal of Integrative Plant Biology

Epigenetic regulation in plant abiotic stress responses[FA]

Ya-Nan Chang[1,2], Chen Zhu[1], Jing Jiang[3], Huiming Zhang[1,3], Jian-Kang Zhu[1,4] and Cheng-Guo Duan[1,3]*

1. Shanghai Center for Plant Stress Biology and Center of Excellence in Molecular Plant Sciences, Chinese Academy of Sciences, Shanghai 201602, China
2. University of Chinese Academy of Sciences, Beijing 100049, China
3. State Key Laboratory of Crop Stress Adaptation and Improvement, School of Life Sciences, Henan University, Kaifeng 475004, China
4. Department of Horticulture and Landscape Architecture, Purdue University, West Lafayette, IN 47907, USA
doi: 10.1111/jipb.12901

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

Abstract In eukaryotic cells, gene expression 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 states for stress-responsive gene expression that is important for adaptation to harsh environmental conditions. Recent studies have revealed that many epigenetic factors participate in abiotic stress responses, and various chromatin modifications are changed when plants are exposed to stressful environments. In this review, we summarize recent progress on the cross-talk between abiotic stress response pathways and epigenetic regulatory pathways in plants. Our review focuses on epigenetic regulation of plant responses to extreme temperatures, drought, salinity, the stress hormone abscisic acid, nutrient limitations and ultraviolet stress, and on epigenetic mechanisms of stress memory.

Edited by: Zhizhong Gong, China Agricultural University, China
Received Dec. 19, 2019; **Accepted** Feb. 20, 2020; **Online on:** Feb. 23, 2020
FA: Free Access

Invited Expert Review

Free Access

INTRODUCTION

Plants live in constantly changing environments that are usually unfavorable or stressful for growth and development. The stressful environmental factors can be either biotic or abiotic. Abiotic stresses mainly include drought, salinity, extreme temperatures, nutrient deficiencies, heavy metal stress, and ultraviolet radiation (Zhu 2016). These adverse environments threaten agricultural productivity. Thus, increasing plant stress resistance is critical for agriculture. 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 mechanisms underlying abiotic stress responses, increased numbers of studies have shown important participation of epigenetic mechanisms in the response of plants to abiotic stresses (Sahu et al. 2013; Kim et al. 2015). A good example of epigenetic regulation in plant response to the environment is the extensive involvements of epigenetic marks in vernalization, a process where plants remember a prolonged low temperature exposure in the winter in order to flower in the spring (Zhao et al. 2018; Luo and He 2020). The epigenetic mechanisms of cold-dependent vernalization have been well documented and will not be discussed in this review. Epigenetic mechanisms participate in the regulation of

stress-responsive genes at the transcriptional and posttranscriptional levels by altering the chromatin status of the genes. Stress treatments can cause changes in the chromatin modifications (Kim et al. 2015; Lamke and Baurle 2017; Luo and He 2020). Moreover, epigenetic mechanisms play vital roles in the formation of stress memory, which may be inherited by the offspring of the stress-treated plants (Friedrich et al. 2019). Therefore, deciphering the epigenetic codes of plant stress responses could be of great significance for breeding stress-tolerant crops.

PROFILE OF PLANT EPIGENETIC MECHANISMS

Epigenetics refers to the study of heritable changes in chromatin function that do not involve changes in DNA sequence. 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 noncoding RNAs (ncRNA), influence the structure and accessibility of chromatin and thereby the biological function of the chromatin (Duan et al. 2018). The effects of epigenetic regulation on gene expression depend on not only the types of epigenetic marks but also their position on the genes. Heterochromatic marks such as DNA methylation and H3K9me2, for example, can display repressive effects on downstream gene expression by inhibiting transcription when they are present within the promoter region. In some cases, 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 high frequency of transposable element (TE) insertion within genes in plant genomes (Makarevitch et al. 2015), particularly within stress-responsive genes, the intragenic heterochromatin-mediated posttranscriptional regulation may play an important role in the dynamic regulation of stress responses. DNA methylation at the 5′ position of cytosines (5mC) is an important epigenetic mark. In plants, DNA methylation occurs in all cytosine sequence contexts, including CG, CHG, and CHH (where H represents A, T, or C). As is best understood in the model plant *Arabidopsis thaliana*, DNA methylation can be established *de novo* through the RNA-directed DNA methylation (RdDM) pathway, and its maintenance mainly requires MET1 at the CG context, CMT3 at the CHG context, and DRM2 or CMT2 at the CHH context (Law and Jacobsen 2010; Duan et al. 2018; Zhang et al. 2018). Epigenetic codes, including DNA methylation, are dynamically regulated through different mechanisms. DNA methylation can be actively removed through a base excision repair pathway that involves the 5-methylcytosine DNA glycosylase/lyase family of enzymes (also known as DNA demethylases), including Repressor of Transcriptional Silencing 1 (ROS1), DEMETER (DME), DEMETER-LIKE 2 (DML2) and DML3 in *Arabidopsis* (Zhang et al. 2018; Liu and Lang 2020). Recent studies have indicated that ROS1 can be recruited to some of its target DNA via two complexes: the Increased DNA methylation (IDM) 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, covalent modifications to histone tails, such as methylation, acetylation, phosphorylation, ubiquitination, sumoylation, glycosylation, and ADP-ribosylation, constitute the other part of the conserved epigenetic code across different kingdoms (Liu et al. 2010). The different types of histone modifications are dynamically determined by specific histone modification enzymes, and are important in specifying chromatin function. For example, histone H3 lysine tri-methylation (H3K27me3) is usually associated with euchromatin, whereas H3K27me1 is a heterochromatic marker (Liu et al. 2010). Strong deposition of H3K4me3 and H3K36me3 marks is often observed on actively expressed genes, whereas H3K9me2 is present within heterochromatic regions (Liu et al. 2010). These histone marks are catalyzed and removed by specific enzyme complexes that are referred to as the writers and erasers, and are recognized by reader proteins (Liu et al. 2010). For example, H3K27me3, which is a representative repressive marker that exhibits high deposition on many 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; meanwhile H3K27me3 is recognized by the PRC1 complex via the H3K27me3 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, H3K4me3 is also present on a large number of stress-responsive genes. In *Arabidopsis*, the COMPASS complex is responsible for the genome-wide deposition of H3K4me3, which is catalyzed by the methyltransferases ARABIDOPSIS TRITHORAX-LIKE PROTEIN 1 (ATX1) and ATX2, and regulates the transcription of various stress responsive genes (Saleh et al. 2008; Fromm and Avramova 2014). Both the H3K4 and H3K27 methylation marks can be removed 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 stress responses (Kim et al. 2015). The dynamic shift in different epigenetic marks is of great significance to biological processes, particularly in response to environmental stimuli (Zhang et al. 2018). For example, several heat stress-responsive genes are dynamically regulated by RdDM pathway-mediated DNA methylation (Popova et al. 2013). The *Arabidopsis* transcription factor MYB74 is normally silenced by RdDM and is desilenced by salt stress treatments (Xu et al. 2015).

EPIGENETIC REGULATION DURING THE EXTREME-TEMPERATURE STRESS RESPONSE

Temperature greatly affects plant growth and development. Due to climate change, heat and cold stresses have become a major challenge for crop productivity. Cold stress has a big 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), while reports on epigenetic regulation during plant responses to heat or cold stress conditions are accumulating.

Cold stress

The C REPEAT BINDING FACTOR (CBF)-COLD RESPONSIVE (COR) pathway is one of the well-characterized mechanisms in the plant cold stress response. In this mechanism, cold stress induces the expression of transcription factors (TFs) such as CBF family proteins, and these TFs bind to the promoters of downstream *COR* genes to activate their expression (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*. The *Arabidopsis pkl* mutants are 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 *pkl* mutants after 3 h of cold treatment compared to that in wild-type plants. Moreover, H3K27me3 deposition occurs in a number of *COR* genes (Kwon et al. 2009). PICKLE 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 with the H3K27me3 methyltransferase CLF in the PRC2 complex (Carter et al. 2018). Consistently, Kwon et al. reported that cold stress caused a decrease of H3K27me3 deposition in two cold-responsive genes, *COR15A* and *GALACTINOL SYNTHASE 3* (*GOLS3*), and that cold-induced decrease of H3K27me3 was maintained even after a return to normal growth temperature, suggesting that H3K27me3 may serve as a memory marker for recent transcriptional activity in *Arabidopsis* (Kwon et al. 2009). Therefore, it is possible that PKL affects plant cold stress response by regulating 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 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. As a result, the transgenic plants were more tolerant to cold treatment (Han et al. 2016). It has been shown that histone acetylation is induced upon cold treatment in the promoter regions of some *COR* genes, such as *COR15A* and *COR47* (Pavangadkar et al. 2010). An early study in 2006 reported that CBF1 could

interact with the ADA2b-GCN5 histone acetylation module (Mao et al. 2006). Cold-responsive gene expression was diminished but not abolished in *gcn5* and *ada2b* mutants, suggesting that GCN5-dependent histone acetylation may mediate transcriptional activation by CBF proteins during cold acclimation in *Arabidopsis*. Another group further confirmed that H3 acetylation increased at *COR* gene promoters upon cold acclimation (Pavangadkar et al. 2010), although they found that GCN5 is not the HAT responsible for histone acetylation at *COR* genes during cold acclimation. Recent studies have indicated that another HD2 family deacetylase, HD2C in *Arabidopsis*, is involved in CBF-dependent transcriptional activation of COR genes upon cold stress. HD2C is a target of HIGH EXPRESSION OF OSMOTICALLY RESPONSIVE GENES 15 (HOS15)-mediated degradation under cold treatment (Park et al. 2018). HIGH EXPRESSION OF OSMOTICALLY RESPONSIVE GENES 15 is a component of the CULLIN 4 (CUL4)-based E3 ubiquitin ligase complex (Zhu et al. 2008). In the absence of cold stress, HOS15 forms a complex with HD2C to repress *COR* gene expression by deacetylation of *COR* promoters. Under cold stress conditions, HOS15 recruits CUL4, resulting in HD2C degradation and increases of H3 acetylation on *COR* promoters. Moreover, HOS15 recruits CBF TFs to the *COR* promoters to activate the expression of *COR* genes (Park et al. 2018) (Figure 1).

It is known that transposon domestication plays an important role in the evolution of plant genomes (Bennetzen and Wang 2014). The anthocyanin level-dependent diversity of fruit color in blood orange was found to be 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, which is required for the biosynthesis of anthocyanin, varies greatly among different varieties. In the varieties of *Ruby*-expression, a retrotransposon is located in the region upstream of *Ruby* transcription start site. Cold-induced retrotransposon transcription activated the transcription of Ruby, and this induction was fruit-specific, suggesting that cold-induced transcription of transposons can lead to desirable agronomic traits in plants.

Heat stress

The transcriptional network of the heat stress response in plants has been nicely 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, HSFBs, and MULTIPROTEIN BRIDGING FACTOR 1C (MBF1C) which are responsible for the activation of downstream heat responsive genes (Ohama et al. 2017). Several 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). Heat shock proteins (HSPs) play a key role in conferring heat tolerance. In general, the principal function of HSPs is to regulate protein folding and unfolding, in conjunction with their subcellular localization and the degradation of unfolded and denatured proteins (Singh et al. 2016). Heat stress induces the sustained accumulation of H3K9Ac and H3K4me3 on *HSP18*, *HSP22.0*, *APX2*, and *HSP70* genes. 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 respond to long-term heat stress (Sanchez and Paszkowski 2014); thus, the activity of this gene contributes to the recovery from heat stress (Popova et al. 2013). The SDC gene is a target of the RdDM pathway and can be epigenetically silenced in normal conditions but is activated by heat stress, suggesting that the transcriptional response of heat stress has to overcome the silencing effect of RdDM at some loci.

EPIGENETIC REGULATION OF THE SALT STRESS RESPONSE

High salinity, which causes ion toxicity (mainly that of Na^+), hyperosmotic stress and secondary stresses such as oxidative damage, inhibits plant growth and development, and a widespread challenge to plant

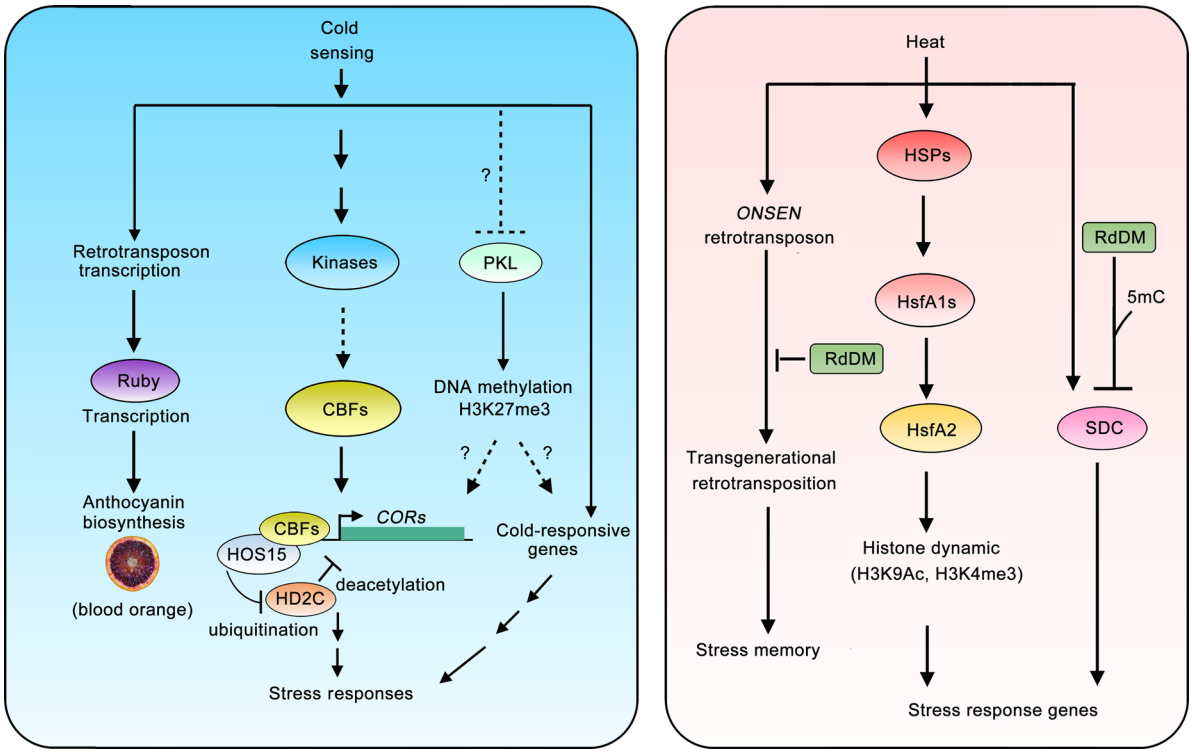

Figure 1. Epigenetic regulation of cold and heat stress responses

Left panel: In the absence of cold stress, HIGH EXPRESSION OF OSMOTICALLY RESPONSIVE GENES 15 (HOS15) interacts with HD2C to repress *COLD RESPONSIVE* (*COR*) gene expression by deacetylation. Under cold stress conditions, HOS15 recruits CULLIN 4 (CUL4) to promote HD2C degradation by ubiquitination, resulting in the increase of H3 acetylation on *COR* promoters. Moreover, HOS15 recruits C REPEAT BINDING FACTOR (CBF) transcription factors (TFs) to the *COR* promoters to activate the expression of *COR* genes. The chromatin regulator PICKLE (PKL) may regulate the chromatin status of *COR* genes and other cold-responsive genes through H3K27me3-dependent silencing. In blood orange, cold stress can induce the activation of a retrotransposon, which leads to the transcription of the downstream *Ruby* gene and the subsequent biosynthesis of anthocyanins specifically in fruits (Butelli et al. 2012). Right panel: HEAT SHOCK TRANSCRIPTION FACTOR As (HSFA1s) are core TFs in heat stress; HSFA2 is one of the direct targets of HSFA1s; Heat shock proteins (HSPs) are heat stress-induced proteins. Upon heat stress treatment, both H3K9Ac and H3K4me3 are increased in some HSP genes; SUPPRESSOR OF DRM1 DRM2 CMT3 (SDC) is a target of RNA-directed DNA methylation (RdDM) pathway, which is also induced by heat stress. Heat stress also activates the transcription of *ONSEN* retrotransposon and the RdDM pathway is required for preventing heat stress-induced transgenerational retrotransposition of *ONSEN*.

agriculture in the world. In plants, Ca^{2+}-CALCINEURIN B-LIKE PROTEIN (CBL)-CBL INTERACTING PROTEIN KINASE (CIPK) module plays an important role in the regulation of cellular ion homeostasis (Zhu 2016) (Figure 2). High Na^+, low K^+, excess Mg^{2+} and high pH cause cytosolic Ca^{2+} signals, which activate the SALT OVERLY SENSITIVE3 (SOS3)-SOS2, CBL1/9-CIPK23, CBL2/3-CIPK3/9/23/26, and SCaBP1-CIPK11/14 to phosphorylate and regulate the activity of SOS1 (Na^+/H^+ antiporter), *Arabidopsis* K^+ TRANSPORTER (AKT1, K^+ channel), putative Mg^{2+} transporter and H^+ ATPase, respectively (Zhu 2016). HIGH-AFFINITY K^+ CHANNEL 1 (HKT1), which mediates Na^+ influx in plants, is an important transporter that coordinates with the SOS pathway to confer salt tolerance (Rus et al. 2001). In *Arabidopsis*, mutation of *HKT1* could suppress the salt hypersensitive phenotype of *sos3* plants (Rus et al. 2001). In wild-type *Arabidopsis*, a putative small RNA target region was identified at about 2.6 kb upstream of *HKT1* and was shown to be heavily methylated (Baek et al. 2011). The level of DNA methylation in this region was decreased in the RdDM mutant *rdr2*, which showed an increased expression of *HKT1*, indicating that RdDM negatively regulates *AtHKT1* gene expression. Similar regulatory activity was also observed in wheat (Kumar et al. 2017). The authors reported

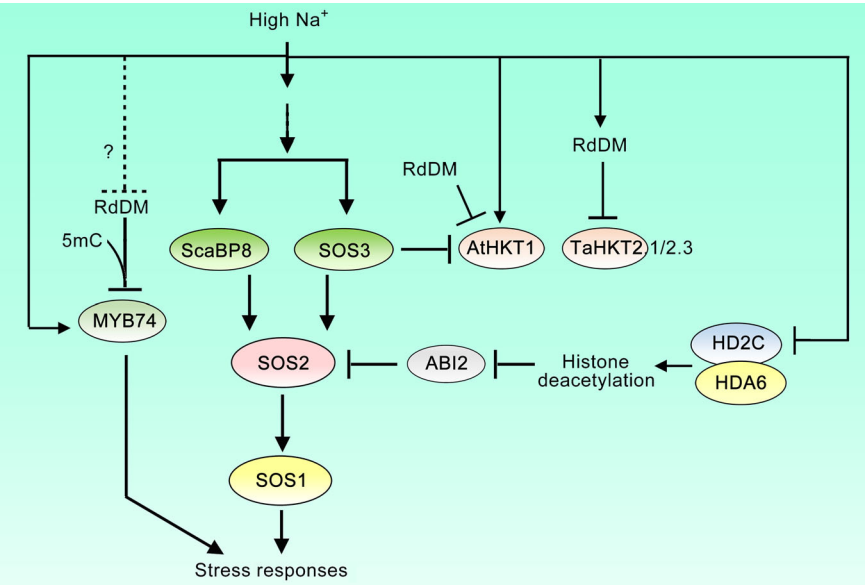

Figure 2. Epigenetic regulation of salt stress response

In *Arabidopsis*, *MYB74* and *HIGH-AFFINITY* K^+ *CHANNEL 1* (*HKT1*) are induced by high salinity. Both *HKT1* and *MYB74* are silenced RNA-directed DNA methylation (RdDM) pathway-dependent DNA methylation in normal conditions. In wheat, salt stress induces DNA methylation that represses the expression of *TaHKT2.1/2.3* in a genotype- and tissue-specific manner. Salt treatment represses HD2C, and HD2C interacts with HISTONE DEACETYLASE 6 (HDA6). HDA6 confers histone deacetylation that supresses the expression of abscisic acid (ABA)-responsive genes *ABA1* and *ABI2* under normal conditions. ABI2 may deactivate SALT OVERLY SENSITIVE (SOS)2 or dephosphorylate the target ion transporters of SOS2.

that cytosine methylation was induced by salt stress in a genotype- and tissue-specific manner, which downregulated the expression of *TaHKT2;1* and *TaHKT2;3* in the shoots and roots of salt-tolerant and salt-sensitive genotypes, although the root-specific downregulation of *TaHKT1;4* was not by the modulation of DNA methylation (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 RdDM pathway under normal conditions; thus, *MYB74* is maintained at a low level of transcription. Interestingly, under salt stress, methylation and 24-nt siRNA levels were nearly undetectable at *MYB74*, which is accompanied by the upregulation of *MYB74* expression (Xu et al. 2015).

In addition to DNA methylation, certain histone modifications are also involved in plant responses to high-salinity stress (Kim et al. 2015). The fine-tuning of acetylation by HATs and HDACs is important for plants to adapt to changing environmental conditions. High-salinity treatments often induce the deposition of active histone marks such as H3K9K14Ac and H3K4me3 and decrease the deposition of repressive marks such as H3K9me2 and H3K27me3 on salt stress-responsive genes (Sokol et al. 2007; Chen et al. 2010; Yolcu et al. 2016). Luo et al. reported that the expression of *HD2C* was repressed by ABA and NaCl, and *hd2c* mutant was more sensitive to ABA and NaCl (Luo et al. 2012). Moreover, HD2C interacts with HISTONE DEACETYLASE 6 (HDA6) to repress ABA-responsive genes *ABA1* and *ABI2* in normal conditions (Luo et al. 2012). The *Arabidopsis HKT1* gene body is highly enriched with H3K27me3 and the expression of *HKT1* is activated by salt treatment at least partly due to the removal of H3K27me3 (Sani et al. 2013). H3 Ser-10 phosphorylation, which is usually related to chromatin density, is another histone modification that can be induced by salinity treatment. Sokol et al. analyzed the histone dynamics of cultured plant cells in response to different abiotic stresses. They found that the levels of H3 Ser-10 phosphorylation, H3 and H4 acetylation underwent a rapid upregulation (Sokol et al. 2007). Interestingly, these three types of modifications do not change in the same way under 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 resistance in plants has been increasingly elucidated (Osakabe et al. 2014). Drought stress induces the synthesis of the phytohormone ABA in plants, and in turn, ABA promotes drought resistance (Shinozaki and Yamaguchi-Shinozaki 2007). An early study in 2007 indicated that the *Arabidopsis* SNF2/Brahma-type chromatin remodeling protein CHROMATIN REMODELING 12 (CHR12) is involved in temporary growth arrest upon perceiving stresses, including drought and heat stresses (Mlynarova et al. 2007). Under high temperature treatment (37°C for 16 h), *atchr12* mutants showed slightly better growth than wild-type, whereas the elongation of the primary stem of *AtCHR12*-overexpressing plants was considerably reduced compared to wild-type plants. Moreover, the growth of *atchr12* was less inhibited by salt treatment than that of wild type at lower salt concentration, suggesting that chromatin remodeling plays an important role in mediating plant response to salt stress. The expression of drought stress-induced genes is closely related to the alteration of histone dynamics (Matsui et al. 2008; Kim et al. 2012; To and Kim 2014; Kim et al. 2015). NINE CIS-EPOXYCAROTENOID DIOXYGENASE 3 (NCED3) is a key enzyme involved in ABA synthesis (Nambara and Marion-Poll 2003). Deposition of H3K4me3 within the *NCED3* gene body region increases after drought stress, which is accompanied by increased transcription of the *NCED3* gene (Ding et al. 2011). Expression of the drought-responsive genes *RD29A*, *RD29B*, *RD22*, and *RAP2.4* is induced under drought stress (Okamuro et al. 1997; Takahashi et al. 2000), and the longer the drought persisted, the more the genes were expressed (Kim et al. 2008). Under drought stress conditions, increasing H3K4me3 and H3K9Ac levels 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 increases in H3K4me3 and H3K9Ac levels are much higher under severe drought stress conditions than under moderate drought stress conditions (Matsui et al. 2008; Kim et al. 2012). After recovery from dehydration, H3K4me3 and H3K9Ac are removed from these gene regions, and the removal of H3K9Ac is more rapid than that of H3K4me3 (Kim et al. 2012). A recent study showed that the decrease in H3K27me3 deposition within the gene body region of drought stress-responsive TFs contributes to drought stress resistance of *Arabidopsis* (Ramirez-Prado et al. 2019). LIKE HETEROCHROMATIN PROTEIN 1 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 response to environmental stimuli, can be induced by ABA treatment (Jiang et al. 2009). A recent study showed that ANAC019 and ANAC055 are target genes of PRC1-LHP1-mediated transcriptional repression (Ramirez-Prado et al. 2019). Mutation of *LHP1* increased ABA sensitivity and drought resistance, 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 resistance via transcriptional repression of the ANAC019 and ANAC055 TFs. In *Populus trichocarpa*, Li et al. (2019) reported that a number of drought-responsive NAC TFs contain ABRE sequences in their promoters. AREB1 binds to the ABRE sequences of NAC genes and recruits the ADA2b-GCN5 histone acetylation module to confer H3K9Ac, leading to activation of the PtrNAC genes and increasing drought resistance.

In addition to regulation of histone dynamics, DNA methylation can also be involved in drought stress response. A study in *P. trichocarpa* found that drought stress treatment induces alterations in the DNA methylation levels and thereby alters 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 in maize, Mao et al. (2015) identified that a miniature inverted-repeat transposable element

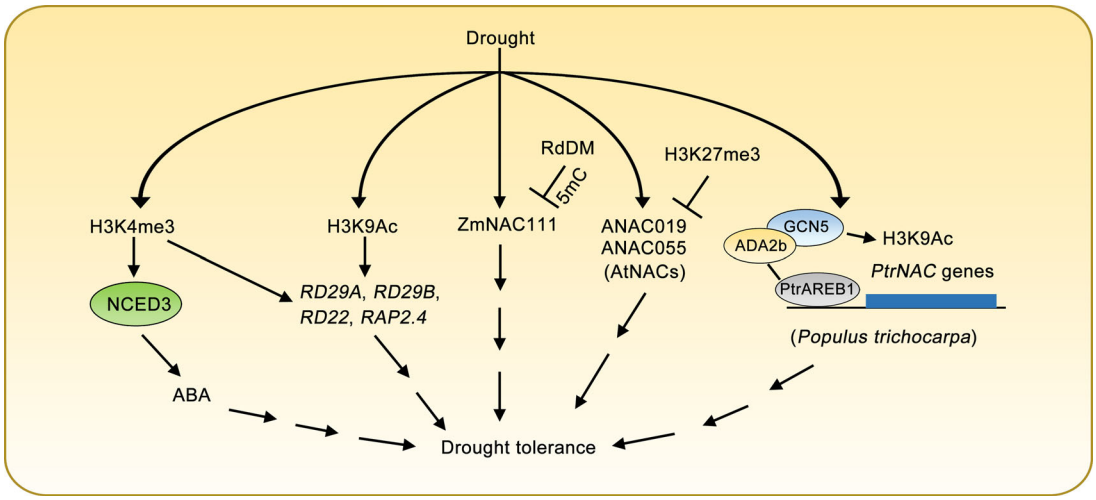

Figure 3. Epigenetic regulation of drought stress response

Drought stress upregulates H3K4me3 and H3K9Ac in the promoter regions of abscisic acid (ABA) biosynthesis enzyme-encoding gene *NINE CIS-EPOXYCAROTENOID DIOXYGENASE 3* (*NCED3*) and drought-responsive genes *RD29A*, *RD29B*, *RD22*, *RAP2.4*, and activates their expression in *Arabidopsis*. The expression of AtNAC transcription factors (TFs) ANAC019 and ANAC055 is repressed by H3K27me3 deposition on these genes. In maize, the expression of the NAC TF gene ZmNAC111 is repressed by RNA-directed DNA methylation (RdDM)-dependent DNA methylation. In *P. trichocarpa*, PtrAREB1 binds to the ABRE motif of *NAC* genes and recruits the ADA2b-GCN5 histone acetylation module to promote H3K9Ac deposition on the *NAC* genes.

(MITE) inserts in the promoter of a *NAC* gene (*ZmNAC111*) represses gene expression through RdDM and H3K9me2 deposition. As summarized in Figure 3, the findings above suggest that the chromatin status shaped by histone modifications and DNA methylation plays crucial roles in the drought stress response.

EPIGENETIC REGULATION OF ABA RESPONSES

Abscisic acid plays a crucial role in the regulation of stress responses in plants. Multiple environmental stresses, such as drought and high salinity, induce the biogenesis of ABA, which controls many important biological processes such as seed germination, stomatal closure, and root growth. The core regulatory pathway of ABA signaling has been identified (Zhu 2016). Under stress conditions, ABA binds to the PYRABACTIN RESISTANCE1 (PYR1)/PYR1-LIKE (PYL)/REGULATORY COMPONENTS OF ABA RECEPTORS (RCAR) ABA receptors, which then bind to and inhibit clade A PROTEIN PHOSPHATASE TYPE 2Cs (PP2Cs), resulting in the release of SNF1-RELATED PROTEIN KINASE 2s (SnRK2s) (Zhu 2016). The activated SnRK2s phosphorylate downstream effectors to regulate multiple biological processes, such as transcription, RNA processing, epigenetic modification, and flowering time regulation (Wang et al. 2013a).

During the past decade, extensive efforts have been made to elucidate the epigenetic mechanisms involved in ABA responses (Liu et al. 2007; Chen and Wu 2010; Luo et al. 2012; Mehdi et al. 2016; Zhu et al. 2018). A recent study demonstrated that an *Arabidopsis* nodulin homeobox protein (AtNDX) could interact with the core components of PRC1 silencing complex, AtRING1A and AtRING1B, thereby negatively regulating the expression of some ABA-responsive genes such as ABI4 (Zhu et al. 2020). Moreover, the expression of *AtNDX* is downregulated by ABA, suggesting an important involvement of AtNDX-PRC1 interaction in ABA signaling pathway. A recent study indicated that the transcription of the ABA receptors PYL4, PYL5 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 interacts with AtMYC2, a regulator of both ABA and jasmonic acid (JA) response 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 SUPRESSOR 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 these genes (Mehdi et al. 2016). In addition to being deposited on ABA receptor genes, H3Ac is also involved in the transcriptional regulation of genes encoding the PP2C family proteins, such as ABA INSENSITIVE 1 (ABI1) and ABI2 (Luo et al. 2012).

In conjunction with FUSCA3 (FUS3) and LEAFY COTYLEDON1 and 2 (LEC1 and LEC2), the ABI3 TF participates in early seed development (Santos-Mendoza et al. 2008). Histone modifications are involved in ABA response in early seedling development (Ryu et al. 2014). 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 H3. Additionally, histone modifications are also involved in the fine-tuning of SnRK2.8 via ABI3 (Wu et al. 2019). Abscisic acid treatment induces the expression of *ABI3*, and then ABI3 binds to the RY motif in the histone demethylase *JMJ30* gene promoter to activate its expression. JMJ30 can remove the repressive marker H3K27me3 from the promoter region of *SnRK2.8*, and hence activates *SnRK2.8* expression; 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 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 critical role in seed dormancy. In summary, the expression patterns of many ABA-responsive genes are dynamically regulated by multiple 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, the expression of some ABA-inducible genes was decreased in *ros1* mutants, and more than 60% of these genes showed hypermethylation in their proximal regions. *NICOTINAMIDASE 3* (*NIC3*) encodes an enzyme that converts nicotinamide to nicotinic acid in the NAD+ salvage pathway and is linked to ABA responsiveness (Kim et al. 2019). *NICOTINAMIDASE 3* is reported to be one of the targets of ROS1 (Kim et al. 2019). There are other ABA-inducible genes under ROS1 regulation which are also potential links between DNA methylation and ABA response. Repressor of Transcriptional Silencing 1-dependent demethylation regulates the imprinting of DOGL4, a negative regulator of seed dormancy (Zhu et al. 2018). *DOGL4* is expressed from the maternal allele in endosperm, and ROS1 negatively regulates imprinting by demethylating the paternal allele. DNA methylation not only alters the expression of ABA stress responsive genes at the transcriptional level but also can mediate the proper subcellular localization 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 and upregulation of stress-responsive genes. Khan et al. showed that, similar to ABA treatment, the malfunctions of several RdDM proteins and HD2C led to a mislocalization of STRS2 and STRS1, respectively (Khan et al. 2014). Moreover, reduced DNA methylation of RdDM target loci was observed in *strs* mutants, suggesting a role for STRSs in epigenetic silencing. Using a genetic screen based on ABA inhibition of seed germination and seedling growth, Yin et al. identified a mutant of *Arabidopsis thaliana POL2a/TILTED1* (*TIL1*), which encodes a catalytic subunit of DNA polymerase ε (Yin et al. 2009). The *til1/abo4* mutant not only displayed ABA hypersensitivity but also release of 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,

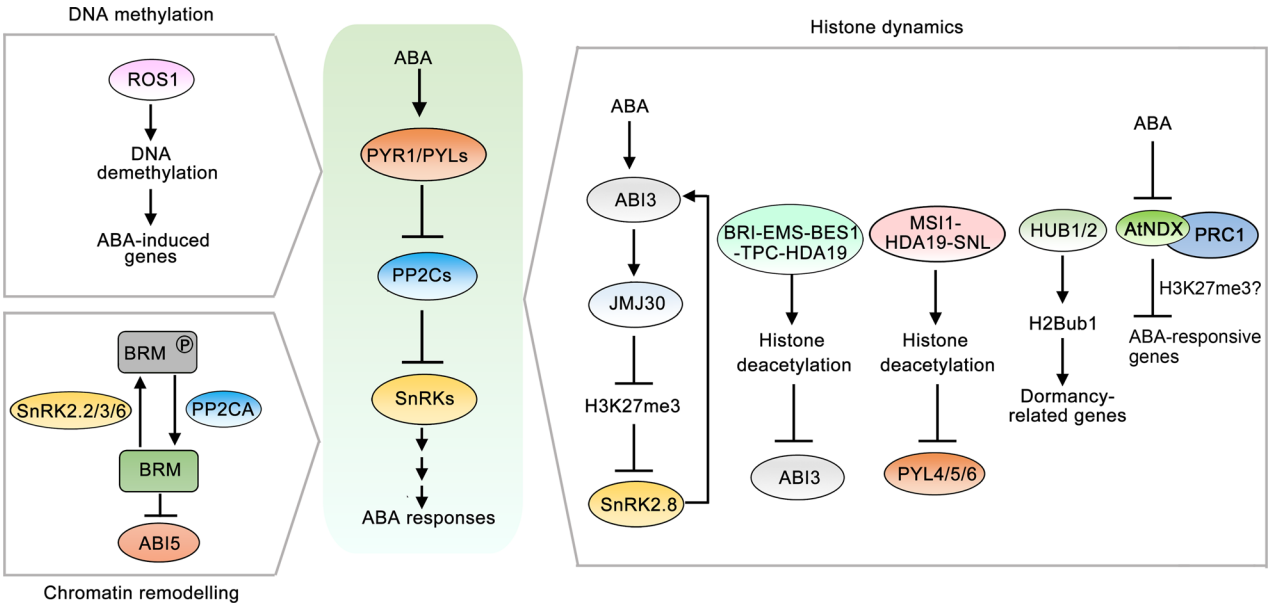

Figure 4. Epigenetic regulation of abscisic acid (ABA) responses
In *Arabidopsis*, ABA induces the expression of ABI3, which binds to the *JMJ30* promoter to activate *JMJ30* expression. JMJ30 can remove the H3K27me3 from *SnRK2.8* and contribute to the activation of *ABI3*, which in turn enhances the activation of *SnRK2.8*; The BRI-EMS-BES1-TPC-HDA19 and MSI1-HDA19-SNL histone deacetylation complexes remove H3K9Ac from the *ABI3* and *PYL4/5/6* loci, respectively, to repress their expression in normal conditions. In seed dormancy, dormancy-related genes, such as *DELAY OF GERMINATION 1 (DOG1)*, *ABI4*, *NCED9*, and *PEROXIREDOXIN ANTIOXIDANT (PER1)*, are positively regulated by HUB1/2-mediated H2B ubiquitination; ABA represses the expression of AtNDX, which could interact with PRC1 core components AtRING1A and AtRING1B to downregulate the expression of some ABA-responsive genes. Repressor of Transcriptional Silencing 1-mediated DNA demethylation is required for the expression of a number of ABA-induced genes; The chromatin remodeling protein BRAHMA (BRM) can be phosphorylated/dephosphorylated by SNF1-RELATED PROTEIN KINASE 2 (SnRK2) kinases/PROTEIN PHOSPHATASE TYPE 2Cs (PP2Cs) and the dephosphorylated BRM represses *ABI5* transcription.

Saez et al. demonstrated that SWITCH/SUCROSE NONFERMENTING 3B (SWI3B), an *Arabidopsis* homolog of the yeast SWI3 subunit of SWITCH/SUCROSE NONFERMENTING (SWI/SNF) chromatin-remodeling complex, participates in ABA 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, although the detailed epigenetic mechanism remains unknown. Interestingly, the same group further found that the chromatin remodeling ATPase BRAHMA (BRM), another subunit of SWI/SNF complex, represses ABA response in the absence of stress stimuli in *Arabidopsis* (Han et al. 2012). They found that BRM binds to the *ABI5* promoter to repress *ABI5* expression by affecting the stability of the associated nucleosome. Moreover, the developmental defects of *brm* mutants could be partially overcome by reduction of ABA response, suggesting a role of BRM in the balance between growth and stress responses. Later on, this group expanded their work 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 the core ABA signaling pathway could directly interact with and phosphorylate BRM. Plants expressing 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, the ABA core signaling pathway can directly control BRM-mediated chromatin status through a rapid phosphorylation-based switch, which in turn affects plant responses to ABA.

EPIGENETIC REGULATION IN THE RESPONSES TO NUTRIENT STRESS AND UV STRESS

Nutrient stress

Proper uptake of nutrients is critical for plant growth and development. Plants have evolved sophisticated mechanisms for adaptation to fluctuating availability of nutrients in the soil (Gojon et al. 2009; Davidian and Kopriva 2010). To date, most of the studies of epigenetic regulation in plant responses to nutrient stresses have focused on histone methylation, histone variants and DNA methylation. High N supply represses the expression of a root nitrogen transporter, NRT2.1; the gene repression requires HIGH NITROGEN INSENSITIVE 9 (HNI9) that participates in the deposition of H3K27me3 on the *NRT2.1* gene (Widiez et al. 2011). Fan et al. reported that PRMT5-mediated histone H4R3 symmetric dimethylation (H4R3sme2) negatively regulates iron homeostasis in *Arabidopsis* (Fan et al. 2014). PRMT5 associated with the chromatin of bHLH genes (*AtbHLH38*, *AtbHLH39*, *AtbHLH100*, and *AtbHLH101*) to symmetrically dimethylate H4R3, although the expression of *PRMT5* itself was not affected by iron (Fan et al. 2014). Xing et al. reported that the histone acetyltransferase 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 H3K6 and H3K14. In *gcn5* mutant plants, iron translocation from the root to shoot was impaired and iron was detained in the root compared with wild type *Arabidopsis* (Xing et al. 2015).

In the response to phosphate (Pi) deficiency, H3K4me3, histone acetylation and histone variant H2A.Z have been shown to play important roles. The PHD protein ALFIN-LIKE 6 (AL6) binds to the H3K4me3 mark and affects transcript maturation and stability of critical genes involved in root hair elongation (Chandrika et al. 2013). 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, and that this phenomenon was mediated through the targeting of HDA19 to genes encoding SPX (SYG1/Pho81/XPR) domain-containing proteins and genes involved in membrane lipid remodeling (Chen et al. 2015). In addition to histone acetylation, 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, for example, in the mutant of ARP6 which is a key component of the SWR1 complex (Smith et al. 2010). Another example is that mutation of IPK1 activates many Pi starvation-induced genes in a way that is related to 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 results in an extensive remodeling of global DNA methylation in *Arabidopsis* and rice (Secco et al. 2015; Yong-Villalobos et al. 2015). Meanwhile, gene expression of some DNA methylases, such as MET1, DRM1, and DRM2, were induced after low Pi treatment (Yong-Villalobos et al. 2015). Some key sulphate responsive genes, such as sulphate transporter genes *SULPHATE TRANSPORTER 1.1* (*SULTR1.1*) and *SULTR1.2*, were subjected to DNA methylation-dependent regulation (Huang et al. 2016). Mutation in MORE SULPHUR ACCUMULATION1 (MSA1), which is required for the biosynthesis of the universal methyl donor S-adenosylmethionine (SAM), resulted in a global reduction of DNA methylation levels and changes of gene expression, including *SULTR1.1* and *SULTR1.2* (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 CHH context, was related to the upregulation of a few Zn deficiency-responsive genes (Chen et al. 2018). Interestingly, the *ddc* (*drm1/drm2/cmt3*) mutant, which lacks non-CG methylation, displayed more severe developmental defects under Zn deficiency (Chen et al. 2018). These results indicated a connection between the Zn deficiency response and DNA methylation dynamics.

UV stress

Lang-Mladek et al. demonstrated that UV-B stress results in an immediate release of the silencing of transgene and endogenous loci through changes in

chromatin conformation and histone acetylation but not DNA methylation in *Arabidopsis* (Lang-Mladek et al. 2010). Moreover, UV stress effects on transgene silencing were heritable and could be passed down to the next two progeny generations in a small number of cells. Pandey and Pandey-Rai evaluated the DNA methylation dynamics in response to UV-B radiation in *Artemisia annua*, which 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 the DBR2 promoter region which contains 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 DNA hypomethylation in the whole genome of *Artemisia annua* L. In particular, UV-B irradiation promoted the demethylation of *AaPAL1* promoter region, which releases the binding sites of several transcription factors and thereby increases the expression of MYB transcription factors, including MYB1, MYC, and WRKY (Pandey et al. 2019).

Epigenetic memory of abiotic stress responses

In the natural environments, it is usually inevitable for plants to experience unfavorable environmental conditions. To some extent, plants can retain the stress response information for at least some specific stress 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 after recovery from stress or even in the progeny (Ding et al. 2012; Sani et al. 2013; Sanchez and Paszkowski 2014; Virlouvet 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 a higher level than that in nontrainable 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 responsive genes (Liu et al. 2014). Sani et al. revealed that the priming treatment could alter the epigenomic landscape. Although these changes were small, they were specific for the treated tissue and varied in number and direction depending on the histone modifications (Sani et al. 2013). Notably, 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 H3K27me3 islands. However, H3K4me2, H3K4me3, and H3K9me2 islands did not show any changes between primed and nonprimed plants. The salt treatment-induced genes with 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 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 put 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 demonstrated the transcriptional memory that was mediated by different histone modifications (Berger 2007; Heard and Martienssen

2014; Zheng et al. 2017), it remains unclear how the adverse conditions trigger the changes in epigenetic modifications.

In addition to the memory during priming, increasing evidence indicates that DNA sequence-independent epigenetic modification could transmit from one generation to the next generation (Lang-Mladek et al. 2010; Iwasaki and Paszkowski 2014; Zheng et al. 2017; Cong et al. 2019), which is referred to as "transgenerational memory" (Heard and Martienssen 2014). The formation of stress-induced transgenerational memory in the progeny benefit plants to achieve a better balance between survival and reproduction (Molinier et al. 2006). A recent study in rice revealed that drought stress induced changes in DNA methylation status and a high percentage (>40%) of these epimutations was inherited in the progeny (Zheng et al. 2017). Meanwhile, the progenies showed decreasing effective tiller numbers (reducing water consumption) and increasing seed setting rates (maintaining the yield). Thus, one possibility 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 drought stress conditions (Zheng et al. 2017). More recently, another study indicated that DNA methylation participates 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 status of a *Tos17* retrotransposon was altered in response to the heavy metal stress and the altered DNA methylation displayed transgenerational inheritance within three generations. Similarly, Ito et al. demonstrated that heat stress treatment could transcriptionally activate a retrotransposon *ONSEN*, and heat-induced *ONSEN* transcription and transposition were promoted in the mutants of siRNA 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. Although these studies have shown the involvement of epigenetic mechanisms in the formation of transgenerational stress memory, the mechanisms underlying the epigenetic alterations remain to be elucidated.

CONCLUSIONS AND PERSPECTIVES

Being exposed to continuously changing conditions in nature, plants have to make a variety of changes to adapt to their environment. As summarized in Figure 5, numerous efforts have been made to explore the epigenetic mechanisms involved in plant abiotic stress responses (Popova et al. 2013; Kim et al. 2015; Lamke and Baurle 2017). It is clear that

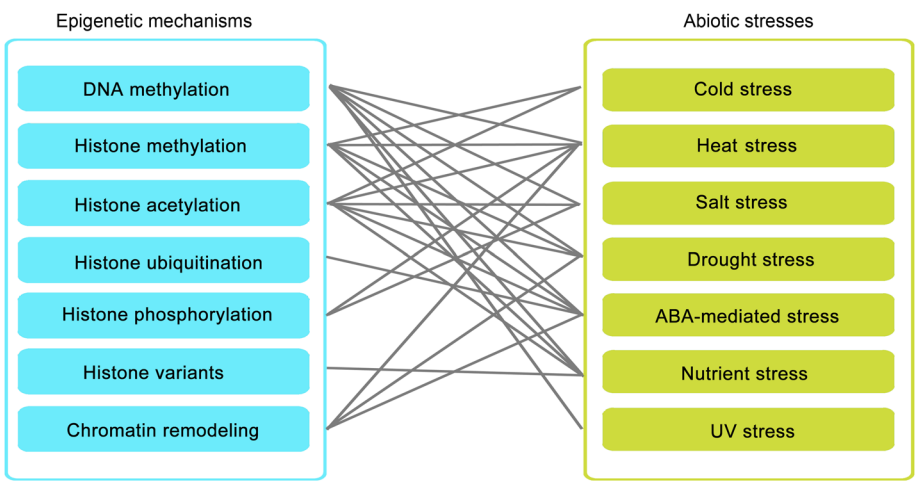

Figure 5. A summary of the cross-talks between epigenetic mechanisms and abiotic stress responses

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 under epigenetic regulation, and the levels of epigenetic marks are activated or 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 various 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, we are far from a full and clear understanding of the roles of epigenetic mechanisms in plant response to abiotic stresses. How stresses regulate the epigenetic machineries to cause chromatin changes and consequent transcriptional reprogramming is poorly understood. It is also unclear how epigenetic changes may be inherited by the offspring as a stress memory mechanism. Undoubtedly, deciphering the epigenetic codes of plant abiotic stress responses deserves more attention in future studies. With the rapid advancement of high-throughput sequencing and various chromatin profiling technologies, the epigenomes of increasing numbers of crop plants are being determined, which will greatly increase the number of studies on the epigenetic mechanisms of stress adaptation in model plants as well as in crops.

ACKNOWLEDGEMENTS

The work of Dr. C.G.D. was supported by the Strategic Priority Research Program of the Chinese Academy of Sciences (XDB27040203) and by the National Natural Science Foundation of China (31970157).

REFERENCES

Abe H, Urao T, Ito T, Seki M, Shinozaki K, Yamaguchi-Shinozaki K (2003) *Arabidopsis* AtMYC2 (bHLH) and AtMYB2 (MYB) function as transcriptional activators in abscisic acid signaling. **Plant Cell** 15: 63–78

Aleman F, Yazaki J, Lee M, Takahashi Y, Kim AY, Li Z, Kinoshita T, Ecker JR, Schroeder JI (2016) An ABA-increased interaction of the PYL6 ABA receptor with MYC2 transcription factor: A putative link of ABA and JA signaling. **Sci Rep** 6: 28941

Avramova Z (2015) Transcriptional 'memory' of a stress: Transient chromatin and memory (epigenetic) marks at stress-response genes. **Plant J** 83: 149–159

Baek D, Jiang J, Chung JS, Wang B, Chen J, Xin Z, Shi H (2011) Regulated *AtHKT1* gene expression by a distal enhancer element and DNA methylation in the promoter plays an important role in salt tolerance. **Plant Cell Physiol** 52: 149–161

Bennetzen JL, Wang H (2014) The contributions of transposable elements to the structure, function, and evolution of plant genomes. **Annu Rev Plant Biol** 65: 505–530

Berger SL (2007) The complex language of chromatin regulation during transcription. **Nature** 447: 407–412

Butelli E, Licciardello C, Zhang Y, Liu J, Mackay S, Bailey P, Reforgiato-Recupero G, Martin C (2012) Retrotransposons control fruit-specific, cold-dependent accumulation of anthocyanins in blood oranges. **Plant Cell** 24: 1242–1255

Carter B, Bishop B, Ho KK, Huang R, Jia W, Zhang H, Pascuzzi PE, Deal RB, Ogas J (2018) The chromatin remodelers PKL and PIE1 act in an epigenetic pathway that determines H3K27me3 homeostasis in *Arabidopsis*. **Plant Cell** 30: 1337–1352

Chandrika NN, Sundaravelpandian K, Yu SM, Schmidt W (2013) ALFIN-LIKE 6 is involved in root hair elongation during phosphate deficiency in *Arabidopsis*. **New Phytol** 198: 709–720

Chen CY, Wu K, Schmidt W (2015) The histone deacetylase HDA19 controls root cell elongation and modulates a subset of phosphate starvation responses in *Arabidopsis*. **Sci Rep** 5: 15708

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 LT, Wu K (2010) Role of histone deacetylases HDA6 and HDA19 in ABA and abiotic stress response. **Plant Signal Behav** 5: 1318–1320

Chen X, Schonberger B, Menz J, Ludewig U (2018) Plasticity of DNA methylation and gene expression under zinc deficiency in *Arabidopsis* roots. **Plant Cell Physiol** 59: 1790–1802

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 J, Zhu JK (2007) Cold stress regulation of gene expression in plants. **Trends Plant Sci** 12: 444–451

Cong W, Miao Y, Xu L, Zhang Y, Yuan C, Wang J, Zhuang T, Lin X, Jiang L, Wang N, Ma J, Sanguinet KA, Liu B, Rustgi S, Ou X (2019) Transgenerational memory of gene expression changes induced by heavy metal stress in rice (*Oryza sativa* L.). **BMC Plant Biol** 19: 282

Davidian JC, Kopriva S (2010) Regulation of sulfate uptake and assimilation–the same or not the same? **Mol Plant** 3: 314–325

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 (2012) Multiple exposures to drought 'train' transcriptional responses in *Arabidopsis*. **Nat Commun** 3: 740

Ding Y, Shi Y, Yang S (2019) Advances and challenges in uncovering cold tolerance regulatory mechanisms in plants. **New Phytol** 222: 1690–1704

Driedonks N, Xu J, Peters JL, Park S, Rieu I (2015) Multi-level interactions between heat shock factors, heat shock proteins, and the redox system regulate acclimation to heat. **Front Plant Sci** 6: 999

Duan CG, Wang X, Xie S, Pan L, Miki D, Tang K, Hsu CC, Lei M, Zhong Y, Hou YJ, Wang Z, Zhang Z, Mangrauthia SK, Xu H, Zhang H, Dilkes B, Tao WA, Zhu JK (2017a) A pair of transposon-derived proteins function in a histone acetyltransferase complex for active DNA demethylation. **Cell Res** 27: 226–240

Duan CG, Wang X, Zhang L, Xiong X, Zhang Z, Tang K, Pan L, Hsu CC, Xu H, Tao WA, Zhang H, Zhu JK (2017b) A protein complex regulates RNA processing of intronic heterochromatin-containing genes in *Arabidopsis.* **Proc Natl Acad Sci USA** 114: E7377–E7384

Duan CG, Zhu JK, Cao X (2018) Retrospective and perspective of plant epigenetics in China. **J Genet Genomics** 45: 621–638

Fan H, Zhang Z, Wang N, Cui Y, Sun H, Liu Y, Wu H, Zheng S, Bao S, Ling HQ (2014) SKB1/PRMT5-mediated histone H4R3 dimethylation of Ib subgroup bHLH genes negatively regulates iron homeostasis in *Arabidopsis thaliana*. **Plant J** 77: 209–221

Friedrich T, Faivre L, Baurle I, Schubert D (2019) Chromatin-based mechanisms of temperature memory in plants. **Plant Cell Environ** 42: 762–770

Fromm M, Avramova Z (2014) ATX1/AtCOMPASS and the H3K4me3 marks: How do they activate *Arabidopsis* genes? **Curr Opin Plant Biol** 21: 75–82

Gojon A, Nacry P, Davidian JC (2009) Root uptake regulation: A central process for NPS homeostasis in plants. **Curr Opin Plant Biol** 12: 328–338

Gonzalez-Guzman M, Pizzio GA, Antoni R, Vera-Sirera F, Merilo E, Bassel GW, Fernandez MA, Holdsworth MJ, Perez-Amador MA, Kollist H, Rodriguez PL (2012) *Arabidopsis* PYR/PYL/RCAR receptors play a major role in quantitative regulation of stomatal aperture and transcriptional response to abscisic acid. **Plant Cell** 24: 2483–2496

Guo X, Liu D, Chong K (2018) Cold signaling in plants: Insights into mechanisms and regulation. **J Integr Plant Biol** 60: 745–756

Han SK, Sang Y, Rodrigues A, Biol F, 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

Han Z, Yu H, Zhao Z, Hunter D, Luo X, Duan J, Tian L (2016) *AtHD2D* gene plays a role in plant growth, development, and response to abiotic stresses in *Arabidopsis thaliana*. **Front Plant Sci** 7: 310

Heard E, Martienssen RA (2014) Transgenerational epigenetic inheritance: Myths and mechanisms. **Cell** 157: 95–109

Hilker M, Schwachtje J, Baier M, Balazadeh S, Baurle I, Geiselhardt S, Hincha DK, Kunze R, Mueller-Roeber B, Rillig MC, Rolff J, Romeis T, Schmulling T, Steppuhn A, van Dongen J, Whitcomb SJ, Wurst S, Zuther E, Kopka J (2016) Priming and memory of stress responses in organisms lacking a nervous system. **Biol Rev Camb Philos Soc** 91: 1118–1133

Huang XY, Chao DY, Koprivova A, Danku J, Wirtz M, Muller S, Sandoval FJ, Bauwe H, Roje S, Dilkes B, Hell R, Kopriva S, Salt DE (2016) Nuclear localised MORE SULPHUR ACCUMULATION1 epigenetically regulates sulphur homeostasis in *Arabidopsis thaliana*. **PLoS Genet** 12: e1006298

Ito H, Gaubert H, Bucher E, Mirouze M, Vaillant I, Paszkowski J (2011) An siRNA pathway prevents transgenerational retrotransposition in plants subjected to stress. **Nature** 472: 115–119

Iwasaki M, Paszkowski J (2014) Identification of genes preventing transgenerational transmission of stress-induced epigenetic states. **Proc Natl Acad Sci USA** 111: 8547–8552

Jiang H, Li H, Bu Q, Li C (2009) The RHA2a-interacting proteins ANAC019 and ANAC055 may play a dual role in regulating ABA response and jasmonate response. **Plant Signal Behav** 4: 464–466

Kazan K, Manners JM (2013) MYC2: The master in action. **Mol Plant** 6: 686–703

Khan A, Garbelli A, Grossi S, Florentin A, Batelli G, Acuna T, Zolla G, Kaye Y, Paul LK, Zhu JK, Maga G, Grafi G, Barak S (2014) The *Arabidopsis* STRESS RESPONSE SUPPRESSOR DEAD-box RNA helicases are nucleolar- and chromocenter-localized proteins that undergo stress -mediated relocalization and are involved in epigenetic gene silencing. **Plant J** 79: 28–43

Kim JM, Sasaki T, Ueda M, Sako K, Seki M (2015) Chromatin changes in response to drought, salinity, heat, and cold stresses in plants. **Front Plant Sci** 6: 114

Kim JM, To TK, Ishida J, Morosawa T, Kawashima M, Matsui A, Toyoda T, Kimura H, Shinozaki K, Seki M (2008)

Alterations of lysine modifications on the histone H3 N-tail under drought stress conditions in *Arabidopsis* thaliana. **Plant Cell Physiol** 49: 1580–1588

Kim JM, To TK, Seki M (2012) An epigenetic integrator: New insights into genome regulation, environmental stress responses and developmental controls by histone deacetylase 6. **Plant Cell Physiol** 53: 794–800

Kim JS, Lim JY, Shin H, Kim BG, Yoo SD, Kim WT, Huh JH (2019) ROS1-dependent DNA demethylation is required for ABA-inducible NIC3 expression. **Plant Physiol** 179: 1810–1821

Kumar S, Beena AS, Awana M, Singh A (2017) Salt-induced tissue-specific cytosine methylation downregulates expression of *HKT* genes in contrasting wheat (*Triticum aestivum* L.) genotypes. **DNA Cell Biol** 36: 283–294

Kuo HF, Chang TY, Chiang SF, Wang WD, Charng YY, Chiou TJ (2014) *Arabidopsis* inositol pentakisphosphate 2-kinase, AtIPK1, is required for growth and modulates phosphate homeostasis at the transcriptional level. **Plant J** 80: 503–515

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

Lamke J, Baurle I (2017) Epigenetic and chromatin-based mechanisms in environmental stress adaptation and stress memory in plants. **Genome Biol** 18: 124

Lamke J, Brzezinka K, Altmann S, Baurle I (2016) A hit-and-run heat shock factor governs sustained histone methylation and transcriptional stress memory. **EMBO J** 35: 162–175

Lang-Mladek C, Popova O, Kiok K, Berlinger M, Rakic B, Aufsatz W, Jonak C, Hauser MT, Luschnig C (2010) Transgenerational inheritance and resetting of stress-induced loss of epigenetic gene silencing in *Arabidopsis*. **Mol Plant** 3: 594–602

Law JA, Jacobsen SE (2010) Establishing, maintaining and modifying DNA methylation patterns in plants and animals. **Nat Rev Genet** 11: 204–220

Lei M, La H, Lu K, Wang P, Miki D, Ren Z, Duan CG, Wang X, Tang K, Zeng L, Yang L, Zhang H, Nie W, Liu P, Zhou J, Liu R, Zhong Y, Liu D, Zhu JK (2014) *Arabidopsis* EDM2 promotes IBM1 distal polyadenylation and regulates genome DNA methylation patterns. **Proc Natl Acad Sci USA** 111: 527–532

Li S, Lin YJ, Wang P, Zhang B, Li M, Chen S, Shi R, Tunlaya-Anukit S, Liu X, Wang Z, Dai X, Yu J, Zhou C, Liu B, Wang JP, Chiang VL, Li W (2019) The AREB1 transcription factor influences histone acetylation to regulate drought responses and tolerance in *Populus trichocarpa*. **Plant Cell** 31: 663–686

Li Z, Fu X, Wang Y, Liu R, He Y (2018) Polycomb-mediated gene silencing by the BAH-EMF1 complex in plants. **Nat Genet** 50: 1254–1261

Liang D, Zhang Z, Wu H, Huang C, Shuai P, Ye CY, Tang S, Wang Y, Yang L, Wang J, Yin W, Xia X (2014) Single-base-resolution methylomes of Populus trichocarpa reveal the association between DNA methylation and drought stress. **BMC Genet** 15(Suppl 1): S9

Liu C, Lu F, Cui X, Cao X (2010) Histone methylation in higher plants. **Annu Rev Plant Biol** 61: 395–420

Liu C, Xin Y, Xu L, Cai Z, Xue Y, Liu Y, Xie D, Liu Y, Qi Y (2018a) *Arabidopsis* ARGONAUTE 1 binds chromatin to promote gene transcription in response to hormones and stresses. **Dev Cell** 44: 348.e7–361.e7

Liu J, Shi Y, Yang S (2018b) Insights into the regulation of C-repeat binding factors in plant cold signaling. **J Integr Plant Biol** 60: 780–795

Liu N, Ding Y, Fromm M, Avramova Z (2014) Different gene-specific mechanisms determine the 'revised-response' memory transcription patterns of a subset of *A. thaliana* dehydration stress responding genes. **Nucleic Acids Res** 42: 5556–5566

Liu R, Lang Z (2020) The mechanism and function of active DNA demethylation in plants. **J Integr Plant Biol** 62: 148–159

Liu Y, Koornneef M, Soppe WJ (2007) The absence of histone H2B monoubiquitination in the *Arabidopsis* hub1 (rdo4) mutant reveals a role for chromatin remodeling in seed dormancy. **Plant Cell** 19: 433–444

Luo M, Wang YY, Liu X, Yang S, Lu Q, Cui Y, Wu K (2012) HD2C interacts with HDA6 and is involved in ABA and salt stress response in *Arabidopsis*. **J Exp Bot** 63: 3297–3306

Luo X, He Y (2020) Experiencing winter for spring flowering: A molecular epigenetic perspective on vernalization. **J Integr Plant Biol** 62: 104–117

Makarevitch I, Waters AJ, West PT, Stitzer M, Hirsch CN, Ross-Ibarra J, Springer NM (2015) Transposable elements contribute to activation of maize genes in response to abiotic stress. **PLoS Genet** 11: e1004915

Mao H, Wang H, Liu S, Li Z, Yang X, Yan J, Li J, Tran LS, Qin F (2015) A transposable element in a *NAC* gene is associated with drought tolerance in maize seedlings. **Nat Commun** 6: 8326

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

Matsui A, Ishida J, Morosawa T, Mochizuki Y, Kaminuma E, Endo TA, Okamoto M, Nambara E, Nakajima M, Kawashima M, Satou M, Kim JM, Kobayashi N, Toyoda T, Shinozaki K, Seki M (2008) Arabidopsis transcriptome analysis under drought, cold, high-salinity and ABA treatment conditions using a tiling array. **Plant Cell Physiol** 49: 1135–1149

Mehdi S, Derkacheva M, Ramstrom M, Kralemann L, Bergquist J, Hennig L (2016) The WD40 domain protein MSI1 functions in a histone deacetylase complex to fine-tune abscisic acid signaling. **Plant Cell** 28: 42–54

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

Molinier J, Ries G, Zipfel C, Hohn B (2006) Transgeneration memory of stress in plants. **Nature** 442: 1046–1049

Mozgova I, Hennig L (2015) The polycomb group protein regulatory network. **Annu Rev Plant Biol** 66: 269–296

Nambara E, Marion-Poll A (2003) ABA action and interactions in seeds. **Trends Plant Sci** 8: 213–217

Nie WF, Lei M, Zhang M, Tang K, Huang H, Zhang C, Miki D, Liu P, Yang Y, Wang X, Zhang H, Lang Z, Liu N, Xu X, Yelagandula R, Zhang H, Wang Z, Chai X, Andreucci A, Yu JQ, Berger F, Lozano-Duran R, Zhu JK (2019) Histone acetylation recruits the SWR1 complex to regulate active DNA demethylation in *Arabidopsis*. **Proc Natl Acad Sci USA** 116: 16641–16650

Ohama N, Sato H, Shinozaki K, Yamaguchi-Shinozaki K (2017) Transcriptional regulatory network of plant heat stress response. **Trends Plant Sci** 22: 53–65

Okamuro JK, Caster B, Villarroel R, Van Montagu M, Jofuku KD (1997) The AP2 domain of APETALA2 defines a large new family of DNA binding proteins in *Arabidopsis*. **Proc Natl Acad Sci USA** 94: 7076–7081

Osakabe Y, Yamaguchi-Shinozaki K, Shinozaki K, Tran LS (2014) ABA control of plant macroelement membrane transport systems in response to water deficit and high salinity. **New Phytol** 202: 35–49

Pandey N, Goswami N, Tripathi D, Rai KK, Rai SK, Singh S, Pandey-Rai S (2019) Epigenetic control of UV-B-induced flavonoid accumulation in *Artemisia annua* L. **Planta** 249: 497–514

Pandey N, Pandey-Rai S (2015) Deciphering UV-B-induced variation in DNA methylation pattern and its influence on regulation of DBR2 expression in *Artemisia annua* L. **Planta** 242: 869–879

Park J, Lim CJ, Shen M, Park HJ, Cha JY, Iniesto E, Rubio V, Mengiste T, Zhu JK, Bressan RA, Lee SY, Lee BH, Jin JB, Pardo JM, Kim WY, Yun DJ (2018) Epigenetic switch from repressive to permissive chromatin in response to cold stress. **Proc Natl Acad Sci USA** 115: E5400–E5409

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

Peirats-Llobet M, Han SK, Gonzalez-Guzman M, Jeong CW, Rodriguez L, Belda-Palazon B, Wagner D, Rodriguez PL (2016) A direct link between abscisic acid sensing and the chromatin-remodeling ATPase BRAHMA via core ABA signaling pathway components. **Mol Plant** 9: 136–147

Popova OV, Dinh HQ, Aufsatz W, Jonak C (2013) The RdDM pathway is required for basal heat tolerance in *Arabidopsis*. **Mol Plant** 6: 396–410

Ramirez-Prado JS, Latrasse D, Rodriguez-Granados NY, Huang Y, Manza-Mianza D, Brik-Chaouche R, Jaouannet M, Citerne S, Bendahmane A, Hirt H, Raynaud C, Benhamed M (2019) The Polycomb protein LHP1 regulates *Arabidopsis thaliana* stress responses through the repression of the MYC2-dependent branch of immunity. **Plant J** 100: 1118–1131

Rus A, Yokoi S, Sharkhuu A, Reddy M, Lee BH, Matsumoto TK, Koiwa H, Zhu JK, Bressan RA, Hasegawa PM (2001) AtHKT1 is a salt tolerance determinant that controls Na (+) entry into plant roots. **Proc Natl Acad Sci USA** 98: 14150–14155

Ryu H, Cho H, Bae W, Hwang I (2014) Control of early seedling development by BES1/TPL/HDA19-mediated epigenetic regulation of ABI3. **Nat Commun** 5: 4138

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

Sahu PP, Pandey G, Sharma N, Puranik S, Muthamilarasan M, Prasad M (2013) Epigenetic mechanisms of plant stress responses and adaptation. **Plant Cell Rep** 32: 1151–1159

Saleh A, Alvarez-Venegas R, Yilmaz M, Le O, Hou G, Sadder M, Al-Abdallat A, Xia Y, Lu G, Ladunga I, Avramova Z (2008) The highly similar *Arabidopsis* homologs of trithorax ATX1 and ATX2 encode proteins with divergent biochemical functions. **Plant Cell** 20: 568–579

Sanchez DH, Paszkowski J (2014) Heat-induced release of epigenetic silencing reveals the concealed role of an imprinted plant gene. **PLoS Genet** 10: e1004806

Sani E, Herzyk P, Perrella G, Colot V, Amtmann A (2013) Hyperosmotic priming of *Arabidopsis* seedlings establishes a long-term somatic memory accompanied by specific changes of the epigenome. **Genome Biol** 14: R59

Santos-Mendoza M, Dubreucq B, Baud S, Parcy F, Caboche M, Lepiniec L (2008) Deciphering gene regulatory networks that control seed development and maturation in *Arabidopsis*. **Plant J** 54: 608–620

Secco D, Wang C, Shou H, Schultz MD, Chiarenza S, Nussaume L, Ecker JR, Whelan J, Lister R (2015) Stress induced gene expression drives transient DNA methylation changes at adjacent repetitive elements. **Elife** 4: e09343

Shinozaki K, Yamaguchi-Shinozaki K (2007) Gene networks involved in drought stress response and tolerance. **J Exp Bot** 58: 221–227

Singh RK, Jaishankar J, Muthamilarasan M, Shweta S, Dangi A, Prasad M (2016) Genome-wide analysis of heat shock proteins in C4 model, foxtail millet identifies potential candidates for crop improvement under abiotic stress. **Sci Rep** 6: 32641

Smith AP, Jain A, Deal RB, Nagarajan VK, Poling MD, Raghothama KG, Meagher RB (2010) Histone H2A.Z regulates the expression of several classes of phosphate starvation response genes but not as a transcriptional activator. **Plant Physiol** 152: 217–225

Sokol A, Kwiatkowska A, Jerzmanowski A, Prymakowska-Bosak M (2007) Up-regulation of stress-inducible genes in tobacco and *Arabidopsis* cells in response to abiotic stresses and

ABA treatment correlates with dynamic changes in histone H3 and H4 modifications. **Planta** 227: 245–254

Sridhar VV, Kapoor A, Zhang K, Zhu J, Zhou T, Hasegawa PM, Bressan RA, Zhu JK (2007) Control of DNA methylation and heterochromatic silencing by histone H2B deubiquitination. **Nature** 447: 735–738

Takahashi S, Katagiri T, Yamaguchi-Shinozaki K, Shinozaki K (2000) An *Arabidopsis* gene encoding a Ca^{2+}-binding protein is induced by abscisic acid during dehydration. **Plant Cell Physiol** 41: 898–903

To TK, Kim JM (2014) Epigenetic regulation of gene responsiveness in *Arabidopsis*. **Front Plant Sci** 4: 548

Virlouvet L, Ding Y, Fujii H, Avramova Z, Fromm M (2014) ABA signaling is necessary but not sufficient for RD29B transcriptional memory during successive dehydration stresses in *Arabidopsis thaliana*. **Plant J** 79: 150–161

Wang P, Xue L, Batelli G, Lee S, Hou YJ, Van Oosten MJ, Zhang H, Tao WA, Zhu JK (2013a) Quantitative phosphoproteomics identifies SnRK2 protein kinase substrates and reveals the effectors of abscisic acid action. **Proc Natl Acad Sci USA** 110: 11205–11210

Wang X, Duan CG, Tang K, Wang B, Zhang H, Lei M, Lu K, Mangrauthia SK, Wang P, Zhu G, Zhao Y, Zhu JK (2013b) RNA-binding protein regulates plant DNA methylation by controlling mRNA processing at the intronic heterochromatin-containing gene IBM1. **Proc Natl Acad Sci USA** 110: 15467–15472

Widiez T, El Kafafi el S, Girin T, Berr A, Ruffel S, Krouk G, Vayssieres A, Shen WH, Coruzzi GM, Gojon A, Lepetit M (2011) High nitrogen insensitive 9 (HNI9)-mediated systemic repression of root NO3- uptake is associated with changes in histone methylation. **Proc Natl Acad Sci USA** 108: 13329–13334

Wu J, Ichihashi Y, Suzuki T, Shibata A, Shirasu K, Yamaguchi N, Ito T (2019) Abscisic acid-dependent histone demethylation during postgermination growth arrest in *Arabidopsis*. **Plant Cell Environ** 42: 2198–2214

Xing J, Wang T, Liu Z, Xu J, Yao Y, Hu Z, Peng H, Xin M, Yu F, Zhou D, Ni Z (2015) GENERAL CONTROL NONREPRESSED PROTEIN5-mediated histone acetylation of FERRIC REDUCTASE DEFECTIVE3 contributes to iron homeostasis in *Arabidopsis*. **Plant Physiol** 168: 1309–1320

Xu R, Wang Y, Zheng H, Lu W, Wu C, Huang J, Yan K, Yang G, Zheng C (2015) Salt-induced transcription factor MYB74 is regulated by the RNA-directed DNA methylation pathway in *Arabidopsis*. **J Exp Bot** 66: 5997–6008

Yang C, Shen W, Chen H, Chu L, Xu Y, Zhou X, Liu C, Chen C, Zeng J, Liu J, Li Q, Gao C, Charron JB, Luo M (2018a) Characterization and subcellular localization of histone deacetylases and their roles in response to abiotic stresses in soybean. **BMC Plant Biol** 18: 226

Yang H, Berry S, Olsson TSG, Hartley M, Howard M, Dean C (2017) Distinct phases of Polycomb silencing to hold epigenetic memory of cold in *Arabidopsis*. **Science** 357: 1142–1145

Yang R, Hong Y, Ren Z, Tang K, Zhang H, Zhu JK, Zhao C (2019) A role for PICKLE in the regulation of cold and salt stress tolerance in *Arabidopsis*. **Front Plant Sci** 10: 900

Yang Z, Qian S, Scheid RN, Lu L, Chen X, Liu R, Du X, Lv X, Boersma MD, Scalf M, Smith LM, Denu JM, Du J, Zhong X (2018b) EBS is a bivalent histone reader that regulates floral phase transition in *Arabidopsis*. **Nat Genet** 50: 1247–1253

Yin H, Zhang X, Liu J, Wang Y, He J, Yang T, Hong X, Yang Q, Gong Z (2009) Epigenetic regulation, somatic homologous recombination, and abscisic acid signaling are influenced by DNA polymerase epsilon mutation in *Arabidopsis*. **Plant Cell** 21: 386–402

Yolcu S, Ozdemir F, Guler A, Bor M (2016) Histone acetylation influences the transcriptional activation of POX in *Beta vulgaris* L. and *Beta maritima* L. under salt stress. **Plant Physiol Biochem** 100: 37–46

Yong-Villalobos L, Gonzalez-Morales SI, Wrobel K, Gutierrez-Alanis D, Cervantes-Perez SA, Hayano-Kanashiro C, Oropeza-Aburto A, Cruz-Ramirez A, Martinez O, Herrera-Estrella L (2015) Methylome analysis reveals an important role for epigenetic changes in the regulation of the Arabidopsis response to phosphate starvation. **Proc Natl Acad Sci USA** 112: E7293–E7302

Zhang H, Lang Z, Zhu JK (2018) Dynamics and function of DNA methylation in plants. **Nat Rev Mol Cell Biol** 19: 489–506

Zhao X, Li J, Lian B, Gu H, Li Y, Qi Y (2018) Global identification of *Arabidopsis* lncRNAs reveals the regulation of MAF4 by a natural antisense RNA. **Nat Commun** 9: 5056

Zheng X, Chen L, Xia H, Wei H, Lou Q, Li M, Li T, Luo L (2017) Transgenerational epimutations induced by multi-generation drought imposition mediate rice plant's adaptation to drought condition. **Sci Rep** 7: 39843

Zhu H, Xie W, Xu D, Miki D, Tang K, Huang CF, Zhu JK (2018) DNA demethylase ROS1 negatively regulates the imprinting of DOGL4 and seed dormancy in *Arabidopsis thaliana*. **Proc Natl Acad Sci USA** 115: E9962–E9970

Zhu J, Jeong JC, Zhu Y, Sokolchik I, Miyazaki S, Zhu JK, Hasegawa PM, Bohnert HJ, Shi H, Yun DJ, Bressan RA (2008) Involvement of Arabidopsis HOS15 in histone deacetylation and cold tolerance. **Proc Natl Acad Sci USA** 105: 4945–4950

Zhu JK (2016) Abiotic stress signaling and responses in plants. **Cell** 167: 313–324

Zhu Y, Hu X, Duan Y, Li S, Wang Y, Rehman AU, He J, Zhang J, Hua D, Yang L, Wang L, Chen Z, Li C, Wang B, Song CP, Sun Q, Yang S, Gong Z (2020) The *Arabidopsis* nodulin homeobox factor atndx interacts with AtRING1A/B and negatively regulates abscisic acid signaling. **Plant Cell** 32: 703–721