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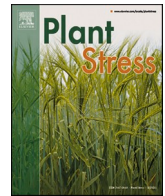
Review

The roles of histone methylation in the regulation of abiotic stress responses in plants

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ABSTRACT

Abiotic stress greatly threaten plants' growth and ultimately impact crop productivity. Plants have evolved sophisticated regulatory mechanisms to cope with stressful conditions, including undergoing physiological changes through genetic and epigenetic regulation of gene expression. Histone methylation takes an essential part in epigenetic regulation of the expression of numerous genes in plant response to abiotic stresses. In this review, we summarize the recent progress on the regulation of histone methylation in plant response to abiotic stress, including drought, high salinity, high temperature, and cold. We also discuss the roles of histone methylation in the formation of plant stress memory, as well as the metabolic regulation of histone methylation under abiotic stress in plants. We posit that a comprehensive understanding of the molecular mechanisms and functional roles of histone methylation in abiotic stress responses will accelerate plant breeding, improve stress resistance and substantially enhance biomass and crop yield.

1. Introduction

Plants, as sessile organisms, usually have to adapt to the stressful environment such as drought, high salinity, high temperature, cold etc. These adverse environmental factors induce various physiological, biochemical, and molecular responses in plants, thereby strongly affecting crop yield and threatening agricultural productivity (Zhang et al., 2022). Epigenetic mechanisms are crucial for plants in response to these abiotic stresses since it can quickly respond to the external environment without genetic mutations (Chang et al., 2020; Kim et al., 2015; Ueda and Seki, 2020). The eukaryotic chromatin is composed of nucleosomes, formed by a core histone octamer (two copies of H3, H4, H2A, and H2B) and 146 bp of DNA (Berger, 2007). Histone modifications refer to the post-translational modifications on the N-terminal tails of histones, including but not limited to methylation, acetylation, ubiquitination, phosphorylation, sumoylation, carbonylation, biotinylation (Strahl and Allis, 2000). Histone methylation status is dynamically regulated by both histone methyltransferase ("writer") and histone demethylase ("eraser") proteins, which deposit and remove methylation marks, respectively. They mainly occur on histone lysine methylation sites (H3K4, H3K9, H3K27, H3K36 and H4K20) and two arginine methylation sites (H3R17 and H4R3), which can be modified by mono-methylation, di-methylation or tri-methylation (Hu and Du, 2022; Liu et al., 2010). Histone methylation may affect chromatin architecture and regulate gene transcription. Generally, H3K4me3 and H3K36me3 are associated with transcriptional activation, while H3K9me2 and H3K27me3 are correlated with transcriptional silencing (Liu et al., 2010; Xiao et al., 2016).

Histone methyltransferases belong to Su(var)3-9, E(z), and Trithorax (SET) domain containing family proteins. According to their methylated residues, histone methyltransferases can be divided into lysine methyltransferases (HKMTs) and arginine methyltransferases (PRMTs). The *Arabidopsis* genome encodes more than 40 SET domain containing proteins, which are for 5 classes of HKMTs and 9 PRMTs (Liu et al., 2010).

The target sites of these HKMTs and PRMTs are as follows: H3K4 methylation (Arabisopsis Trithorax-like 1-5 (ATX1-5) and ATX–related 3/7 (ATXR3/7)); H3K9 methylation (SU(VAR)3-9 homologs 1-10 (SUVH1-10) and SU(VAR)3-9 related 1-5 (SUVR1-5)); H3K27 methylation (ATXR5/6, CURLY LEAF (CLF), SWINGER (SWN), and MEDEA (MEA)); H3K36 methylation (SET domain group 4/8/26 (SDG4/8/26)); H4K20 methylation (SUVH2); H3R17 methylation (PRMT4A/4B); and H4R3 methylation (PRMT1A/1B/5/10) (Fig. 1). Among them, the biochemical activities of ATX1/2/5/6, SUVH1/4/5/6, SUVR4, SDG8/25, and PRMT1A/1B/4A/4B/5/10 have been demonstrated (Hu and Du, 2022; Liu et al., 2010).

Histone demethylases, removal of methyl group from histone residues, are classified as lysine-specific demethylases (LSD) and jumonjiC (jmjC) domain-containing proteins (JMJ). The *Arabidopsis* genome encodes 4 *LSD* and 21 *JMJ* genes. The target sites of LSD and JMJ proteins are described as follows: H3K4 demethylation (FLOWERING LOCUS D, LSD1-LIKE1-3, and JMJ14-18); H3K9 demehtylation (IBM1/JMJ25, JMJ27-29, JMJ16); H3K27 demetylation (EARLY FLOWERING 6 (ELF6)/JMJ11, RELATIVE OF EARLY FLOWERING6 (REF6)/JMJ12, JMJ13, JMJ30, JMJ32); H3K36 demethylation (JMJ30, ICU11); H4R3 demethylation (JMJ20, JMJ22) (Fig. 1). However, the specific binding substrates of some JMJ proteins are still controversial. For example, JMJ30 has been revealed the H3K27me2/3 demethylase activity (Gan et al., 2014; Maruoka et al., 2022), which is contradictorily reported to its demehylation activity at H3K9 and H3K36 sites (Jones et al., 2019; Lee et al., 2018). Among these JMJs, the crystal structures of JMJ14 and REF6 with their complexes have been reported, revealing their different catalytic and substrate binding mechanisms of various plant JMJ proteins (Tian et al., 2020; Yang et al., 2018). In addition, a set of effector proteins ("readers"), containing various functional domains, such as Chromo, Tudor, MBT, WD40, PHD and PWWP domains, recognize different histone methylation status and generate specific transcriptional outcomes (Zhao et al., 2019b). In this review, we will mainly discuss the regulatory roles of histone methylation in response to four major abiotic stresses (drought, high salinity, high temperature and cold) (Fig. 1), as well as histone methylation memory induced by abiotic stress and metabolic regulation of plant histone methylation under abiotic stress, which can give more evidence to understand the complexity of the epigenetic landscape.

2. Histone methylation in drought stress

Drought stress severely limits plant growth and development, which is highly related to abscisic acid (ABA) (Osakabe et al., 2014). When plants sense the water-deficit signal, ABA is synthesized and then activates many proteins that regulate stomatal aperture to resist drought stress (Osakabe et al., 2014). Genome-wide H3K4 methylation status in response to drought stress reveals that inducible genes by dehydration with atypical broader H3K4me3 distribution profiles, indicating that H3K4me3 has important roles in transcriptional response of implicated genes (van Dijk et al., 2010). Under drought conditions, the expression levels of drought-responsive genes, such as *RESPONSIVE TO DESICCATION 29A* (*RD29A*), *RD29B, RD22* and *RELATED TO AP2.4* (*RAP2.4*) were induced (Matsui et al., 2008). The levels of histone modification H3K4me3 were also increased on these drought stress-induced genes, contributing to the active expression of these genes under drought stress (Kim et al., 2008). Moreover, H3K4me3 mark was more highly enriched under severe drought than under mild drought conditions (Kim et al., 2008). After recovery from drought stress, H3K4me3 mark was removed from these drought stress-upregulated genes, indicating that H3K4me3 is closely related to the expression of drought-responsive genes (Kim et al., 2008).

Several histone methylation enzymes have been reported to involve in drought stress response. *9-cis-EPOXYCAROTENOID DIOXYGENASE 3* (*NCED3*) encodes a crucial enzyme for ABA synthesis (Tan et al., 2003). Histone methyltransferase ATX1 is involved in regulation of H3K4me3
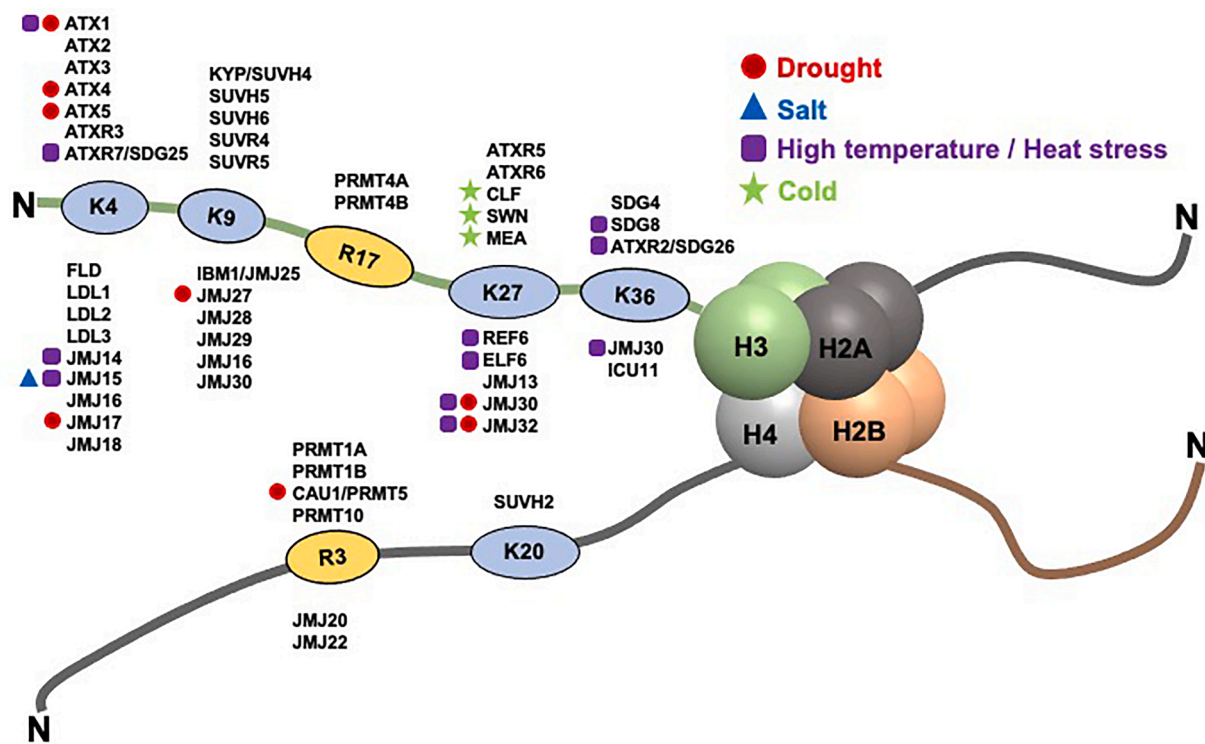
Fig. 1. Histone methylation sites and their methylation/demethylation enzymes involved in abiotic stress response in *Arabidopsis*. Histone lysine methylation sites are shown in pink ellipses and histone arginine methylation sites are shown in grey ellipses. The reported histone methyltransferases and demethylases in *Arabidopsis* are listed upper and lower sites, respectively. The enzymes involved in drought, salt, high temperature/heat stress and cold stress are marked with red cycle, blue triangle, purple square and green star, respectively.

on the responsive genes including *NCED3* in drought stress response. Drought stress recruits more ATX1 to the chromatin of *NCED3* gene, accompanied with the enhanced deposition of H3K4me3, which are preceded by upregulation of *NCED3*, indicating that ATX1 regulates drought responsive genes by modulating H3K4me3 levels (Ding et al., 2011). In addition to ATX1, other ATX group members, ATX4 and ATX5 redundantly regulate *ABA-HYPERSENSITIVE GERMINATION3* (*AHG3*) expression via directly targeting to *AHG3* and increasing H3K4me3 level at this locus (Liu et al., 2018). Thus, *atx4/5* loss-of-function mutants showed drought-tolerant and ABA-hypersensitive phenotypes (Liu et al., 2018). OsSDG708 is a specific H3K36 methyltransferase in rice and functions as a positive regulator of drought tolerance (Chen et al., 2021). OsSDG708 was found to activate the ABA biosynthesis genes *OsNCED3* and *OsNCED5* via regulating H3K36me3 levels (Chen et al., 2021). Several histone demethylases have also been reported to function in drought stress response. For example, *JMJ17* knockout mutants show the increased drought tolerance (Huang et al., 2019). In detail, JMJ17 directly binds to the chromatin of *OPEN STOMATA 1* (*OST1*) and regulates *OST1* transcript levels via demethylating H3K4me3 (Huang et al., 2019). H3K9me2 is generally related to heterochromatin formation and transcriptional repression in plants (Zhao et al., 2019a). JMJ27 positively regulates drought-stress responses through demethylating H3K9me2 (Wang et al., 2021). In particular, JMJ27 directly associates with positive drought-stress regulators, *GALACTINOL SYNTHASE 2* (*GOLS2*) and *RESPONSE TO DESICCATION 20* (*RD20*), to reduce their H3K9me2 levels. Drought stress leads to increase the abundance of JMJ27 at the chromatin loci of *GOLS2* and *RD20* chromatin loci and induce transcription of these two genes (Wang et al., 2021). Moreover, JMJ30 and JMJ32 may function redundantly in drought-stress response through targeting *SNF1-related protein kinase 2.8* (*SnRK2.8*) (Wu et al., 2019). *SnRK2.8* encodes a kinase that activates ABA-insensitive 3 (ABI3) and participates in drought-stress response (Kim et al., 2012). JMJ30/32 can remove H3K27me3 from *SnRK2.8* promoter and hence derepress *SnRK2.8* expression, suggesting that JMJ30/32 play important roles in ABA-dependent signaling in response to drought stress. LIKE HETERO-CHROMATIN PROTEIN 1 (LHP1) recognizes Polycomb-deposited H3K27me3 and represses many Polycomb target genes in plants (Turck et al., 2007). *NAC019* and *NAC055*, belonging to *Arabidopsis* NAC family transcription factors, were described as positive regulators of drought tolerance (Tran et al., 2004). Loss of *LHP1* reduced the deposition of H3K27me3 on *NAC019* and *NAC055*, and consequently induced the expression of these two genes (Ramirez-Prado et al., 2019). LHP1 thus negatively regulates drought tolerance process via transcriptional repression of *NAC019* and *NAC055* (Ramirez-Prado et al., 2019). Besides histone lysine methylation enzymes, CALCIUM UNDER-ACCUMULATION1 (CAU1)/PRMT5, mediating symmetric dimethylation of histone H4 Arginine 3 (H4R3sme2), is also involved in drought stress response (Fu et al., 2013). Drought stress can reduce the accumulation of CAU1 protein and then derepress the stress-related genes *NAC055* and *CALCIUM SENSOR* (*CAS*) by regulating H4R3sme2 level, thus *cau1* mutants displaying enhanced drought tolerance and stomatal closure (Fu et al., 2018; Fu et al., 2013). As summarized in Fig. 2, these findings above suggest that histone methylation/demethylation play crucial roles in drought stress response and tolerance.

3. Histone methylation in salt stress

High salinity, one of most detrimental environmental stresses, causes ion toxicity, osmotic stress and secondary stresses such as oxidative damage in plants (Zhang et al., 2022; Zhu, 2016). It has been well elucidated the sensing signal pathways and transcriptional regulation of a cascade of genes under salt stress (Paes de Melo et al., 2022; Zhang et al., 2022; Zhao et al., 2021). Histone methylation has been reported to regulate the transcripts of the salt stress responsive genes (Kim et al., 2015; Liu et al., 2022; Singroha et al., 2022). Salt stress increases H3K4me3 and reduces H3K9me2 levels at the salt-responsive transcription factor genes such as *RD29A, RD29B, COLD-REGULATED 15A* (*COR15A*) and *COR15B* in plants (Shen et al., 2022; Song et al., 2012). Moreover, genome-wide analysis shows that salt stress leads to more than 4000 genes with H3K4me3 changes in *Arabidopsis*, and these changed H3K4me3 genes are most enriched in the category of response to abiotic stress, indicating that H3K4me3 plays essential roles in
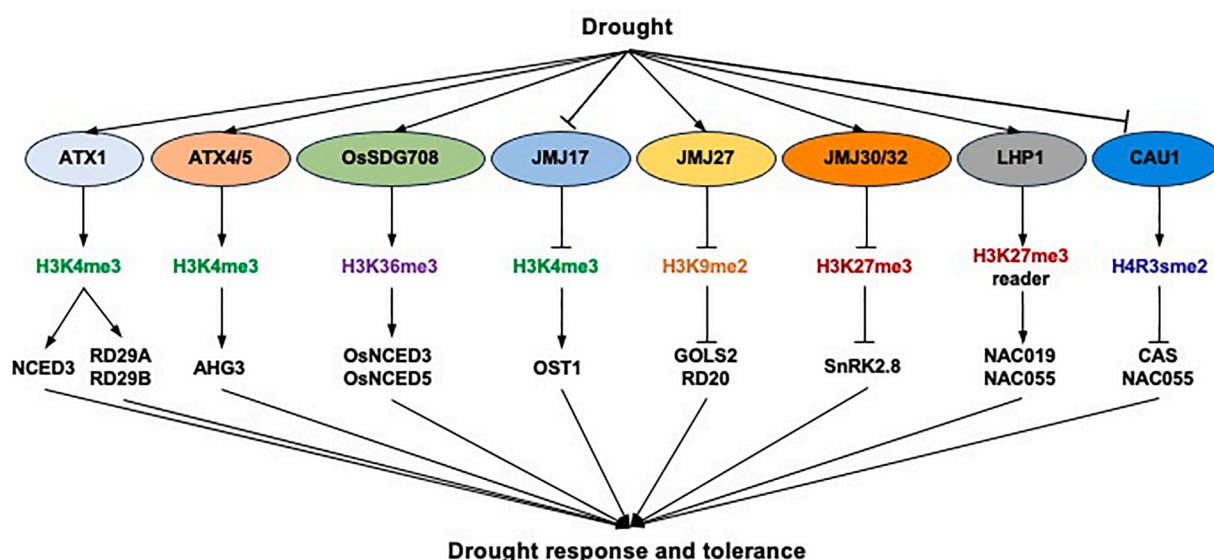

Fig. 2. Histone methylation/demethylation regulation of drought stress response. Drought stress induces the expression levels of drought-responsive genes like RD29A, RD29B, NCED3 by regulating H3K4me3 via ATX1. ATX4/5 also promote transcription of AHG3 by increasing H3K4me3 level. OsSDG708 functions as a positive regulator of drought tolerance by regulating H3K36me3 on ABA biosynthesis genes OsNCED3 and OsNCED5. Histone demethylase JMJ17 involves in drought stress response by demethylating H3K4me3 on OST1, thereby inhibiting its transcript level and affecting stomatal closure. JMJ27 positively regulates drought-stress responses through demethylating H3K9me2 on GOLS2 and RD20. JMJ30/32 function redundantly in ABA-dependent growth arrest through activating SnRK2.8 by demethylating H3K27me3. LHP1 negatively regulates drought tolerance process via transcriptional repression of NAC family transcription factors, NAC019 and NAC055. Drought stress decreases the accumulation of CAU1 protein and then derepresses the stress-related genes NAC055 and CAS by regulating H4R3sme2 levels. Thus, cau1 mutants display increased drought tolerance and stomatal closure.

transcriptional regulation under the salt stress (Shen et al., 2022). Similarly, salinity treatment in soybean induced dramatic alterations of H3K4me3 and H3K4me2 on many genes, which coordinately mediated ion homeostatsis and cell wall modification (Yung et al., 2022). In addition, variation in methylation levels of H3K4me3 and H3K27me3 were shown at the salt responsive gene *OsBZ8* locus in salt-tolerant rice varieties Nonabokra and salt-sensitive rice varieties IR64 (Paul et al., 2017). *RADIALIS-LIKE SANT* (*RSM1*), a MYB transcription factor involved in ABA-mediated salt stress response, was transcriptionally regulated by the balance of H3K4me3 and H3K27me3 in castor bean (Han et al., 2020). These observations evidently established the essential roles of histone methylation in modulating salt stress response and imparting stress tolerance in plants.

Histone methylation/demethylation enzymes have also been reported to involve in salt stress response. *HIGH-AFFINITY K$^+$ CHANNEL* (*HKT*), encoding the plant Na$^+$ transporter, is a salt tolerance determinant which coordinates with salt overly sensitive pathway (Rus et al., 2001). The *HKT1* is highly enriched with H3K27me3 in its gene body and the activation of *HKT1* under salt stress is due to the removal of H3K27me3 (Sani et al., 2013). *OsHKT1;5* mediates Na$^+$ transport in rice and its expression is regulated by a SET DOMAIN GROUP protein SDG721 via modulating H3K4me3 level (Liu et al., 2021). Moreover, *Arabidopsis* H3K4me3 demethylase, JMJ15, has been shown to involve in salt stress. Gain-of-function *jmj15* mutants exhibited increased tolerance to salinity stress (Shen et al., 2014). Further study showed that JMJ15 was directly bound to the negative salt-stress regulators, *WRKY46* and *WRKY70*, and repressed their expression by demethylating H3K4me3 (Shen et al., 2022). Moreover, some *JMJ* genes were induced by salt treatment in rice and cotton. When these *JMJ* members were overexpressed in yeast cells, they were found to greatly improve salt tolerance, also indicating that these *JMJ* demethylases function in salt stress response (Chowrasia et al., 2018; Sun et al., 2021). In soybean, CCCH zinc-finger protein GmZF351 is an oil level regulator and overexpression of GmZF351 confers stress tolerance. The expression of GmZF351 is regulated by GmJMJ30-1/2 via reduction of H3K27me3

level, and thus overexpression of *GmJMJ30-1/2* in transgenic hairy roots improves salt stress tolerance (Wei et al., 2023). In addition, GmPHD6 is a histone reader which recognizes H3K4me0/1/2 in soybean. It has been reported that GmPHD6 specifically affects the transcription of some salt-tolerance genes including *GmCYP75B1* and *GmCYP82C4* (Wei et al., 2017). Taken together, these findings suggest that histone methylation plays important roles in salt stress response and tolerance (Fig. 3).

4. Histone methylation in high temperature stress

As a consequence of global warming, plants have to face more acute and more frequent high-temperature stress. High-temperature stress adversely affects cellular events such as photosynthesis, cell membrane integrity, and ROS signaling, thereby limiting plant growth and production. The transcriptional network involving heat stress response and thermotolerance in plants has been elucidated, of which heat shock transcription factors (HSFs) and heat shock proteins (HSPs) play crucial roles in this process (Huang et al., 2022; Ohama et al., 2017). Recent studies have shown that the expression of heat stress-induced genes is correlated with changes in histone methylation (He et al., 2021). For example, heat stress induces the accumulation of H3K4me3 on *HSP18, HSP22, HSP70* and *ASCORBATE PEROXIDASE 2* (*APX2*) genes (Lamke et al., 2016). Histone lysine methyltransferases and demethylases are also required for heat stress response and tolerance. *SDG25* and *ATX1*, H3K4 methyltransferases, are up-regulated during heat stress. Mutations of *SDG25* and *ATX1* showed the decreased H3K4me3 level, the reduced heat stress gene expression, and more sensitive to heat stress (Song et al., 2021). Histone demethylases JMJ proteins also participate in heat acclimation. *Arabidopsis* histone H3K27 demethylases, JMJ30/JMJ32/REF6/ELF6, function redundantly in sustained H3K27me3 demethylation at *HSP22* and *HSP17.6* loci in response to heat stress (Yamaguchi et al., 2021). Thermomorphogenesis is a particular response to ambient high temperatures in plants, including a suite of morphological adaptations such as upward leaf movement, hypocotyl and petiole elongation, and formation of thinner leaves (Quint
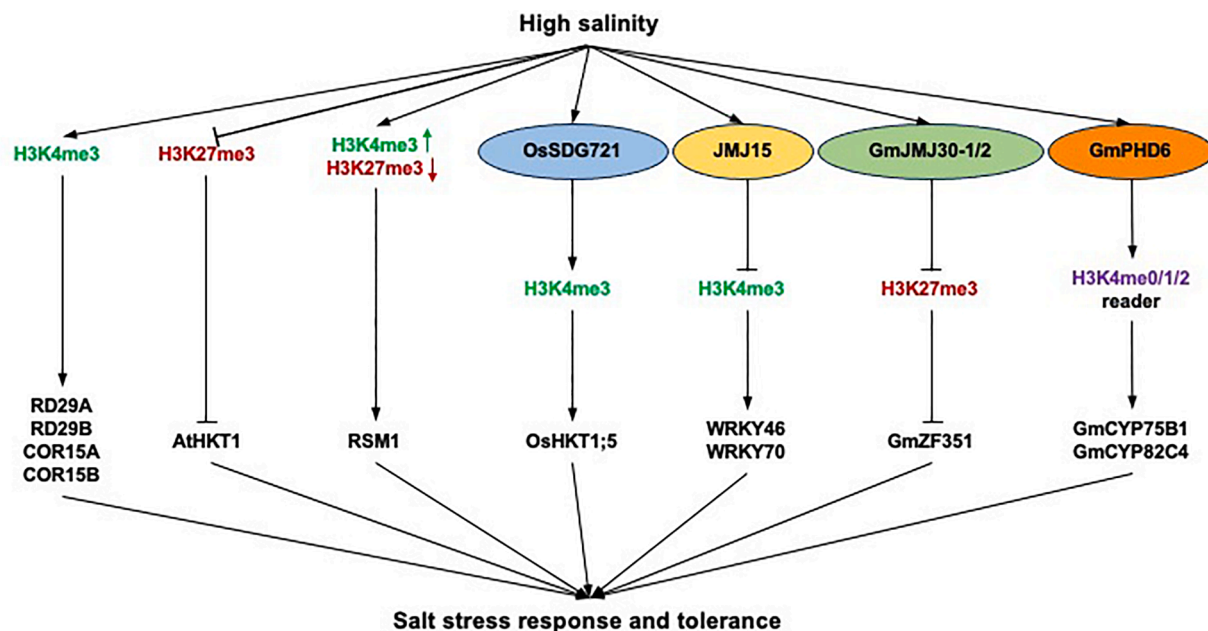
Fig. 3. Role of histone methylation in the plant response to high salinity stress. Salt stress induces the expression levels of responsive genes such as RD29A, RD29B, COR15A and COR15B via elevating the H3K4me3 levels in Arabidopsis. Salt stress decreases the H3K27me3 level on HKT1 gene, thereby derepressing its expression in Arabidopsis. In castor bean, the transcript level of salt-responsive regulator RSM1 is controlled by the the balance of H3K4me3 and H3K27me3. Rice histone methyltransferase OsSDG721 is induced by salt treatment. OsSDG721 subsequently increases the H3K4me3 level at Na$^+$ transporter OsHKT1;5 to elevate its expression. Arabidopsis JMJ15 positively regulates salt tolerance process at least partially via demethylating H3K4me3 at the negative stress regulators WRKY46 and WRKY70. Soybean GmJMJ30-1/2 involve in salt stress by demethylating H3K27me3 at oil level regulator GmZF351. Soybean GmPHD6 recognizes H3K4me0/1/2 and regulates the transcription of the salt-tolerance genes CYP75B1 and CYP82C4.

et al., 2016). JMJ14 functions redundantly with JMJ15 and JMJ18 in the plant response to ambient high temperature (Cui et al., 2021). During the plant thermosensory process, JMJ14 and JMJ15 regulate the transcription of high temperature-repressed genes by demethylating H3K4me3, such as *sugar transporter 14* (*STP14*), *phytochrome kinase substrate 4* (*PKS4*), *dormancy/auxin associated family protein* (*DRM2*), zinc finger homeodomain 1 (*ZFHD1*). Thus, JMJ14/15/18 are positive regulators in ambient high temperature-mediated changes in gene expression and thermomorphogenesis (Cui et al., 2021). The auxin biosynthetic enzyme, YUCCA8 (YUC8), is critical for thermomorphogenesis in plants. The RNA binding protein FLOWERING CONTROL LOCUS A (FCA) is recruited to and triggers H3K4me2 demethylation at the chromatin of *YUC8* loci during exposure to ambient high temperature. Therefore, FCA mediates thermal adaptation partially through attenuating *YUC8* expression (Lee et al., 2014). REF6 also involves in thermomorphogenesis. The loss-of-function mutants of *REF6* exhibit reduced hypocotyl elongation and inefficiently induced genes with high levels of H3K27me3 at the loci of *GIBBERELLIN 20-OXIDASE 2* (*GA20ox2*) and *BASIC HELIX-LOOP-HELIX 87* (*bHLH87*) under ambient high temperature. Therefore, REF6 may control thermomorphogenesis through demethylating H3K27me3 and upregulating genes of *GA20ox2* and *bHLH87* (He et al., 2022). Furthermore, H3K36me3 is involved in modulating ambient high temperature-induced alternative splicing and temperature-dependent flowering time control (Pajoro et al., 2017). In addition, the ATP-dependent chromatin remodeling factor, PICKLE (PKL), is reported to participate in thermomorphogenesis (Zha et al., 2017). *PKL* expression is induced in response to ambient high temperature, while *pkl* mutant seedlings reduce sensitivity in hypocotyl elongation at high temperature. Furthermore, PKL affects H3K27me3 levels

and gene expression levels of auxin-responsive genes *IAA19* and *IAA29*. Thus, PKL may control plant growth in response to high temperature through modulating H3K27me3 levels on the auxin-responsive genes (Zha et al., 2017). As summarized in Fig. 4, the findings above suggest the important roles of histone methylation in heat stress response and thermomorphogenesis.

5. Histone methylation in cold stress

Cold stress is an environmental factor that limits the geographical distribution, affecting the crop productivity and quality. Plants occur many physiological and molecular changes to cold adaption. The C REPEAT BINDING FACTOR (CBF) transcription factors are rapidly induced by cold stress and then activate COLD RESPONSIVE (COR) gene expression (Kidokoro et al., 2022). It has been shown that histone methylation involves in transcriptional regulation of genes in response to cold stress in plants (Banerjee et al., 2017; Hereme et al., 2021; Kidokoro et al., 2022). During exposure to cold temperature, H3K27me3 levels in cold responsive genes, *COR15A* and *galactinol synthase 3* (*GOLS3*), decreased in *Arabidopsis* (Kwon et al., 2009). PKL is also found to participate in CBF-dependent cold stress response (Yang et al., 2019). The mutants of *PKL* showed more sensitive to chilling and cold stress treatment. Moreover, defect of PKL led to downregulation of *CBF3*, as well as its downstream *COR15A, COR15B* and *RD29A* genes under cold stress, indicating the positive roles of PKL in cold stress (Yang et al., 2019). Vernalization response is a process that plants have evolved to cope with low temperature stress. During vernalization, the floral repressor locus *FLOWERING LOCUS C* (*FLC*) is epigenetically silenced mainly through POLYCOMB REPRESSIVE COMPLEX 2 (PRC2)
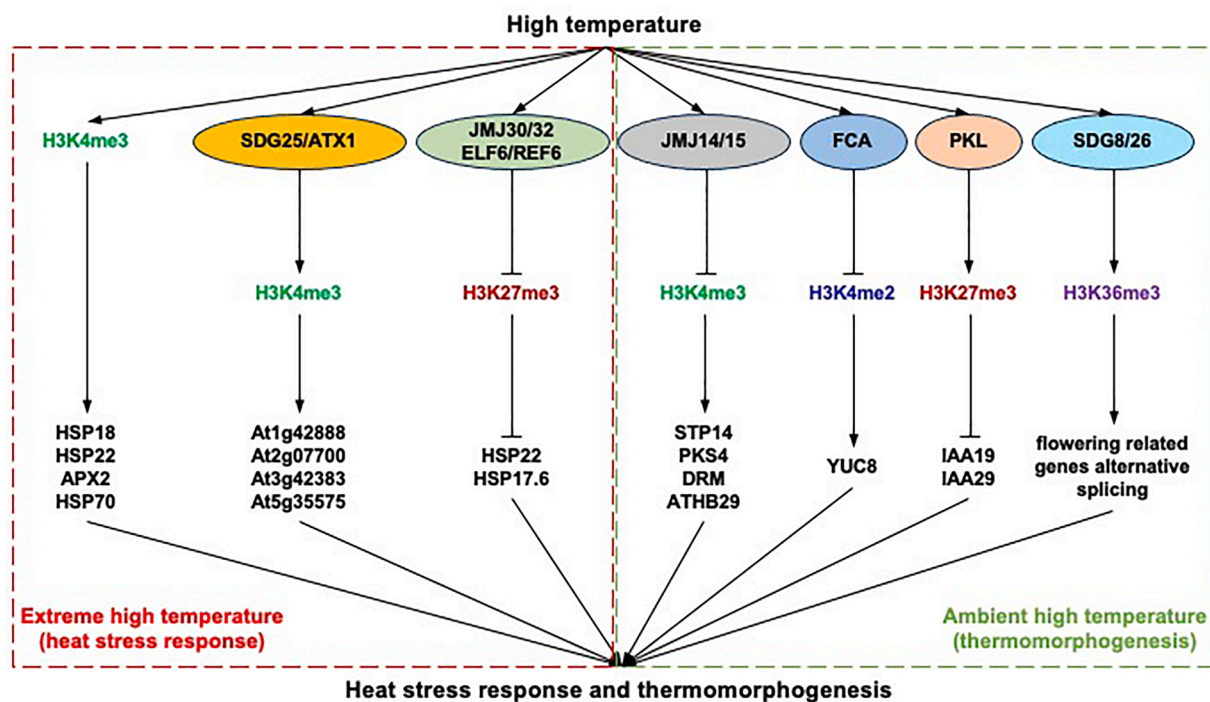
Fig. 4. Role of histone methylation in the plant response to high temperature. Heat stress induces the expression of heat responsive genes such as HSP18, HSP22, HSP70 and APX2 by regulating H3K4me3. H3K4 methyltransferases SDG25 and ATX1 are induced by heat stress, and subsequently increase the H3K4me3 levels in some target genes. JMJ30/JMJ32/REF6/ELF6, function redundantly in sustained H3K27me3 demethylation at HSP22 and HSP17.6 loci in the response to heat stress, thus poising both genes for subsequent activation. JMJ14/15 act redundantly as positive regulators in thermomorphogenesis via demethylating H3K4me3 at the high temperature-repressed genes during the plant thermosensory process. FCA mediates hypocotyl elongation at ambient high temperatures partially through demethylaing H3K4me2 and attenuating the expression of YUC8. REF6 also involves in thermomorphogenesis through demethylating H3K27me3 and upregulating expression of GA20ox2 and bHLH87 at ambient high temperature. High temperature induces PKL expression. PKL regulates H3K27me3 levels on auxin-responsive genes IAA19 and IAA29, and thus controls thermosensory hypocotyl elongation. Ambient high temperature leads to the deposition of H3K36me3 on flowering-related genes such as Flowering Locus M (FLM) and MADS Affecting Flowering 2 (MAF2), then affecting high temperature-induced alternative splicing and flowering time.

increasing H3K27me3 levels (Yang et al., 2017). Transcriptional repression of *FLC* also correlates with decreased levels of H3K36me3 and H3K4me3 in *Arabidopsis* (Yang et al., 2014), indicating that histone methylation is required for cold-induced epigenetic switch at *FLC*. In potato, cold stress affects the bivalent arrangement of H3K4me3 and H3K27me3 of active genes (Zeng et al., 2019). In rice seedlings, the most chromosomes exhibited a decrease in H3K27me3 and an increase in H3K27ac peaks on the responsive genes such as *OsDREB1A* and *OsDREB1B* during cold stress treatment (Dasgupta et al., 2022). Histone methyltransferases/demethylases are also reported to involve in plant cold stress process. For example, MtJMJC5, the JMJ30/JMJD5 ortholog in *Medicago truncatula*, revealed circadian oscillation and reversible cold-induced alternative splicing, indicating that MtJMJC5 may act in epigenetic regulation of the link between the circadian clock and cold stress response in *Medicago* (Shen et al., 2016b). Together, these findings suggest that histone methylation is a critical factor affecting cold stress responses in plants (Fig. 5).

6. Role of histone methylation in abiotic stress memory

In the natural environments, plants often face recurrent unfavorable environmental conditions. To cope with recurrent stress, plants have developed the ability to remember the adverse conditions and prepared to adapt to the same adversity more rapidly and effectively (Avramova, 2015). Recent studies have shown that histone methylation plays vital roles in the establishment of plant stress memory (Ding et al., 2012; Friedrich et al., 2019; Lamke and Baurle, 2017; Lamke et al., 2016). H3K4me3, the active marker of gene expression, is often associated with transcriptional memory at several abiotic stress-responsive genes. For example, the H3K4me3 level at the dehydration memory genes accumulates and lasts for a period after the dehydration seizes (Ding et al., 2012). It is also found that the H3K4me3 level at these memory trained genes is higher than that in untrained genes after repeated drought stress treatments (Ding et al., 2012), indicating that H3K4me3 participates in maintaining the drought stress memory. Similarly, Δ^1-*pyrroline-5--carboxylate synthetase 1* (*P5CS1*) encodes a proline biosynthetic enzyme, the expression of which is induced by primary salt stress, reduced to basal level during the recovery, and more induced by reoccurring salt stress. Further studies showed that salt-induced transcriptional memory of *P5CS1* is related to the maintenance of enhanced H3K4me3 level at *P5CS1* locus during the recovery stage after salt stress (Feng et al., 2016). Additionally, the accumulation of H3K4me2/3 is observed in heat stress-primed plants (Lamke et al., 2016; Liu et al., 2018). The heat memory genes displayed H3K4 hypermethylation that sustained for several days after the heat seized (Lamke et al., 2016; Liu et al., 2018). And the high level of H3K4 methylation was connected with hyper-induction of gene expression under the reoccurring heat stress. Together, these observations suggest that H3K4me3 may be a general machinery for stronger reactivation of abiotic stress memory genes upon the reoccurring stress. Recently, H3K27me3 is also reported to associate with transcriptional memory for abiotic stress (Yamaguchi et al., 2021). For instance, it is observed that the sustained removal of H3K27me3 at *HSP22* and *HSP17.6C* loci in plants primed by heat stress, poising both *HSP* genes for subsequent activation (Yamaguchi et al., 2021). It is also found that H3K27 demethylases JMJ30/JMJ32/REF6/ELF6 function redundantly in removing H3K27me3 at the heat memory genes in plants (Yamaguchi et al., 2021). Similarly, cold stress triggered the decrease of H3K27me3 abundance in responsive genes such as *COR15A* and *GOLS3*, and this decrease was maintained for a few days after plants returned to normal conditions, suggesting that H3K27me3 serves as a memory marker for cold stress (Kwon et al., 2009). In addition, *FLC* is mainly transcriptionally repressed by recruiting PRC2 to increase H3K27me3 during vernalization and this repression is maintained when temperature rises, suggesting that PRC2-mediated H3K27me3 are required for
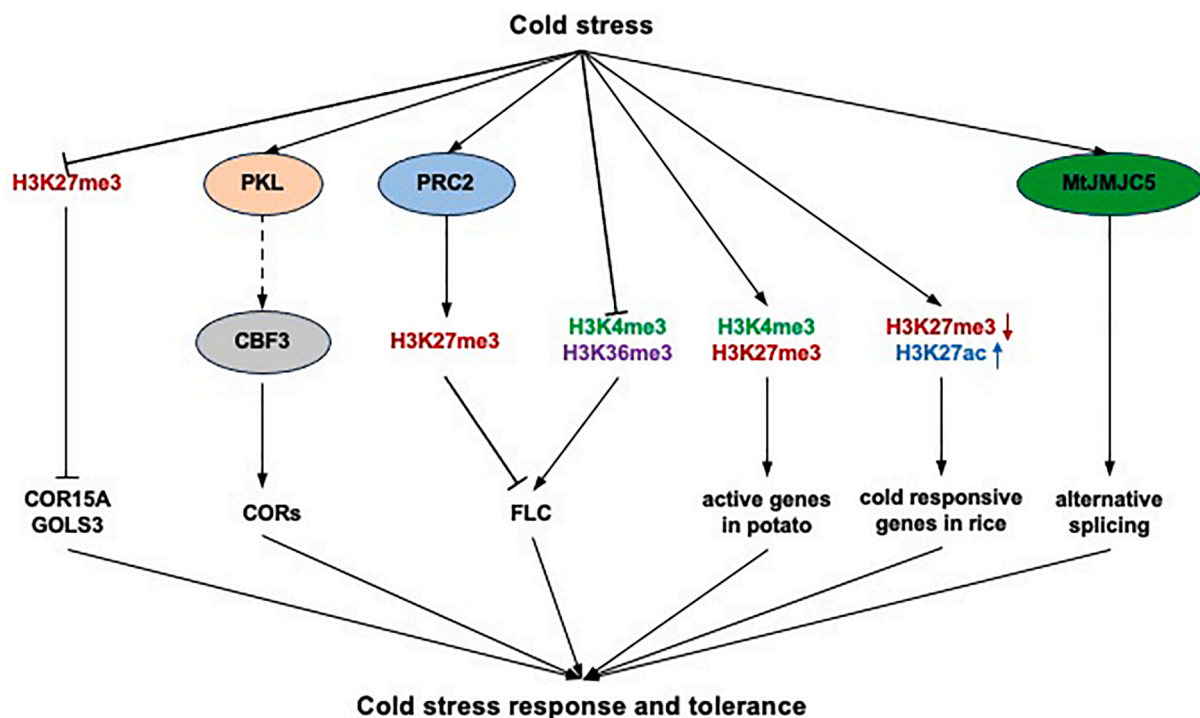

Fig. 5. Histone methylation/demethylation regulate cold stress response in plants. Cold stress suppresses H3K27me3 levels at the cold responsive genes, such as *COR15A* and *GOLS3*. PKL participates in CBF-dependent cold stress response in *Arabidopsis*. In *pkl* mutants, the expression levels of *CBF3*, as well as its downstream COR family genes *COR15A*, *COR15B* and *RD29A*, are downregulated under cold stress. *FLC* is silenced mainly through PRC2 via increasing H3K27me3 levels. Transcriptional repression of *FLC* also correlates with decreased levels of H3K36me3 and H3K4me3. In potato, cold stress induces enhanced chromatin accessibility and bivalent histone modifications H3K4me3 and H3K27me3 of active genes. In rice, cold stress leads to a decrease in H3K27me3 and an increase in H3K27ac on responsive genes. *MtJMJC5* showed reversible cold-induced alternative splicing, indicating that MtJMJC5 involves in cold stress response in *Medicago*.

cold stress memory (Gao et al., 2023; Yang et al., 2017). Another study showed that salt priming changed the epigenomic landscape, leading to a shortening and fractioning of H3K27me3 islands (Sani et al., 2013). Priming induced 'etching' of H3K27me3 islands may affect the expression of genes, such as Na$^+$ transporter *HKT1*. Then *HKT1* responds more strongly and effectively in the primed plants upon the recurrent salt stress (Sani et al., 2013). Therefore, histone methylation, in particular H3K4me3 and H3K27me3, confer plant transcription memory of abiotic stresses.

7. Metabolic regulation of histone methylation in abiotic stress

Under abiotic stress, plants adjust metabolic activities to adapt stressful environment. Histone methylation/demethylation enzymes require primary metabolic intermediates such as S-adenosyl-methionine (SAM) or alpha-ketoglutarate (α-KG) as substrates or cofactors. The levels of these key metabolites are strongly affected by stress and growth conditions in plants. Therefore, the interplay between histone

methylation dynamics and metabolic activity controls plant response to abiotic stress (Lu et al., 2023; Shen et al., 2016a). Histone methyltransferases utilize SAM as the methyl group donor. SAM is synthesized from methionine by SAM synthetases (SAMS) and converted to S-adenosylhomocysteine (SAH) after serving as a methyl donor. Several studies have shown that the SAM biosynthesis and metabolism affect histone methylation in plants (Fig. 6) (Meng et al., 2018). For instance, methionine adenosyltransferase 4 (MAT4)/SAM synthetase 3 (SAMS3) catalyzes the synthesis of SAM in *Arabidopsis*. Mutations of *MAT4/-SAMS3* decrease the level of CHG and CHH DNA methylation and H3K9me2 (Meng et al., 2018). Similarly, Methionine Synthase 1 (ATMS1) and homologous gene silencing 1 (HOG1) catalyze the synthesis of methionine and the transformation of SAH to homocysteine (Hcy) in *Arabidopsis*, respectively. Mutations of *ATMS1* and *HOG1* cause a significant decrease in the ratio of SAM/SAH, resulting in the decreased levels of DNA methylation and H3K9me2 (Yan et al., 2019). In mammalian and nematode cells, it has been reported that stresses disrupt methionine metabolism, thereby lowering intracellular levels of
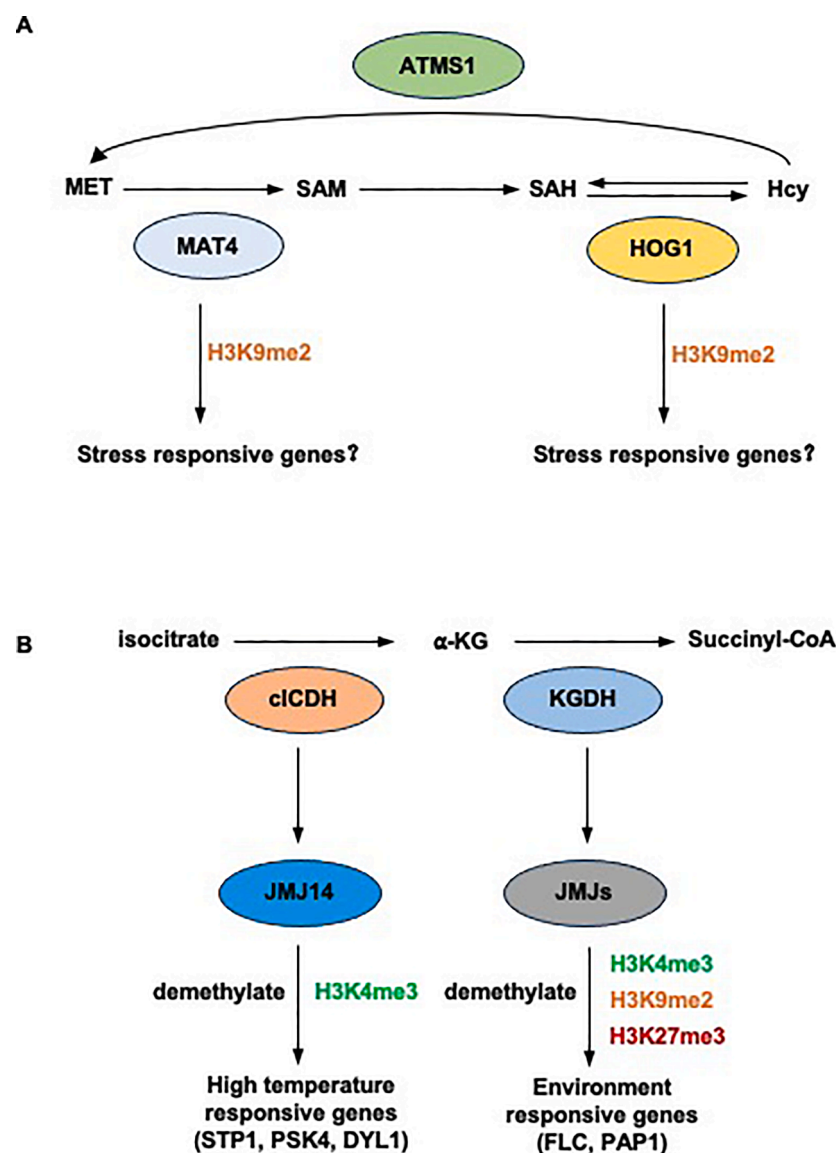

Fig. 6. Metabolic control of histone methylation/demethylation in plant response to abiotic stress. A. SAM is utilized as the methyl group donor for histone methylation. The homeostasis of SAM is regulated by ATMS1, MAT4 and HOG1 in *Arabidopsis*. The mutations of ATMS, MAT4 and HOG1 reduce the level of H3K9me2 in plants. B. α-KG associated enzymes interact with JMJs to control gene expression in plant response to abiotic stress. cICDH catalyzes isocitrate to α-KG in cytosol. The absence of cICDH upregulates H3K4me3 level and enhances JMJ14 mutation defect in the plant response to high temperature stress. KGDH catalyzes α-KG to succinyl-CoA. KGDH regulates histone demethylation and the expression of environment responsive genes by affecting JMJs activity.

SAM and resulting in loss of the selective histone methylation which may misregulate stress-related genes and impair stress response (Bian et al., 2020; Ding et al., 2018; Roy et al., 2020; Yu et al., 2019). In plants, this aspect remains to be explored, especially the alteration of abiotic stress in SAM metabolism, the sensitivity of histone methyltransferases to SAM level, and the regulatory function of SAM in histone methylation.

JmjC histone demethylases require α-KG for their demethylase activity. In plants, α-KG is produced by isocitrate dehydrogenases (IDHs) in different metabolic pathways (Nunes-Nesi et al., 2013). Loss of the *cytosolic IDH* (*cICDH*) results in decreased α-KG levels, subsequently upregulating H3K4me3 by influencing the activity of histone demethylase JMJ14 (Cui et al., 2021). The H3K4me3 alteration in *cICDH* and *JMJ14* mutants affect the expression of stress-responsive genes in plant thermosensory response, indicating that H3K4 demethylases coordinating primary metabolic intermediate α-KG, involve in the plant response to high temperature (Cui et al., 2021). In the tricarboxylic acid (TCA) cycle, α-KG is decarboxylated oxidatively by a-ketoglutarate dehydrogenase (KGDH) in plants (Nunes-Nesi et al., 2013). A more recent study has revealed that *Arabidopsis* KGDH enters the nucleus and regulates the activities of JMJ demethylases (Huang et al., 2023). Nuclear KGDH reduces local α-KG concentration and interacts with various JMJs, thus inhibiting histone demethylation to regulate expression of genes, including some environmental stress responsive genes such as cold responsive gene *FLC* and stress-responsive MYB-domain transcription factor *PAP1* (Huang et al., 2023). These results illustrate that metabolic enzymes function together with JMJs to control histone demethylation and gene expression in plant response to abiotic stress (Fig. 6).

8. Conclusions and perspectives

Abiotic stress threatens the the growth, development and productivity of plants during their life cycles. To properly adapt to the stressful conditions, epigenetic changes are widely involved in plant responses to abiotic stresses. In this review, we discussed the mechanisms underlying the dynamic regulation of histone methylation in plant response to stress. As summarized above, a plethora of stress-responsive genes have been shown the dynamic changes in histone methylation, which modulate them activated or repressed during abiotic stress treatment. Several histone methylation/demethylation enzymes have been found to participate in various abiotic stress responses. Despite a great number of studies concerning this field, the comprehensive regulatory mechanism of histone methylation in plant response to abiotic stress is far from elucidated. What histone methylation regulators are involved in each different abiotic stress is unclear. How histone methylation enzymes are appropriately recruited to target loci under different abiotic stresses is poorly understand. The mechanism of abiotic stress memory is of great interest to explore further, such as the persistence of histone methylation during the memory phase after stress treatment and the role of histone methylation in transmission of stress memory to the next generation. As sessile organisms, plants possess highly dynamic cellular metabolism, signaling pathways and biological activities in response to environmental stresses. Metabolic fluctuations affect the activity of histone methylation enzymes and histone methylation landscape. How histone methylation integrating cellular metabolism modulates the response to abiotic stress in plants needs to be addressed. Since the chromatin status is controlled by complex epigenetic regulations, the crosstalk between histone methylations with other chromatin modifications to either solidify or overturn its effect on transcription, genome accessibility or chromatin topology during the abiotic stress also requires further investigation. For example, histone variants, histone acetylation and chromatin remodeling factors have also been reported to regulate thermoresponsiveness. How histone methylation interplays with other epigenetic modifications during transcriptional regulation under high temperatures needs to be considered in future research. Recent development of new technologies such as high-throughput sequencing technology and single cell-omics techniques including high-throughput chromosome conformation capture (Hi-C), *in-situ* Hi-C followed by chromatin immunoprecipitation (HiChIP), single cell RNA-sequencing (scRNA-seq), scChIP-seq, scATAC-seq, scHi-C, etc. are driving discoveries of molecular mechanisms of epigenetic regulation in plant adaption to abiotic stress. Further studies on plant epigenetic regulation will facilitate the breeding of cultivars with enhanced tolerance to abiotic stress, as well as contribute to the improvement of biomass and grain yield.

CRediT authorship contribution statement

Lei Shi: Conceptualization, Writing – original draft. **Xiaoyun Cui:** Writing – original draft, Writing – review & editing. **Yuan Shen:** Conceptualization, Writing – original draft, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.stress.2023.100303.

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