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Histone modifications and chromatin remodelling in plants in response to salt stress

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Abstract

In the face of global food security crises, it is necessary to boost agricultural production. One factor hampering the attempts to increase food production is elevated soil salinity, which can be due to salt that is naturally present in the soil or a consequence of excessive or prolonged irrigation or application of fertiliser. In response to environmental stresses, plants activate multiple molecular mechanisms, including the timely activation of stress-responsive transcriptional networks. However, in the case of salt stress, the combined effects of the initial osmotic shock and the subsequent ion-specific stress increase the complexity in the selective regulation of gene expressions involved in restoring or maintaining osmotic balance, ion homeostasis and reactive oxygen species scavenging. Histone modifications and chromatin remodelling are important epigenetic processes that regulate gene expressions by modifying the chromatin status and recruiting transcription regulators. In this review, we have specifically summarised the currently available knowledge on histone modifications and chromatin remodelling in relation to plant responses to salt stress. Current findings have revealed the functional importance of chromatin modifiers in regulating salt tolerance and identified the effector genes affected by epigenetic modifications, although counteraction between modifiers within the same family may occur. Emerging evidence has also illustrated the crosstalk between epigenetic modifications and hormone signalling pathways which involves formation of protein complexes. With an improved understanding of these processes, plant breeders will be able to develop alternative strategies using genome editing technologies for crop improvement.

1 | INTRODUCTION

Salt stress is a major abiotic stress that negatively impacts agricultural production. A recent study reported a consistent estimation that around 1 billion hectares of land in the world was affected by soil salinity (Ivushkin et al., 2019). From 1992 to 2013, salinity led to a loss in agricultural production of more than 120 trillion kilocalories per year (Russ et al., 2020). The osmotic component of salt stress reduces water uptake, leading to the inhibition of photosynthesis and plant growth (Flowers et al., 2015; van Zelm et al., 2020). Accumulation of sodium and chloride ions induces cytotoxicity and perturbs metabolism (Flowers et al., 2015, van Zelm et al., 2020).

Plants develop multiple cellular and molecular mechanisms for adaptation to salt stress, which include activation of transport systems, metabolic adjustment and modulation of transcriptional responses (van Zelm et al., 2020). While transcriptional reprogramming is primarily regulated by transcription factor networks, emerging evidence has demonstrated that epigenetic modifications of

the chromatin present another level of regulation. In eukaryotes, the nucleosome is the basic unit of chromatin. DNA is wrapped around the histone octamers composed of two copies of each of the core histones, H2A, H2B, H3 and H4, to form a nucleosome. In addition to the canonical histone proteins, histone variants can be incorporated to form nucleosomes at different genomic regions according to their functions (Armeev et al., 2019; Martire & Banaszynski, 2020). Under salt stress, the packaged DNA harbouring stress-responsive genes is expected to be made accessible to the protein factors or complexes to facilitate transcription. In the nucleosomal context, the accessibility of a DNA region can be modulated by post-translational modifications (PTMs) on the histone proteins as well as the chromatin-remodelling complexes that regulate nucleosome assembly and spacing (Clapier et al., 2017; Hargreaves & Crabtree, 2011; Lusser & Kadonaga, 2003).

The protruding N-terminal tails of the core histone proteins contain extensive numbers of amino acid residues which are subjected to covalent modifications. For example, the acetylation of lysine residues neutralises the positive charge and reduces the electrostatic interaction between DNA and histones, thus loosening the DNA packing and allowing the transcription machinery to gain access to the targeted DNA region (Bannister & Kouzarides, 2011). Besides, modified histones are recognised by other proteins such as the ATP-dependent chromatin remodelers to further modify local chromatin status or regulate gene expression (Clapier et al., 2017; Oliver & Denu, 2011). The deposition of histone variants also influences nucleosome stability and interactions with mRNA processing factors (Martire & Banaszynski, 2020).

In this article, the progress in deciphering the transcriptional regulation by histone modifications and chromatin remodelling in plant responses to salt stress are reviewed (Figure 1). While the significance of these mechanisms in regulating salt tolerance was revealed by genetics or chemical inhibition experiments, synergistic or antagonistic relationships were also present between members of different protein families. Therefore, integrating the available knowledge is necessary to dissect the interactions between the regulatory pathways. In addition, analyses of global chromatin status in recent studies have enabled the examination of dynamic fluctuations and persistent marks linked to salt stress responses, which provide clues for the consequences of the complex interactions. By combining the available working models, we have uncovered the subtle relationships between epigenetic components and hormone signalling pathways, which address the potential factors underlying the indirect effects of epigenetic mechanisms on regulating salt stress response. As most of the findings are focused on the model plant *Arabidopsis thaliana*, more efforts are needed to identify targets for selection and modification by genome-editing techniques to improve salt tolerance in crops.

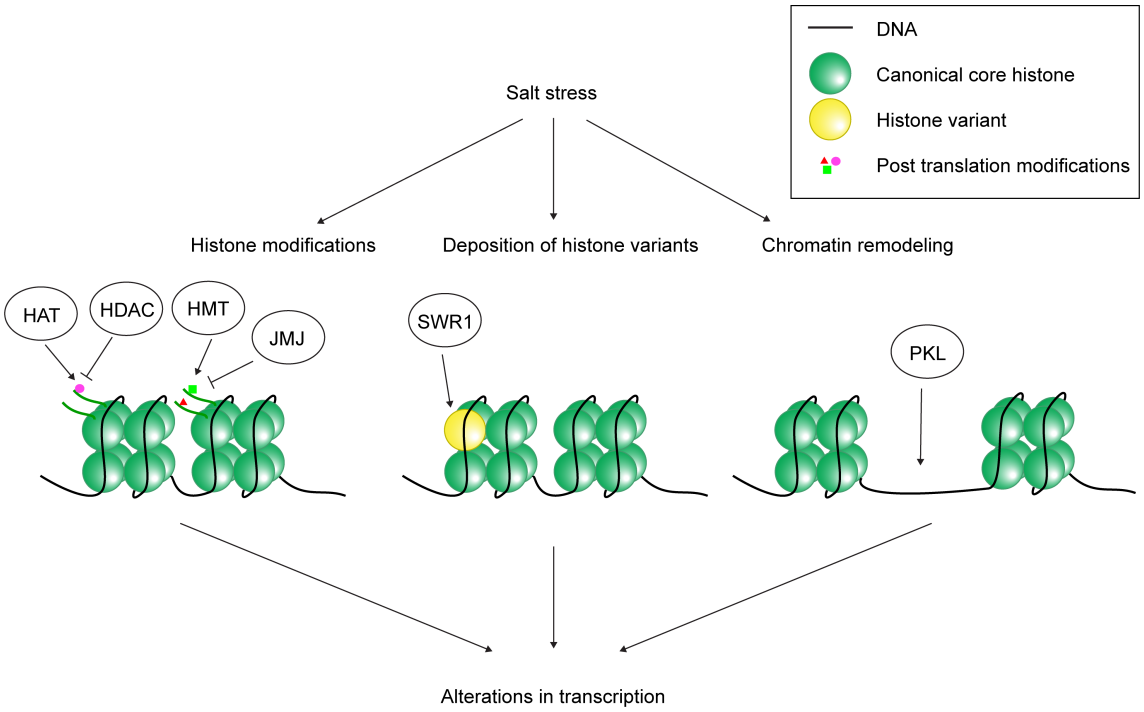

FIGURE 1 A schematic diagram of epigenetic mechanisms at the nucleosomal level in plant responses to salt stress. Under salt stress, alterations in various histone modifications were documented. For example, histone acetyltransferases (HAT) and histone deacetylases (HDAC) determine the level of acetylation (pink dot) of histone proteins. Histone methyltransferase (HMT) and demethylase (represented by JUMONJI domain-containing protein, JMJ) regulate the level of methylation (green square). It should be noticed that alternations in other histone modifications such as methylglyoxalation, phosphorylation and ubiquitination (represented by red triangle for simplicity) are also involved in salt stress response. Histone variants such as H2A.Z (yellow sphere) are deposited by the SWI2/SNF2-RELATED 1 (SWR1) complex. In addition, the chromatin-remodelling factor, PICKLE (PKL), modulates the accessibility of DNA to other transcriptional regulators, leading to alterations in gene expression

2 | HISTONE MODIFICATIONS AND THEIR ROLES IN PLANT RESPONSES TO SALT STRESS

The PTMs of histone proteins, which include, but are not limited to, acetylation, methylation, ubiquitination and phosphorylation, may alter gene expressions by restructuring chromatin or recruiting specific regulatory proteins. Regarding their roles in regulating gene expressions, most of the histone acetylations have been demonstrated to be involved in transcriptional activation (Allis & Jenuwein, 2016). One hypothesis is that acetylation reduces the interactions between histones and DNA and relaxes the chromatin structure, resulting in increased accessibility to the DNA (Allis & Jenuwein, 2016). Transcriptional regulation is also facilitated by different types of histone methylation, which act by changing the association between histone proteins and DNA, thus influencing the chromatin structure (Xiao et al., 2016). For example, H3K9me2 (histone H3 lysine 9 dimethylation) established by SUPPRESSOR OF VARIEGATION 4/5/6 (SUVH4/5/6) is essential in maintaining DNA methylation at the heterochromatin regions in *A. thaliana* (Du et al., 2012; Zhang et al., 2018). Additionally, the ubiquitination at histone H2A and H2B is linked to transcriptional repression and activation, respectively (Zhou et al., 2017). Numerous studies have reported that these marks are involved in flowering, seed development, nitrogen fixation, biotic and abiotic stress responses (Cao et al., 2008; Huang et al., 2016; Wang et al., 2020; Zhou et al., 2017; Zou et al., 2014). In later sections, we will focus on the progress made in understanding the role of histone modifications in plants under salt stress.

2.1 | Functional studies of histone-modifying enzymes in response to salt stress

2.1.1 | Histone acetyltransferases

The histone acetyltransferase (HAT), GENERAL CONTROL NONDEREPRESSIBLE 5 (GCN5), was demonstrated to positively regulate salt tolerance in *A. thaliana* (Zheng, Liu, et al., 2019). Under salt stress, the *gcn5* mutant displayed inhibited growth and higher accumulation of sodium ions compared to wild type. As indicated by transcriptomic analyses, the group of salt stress-induced genes in wild type, which was repressed by the *gcn5* mutation under saline condition, included cell wall biosynthetic genes. In line with the reduced cellulose content, abnormal cell wall structure was observed in mutants exposed to salt stress. Further chromatin-immunoprecipitation experiments confirmed that GCN5 could bind to the cell wall synthesis genes *CHITINASE-LIKE 1* (*CTL1*), *POLYGALACTURONASE INVOLVED IN EXPANSION-3* (*PGX3*) and *MYB54*. Importantly, H3K9ac (histone H3 lysine 9 acetylation) and H3K14ac (histone H3 lysine 14 acetylation) levels were diminished in *gcn5* mutants under salt stress. Moreover, overexpressing *TaGCN5* from wheat could rescue the defect of *A. thaliana gcn5* mutants, suggesting that GCN5 is a conserved epigenetic regulator in the plant response to salt stress (Zheng, Liu, et al., 2019). Recently, TaGCN5 was also reported to target genes controlling hydrogen peroxide production, which was important for salt stress adaptation in wheat (Zheng et al., 2021). These studies around GCN5 reinforce its regulatory role in multiple aspects of salt tolerance mechanisms.

2.1.2 | Histone deacetylases

The majority of the functional analyses of histone-modifying enzymes in plants that respond to salt stress have focused on histone deacetylases (HDACs), which are classified into three major groups. Mutants of various members within the REDUCED POTASSIUM DEPENDENCY 3 (RPD3/HDA1) superfamily have been characterised to alter the sensitivity to salt stress in different species. Two members of the class I RPD3/HDA1-type HDAC, HDA6 and HDA19, were shown to have a positive role in salt tolerance in the ecotype Wassilewskija (Ws) of *A. thaliana* (Chen et al., 2010; Chen & Wu, 2010). The splicing mutant of *HDA6* (*axe1-5*), *HDA6*-RNAi and *hda19-1* plants had lower germination rates and/or survival rates at the seedling stage under salt treatment (Chen et al., 2010, Chen & Wu, 2010). Reduced gene expressions and H3K9K14ac levels of *DREB2A*, *RD29A* and *RD29B* were observed in *axe1-5* and *HDA6*-RNAi plants when compared to wild type, suggesting that HDA6 regulates the key molecular pathway of salt stress responses (Chen et al., 2010, Chen & Wu, 2010). However, it is surprising that the mutation in HDAC led to a reduction in H3K9K14ac. Further studies are needed to dissect the mechanisms by which HDA6 indirectly regulates the expression of those salt stress-responsive genes. Interestingly, a mutation in *HDA19* had opposite effects on salt sensitivity in the ecotype Columbia-0 (Col-0), in which the *hda19-3* mutant showed higher survival rates than the wild type under salt treatment. Enhanced expressions of the ABA signalling regulator *ABI5* and positive regulators of stress tolerance such as *ANAC019*, *P5CS1* and *LEA4_2*, were also observed in the *hda19-3* mutant (Ueda et al., 2017).

However, in rice, the overexpression of *HDA705*, which is the closest homologue to the *A. thaliana HDA6*, led to delayed germination under salt treatment when compared to wild type (Zhao et al., 2016). The knockout mutant of rice *HDA710*, which is the closest homologue to the *A. thaliana HDA19*, displayed a higher survival rate at the seedling stage. In addition to the global increase in the levels of acetylated H3 and H4 under normal condition, the increase in H4ac observed at the promoter and genic regions of rice Na^+/H^+ *EXCHANGER 1* (*OsNHX1*) was consistent with the enhanced gene expression under salt stress (Ullah et al., 2020).

In contrast to *HDA6*, the loss of a functional *HDA9* in *A. thaliana* resulted in reduced sensitivity to salt in seedlings, along with the up- and down-regulation of 47 and 13 drought response-associated genes, respectively, when under salt stress (Zheng et al., 2016). As expected, the differential gene expressions were positively associated with the changes in the H3K9ac level in the *hda9* mutants

(Zheng et al., 2016). Recently, HDA9 was found to deacetylate the histones associated with *WRKY53*, resulting in the inhibition of transactivation of this stress-responsive regulator. Interestingly, WRKY53 could also inhibit *HDA9*, and the mutation of these two genes had opposite effects on salt tolerance (Zheng et al., 2020). Overall, the findings in *A. thaliana* and rice suggest that different members within the class I RPD3/HDA1-type HDAC play different roles in regulating salt tolerance.

The role of the class II RPD3/HDA1-type HDACs in salt stress responses was characterised using a quadruple *hda5/14/15/18* mutant in *A. thaliana*, which showed a lower survival rate than wild type under salt stress when grown in a liquid medium (Ueda et al., 2017). In comparison to the more salt-tolerant *hda19-3* mutant under the same treatment condition, salinity triggered different sets of upregulated genes in these two mutants relative to the wild type as indicated by the transcriptomic analysis. Interestingly, the quintuple *hda5/14/15/18/19* mutant rescued the salt-sensitive phenotype of the quadruple mutant, suggesting that the overall class II HDAC-mediated salt stress response could be either repressed or outcompeted by the class I HDAC-mediated response (Ueda et al., 2017). Also, although HDA19 exerted a stronger regulation of the salt stress response as supported by a later study, the activation of *NAC016* expression under salt stress was not affected by the loss of *HDA19* in addition to the quadruple class II HDAC mutation, suggesting the existence of a response pathway independent of *HDA19* (Ueda et al., 2019). Future studies may consider the construction of mutants for further investigation on the interactions between different members from the two classes of RPD3/HDA1-type HDACs. Also, the observations that several HDAC mutants had lower salt tolerance suggest the importance of HDAC-mediated gene repression in establishing salt tolerance. The role of class III RPD3/HDA1-type HDACs in regulating salt tolerance has only been studied in tomato. Knocking down *SlHDA5* resulted in shorter hypocotyl and root length and lower chlorophyll content after salt treatment compared to wild type (Yu et al., 2018). This study demonstrated that class III RPD3/HDA1-type HDACs also can regulate salt tolerance, and the mechanism through which they do so is worth further investigation.

Regarding the studies on the Histone Deacetylase 2 (HD2) superfamily of HDAC, the *hd2c-1* mutation led to an increase in the global H3K9K14ac and H3K4me3 levels and a decrease in the global H3K9me2 level in *A. thaliana*. Under high salt stress, the *hd2c* mutant displayed a lower seed germination rate and survival rate at the seedling stage (Luo et al., 2012). Higher basal expression levels of negative regulators of ABA responses such as *ABI1*, *ABI2* and *AtERF4* were associated with either higher H3K9K14ac or lower H3K9me2 levels in the *hd2c* mutant compared to wild type (Luo et al., 2012). These suggest that HD2C may function in fine-tuning the ABA-responsive pathways under salt stress. Interestingly, it was reported that HD2C could interact with HDA6 and the loss of *hda6* function in the *hd2c* background further enhanced the *hda6*-mediated salt stress response (Luo et al., 2012). This suggests that HDACs from different superfamilies can cooperate to regulate salt stress responses. In rice, the overexpression of *HDT701* led to enhanced chlorophyll contents and survival rates of seedlings under salt stress when compared to wild type (Zhao, Zhang, et al., 2014). However, the downstream molecular responses leading to enhanced salt tolerance were not reported in the study. On the other hand, in poplar, the overexpression of *PtHDT902* repressed the expression of the *HIGH-AFFINITY K^+ TRANSPORTER 1* (*HKT1*) and led to lower salt tolerance than wild type (Ma et al., 2020).

2.1.3 | Histone methyltransferases and demethylases

Gain-of-function mutants of the *A. thaliana JMJ15*, which encodes a JUMONJIC (JMJC) domain-containing H3K4 demethylase, were reported to enhance seed germination rates under salt treatment (Shen et al., 2014; Yang et al., 2012). Although the overexpression of *JMJ15* repressed the expressions of a group of stress response regulators such as *WRKYs* and *ERFs* under normal condition, the expressions of *RD22* and *RD29A* were induced at a higher level by salt treatment in comparison with wild type (Shen et al., 2014). It is worth mentioning that the accumulation of lignin in the mutants may have contributed to the increased salt tolerance observed, so further analyses are needed to dissect the regulation of lignin biosynthetic genes by JMJ15 and to investigate whether JMJ15 and GCN5 participate in a common regulatory pathway in cell wall modification.

In another study, the mutation of the *SHK1 KINASE-BINDING PROTEIN 1* (*SKB1*), which encodes a protein arginine methyltransferase, led to a reduction in the total H4R3sme2 (symmetric dimethylation of histone H4 arginine 3) level as well as hypersensitivity to salt stress as indicated by shorter root lengths and lower survival rates in *A. thaliana* (Zhang et al., 2011). Unexpectedly, the reduction in the repressive mark H4R3sme2 was inconsistent with the reduced *RD29A* and *RD29B* expression levels in salt-stressed mutants. In addition, the higher expression levels of various negative regulators of the ABA signalling pathway, such as *HAB1*, *MEK1* and *MRK1*, may have also influenced the salt sensitivity in the *skb1-1* mutant (Zhang et al., 2011).

2.1.4 | Histone ubiquitination enzymes

In *A. thaliana*, E3 ubiquitin ligase (HUB1 and HUB2) and E2 ubiquitin conjugase (UBC1 and UBC2) were reported to be responsible for histone H2B mono-ubiquitination (H2Bub1) (Cao et al., 2008). Regarding their roles in salt stress responses, loss-of-function mutants of *HUB1* and *HUB2* displayed hypersensitivity and reduced microtubule depolymerisation, which was involved in stress signalling under salt treatment (Zhou et al., 2017). In addition, the induction of *AtPTP1* and *AtMKP1*, which regulate the activities of MPK3 and MPK6 through protein dephosphorylation, was weaker in the *hub1-4* and *hub2-2* mutants under salt treatment (Zhou et al., 2017).

TABLE 1 Mutant phenotypes of histone-modifying enzymes in response to salt stress in plants

Species	Gene(s)	Functions	Salt treatment conditions	Mutant phenotypes compared to wild type	References
Histone acetyltransferase					
Arabidopsis thaliana	*GCN5*	Encoding GCN5 histone acetyltransferase	10-day-old seedlings, 200 mM NaCl; 12-day-old plants, irrigated with 200 mM NaCl for every 3 days	*gcn5* mutant showed shorter root length, reduced leaf area, inhibited growth with lower fresh weight, accumulation of sodium ion and abnormal cell wall structure	Zheng, Liu, et al. (2019)
Triticum aestivum	*TaHAG1*/*TaGCN5*	Encoding GCN5 histone acetyltransferase	7-day-old seedlings, 200 mM NaCl for 3 or 4 weeks; 10-day-old seedlings, 250 mM NaCl until maturity	*TaHAG1*-OE plants showed longer root length, higher shoot fresh weight, higher K^+/Na^+ ratio, higher spike length and higher yield. Phenotypes in *TaHAG1*-RNAi and *TaHAG1* knockout lines were opposite to those in *TaHAG1*-OE lines	Zheng et al. (2021)
Histone deacetylase (HDAC): Class I RPD3/HDA1-type HDACs					
A. thaliana	*HDA6*	Encoding a histone deacetylase	Seeds, 100 mM, 150 mM or 200 mM NaCl; 5-day-old seedlings, 125 mM NaCl	The splicing mutant of *HDA6* (*axe1-5*) and *HDA6*-RNAi had lower germination rate and survival rate at the seedling stage	Chen et al. (2010)
A. thaliana	*HDA9*	Encoding a histone deacetylase	Seeds, 160 nM NaCl-infused medium; 4-day-old seedlings, 160 nM NaCl-infused medium	*hda9* mutant showed higher germination rate, longer root length and reduced sensitivity to salt at the seedling stage	Zheng et al. (2016)
A. thaliana (Ws)	*HDA19*	Encoding a histone deacetylase	Seeds, 150 or 200 mM NaCl	*hda19-1* plants showed lower germination rate	Chen and Wu (2010)
A. thaliana (Col-0)	*HDA19*	Encoding a histone deacetylase	5-day-old seedlings, 100 mM NaCl; 5-day-old seedlings, 125 mM NaCl for 2 h	*hda19-3* mutant showed higher survival rate	Ueda et al. (2017)
Oryza sativa	*HDA705*	Closest homologue of *Arabidopsis* HDA6	Seeds, 50, 100 or 150 mM NaCl; 2-day-old seedlings, 300 mM NaCl	Overexpression of *HDA705* led to delayed seed germination	Zhao et al. (2016)
Oryza sativa	*HDA710*	Closest homologue of *Arabidopsis* HDA19	2-week-old seedlings, 150 mM NaCl	*hda710* mutant displayed a higher survival rate at the seedling stage, greener leaves and higher fresh weight	Ullah et al. (2020)
Class II RPD3/HDA1-type HDACs					
A. thaliana	*HDA5*/*HDA14*/*HDA15*/*HDA18*	Encoding histone deacetylases	5-day-old seedlings, 100 mM NaCl; 5-day-old seedlings, 125 mM NaCl for 2 h	The quadruple *hda5/14/15/18* mutant showed lower survival rate	Ueda et al. (2017)
Class III RPD3/HDA1-type HDACs					
Solanum lycopersicum	*SlHDA5*	Encoding a histone deacetylase	Seeds, 100 mM; seedlings, 50 or 100 mM; leaves, dipped in 300 mM NaCl for 4 days; 35-day-old plants, irrigated with 400 mM NaCl for every 3 days	Knockdown of *SlHDA5* resulted in shorter hypocotyl length, root length, lower chlorophyll content and severely wilted and yellowed leaves	Yu et al. (2018)

(Continues)

TABLE 1 (Continued)

Species	Gene(s)	Functions	Salt treatment conditions	Mutant phenotypes compared to wild type	References
HD2 family					
A. thaliana	*HD2C*	Encoding a histone deacetylase	Seeds, 100 mM, 125 mM or 150 mM NaCl; 5-day-old seedlings, 150 mM NaCl	*hd2c-1* displayed lower seed germination rate, survival rate and less-green leaves at the seedling stage	Luo et al. (2012)
Oryza sativa	*HDT701*	Encoding a histone H4 deacetylase	Seeds, 100 or 150 mM NaCl; 2-week-old seedlings, 150 mM NaCl	Overexpression of *HDT701* mutant delayed seed germination but enhanced chlorophyll content and survival rate after salt treatment	Zhao, Zhang, et al. (2014)
Populus trichocarpa	*PtHDT902*	Encoding a histone deacetylase	4-week-old seedlings, 200 mM NaCl; 3-week-old shoots developed from the axillary buds, 50 mM NaCl	Overexpression of *PtHDT902* led to shorter plants, lower fresh weight, yellow leaves and lower chlorophyll content	Ma et al. (2020)
Histone methyltransferases/demethylases					
A. thaliana	*JMJ15*	Encoding a JmjC domain containing H3K4 demethylase	Seeds, 130 or 150 mM NaCl; 8-day-old plants, 100 or 150 mM NaCl for 1 or 5 h	Gain-of-function *JMJ15* mutant enhanced seed germination rate and accumulation of lignin	Shen et al. (2014)
A. thaliana	*SKB1*	Encoding a protein arginine methyltransferase	4-day-old seedlings, 80 mM, 120 mM or 160 mM NaCl; 4-day-old seedlings, 100 mM NaCl for root measurement	*SKB1* mutants showed shorter root length and lower survival rate	Zhang et al. (2011)
Histone ubiquitination enzymes					
A. thaliana	*HUB1 and HUB2*	Encoding E3 ubiquitin ligases	6-day-old seedlings, 150 mM NaCl; 7-day-old seedlings, 150 mM NaCl; 3-day-old seedlings, 100 mM for root measurement; 14-day-plants, irrigated with 400 mM NaCl for every 4 days	*hub1-4* and *hub2-2* displayed chlorotic leaves, shorter root length, smaller seedlings and reduced microtubule depolymerization	Zhou et al. (2017)
A. thaliana	*UBC1 and UBC2*	Encoding E2 ubiquitin conjugases	5-day-old seedlings, 175 mM NaCl; 5-day-old seedlings, 100 mM NaCl for root measurement	*ubc1-1*, *ubc2-1* and *ubc1,2* double mutants showed reduced root lengths and lower survival rates	Sun et al. (2020)

Similar to *hub1* and *hub2* mutants, *A. thaliana ubc1-1*, *ubc2-1* and *ubc1/2* double mutants were all hypersensitive to salt when compared to wild type (Sun et al., 2020). In these mutants, lower H2Bub1 and H3K4me3 (histone H3 lysine 4 trimethylation) levels were observed at *MYB42* and *MPK4*, the expressions of which were downregulated under salt stress (Sun et al., 2020). In the same study, MYB42 was confirmed to activate *SALT OVERLY SENSITIVE 2* (*SOS2*) expression and act as a positive regulator of salt tolerance (Sun et al., 2020), supporting the key role of UBC1 and UBC2 in the salt stress response.

2.1.5 | Insights from chemical inhibitor experiments

Chemical inhibitors which exert broad effects on certain classes of histone-modifying enzymes may facilitate the understanding of their coordinated regulation of salt stress responses. In *A. thaliana*, the addition of a HDAC inhibitor, Ky-2, led to an increased global H4ac (acetylated H4) level (Sako et al., 2016). The enhanced expressions of *SOS1* and *SOS3* under salt stress were facilitated by the increase in H4ac levels at these genes, resulting in a lower accumulation of Na^+ in the plant and better salt tolerance (Sako et al., 2016).

In line with the *A. thaliana* study, another HDAC inhibitor, suberoylanilide hydroxamic acid (SAHA), enhanced the H3ac (acetylated H3) and H4ac levels in the roots of cassava and led to the upregulation of *MeSOS1* expression, whereby conferring salt tolerance (Patanun et al., 2016). The SAHA application to cotton also led to a similar phenotype and consistent changes in the expressions of genes related to ion homeostasis, including those along the SOS pathway (He et al., 2020). Together with the findings from the mutants with altered H2Bub1 levels, these studies revealed that histone ubiquitination and acetylation might target different components in the SOS pathway to coordinate the regulation of salt tolerance in plants.

As indicated by the studies mentioned above, histone-modifying enzymes from the same family may have divergent effects towards salt tolerance, and these effects also vary across different species (Table 1). Notably, most of the experiments, including those utilising chemical inhibitors, were focused on histone acetylation/deacetylation. In addition, synergistic (e.g., between HDA6 and HD2C) or antagonistic (e.g., between HDA19 and class II RPD3/HDA1-type HDACs) interactions between enzyme classes or families were evidenced. Thus, more efforts are needed to dissect the molecular pathways regulated by individual or classes of histone-modifying enzymes.

2.2 | Crosstalk between histone-modifying processes and hormone signalling pathways under salt stress

Emerging evidence has suggested that histone-modifying enzymes may extend their roles in regulating stress signalling pathways through direct protein–protein interactions or the formation of protein complexes with the components of hormone signalling pathways. These findings, which are summarised below according to individual enzymes, provide insights on how stress signalling and histone modification regulate each other to fine-tune salt stress responses.

2.2.1 | HISTONE DEACETYLASE 6

Histone deacetylase HDA6 was reported to interact with a GLYCOGEN SYNTHASE KINASE 3 (GSK3)-like kinase, BR-INSENSITIVE 2 (BIN2), which is a key regulator in the brassinosteroid (BR) signalling pathway. In *A. thaliana*, BIN2 was inhibited by the deacetylation of the K189 residue by HDA6, which could then enhance BR signalling (Hao et al., 2016). It is known that BIN2 negatively regulates SOS2 activity by phosphorylating the T172 residue of the kinase domain of SOS2. Thus, the salt stress response is further repressed by BIN2 (Li et al., 2020). Hence, HDA6 might inhibit BIN2 kinase activity and dampen the function of BIN2 in the salt response pathway and promote salt stress response indirectly.

On the other hand, HDA6 is also a component of the Skp1/Cullin1/F-box protein CORONATINE INSENSITIVE1 (SCF^{COI1}) complex and interacts with the JASMONATE-ZIM-DOMAIN (JAZ) protein involved in the jasmonate (JA) signalling pathway (Devoto et al., 2002). In rice, jasmonoyl-isoleucine (JA-Ile) promotes the COI1-JAZ protein interaction (Thines et al., 2007), and the level of JA-Ile was accumulated under salt stress (Hazman et al., 2019). Upon the binding of JA-Ile to the SCF^{COI1} complex, OsJAZ9 interacts with OsCOI1a to regulate JA-responsive gene expressions. *OsbHLH062* is then induced to activate ion transporter genes which modulate K^+ homeostasis, part of the mechanism involved in regulating salt tolerance (Wu et al., 2015). At the same time, the release of OsbHLH094 may also activate the transcription of JA-responsive and salt-responsive genes (Toda et al., 2013). Therefore, HDA6 is involved in repressing salt-responsive genes under normal condition by interacting with the JA pathway.

2.2.2 | HISTONE DEACETYLASE 9

It was found that HDA9 formed a protein complex with HIGH EXPRESSION OF OSMOTICALLY RESPONSIVE GENES 15 (HOS15), a WD40-repeat protein. HOS15 interacts with the positive (OST1/SnRK2.6 protein) and negative (ABI1/2 phosphatase) regulators of ABA signalling (Ali et al., 2019). In *A. thaliana*, HOS15 interacts with histone H4 along with HDA9 to promote histone deacetylation. In *hos15* mutant plants, H4 was more acetylated, and the associated *RD29A* promoter was more active (Zhu et al., 2008). Thus, HOS15 and HDA9 can form a transcriptional corepressor complex and contribute to the fine-tuning of chromatin status at *RD29A* during salt stress.

In addition, it was reported that HDA9 also interacted with POWERDRESS (PWR) and then bound to ABA INSENSITIVE 4 (ABI4), which is an ABA-responsive transcription factor (Baek et al., 2020). The complex could bind the promoters of stress-responsive genes as a repressor (Khan et al., 2020). In a genetic study, the *abi4* mutant displayed increased salt tolerance while the overexpression of *ABI4* enhanced salt sensitivity via modulating the *HKT1;1* expression in *A. thaliana* (Shkolnik-Inbar et al., 2013). Thus, this triple complex (PWR, HDA9 and ABI4) may act as a transcriptional repressor complex involved in ABA signalling under salt stress.

2.2.3 | HISTONE DEACETYLASE 19

HDA19 interacts with MULTICOPY SUPPRESSOR OF IRA1 (MSI1) and responds to salt stress via mediating ABA signalling. The MSI1-HDA19 complex associates with the SIN3-LIKE proteins, SNL4 and HISTONE DEACETYLATION COMPLEX1 protein (HDC1), to form a SIN3-like complex. The complex represses the ABA-responsive genes by directly binding to the chromatin of ABA receptor genes such as *PYL4*. In the genetic study, *msi1-as* and *hda19* mutants had elevated expressions of ABA-responsive genes and the salt-responsive gene, *RD29B*, to enhance salt tolerance in *A. thaliana* (Mehdi et al., 2016). This implies that MSI1 and HDA19 function together to repress both ABA-responsive and salt-responsive genes.

Moreover, HDA19 interacts with the transcriptional repressor AtERF7 to regulate salt stress-responsive genes. AtERF7 is an APETALA/EREBP-type transcription factor involved in ABA signalling. AtERF7 binds to the GCC-box and forms a protein complex with the co-repressors, AtSIN3 and HDA19, to repress transcription (Song et al., 2005). Meanwhile, AtERF4 is also involved in regulating ABA and abiotic stress responses and can act as a substitute for AtERF7 in the protein complex (Kazan, 2006). These transcriptional complexes work together to repress the ABA-responsive and salt-responsive gene expressions.

Also, HDA19 cross-talks with the SIN3 ASSOCIATED POLYPEPTIDE P18 (AtSAP18), which is involved in regulating ethylene signalling and salt stress responses. In *A. thaliana*, *AtSAP18*-knockout mutant showed a sensitive phenotype to salt treatments. HDA19 and AtSAP18 interact with ETHYLENE RESPONSIVE ELEMENT BINDING FACTOR 3 (ERF3), which is a negative regulator in ethylene signalling, to form a triple complex to repress transcription by binding to the GCC-box of ethylene- or stress-responsive genes (Song & Galbraith, 2006).

2.2.4 | GENERAL CONTROL NONDEREPRESSIBLE 5

Lastly, GENERAL CONTROL NONDEREPRESSIBLE 5 (GCN5) was reported to interact with a PROTEIN PHOSPHATASE 2C (AtPP2C-6-6). AtPP2C-6-6 belongs to the fifth group of PP2C members and is involved in the ABA signalling pathway. In *A. thaliana*, the expression of *AtPP2C-6-6* is responsive to salt (Servet et al., 2008). AtPP2C-6-6 can dephosphorylate GCN5 and prevent it from functioning. Thus, AtPP2C-6-6 may act as a negative regulator of GCN5 under salt stress.

2.3 | Alterations in histone modifications in response to salt stress

Profiling the changes in the enrichment of different histone modifications in response to salt stress may provide clues to the regulatory mechanisms and their phenotypic consequences. Such changes have been reported in several plant species. According to previous reports, salt stress led to an increase in the global level of at least one type of histone acetylation marks in *A. thaliana*, cassava, cotton, maise, rice and tobacco (He et al., 2020; Patanun et al., 2016; Sokol et al., 2007; Zhao, Wang, et al., 2014; Zheng, Wang, et al., 2019). As histone acetylation is considered to be an activation mark, it was believed that its increase was important for facilitating the transcriptional responses to salt stress. Besides, an increase in H3S10pho (histone H3 serine 10 phosphorylation) was detected in *A. thaliana* and tobacco shortly after exposure to high salt concentrations, followed by the peaking of sequential H3S10phoK14ac marks (Sokol et al., 2007). This demonstrates that temporal differences exist in the establishment of different histone marks in response to salt stress. In *Brassica napus*, an increase in the H3K4me3 level and a decrease in H3K9me2 were observed in the root tip meristem cells under low-salt treatment (25 mM), which improved the germination rate and root growth, while treatment with higher salt concentrations (50 and 100 mM) led to totally opposite phenotypes and changes in the histone marks (Fang et al., 2017). In addition, an increase in the activating mark H3K4MG (histone H3 lysine 4 methylglyoxalation) and a decrease in the repressive mark H4R3sme2 were also reported in *A. thaliana* under salt treatment (Fu et al., 2021; Zhang et al., 2011). Although the global increase in activating histone marks or decrease in repressive histone marks seem to be a conserved strategy for salt stress responses in several species, the study in rice reported dissimilar patterns in the global levels of various histone modifications. In this case, except for H3K9ac, other modifications linked with gene activation, including H3K4me3, H3K27ac (histone H3 lysine 27 acetylation) and H4K12ac (histone H4 lysine 12 acetylation) and the repressive mark H3K27me3 (histone H3 lysine 27 trimethylation) were all decreased upon salt treatment (Zheng, Wang, et al., 2019). Further bioinformatics analyses revealed that the effects of combinations of histone modifications on gene expressions might be tissue-specific, for example, the combination of H3K9ac, H3K27ac and H4K12ac was responsible for influencing salt-responsive genes in leaves but not roots (Zheng, Wang, et al., 2019).

To investigate how alterations in histone modifications might regulate transcriptional responses when under salt stress, chromatin immunoprecipitation-quantitative polymerase chain reaction (ChIP-qPCR) was performed in multiple studies to assay the local histone modification status at key genes involved in salt stress signalling and tolerance. Regarding the genes involved in ABA signalling, increases in the H3ac and H3K4me3 levels were observed in *ABI1*, *ABI2* and *HAI1* (which encode protein phosphatase 2C) in *A. thaliana* (Nguyen et al., 2019). Within the same gene family, *HAB1* was marked with reduced levels of the repressive mark H4R3sme2 (Zhang et al., 2011). In addition, an increase in the H3K4me3 level was found at *ATAF1* and *NCED3*, which are involved in ABA biosynthesis (Fu et al., 2021). In a comparison between the salt-tolerant rice cultivar Nonabokra and the salt-sensitive cultivar IR64, the epigenetic status of *BZIP PROTEIN 8* (*OsBZ8*), which is involved in ABA-mediated stress responses, was monitored. The higher expression of *OsBZ8* in Nonabokra in the control condition and during early salt stress response was associated with higher H3K9ac, H3K14ac and H3K27ac levels around the transcription start site. In the sensitive cultivar IR64, the increase in *OsBZ8* expression was accompanied by increased H3K4me3 level and decreased H3K27me3 level (Paul et al., 2017). These studies indicate that differential enrichment of histone modifications is involved in the induction of the ABA-dependent pathway components under salt stress. Moreover, the expressions of other salt stress-responsive genes also showed similar relationships with changes in histone modifications. In *A. thaliana*, it was reported that salt stress led to increases in H3K4me3 and H3K9K14ac levels and a reduced H3K9me2 level at the *DREB2A* and *RD29A* loci (Chen et al., 2010). Enhanced expression of *COR6.6* and *RAB18* were also associated with the increase

in H3K9K14ac or H4ac levels in *A. thaliana* (Kaldis et al., 2011). In *Medicago sativa*, enhanced levels of H3K4me3 and H3K9ac were observed at the salt-inducible gene *MsMYB4* (Dong et al., 2020). In soybean, increases in H3K4me3 or H3K9ac levels were observed with a decrease in H3K9me2 level at salt-induced genes encoding one member from each of the AP2/DREB, MYB and NAC transcription factor families (Song et al., 2012). Apparently, the *A. thaliana RD29B* possessed the most diversified changes in histone marks among plant responses to salt stress, including increased H3K9K14ac and H3K4me3 levels and decreased H3K9me2 and H4R3sme2 levels (Figure 2) (Chen et al., 2010; Zhang et al., 2011). Recently, H3 methylglyoxalation (H3MG) was discovered and demonstrated to be important for salt stress responses in *A. thaliana* (Fu et al., 2021). In that study, the increases in H3MG and H3K4MG levels were associated with the upregulation of *ABCG6*, *ATAF1*, *NCED3* and *RD29B*.

Upregulated genes involved in ion homeostasis were also tagged by differential histone modifications in response to salt stress. In *A. thaliana*, the genes encoding MYB42 and its regulator MPK4 were marked with higher H2Bub1 and H3K4me3 levels after salt treatment. These changes were revealed to be crucial for activating *SOS2* to positively regulate salt tolerance (Sun et al., 2020). Alterations in histone modifications were also linked to genes controlling cell wall modification and integrity, which are also important processes for enhancing salt tolerance. In *A. thaliana*, increases in H3K9ac and H3K14ac levels were associated with the activated genes *CTL1*, *PGX3* and *MYB54* when under salt stress (Zheng, Liu, et al., 2019). CTL1 was involved in cellulose biosynthesis and was previously shown to be essential for salt tolerance (Kwon et al., 2007). While the MYB transcription factor MYB54 was also involved in secondary cell wall biosynthesis, PGX3 was reported to regulate pectin degradation (Zheng, Liu, et al., 2019). Similarly, in maize, an increase in H3K9ac levels was observed at

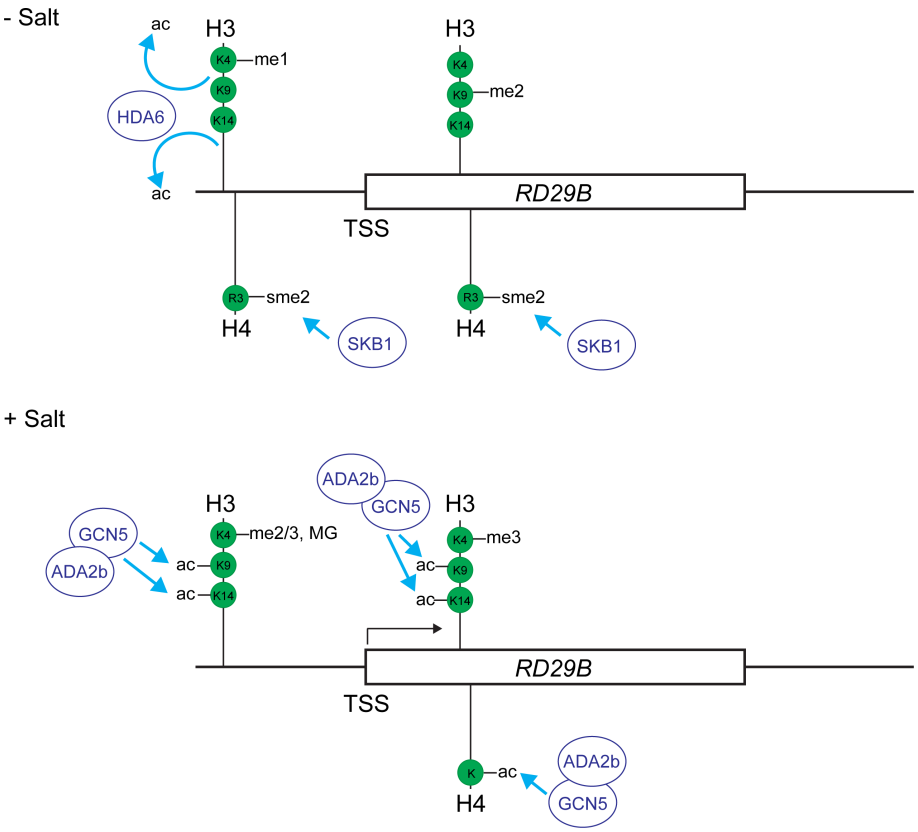

FIGURE 2 Chromatin status at the *RD29B* locus under control condition or salt stress. The *RD29B* locus of *Arabidopsis* is picked to illustrate the dynamic changes in histone modifications under salt stress. For the sake of simplicity, the types of histone modifications are only indicated at the condition that showed a higher level. Under control condition, histones H3 and H4 at both the promoter and genic regions of *RD29B* are modified by repressive marks. SKB1 is responsible for the establishment of H4R3sme2, and HDA6 deacetylates H3K9 and H3K14. Upon salt treatment, the GENERAL CONTROL NONDEREPRESSIBLE 5 (GCN5)-complex is recruited by the interaction of ADA2b with an unknown factor to the locus and acetylates H3K9, H3K14 and H4. SHK1 KINASE-BINDING PROTEIN 1 (SKB1) binding to H4 is reduced at the target genes, and leads to lower H4R3sme2 levels, whereas the specific proteins responsible for the increase in H3K4me2, H3K4me3 and H3K4MG are still unknown. The overall 'active' chromatin status facilitates the induction of *RD29B* expression, which is important for salt tolerance. The N-terminal tails of histone proteins are represented by perpendicular lines. Green circles represent individual residues of the tails. The symbols me1, me2, me3, ac, sme2 and MG represent monomethylated, dimethylated, trimethylated, acetylated, symmetrically dimethylated and methylglyoxalated residues, respectively. TSS, transcriptional start site

ZmEXPB2 and *ZmXET1*, which regulate cell wall extensibility in response to salt stress (Li et al., 2014). Differences in histone modification levels were also detected at the gene encoding peroxidase in the study on sugar beet and wild beet. Although the *POX* gene was induced by salt stress in both types of beets, an increase in the H3K9ac level at *POX* was observed in the wild beet, in contrast to an increase in the H3K27ac level in the sugar beet when exposed to high salinity stress (Yolcu et al., 2016).

While investigations of key genes have linked the regulatory effects of histone modifications to salt stress responses, comprehensive profiling of the genome-wide distribution of histone modifications may provide novel insights into different pathways affected by the differential enrichment of histone modifications in response to salt stress. Han et al. (2020) reported a ChIP-Seq analysis in castor bean subjected to salt stress treatment for 23 days. Consistent with previous findings, the H3K4me3 level was positively correlated with the transcription level, whereas the H3K27me3 and transcription levels were negatively correlated. When comparing leaf tissues from salt-treated seedlings to control, 440 and 192 genes were differentially marked by H3K4me3 and H3K27me3, respectively. Among the genes with a differential H3K4me3 level, those involved in metabolic pathways were enriched, as identified in Kyoto Encyclopedia of Genes and Genomes (KEGG) analysis, whereas Gene Ontology (GO) terms involved in signalling and nucleotide-related pathways were enriched in those with a differential H3K27me3 level, suggesting that the two histone marks were involved in regulating distinct processes. However, integrating the transcriptomic data and the histone modification profile only identified 45 genes showing expected differential expressions (Han et al., 2020). On the other hand, the dynamic fluctuation in H3K4me3 and H3K27me3 was tightly associated with the expression pattern of *RADIALIS-LIKE SANT/MYB 1* (*RSM1*), which was previously reported to be a positive regulator of salt tolerance (Han et al., 2020; Yang et al., 2018). The genome-wide H3K27me3 pattern was also investigated in soybean roots under salt stress, in which 336 expressed genes showed a lower H3K27me3 level when compared to control (Sun et al., 2019). Interestingly, there were only five expressed genes associated with an increase in the level of existing H3K27me3, whereas 294 expressed genes were marked with de novo H3K27me3 when under salt stress (Sun et al., 2019). Further comparison of the transcriptomic data with the histone modification profile identified a group of genes showing the expected relationship between differential expression and differential modification, which included 170 and 99 differentially expressed genes marked by increased and decreased H3K27me3 levels, respectively (Sun et al., 2019). Compared to the soybean study, the correlation between differential expression and differential modification was weaker in the castor bean study. This might be due to the longer duration of salt treatment in the castor bean experiment, as the plants could have adapted to salinity and adjusted the transcriptional responses for the long-term metabolic state. Meanwhile, epigenetic marks could be retained at initial loci for the record of stress onset, which is sometimes known as stress memory (Avramova, 2015).

It is well documented that plants pre-exposed to stress have altered response or tolerance to the same or related stress. There is increasing evidence to suggest that changes in histone modifications can mediate this process. In *A. thaliana*, it was reported that mild salt treatment (50 mM NaCl) improved the tolerance to subsequent higher salt (80 mM NaCl) or drought treatment even if the two treatments were separated by a recovery period of 10 days (Sani et al., 2013). Although there was a lack of association between the differential patterns of H3K4me3 or H3K27me3 and differential gene expressions after 24 h in the initial mild salt treatment, a reduction in the H3K27me3 level was identified at the sodium ion transporter gene *HKT1*, which was then expressed at a higher level in pre-treated seedlings compared to untreated seedlings exposed to the second higher salt stress. The reduction in the H3K27me3 level was retained at *PIP2E*, which encodes an aquaporin, after the recovery period of the first salt treatment, and the *PIP2E* expression was subsequently higher in the pre-treated seedlings when exposed to the second stress (Sani et al., 2013). In another study, the deposition of H3K4me3 was observed at *P5CS1*, which encodes a delta1-pyrroline-5-carboxylate synthase, in *A. thaliana* after two salt pre-treatments (Feng et al., 2016). In a subsequent salt treatment, higher *P5CS1* expression and proline accumulation were observed in pre-treated seedlings compared to seedlings without pre-treatment. Interestingly, the induction of *P5CS1* expression and H3K4me3 deposition were both affected by light regimes and were abolished in the *hy5 hyh* (*elongated hypocotyl 5/hy5-homologue*) mutant. This suggests that light is an essential factor in establishing the transcriptional memory of *P5CS1* (Feng et al., 2016).

3 | CURRENT UNDERSTANDING ABOUT THE ROLES OF HISTONE VARIANTS IN PLANT SALT STRESS RESPONSES

In the previous sections, we have reviewed the roles of histone modifications in salt stress responses, ranging from transcriptional regulation to coordination of signalling pathways. Apart from that, the displacement of canonical histones by their variants could also affect the nucleosome packing and thus transcription (Fang et al., 2017; Lei & Berger, 2020).

The roles of H1 in plant salt stress responses are less known. H1.1 H1.2, H1.3 are the major variants of H1 found in *A. thaliana*. However, it seems that there is no direct evidence showing that H1 variants play a role under salt stress, other than some indirect clues. Although HDC1 is responsible for the deacetylation of H3K9/K14, HDC1 was found to be an interacting partner of *A. thaliana* H1.1, H1.2 and H1.3 with descending affinity (Perrella et al., 2016). Since the expression of *H1.3* has been demonstrated to be stress responsive and H1.3 is essential for stomatal functions (Rutowicz et al., 2015), it is sensible to speculate that H1.3 could play a role in salt tolerance.

The *A. thaliana* genome encodes the canonical H2A and its variants, including H2A.X, H2A.Z and the plant-specific H2A.W (Jiang & Berger, 2017; Lei & Berger, 2020). The ratio of H2A and H2A.Z is

TABLE 2 Genetic studies of histone variants, histone chaperones, and chromatin remodelling factors in response to salt treatments

Species	Gene(s)	Functions	Salt treatment conditions	Mutant phenotypes compared to wild type	References
Histone variants					
A. thaliana	*HTA9*, *HTA11*	Encoding H2A.Z	Seeds and seedlings, 150 mM NaCl	*hta9 hta11* double mutant showed a slight but insignificant delay in radicle tip emergence, but a faster green cotyledon development	Sura et al. (2017)
Histone chaperones					
A. thaliana	*DEK3*	Encoding a DEK domain containing protein that potentially served as H3/H4 histone chaperone	Seeds and seedlings, 200 mM	*dek3* knockout mutant showed higher seed gemination and seedling survivability	Waidmann et al. (2014)
A. thaliana	*MSI1*	Encoding the MSI1 subunit of the Chromatin Assembly Factor-1 complex	7-day old seedlings, 150 mM NaCl	*msi-as* (antisense) showed delayed chlorophyll loss	Mehdi et al. (2016)
A. thaliana	*NAP1;1*	Encoding a histone chaperone for H2A/H2B	Seedlings, 150 mM NaCl	*Atnap1;3–2* (*AtNAP1;3 T*), a dominant negative mutant with truncated C-terminus, showed ABA-hyposensitive and salt-sensitive phenotype	Liu, Gao, et al. (2009)
Oryza sativa	*OsNAPL6*	Encoding a histone chaperone for H3/H4	2-month-old plants, 50 mM NaCl, 3.75 mM $MgCl_2$, 15 mM $MgSO_4$, and 6.25 mM $CaCl_2$ (soil electrical conductivity [EC] of 10 dS/m)	Overexpressor possessed lower leaf Na^+/K^+ ratio and higher relative water content, better yield components (total biomass, number of panicles, number of filled grains, harvest index). Knockdown mutant did the opposite	Tripathi et al. (2016)
Chromatin-remodelling factors					
A. thaliana	*ARP6*	Encoding the subunit of SWR1 chromatin-remodelling complex, which is required for H2A.Z deposition	Seeds and seedlings, 150 mM NaCl	*arp6* showed delayed germination and cotyledon greening	Sura et al. (2017)
A. thaliana	*CHR12*	Encoding a SNF2/Brahma-type ATPase	Seedlings, 0–150 mM NaCl	*atchr12* mutant suffered less root growth inhibition but overexpression of *AtCHR12* showed no significant difference in root length when compared to wild type.	Mlynarova et al. (2007)
A. thaliana	*PIE1*	Encoding the subunit of SWR1 chromatin-remodelling complex, which is required for H2A.Z deposition	Seeds and seedlings, 150 mM NaCl	*pie1-5* showed severely delayed germination and cotyledon greening	Sura et al. (2017)
A. thaliana	*PKL(CHR6)*	Encoding CHD3-type chromatin-remodelling factor PICKLE/GYMNOS	Seeds and seedlings, 150 mM NaCl	*pkl-1* mutant showed substantial reduction in cotyledon greening and slight but significant reduction in root length	Yang et al. (2019)

(Continues)

TABLE 2 (Continued)

Species	Gene(s)	Functions	Salt treatment conditions	Mutant phenotypes compared to wild type	References
A. thaliana	*EEN*(*IES6*), *EIN6*(*REF6*)	*IED6* Encoding a subunit (INO 80 subunit 6) of INO80 chromatin remodelling complex	Seedlings, Linsmaier and Skoog medium	Either *een* or *ein6* single mutant showed transcriptional responses similar to wild type *ein6-1 een-1* double mutant showed impaired *EIN2*, an important salt tolerance gene, expression due to exceptionally increased H2A.Z and H3K27me3 deposition within the gene body	Zander et al. (2019)

likely to be subjected to transcription regulation under salt stress. For example, it has been demonstrated that H2A and H2A.Z were differentially expressed in leaves and roots under 200 mM NaCl treatment in a 24-h time course experiment (Lv et al., 2019). The changes in expression seemed to be locus-specific. Another study showed that the expressions of H2A.X and H2A were reduced at least 3-folds in a salt-tolerant grapevine rootstock 1616C at 6 and 24 h after salt treatment (Aydemir et al., 2020).

In general, the major sequence differences between canonical H2A and H2A variants were demonstrated to affect intra- and inter-nucleosome interactions, thus directly affecting the packing of the chromatin (Kawashima et al., 2015). Chromatin remodelling under stress could be achieved by displacing the H2A-H2B dimer with H2A.Z-H2B or directly evicting the H2A-H2B dimer to relax the nucleosome wrapping and thus activate transcription (Jiang & Berger, 2017). Although sequence variants of H2B exist, they are functionally indistinguishable from one another.

H2A.Z occupancy in the gene body is significantly positively correlated with the responsiveness of gene expression under stress conditions in *A. thaliana* (Sura et al., 2017). At the same time, under control condition, stress-induced genes have lower H2A.Z in +1 nucleosome while suppressed genes have higher H2A.Z in +1 nucleosome (Sura et al., 2017). It has been demonstrated that the depletion of H2A.Z in the *hta9 hta11* double mutant resulted in slightly slower germination rates but slightly earlier greening of cotyledons under salt treatment (Table 2) (Sura et al., 2017). Furthermore, the loss-of-function mutation in chromatin-remodelling proteins that are required for H2A.Z incorporation would lead to severe salt sensitivity phenotype (see below) (Sura et al., 2017).

For example, *AtMYBR1/AtMYB44* is a well-characterised salt stress-responsive gene regulated by H2A.Z occupancy. The ectopic expression of *AtMYB44* could enhance salt tolerance through stimulating stomatal closure by enhancing ABA sensitivity (Jaradat et al., 2013; Jung et al., 2008). The expression of *AtMYB44* was highly inducible by salt stress and was associated with reduced H2A.Z in both the promoter and the gene body and increased RNA polymerase II near the transcription start site, without any alteration in the H3K4me3, H3K9ac, H3ac and H4ac levels (Nguyen & Cheong, 2018). This suggests that H2A.Z has a preferential role in regulating *AtMYB44* in the salt stress response.

H3.1 and H3.3 are the major variants of H3 in *A. thaliana*. The ratio of canonical H3 and its variants are also transcriptionally regulated (Aydemir et al., 2020; Lv et al., 2019). The sequences of the canonical H3 and its variants are relatively conserved. For example, there are only four different amino acids between H3.1 and H3.3. However, these amino acid differences have been demonstrated to influence the assembly and disassembly of the nucleosome (Shi et al., 2011). As discussed in a previous section, HDC1 is a positive regulator of salt stress tolerance and enhances the expression of salt stress-responsive genes by mediating the deacetylation of H3K9/K14 (Perrella et al., 2013). HDC1 itself cannot interact directly with H3.1 or H3.3, but it can interact with the interacting proteins of H3 such as SHL1, ING2, MSI1, SAP18, SNL3, HDA6, and HDA19 (Perrella et al., 2016). On the other hand, while the de-novo establishment of H3K27me3 has been observed at inactive genes during salt stress (Sun et al., 2019), it was shown that H3.1 enrichment was in general associated with the enrichment of H3K27 methylation (including H3K27me1, H3K27me2, and H3K27me3) (Stroud et al., 2012). Besides, H3.3 occupancy is negatively correlated with that of H2A.Z (Stroud et al., 2012), which is normally redistributed under stress. Altogether, this implies that the interplay of H3 variants is involved in transcriptional regulation in response to salt stress.

4 | ROLES OF HISTONE CHAPERONES IN SALT STRESS RESPONSES

Histone chaperones generally carry a net negative charge at cellular pH, and therefore can neutralise the net positive charge of histone proteins to assist the latter's folding and interactions with DNA (Hammond et al., 2017). Histone chaperones are also responsible for the escorting, storage and turnover of histones, and for mediating the nucleosome assembly (Hammond et al., 2017). A summary of *A. thaliana* histone variants and their potential chaperones can be found in a previous review (Jiang & Berger, 2017). So far, only a few

studies have investigated the roles of histone chaperones in salt stress responses in plants (Table 2).

NUCLEOSOME ASSEMBLY PROTEIN 1 (NAP1) is a eukaryotic conserved histone chaperone (Park & Luger, 2006). They are primarily H2A and H2B chaperones that interact with the nascent H2A and H2B to assist their folding as well as displacing the canonical H2A-H2B from the nucleosome and replacing them with their variants (Park & Luger, 2006). There are multiple NAP1-encoding genes in the *A. thaliana* genome, including *NAP1;1*, *NAP1;2*, *NAP1;3*, *NAP1;4* (Liu, Zhu, et al., 2009), *NAP1-RELATED PROTEIN 1* (*NRP1*) and *NRP2* (Zhu et al., 2006). The somatic homologous recombination of DNA, inducible by UV radiation, mutagenic chemicals and abiotic stresses such as salt stress, was suppressed in the *npr1 npr2* double mutant (Gao et al., 2012). It was speculated that in the absence of NRP1 and NRP2, due to the reduction in nucleosome disassembly, the damaged DNA was less accessible to the DNA-repairing machinery, which repairs the double-strand break by homologous recombination.

Specifically, there are two characterised mutant alleles of *AtNAP1;3*, namely *nap1;3-1* and *nap1;3-2*. The initial screening of *nap1;1 nap1;2 nap1;3-1* (*m123-1*) and *nap1;1 nap1;2 nap1;3-2* (*m123-2*) triple mutants showed contradictory phenotypes, where seedlings of the former were hypersensitive to ABA while those of the latter were hyposensitive to ABA and hypersensitive to salt stress (Liu, Gao, et al., 2009). It turned out that *nap1;3-1* was a knockout mutant while *nap1;3-2* was a dominant negative gain-of-function mutant. The *nap1;3-2* mutation alone could alleviate the chlorosis of *A. thaliana* seedlings under salt treatment (Liu, Gao, et al., 2009). The phenotype could be linked to the altered expression of ABA-responsive genes in the mutant. *nap1;3-2* encodes NAP1;3 T with a truncation of 34 amino acid residues at the C-terminus (Liu, Gao, et al., 2009). The exact mechanism of how NAP1;3 T alters ABA and salt sensitivity is still unknown. Since NAP1;3 T was still able to interact with other NAP1 proteins and the H2A-H2B heterodimer (Liu, Gao, et al., 2009), and the truncated C-terminus was required for H2A-H2B dissociation from the nucleosome (Park et al., 2005; Park & Luger, 2006), it was proposed that NAP1;3 T acts as an inhibitor of canonical H2A-H2B displacement by their variants. Thus, manipulation of the protein sequence of NAPs in plant could possibly be a way to improve salt tolerance. In addition, *A. thaliana* NAP1 may also play roles in controlling the H3.3:H3.1 ratio. FASCIATA1 (FAS1) is one of the subunits of CHROMATIN ASSEMBLY FACTOR 1 (CAF-1). The *fas1* mutant possessed a significantly increased H3.3:H3.1 ratio (Kolarova et al., 2020). Although the *m123-2* triple mutant alone did not show a significant change in the H3.3:H3.1 ratio, this triple mutation could restore the H3.3:H3.1 ratio to a lower level in the *fas1 m123-2* quadruple mutant (Kolarova et al., 2020).

There are 11 OsNAP-encoding genes in the rice genome, among which, *OsNAPL6* is the only one inducible by salt regardless of the genotype (Tripathi et al., 2015). Unexpectedly, OsNAPL6 has a higher affinity for H3/H4 than for H2A/H2B, deviating from the general belief that NAPs are solely H2A/H2B chaperones (Tripathi et al., 2016). It has also been demonstrated that OsNAPL6 is involved in nucleosome assembly (Tripathi et al., 2016). Knocking down *OsNAPL6* led to higher sensitivity to stresses, including salinity, while overexpressing *OsNAPL6* could improve salt tolerance and reduce the yield penalty due to salt stress in the transgenic plant (Tripathi et al., 2016). The expressions of around 500 genes, mostly related to transcription, translation and stress responses, showed an opposite trend between the *OsNAPL6*-overexpressor and *OsNAPL6*-knockdown plants when compared to wild type. At the same time, OsNAPL6 was demonstrated to be enriched at the promoters of some of these genes, suggesting that their expressions are directly regulated by OsNAPL6 (Tripathi et al., 2016). Furthermore, the overexpression of *OsNAPL6* could also reduce the DNA damage caused by salt stress, which is consistent with the phenotype of *A. thaliana npr1 npr2* double mutant (Gao et al., 2012).

The DEK domain-containing protein is also considered to be a histone chaperone as the DEK protein from *Drosophila* was found to be involved in incorporating core histones, mainly H3.3, into chromatin to form nucleosomes (Sawatsubashi et al., 2010). There are four DEK domain-containing protein-encoding genes (*DEK1-4*) in the *A. thaliana* genome (Pendle et al., 2005). DEK3 was found to specifically interact with H3/H4 but not with H2A/H2B in western blot and co-immunoprecipitation experiments (Waidmann et al., 2014). Furthermore, DEK3 was also co-immunoprecipitated with a type-I DNA topoisomerase (Top1α), a cohesion protein (SSC3), a cohesion-associated protein (PDS5), a histone deacetylase (HDA3/HDT1), a PHD-finger chromatin-remodelling factor (SHL1) and a salt tolerance-related protein (At1g13930) (Waidmann et al., 2014). ChIP-seq demonstrated that DEK3-CFP was associated with 161 gene loci (Waidmann et al., 2014). A further study of the *dek3* mutant and *DEK3*-overexpressor showed that the histone H3 occupancies at the DEK3-associated genes increased with the increase in DEK3, while chromatin accessibility and the expression of most of the DEK3-associated genes decreased (Waidmann et al., 2014). While a study of the role of DEK proteins under salt stress is lacking, results of the genetic study inferred that DEK proteins could possibly be playing a negative role in salt stress tolerance as DEK proteins apparently reduce chromatin accessibility, which is unfavourable for gene expression and DNA repairing.

5 | ROLES OF CHROMATIN REMODELLING FACTORS IN SALT STRESS RESPONSES

Chromatin-remodelling complexes are responsible for the ATP-dependent repositioning of nucleosomes and alterations in the core histone composition of the nucleosome (Han et al., 2015), which serve to regulate the accessibility of the genomic DNA, possibly in a locus-specific manner under specific conditions. It has been found that in *A. thaliana*, salt stress tended to reduce chromatin accessibility, in contrast to the increase in chromatin accessibility under heat or cold treatment (Raxwal et al., 2020). Although the same study suggested that the global change in chromatin packing under salt treatment may be due to the change in cellular ionic strength (Raxwal et al., 2020), other studies have demonstrated the potential roles of chromatin

remodelling under salt stress (Table 2). There are multiple chromatin-remodelling complexes, which are conserved among eukaryotes. The better-characterised chromatin-remodelling proteins are from the SUCROSE NON-FERMENTING 2 (SNF2) family and the SWI2/SNF2-RELATED 1 (SWR1) family. The SNF2 family consists of the SNF2/BRAHMA (BRM), IMITATION SWITCH (ISWI), CHROMODOMAIN-DOMAIN-HELICASE-DNA-BINDING PROTEIN (CHD), and some less-characterised subfamilies, while the SWR1 family is divided into the SWR1 and INOSITOL REQUIRING 80 (INO80) subfamilies (Han et al., 2015; Knizewski et al., 2008; Verbsky & Richards, 2001). The expressions of some of these factors have been demonstrated to be responsive to salt stress (Li et al., 2011).

A phylogenetic study showed that *A. thaliana CHROMATIN REMODELLING 12* (*AtCHR12*), *AtCHR23*, *AtCHR2*/*BRM* and *AtCHR3*/*SPLAYED* (*SYD*) encode for SNF2/BRM-type chromatin-remodelling proteins (Verbsky & Richards, 2001). While the primary function of AtCHR12 is potentially related to growth, knocking out *AtCHR12* abolished the inhibition on root growth by salt stress at low NaCl concentration (Mlynarova et al., 2007). Furthermore, although there is no direct evidence showing BRM plays a role in salt tolerance, the *A. thaliana* loss-of-function *brm* mutant was more sensitive to ABA and had higher tolerance to dehydration stress (Han et al., 2012). 'Hormone responses' and 'stress and environmental responses' are the two most significantly enriched GO terms of BRM targets as identified by ChIP-chip, while the GO terms 'response to drought', 'response to salt stress', 'response to osmotic stress' and 'response to light' were also significantly enriched (Archacki et al., 2017). The *brm-3* mutant was demonstrated to have higher expressions of ABA-related *PP2C* genes (*ABI1*, *ABI2* and *HAI1*) in response to NaCl treatment (Nguyen et al., 2019), suggesting that BRM may act as a repressor of these genes. Immunoprecipitation of BRM-GFP successfully isolated the subunits of the SWI/SNF complex in *A. thaliana*, including SWP73A, SWP73B, SWI3A, SWI3B, SWI3C, SWI3D, and SYD (Li et al., 2016). ChIP-seq also demonstrated that SYD and BRM targeted a common set of genes under normal conditions (Shu et al., 2021).

PICKLE (*PKL*) is a relatively well-characterised CHD3-type chromatin-remodelling factor-encoding gene from *A. thaliana*, and PICKLE was found to mediate the trimethylation of H3K27 at its target gene (Yang et al., 2019). *PHOTOPERIOD INDEPENDENT EARLY FLOWERING 1* (*PIE1*) and *ACTIN-RELATED PROTEIN 6* (*ARP6*) encode components of the SWR1 chromatin-remodelling complex (Carter et al., 2018). The SWR1 complex mediates the incorporation of H2A.Z into nucleosomes (Deal et al., 2007; Kumar, 2018). PICKLE, PIE1 and APR6 were identified to be involved in salt stress tolerance (Sura et al., 2017; Yang et al., 2019), and that the mutation of any one of them would lead to a salt-sensitive phenotype in *A. thaliana*. A transcriptomic study comparing *pie1-5*, *pkl-1*, *curly leaf* (*clf-28*) mutants in *A. thaliana* to the wild type showed that they regulate the expressions of a common set of genes (Carter et al., 2018). *CLF* encodes an enhancer of zeste-family histone methyltransferase as a subunit of Polycomb Repressive Complex 2 (PRC2), which is responsible for H3K27me3 (Mozgova et al., 2015). Based on the observation that H2A.Z-enriched nucleosomes were also enriched in H3K27me3 modifications at specific gene loci, it was suggested that PIE1 is responsible for the incorporation of H2A.Z into nucleosomes, which subsequently mediates the deposition of H3K27me3. PICKLE, on the other hand, directly mediates and maintains the H3K27me3 mark (Carter et al., 2018).

The *ein6 een* double mutant was first identified as an ethylene-insensitive mutant in the screening of *A. thaliana* mutants with altered ethylene responses. The corresponding gene of *ein6* is *RELATIVE OF EARLY FLOWERING 6* (*REF6*), which encodes an H3K27me3 demethylase, while that of *een* (*enhancer of ein6*) is *INO80 subunit 6* (*IES6*), which encodes a subunit of the INO80 chromatin-remodelling complex (Zander et al., 2019). While *EIN2* expression was induced by ethylene treatment in wild type, *ein6-1* and *een-1* single mutants, *EIN2* was strongly repressed with or without the ethylene treatment in the *ein6-1 een-1* double mutant (Zander et al., 2019). The repression of *EIN2* could be explained by the enrichment of H3K27me3 and H2A.Z, which are directly linked to the functions of REF6 and IES6 (Zander et al., 2019). Although there was no direct report on the roles of REF6 and IES6 in salt stress responses, since EIN2 is essential for salt tolerance (Zander et al., 2019), one cannot rule out the possibility that REF6 and IES6 are also involved. Therefore, this requires further investigation.

6 | FUTURE PERSPECTIVES

Current studies of histone modifications and chromatin remodelling in plant responses to salt stress have still mostly been done in the model plant *A. thaliana*. Crop genomes are usually much more complicated than that of *A. thaliana* in terms of the epigenome, especially those that have recently experienced whole-genome duplication or exhibit polyploidy (Concia et al., 2020; Zhang et al., 2019). Moreover, specific mutants of histone-modifying enzymes, histone variants, histone chaperones and chromatin-remodelling factors are often not readily available in most crop species. Thus, the translation of knowledge from *A. thaliana* to crops for basic research and real-life application is still challenging.

Genome-wide analyses of chromatin structures using next-generation sequencing have been useful in mapping the distribution of histone variants or modified histones under salt stress using ChIP-seq or ChIP-chip. Also, chromatin accessibility can be comprehensively assessed by DNase-seq, MNase-seq, ATAC-seq and FAIRE-seq. To add to the knowledge on the global trends of epigenetic mark alterations reported in published studies, future analyses should focus on integrating the epigenetic marks with transcriptional profiles to dissect the complex gene networks regulating salt stress responses. Moreover, there are very few studies on the specific DNA sequences or protein determinants responsible for the locus-specific histone modifications or chromatin remodelling under salt stress. One example is a study that reported that the transcriptional co-activator *ALTERATION DEFICIENCY IN ACTIVATION 2b* (*ADA2b*) and *SAGA-ASSOCIATED FACTOR 29a* (*SGF29a*), which are the components of the

GCN5 complex, were involved in mediating salt stress responses in *A. thaliana* (Kaldis et al., 2011). Another example is one that showed that the histone deacetylase OsHDA1 is recruited to repress *OsSOS1* in rice through interacting with the recruiter INDETERMINATE SPIKELET1 (OsIDS1) (Cheng et al., 2018). In addition, the discovery of protein readers of histone modifications could enhance our understanding of the mechanisms by which salt-induced changes in these marks regulate gene expressions and chromatin status. In soybean, it was reported that the PLANT HOMEODOMAIN 5 (GmPHD5) protein, which reads H3K4me2 could also interact with a histone acetyltransferase and the Soybean IMITATION SWITCH (GmISWI) protein (Wu et al., 2011). GmPHD5 was also reported to bind to the salt-responsive genes *GmRD22* and *GmGST* (Wu et al., 2011). Also, the overexpression of GmPHD6, which reads histone H3K4me0/1/2, decreased the soybean sensitivity to salt stress (Wei et al., 2017). Additionally, PLANT HOMEODOMAIN 6 (GmPHD6) was shown to interact with the co-factor LIKE HETEROCHROMATIN PROTEIN 1 (LHP1-1/2) to activate gene expressions under salt stress (Wei et al., 2017). Future studies should expand the research to the protein readers of other histone modifications.

Moreover, plants normally receive short-term stress treatments in mechanistic studies. However, crops planted in the salt-affected field are subjected to such stress for the whole life cycle and into subsequent generations. Several studies have addressed the histone modifications constituting the transcriptional memory over a longer period (Feng et al., 2016; Sani et al., 2013). Also, epigenetic changes were assessed in the progeny of *A. thaliana* exposed to salt stress for three weeks (Bilichak et al., 2012). In that study, alterations in H3K9ac and H3K9me2 levels were identified at the genes that regulate epigenetic pathways, suggesting the existence of a self-regulating mechanism (Bilichak et al., 2012). However, whether changes in histone modifications can also be found at genes involved in salt tolerance and inherited to the next generation require further investigation by prolonged salt treatment over the whole life cycle.

Epigenetic marks have been demonstrated to be associated with the selection of important agricultural traits (Hauben et al., 2009). In canola, epigenetic variations among the isogenic population of a commercial breeding line were linked to variations in energy use efficiency and drought tolerance. By selecting individuals with high performance over generations, the epigenome could be fixed to facilitate the expression of drought-responsive genes, suggesting that epigenetic loci could be traced during crop breeding (Verkest et al., 2015). Also, genes with alterations in chromatin status under salt stress are potential targets of genome editing by CRISPR-Cas9 systems in the future development of salt-tolerant crops. In addition, CRISPR-based technologies with the incorporation of modification enzymes could facilitate editing of locus-specific epigenetic status to modulate expression of key genes involved in salt tolerance (Roca Paixao et al., 2019).

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Hon-Ming Lam conceived the work. Wai-Shing Yung, Man-Wah Li, Ching-Ching Sze and Qianwen Wang drafted the manuscript. Hon-Ming Lam, Wai-Shing Yung, and Man-Wah Li wrote the final manuscript.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analysed in this study.

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