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Redox regulation of chromatin remodelling in plants

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Abstract

Changes in the cellular redox balance that occur during plant responses to unfavourable environmental conditions significantly affect a myriad of redox-sensitive processes, including those that impact on the epigenetic state of the chromatin. Various epigenetic factors, like histone modifying enzymes, chromatin remodelers, and DNA methyltransferases can be targeted by oxidative post-translational modifications. As their combined action affects the epigenetic regulation of gene expression, they form an integral part of plant responses to (a) biotic stress. Epigenetic changes triggered by unfavourable environmental conditions are intrinsically linked with primary metabolism that supplies intermediates and donors, such acetyl-CoA and S-adenosyl-methionine, that are critical for the epigenetic decoration of histones and DNA. Here, we review the recent advances in our understanding of redox regulation of chromatin remodelling, dynamics of epigenetic marks, and the interplay between epigenetic control of gene expression, redox signalling and primary metabolism within an (a)biotic stress context.

KEYWORDS
abiotic stress, epigenetics, redox signalling

1 | INTRODUCTION

Nuclear gene expression is drastically altered when plants are facing abiotic and biotic stresses. A complex interplay between general transcriptional complexes, RNA polymerases, transcription factors (TFs), and cis-regulatory promoter elements create cooperative feedforward and feedback regulatory circuits that reshape the transcriptional landscape to adapt to the adverse environment (Ding et al., 2020). Transcript stability, translational control, and protein turnover add further regulatory levels to fine-tune protein and metabolite abundances (Nouaille et al., 2017; Teixeira and Lehmann, 2019). Although often overlooked, transcriptional activity is largely affected by the chromatin state. The chromatin consists of genomic DNA wrapped around histone proteins and is essential for packaging and protecting the genomic information. Apart from underlying the activity of the transcriptional machinery, chromatin state is vital for DNA replication, repair, and recombination, which are not only implicated in plant growth and development, but also in acclimation to adverse environmental conditions (Pedroza-Garcia et al., 2022). In a silent status, the chromatin has a compact structure and represents an obstacle to the transcriptional machinery that needs to be dynamically rearranged to allow access to those genomic regions encoding for the proteins that are crucial for launching and execution of developmental and defence programs (Gan et al., 2021; Seni et al., 2023; Wang et al., 2023). In general, the chromatin structure is shaped by the combined activity of enzymes that methylate DNA, deposit histone variants, use energy from ATP to disrupt chromatin-DNA interactions and covalently modify the nucleosome core histone proteins H2A, H2B, H3, and H4 (Long et al., 2023; Shang and He, 2022). These histones proteins can be acetylated, methylated, phosphorylated, ubiquitinated, ADP-ribosylated, crotonylated, butyrylated and

sumoylated, to name only the most prominent modifications (Zhao and Garcia, 2015). These histone marks occur at particular sites (usually at the protruding N-terminal histone tails) and their pattern and genome-wide distribution underlies specific transcriptional effects. The wide range of possible histone patterns potentially allows the existence of a myriad signalling mechanisms that can have either positive or negative effect on gene expression. For example, acetylation of lysine residues which is one of the most abundant and well-studied histone modifications neutralises the negative histone charges which relaxes the chromatin structure and is associated with transcriptionally active chromatin (Shvedunova and Akhtar, 2022). The physiochemical consequences of histone methylation are less understood and can have both positive and negative effects on gene expression (He et al., 2021).

A common theme between (a)biotic stresses is the perturbation of the cellular redox homoeostasis that reflects the combined changes in production and scavenging of reactive oxygen species (ROS) and disruption of the balance of redox couples such as NAD(P)(H)/NAD(P)+, glutathione (GSH/GSSG), and ascorbate (ASC/DHA) (Devireddy et al., 2021; Fichman et al., 2023). Redox-active cysteine residues are the main targets of ROS such as hydrogen peroxide (H_2O_2) which initiates signalling cascades that relay information about the cellular redox status (García-Santamarina et al., 2014). Previous transcriptome studies have extensively documented changes in gene expression associated with specific ROS types, such as H_2O_2 or singlet oxygen ($^1O_2$), and their subcellular production sites (Laloi et al., 2007; Queval et al., 2012). Distinct ROS transcriptional footprints can be identified during abiotic and biotic stress conditions further corroborating the central role of redox signalling in gene expression (Rosenwasser et al., 2013; Willems et al., 2016). These insights mainly originate from studies with Arabidopsis mutants with disrupted redox homoeostasis and chemical treatments leading to excess production of ROS in specific organelles. Unfortunately, such experimental model systems have not been used until now to characterise the impact of ROS on the epigenetic landscape in plants with methods such as ChIP-Seq, bisulfite sequencing, or CUT& Tag. However, despite the limited information on chromatin remodelling during abiotic stresses, it is clear that histone marks, DNA methylation, and histone variants are dynamically regulated under stress conditions and functionally implicated in plant stress responses.

Here, we summarise the state-of-the art knowledge of how perturbations of the redox homoeostasis impact chromatin remodelling and thereby affect biological processes coordinated at the epigenetic level. We discuss cases of oxidative posttranslational modifications on epigenetic regulators that might directly affect their activity and/or stability alongside the integration of the cellular redox homoeostasis and metabolism that orchestrate DNA and histone methylation, as well as histone acetylation in plants.

1.1 | Dynamics of the epigenetic landscape during (a)biotic stress

Covalent histone modifications are deposited by enzymes commonly referred to as "writers", while "erasers" can enzymatically remove the modifications. The combined activity of "erasers" and "writers" provides a versatile way for dynamically decorating the histone cores and regulating gene expression by controlling the persistence and genome-wide distribution of histone marks. Histone acetylation and deacetylation of lysine residues is catalysed by histone acetyltransferases (HATs) and histone deacetylases (HDAs), respectively. Similarly, histone methylation marks (at lysine and arginine residues) are deposited by histone methyltransferases (HMTs) and removed by histone demethylases (HDM). Summarising the numerous functional studies on individual chromatin modifiers that have revealed versatile and often pleiotropic effects on plant growth, development and defence is outside the scope of this review (Kim et al., 2018; Li et al., 2020; Mozgová et al., 2017; Zheng et al., 2021). Here, we summarise how the abundance and genome-wide distribution of histone marks and DNA methylation is altered during unfavourable environmental conditions.

1.1.1 | Histone acetylation

The profound impact of (a)biotic stresses on gene expression also entails changes in the transcript abundances of genes encoding chromatin modifying enzymes. Interestingly, among the early (30 and 60 min) photosynthetically redox-regulated genes in *Arabidopsis* were transcripts of histone acetyltransferases and histone deacetylases suggesting that rearrangement of the epigenetic landscape is likely implicated in the redox control of nuclear gene expression (Dietzel et al., 2015). The histone acetyltransferase *GENERAL CONTROL NON DEREPRESSIBLE 5* (*GCN5*) accumulated in maize seedlings exposed to heat stress, whereas the expression of histone deacetylase *HDAC101* was repressed (Wang et al., 2015). This was accompanied with increase of H3K9ac and H4K5ac acetylation marks and depletion of dimethylation on H3K9 (Figure 1). Similarly, salt-treated maize plants showed enhanced expression of two histone acetyltransferases (*ZmGCN5* and *ZmHATB*) and elevated histone acetylation marks H3K9ac and H4K5ac (Li et al., 2014). Apart from regulating gene expression by depositing activating histone acetylation marks, an alternative role of GCN5 and potentially other histone modifying enzymes can be glimpsed from a study in yeast where induction of the H_2O_2-responsive heat shock protein HSP12 by GCN5 relied on recruitment of chromatin remodelling complexes in addition to its histone acetyltransferase activity (Antonazzi et al., 2021). The histone deacetylase *HDT701* in rice is transcriptionally upregulated upon infection with the fungal pathogen *Magnaporthe oryzae* (Ding et al., 2012). Silencing of *HDT701* in transgenic rice caused elevated levels of histone H4 acetylation and enhanced generation of ROS upon treatment with the pathogen-associated molecular pattern elicitors chitin and flg22. HDT701 is likely to modulate ROS production by targeting the promoter region of *SGT1*, an important component of plant immunity which regulates NADPH oxidase activity required for H_2O_2 production. Incubation of *Arabidopsis* tissue cultures with trichostatin A, a histone deacetylase inhibitor, resulted in ROS accumulation which was more pronounced under stress conditions

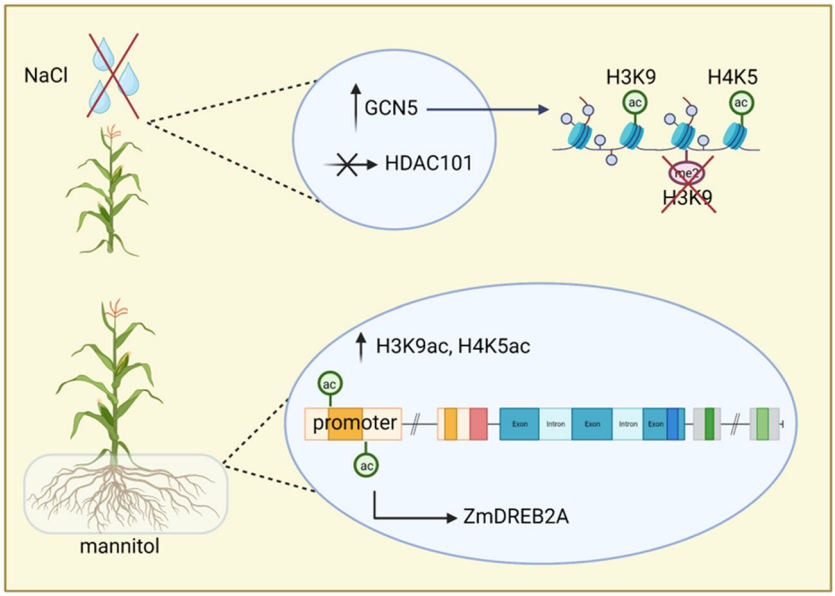

FIGURE 1 Impact of abiotic stress conditions on the transcript abundances of histone acetyltransferase *GENERAL CONTROL NON DEREPRESSIBLE 5 (GCN5)* and histone deacetylase *HDAC101* and deposition of histone acetylation (ac) and methylation (me) marks (Wang et al., 2015; Zhao et al., 2014). Figure created with BioRender. com.

further corroborating the role of histone deacetylases in modulation of the cellular redox homoeostasis (Jadko, 2015).

Changes of global histone acetylation patterns induced by various stresses largely entail accumulation of histone H3 and H4 acetylation marks (Hu et al., 2019). For example, histone H3K9ac and H4K5ac marks increased upon mannitol treatment in maize, but interestingly, this effect was only observed in root tissues (Zhao et al., 2014). Their deposition was specifically observed in the promoter region of the osmotic stress responsive gene *ZmDREB2A* which likely promotes its increased expression in the presence of mannitol (Figure 1). Even though it is largely assumed that histone acetylation is essential for activation of gene expression, the precise sequence of events and causal relationship between chromatin changes and transcriptional activation under stress is still a matter of debate (Asensi-Fabado et al., 2017). Moreover, information about global histone acetylation levels can be convoluted since acetylation of discrete genome locations important for stress responses does not always correlate with the global amount of histone acetylation marks. For example, exposure of rice plants to cold had no effect on global H3K9ac and H3K27ac levels and led to a decrease of H3K14ac (Roy et al., 2014). Nevertheless, the locus encoding *OsDREB1b*, a major transcription factor that regulates cold responses, was enriched with all three histone acetylation marks. In rice plants undergoing starvation induced by prolonged darkness over 1000 genes had increased levels of H3K9ac, whereas over 2000 genes displayed decreased deposition of H3K9ac (Lu et al., 2018). In addition to acetylation, H3K9 can also be subjected to crotonylation (cr) and butyrylation (bu), and even though these two marks overlap with H3K9ac in target sites, their deposition seems to be less dynamic than H3K9ac. The submergence marker *Sub1C* can be decorated with all three marks (H3K9ac/cr/bu) suggesting an interplay between them (Lu et al., 2018).

Histone posttranslational modifications are predominantly enriched in genic regions although they can also be found at *cis*-regulatory elements, such as enhancers (Calo and Wysocka, 2013). In *Paulownia*, histone marks H3K9ac, H3K36me3, and H3K4me3 were found distributed mainly among promoters, 5′UTRs, 3′UTRs, CDS and introns. Interestingly, H3K9ac and H3K4me3 were similarly distributed between CDS and introns, while deposition of H3K36me3 was more common at introns. Phytoplasma infection on *Paulownia* caused changes in the distribution of histone marks H3K9ac and H3K4me3 (Yan et al., 2019).

In summary, the above examples highlight the significant impact of stress responses on histone-modifying enzymes, leading to widespread epigenetic changes. Changes of histone acetylation marks observed under stress ultimately reflect alterations of histone acetyltransferase and deacetylase activities which can entail transcriptional regulation. As described further, histone modifying enzymatic activities are also be fine-tuned by posttranslational modifications (PTMs) thereby adding another layer of complexity to epigenetic control mechanisms.

1.1.2 | DNA methylation

Changes in DNA methylation have been observed following various abiotic stresses and oxidative stress treatments (Zhang et al., 2018). Transgenic tobacco plants overproducing H_2O_2 were used to assess whole-genome DNA methylation changes using bisulfite sequencing (Villagómez-Aranda et al., 2021). Even though the study revealed a trend toward hypomethylation, the overall impact on distribution and global DNA methylation levels was minimal which could reflect an adaptation to the constitutively high H_2O_2 levels. The effects were pronounced following incubation of tobacco BY-2 cell suspension culture with the oxidative stress promoting cytotoxic metabolite juglone which caused global DNA hypomethylation (Poborilova et al., 2015). Paraquat-induced oxidative stress in tobacco led to DNA demethylation of a genomic region coding for a stress responsive

glycerophosphodiesterase-like protein which was accompanied with increased expression levels (Choi and Sano, 2007). Salt and low temperature treatment resulted in a similar demethylation pattern suggesting that ROS accumulation is likely a primary trigger of DNA demethylation. Rice seedlings exposed to the NO donor sodium nitroprusside (SNP) displayed DNA hypomethylation changes and altered expression of major chromatin remodelling and DNA methylation players (Ou et al., 2015). UV-induced DNA hypomethylation was also observed in Arabidopsis and *Artemisia annua* (Jiang et al., 2021; Pandey and Pandey-Rai, 2015). Cold exposure decreased DNA methylation in maize roots and induced demethylation of the promoters of important stress regulated genes in rice and *Hevea brasiliensis* (Steward et al., 2002; Guo et al., 2019; Tang et al., 2018). Heat stress resulted in genome-wide DNA hypomethylation in *Brassica napus* and soybean (Hossain et al., 2017; Li et al., 2016). DNA demethylation under heat stress is most probably not a random process and has been shown to occur as specific loci in *Arabidopsis* (Korotko et al., 2021).

Oxidative stress triggered DNA hypomethylation likely involves negative regulation of crucial redox-sensitive components involved in SAM synthesis which serves as a methyl donor for DNA methyltransferases as described below. Such regulation is likely to lead to global and indiscriminate changes in the DNA methylation patterns. However, specific mechanisms unrelated to perturbations of the cellular redox homoeostasis leading to DNA methylation changes have also been reported. In *Arabidopsis* plants exposed to UVB radiation, the UVB photoreceptor UVR8 interacts with DNA methyltransferase (DRM2) and inhibits its methyltransferase activity (Jiang et al., 2021). Intriguingly, transposons with high DNA methylation are more sensitive to UVB radiation. Even though similar mechanistic insights for inhibition of DNA methylation under other abiotic stresses are currently lacking, it is highly possible that such mechanisms operate alongside the redox-sensitive perturbation of SAM metabolism.

1.1.3 | Histone methylation

Histone methylation and demethylation on lysine and arginine residues of histone H3 and H4 are actively involved in response to environmental stimuli. In contrast to histone acetylation that is linked to actively transcribed genomic regions, histone methylation which can occur as mono- (me1), di-(me2), and trimethylation (me3) can have varying effects on gene expression depending on the site and methylation pattern (Cheng et al., 2020; Liu et al., 2010). Tri- and dimethylation of H3K27 and H3K9, respectively, are associated with silenced genomic regions, whereas H3K4me3 and H3K36me3 activate gene expression (Liu et al., 2010). The various examples described below give rather complex and species-specific insights into the regulation of histone methylation under adverse environmental conditions. Soybean plants exposed to salinity displayed accumulation of the histone methylation marks H3K4me2 and H3K4me3 (Yung et al., 2022). Similarly, the levels of H3K4me2 in maize increased under heat stress (Hou et al., 2019). On the contrary, heat stress resulted in depletion of the H3K9me2 mark in *Arabidopsis* (Pecinka et al., 2010). Interestingly, self-grafting in tomato plants that led to acquisition of drought tolerance was accompanied with deposition of H3K4me3 and H3K27me3 marks on the majority of differentially methylated genes (Fuentes-Merlos et al., 2023). The accumulation of these histone marks can be partially governed by perturbations of the cellular redox homoeostasis triggered by the wounding process. In fact, a rapid systemic signal whose propagation depends on ROS accumulation mediated by the respiratory burst oxidase homologue D (RbohD) gene is triggered by wounding (Miller et al., 2009).

Although studies on genome-wide changes of histone marks and DNA methylation patterns in plants exposed to unfavourable environmental conditions give us a glimpse in the regulation of the epigenetic landscape, a significant part of the information is likely obscured by the use of whole seedlings. Readouts from individual cell and tissue types and discrete genome locations will be needed to fully understand the exact molecular mechanisms. Even though quantification of histone marks can be challenging and requires large amount of material especially for mass spectrometry-based methods that allow systemic and unbiased simultaneous detection of multiple histone marks, assessing the DNA methylation landscape in specific cell types is technically feasible by either combining the Isolation of Nuclei in Tagged Cell Types (INTACT) method with whole-genome bisulfite sequencing or single cell DNA methylation profiling (Deal and Henikoff, 2011). Targeting histone modifying enzymes or DNA (de)methyltransferases to specific genome locations using nuclease-dead Cas molecules can be another way to explore the functional links between chromatin remodelling and stress responses.

1.2 | Redox regulation of histone modifying enzymes, DNA methyltransferases, and chromatin remodelers

The exploration of how adverse environmental conditions impact nuclear redox homoeostasis, including regulatory mechanisms and alterations, is an ongoing area of research. The presence of enzymatic and nonenzymatic antioxidants in the nucleus points toward an actively regulated process rather than a mere reflection of the global cellular redox homoeostasis (He et al., 2018). For example, following ROS induced DNA damage, the antioxidant enzyme peroxiredoxin 1 (PRDX1) is recruited to the nucleus. This happens mainly during the G2 phase of the cell cycle which correlates with elevated ROS levels (Kirova et al., 2022; Moretton et al., 2023). Interestingly, in plants H_2O_2 can be directly transferred from chloroplasts to the nucleus (Exposito-Rodriguez et al., 2017; Foyer and Hanke, 2022). Ultimately, changes of the nuclear redox homoeostasis can impact not only redox-regulated epigenetic enzymes as described below, but essentially all redox-active nuclear proteins including TFs (Figure 2).

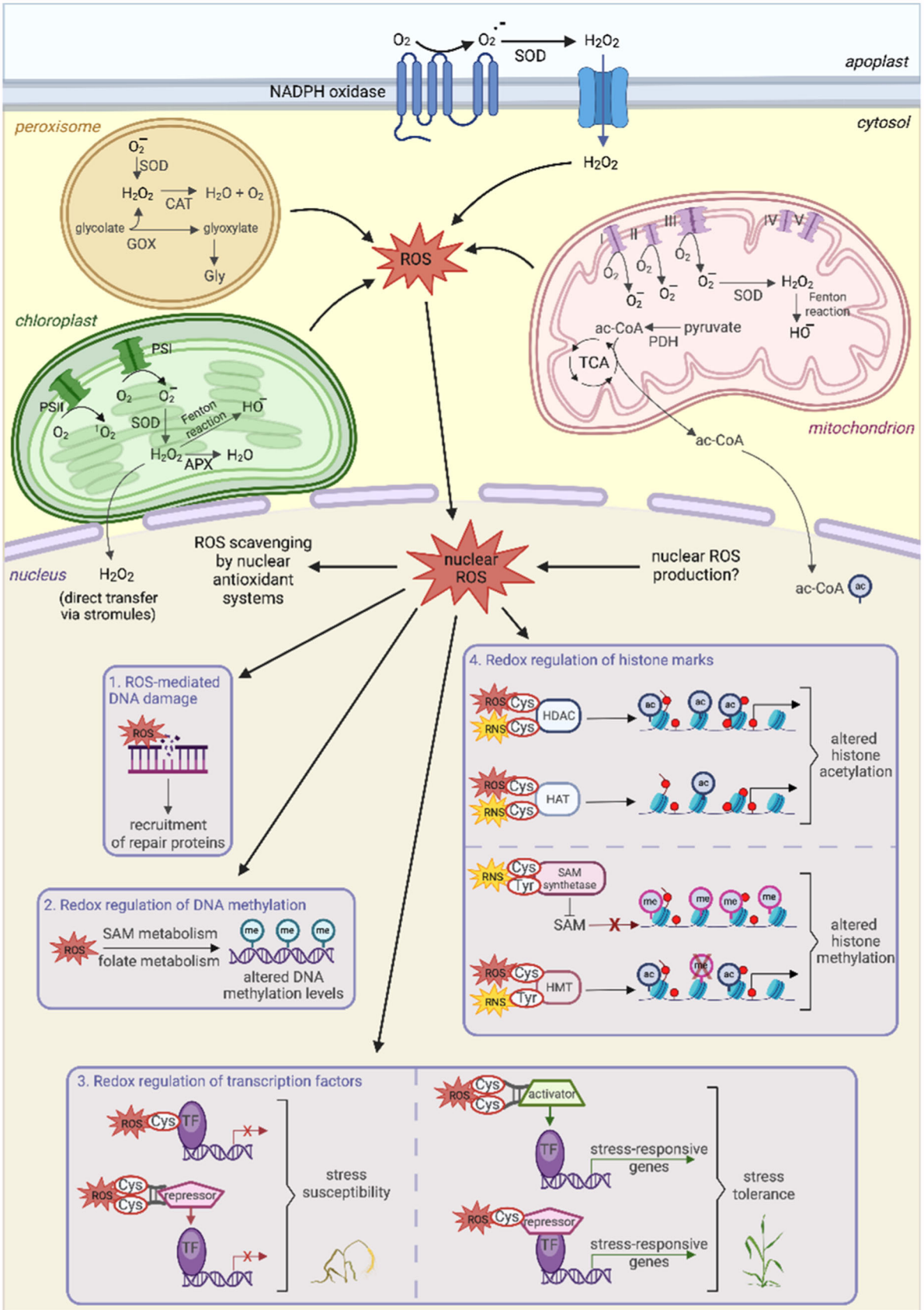

FIGURE 2 (See caption on next page).

1.2.1 | Oxidative posttranslational modification of histone deacetylases

Direct redox regulation of chromatin modifying enzymes has been mainly described in animal systems but experimental evidence for oxidative posttranslational modification of epigenetic enzymes in plants is slowly accumulating. Redox-active cysteine or tyrosine residues are likely to be the hot spots for oxidative posttranslational modifications. Given the high evolutionary conservation of many chromatin modifying enzymes, such regulation is likely to occur more often in plants than currently thought. For example, both *Arabidopsis* HDA6 and its closest human ortholog HDAC2 are direct targets of NO (Ageeva-Kieferle et al., 2021; Ito et al., 2004). NO-mediated modifications of *Arabidopsis* HDAs inhibit their enzymatic activity resulting in accumulation of acetylation marks on stress-responsive genes (Mengel et al., 2017). Treatment of *Arabidopsis* with S-Nitrosoglutathione (GSNO), the principal bioactive form of NO, led to accumulation of H3K9ac in the wild type, but did not affect the abundance of this histone mark in mutant plants deficient in HDA6 activity (Ageeva-Kieferle et al., 2021). Intriguingly, HDA6 acts as a molecular switch that regulates the metabolic flux from glycolysis into acetate synthesis which stimulates jasmonate (JA) signalling and enhances drought tolerance (Kim et al., 2018). Exogenous treatment with acetic acid results in activation of JA synthesis and deposition of histone H4 acetylation marks, which correlates with increased drought tolerance in a range of plant species. Whether NO-mediated HDA6 modifications play a role in drought response will be interesting to explore. Since tyrosine nitration of the human ortholog HDAC2 reduces its histone deacetylase activity and results in hyperacetylation and activation of gene expression, a similar scenario can be envisaged in plants (Ito et al., 2004).

Application of salicylic acid (SA) activates plant defence and leads to perturbation of the cellular redox homoeostasis making it a good model system to identify redox-sensitive proteins involved in plant immunity. *Arabidopsis* HDA19 and HDA9 have been found among the proteins oxidised upon treatment of suspension cells with SA in an Oxi-TRAQ-based proteomics study (Liu et al., 2010). *Arabidopsis* HDA19 is also S-nitrosylated upon treatment with SA and the catalase inhibitor 3-amino-1,2,4-triazole (Zheng et al., 2023). Although HDA19 has four cysteines which can potentially be S-nitrosylated, only Cys137 has been shown to play a role in plant development and stress responses. The stress-induced S-nitrosylation promotes the nuclear sequestration of HDA19, stimulates its deacetylase activity, and preferential removal of the H3K14 mark at its target loci which are enriched in oxidative stress-induced genes both under normal and stress conditions (Zheng et al., 2023). Intriguingly, plants deficient in HDA19 accumulate SA, display enhanced expression of pathogenesis related (*PR*) genes, and increased resistance to the biotrophic pathogen *Pseudomonas syringae* (Choi and Sano, 2007). HDA19 targets the promoter regions of *PR1* and *PR2* which are hyperacetylated in the *hda19* mutant background. Taken together, these findings point towards a role of HDA19 in repression of SA-mediated defence response by maintaining a repressive chromatin state. Even though it is tempting to speculate that a single oxidative posttranslational modification at HDA19 can modulate the SA signalling pathway, the reality is likely more convoluted and numerous regulatory layers probably contribute to activation and repression of defence pathways and their integration with growth and developmental processes. For example, mutants lacking the histone acetyltransferase GCN5 also accumulate SA and show enhanced resistance *P. syringae* (Kim et al., 2020). GCN5 in *Arabidopsis* is part of the evolutionary conserved SAGA complex, but at the same time is present in the plant specific PAGA complex (Wu et al., 2023). PAGA and SAGA mediate moderate and high levels of histone acetylation, respectively and display antagonistic regulation of gene expression incl. *PR* genes.

Examples from mammalian systems can offer a glimpse into other possible scenarios of oxidative posttranslational modifications of epigenetic enzymes and their impact. Mammalian HDAC4, for example, forms an intramolecular disulphide bridge under oxidative stress promoting conditions which underlies its exclusion from the nucleus in cardiac muscle cells (Ago et al., 2008). The interplay between oxidation and phosphorylation of HDAC4 modulates its protein-protein interaction with Mef2A, a transcription factor essential for activating stress-responsive genes in endothelial cells. The oxidation of HDAC4 mediated by H_2O_2 led to its phosphorylation, resulting in the dissociation of the complex between HDAC4 and Mef2A (Schader et al., 2020).

1.2.2 | Oxidative posttranslational modification of histone (de)methyltransferases

The histone methyltransferase MLL1 from *Caenorhabditis elegans* is inhibited in the presence of H_2O_2 (Bazopoulou et al., 2019). The loss of enzymatic activity is likely contributed to cysteine oxidation since the effect can be reverted in the presence of the thiol-reducing agent dithiothreitol. MLL1 is part of the highly conserved histone methylation complex COMPASS that deposits H3K4me3 marks during early development. H3K4me3 levels remain stable throughout

FIGURE 2 A schematic overview depicting possible mechanisms contributing to the nuclear redox homoeostasis and the impact of reactive oxygen (ROS) and reactive nitrogen (RNS) species on epigenetic enzymes involved in histone (de)acetylation and de(methylation), DNA methylation, and redox-regulated transcription factors. APX, ascorbate peroxidase; CAT, catalase; GOX, glycolate oxidase; HAT, histone acetyltransferase; HDAC, histone deacetylase; HMT, histone methyltransferase; PDH, pyruvate dehydrogenase; POD, peroxidase; SAM, S-Adenosylmethionine; SOD, superoxide dismutase; TF, transcription factor. Figure created with BioRender. com. [Color figure can be viewed at wileyonlinelibrary.com]

life and this mark has been named redox-sensitive because its global levels are depleted by transient ROS increase, which occurs naturally during early development (Bazopoulou et al., 2019). Ultimately, this underlies enhanced stress resistance, improved redox homoeostasis, and prolonged lifespan. This effect is not limited to *C. elegans* and redox-sensitivity of H3K4me3 marks has been also shown in mammalian cell cultures. Several conserved COMPASS subunits have been also identified in *Arabidopsis*. However, whether the *Arabidopsis* COMPASS complex contains subunits that can be redox-regulated remains to be explored.

Arabidopsis PROTEIN ARGININE METHYLTRANSFERASE 5 (PRMT5) performs histone arginine dimethylation and methylation of non-histone proteins and has been implicated in shoot regeneration, flowering time, RNA interference, DNA damage, and stomatal closure (Fu et al., 2013; Liu et al., 2016; Wang et al., 2007). PRMT5 is *S*-Nitrosylated at Cys125, which positively regulates the methyltransferase activity of the recombinant protein (Hu et al., 2017). The accumulation of *S*-Nitrosylated PRMT5 increases under salt stress that is accompanied by an NO burst. Interestingly, complementation of the *prmt5* mutant, which displays developmental defects and hypersensitivity to abiotic stresses, with a construct carrying a mutated cysteine to serine ($PRMT5^{C125S}$) rescued the developmental phenotypes. However, the complementation failed to revert the hypersensitive to NaCl and ABA observed in *prmt5* mutant plants, pointing toward an important role for *S*-nitrosylation of PRMT5 in stress responses. No changes in histone H4R3 symmetric dimethylation were observed under control and salt treatment suggesting that the observed effects are likely due to dimethylation of non-histone proteins, such as key components of the spliceosome (Hu et al., 2017). However, given that many of the PRMT5 related phenotypes are linked to dimethylation of specific gene loci, the role of PRMT5 S-nitrosylation might be worth investigating using more advanced methods.

1.3 | Redox regulation of chromatin remodelers

The chromatin modifier PICKLE has been found to be nitrosylated in Arabidopsis (Lozano-Juste et al., 2011). PICKLE associates with HDA9 which is also likely to be redox regulated as described above and both of them jointly control the abundance of the H3K27ac mark at the loci encoding miR156, a major determinant of juvenile-to-adult phase transition (Hu et al., 2022). Interestingly, PICKLE interacts with ABI5, a central hub repressing growth. ABI5 is also S-nitrosylated at cysteine 153 which destines it for degradation and promotes seed germination (Albertos et al., 2015). Whether the nitrosylation of PICKLE has a regulatory function can only be speculated. Similar to other histone modifying enzymes which have been reported to by nitrosylated, such as histone acetyltransferase HAC12 and HAC2, Histone-lysine N-methyltransferase ASHH2, histone deacetylase 2C and 2B (Chaki et al., 2015; Lozano-Juste et al., 2011), the precise consequences of these oxidative posttranslational modifications remain to be explored. Taken together, the above cases remind us that perturbations of the cellular redox homoeostasis can potentially impact simultaneously multiple redox-sensitive proteins including ones that can also function together in complexes. What could be the interplay between oxidative posttranslational modifications found on interacting proteins is a topic of future interest.

1.4 | Redox-sensitive histone modifications

Apart from the canonical histone marks discussed above, less abundant, and rare modifications can also have biological function. Mammalian histone H3, for example, can be S-glutathionylated at Cys110 during cell proliferation (García-Giménez et al., 2013). S-glutathionylation is a redox-sensitive posttranslational modification that is formed through the reaction between a protein's cysteine residue and glutathione. This modification is removed with the progression of aging leading to changes of nucleosome stability. Given the evolutionary conserved nature of Cys110 of histone H3 (the only histone containing cysteine), it is likely that similar regulation can also occur in plants. Advanced mass spectrometry-based methods that can detect and quantify a wide range of histone modifications in a systemic and unbiased manner will be especially useful to detect not only whether histone H3 can be S-glutathionylated in plants but also the full repertoire of plausible oxidative histone posttranslational modifications (García-Giménez et al., 2021).

1.5 | Interplay between metabolism and epigenetic regulation from a redox perspective

Alterations of major metabolic fluxes (e.g., photorespiration, photosynthesis, and respiration) that accompany stress responses are also intrinsically linked with chromatin remodelling since chromatin modifying enzymes consume central metabolites such as acetyl-CoA, SAM, and ATP. Elevated levels of acetyl-CoA in *Arabidopsis* mutants lacking cytosolic acetyl-CoA carboxylase1 (ACC1) led to histone hyperacetylation at lysine 27 of histone H3 which was dependent on GCN5 (Chen et al., 2017). Apart from showing that histone acetylation is directly related to acetyl-CoA availability, these results hint towards a role in redox homoeostasis because the upregulated genes in the *acc1* mutant background were enriched in reactive oxygen species metabolism category. Nearly all high flux metabolic processes affect the redox homoeostasis and/or possess components that are under redox control. Thus, the impact of primary metabolism of chromatin remodelling can be seen as largely fine-tuned by the cellular redox status. Conversion of pyruvate to acetyl-CoA by the pyruvate dehydrogenase (PDH) complex requires NAD+ which is directly intertwined with the cellular redox homoeostasis. How fine-tuning of PHD activity impacts global histone acetylation in plants remains to be explored.

1.5.1 | SAM metabolism

In animal systems, the availability of SAM that is used in DNA and histone methylation is tightly regulated by the cellular redox state (Lennicke and Cocheme, 2021). The enzymatic activities of methionine synthase (MS) and betaine homocysteine methyltransferase (BHMT) that act on homocysteine, an important intermediate in the methionine cycle leading to SAM production, are inhibited by oxidants (Murray et al., 2015). Whereas evidence for redox regulation of SAM metabolism in plants has yet to be unequivocally shown and not all components are conserved between plants and animals, it is expected that some of the enzymes might be similarly regulated (Shen et al., 2016). Following treatment of *Arabidopsis* cell suspension cultures with the NO donor S-nitrosoglutathione and whole plants with gaseous NO, important players in methionine and SAM metabolism (S-adenosyl-L-homocysteine hydrolase, METHIONINE SYNTHESIS (METS1), and S-ADENOSYLMETHIONINE SYNTHETASE 3 (SAM3)) have been shown to undergo S-nitrosylation of cysteine residues (Lindermayr et al., 2005). The degree of S-nitrosylation on S-adenosyl-L-homocysteine hydrolase was found to increase upon cold exposure in *Arabidopsis* (Puyaubert et al., 2014). METS1 has also been shown to undergo thiolation upon oxidative treatment (Dixon et al., 2005). The enzymatic activity of recombinant *Arabidopsis* SAM1 is inhibited by GSNO, whereas the other two *Arabidopsis* isoforms SAM2 and 3 were not significantly affected by pretreatment with GSNO (Lindermayr et al., 2006). Interestingly, *S*-nitrosylation of SAM1 happens at Cys114 which is absent in SAM2 and 3, further corroborating the idea that a reversible inhibition of SAM1 might be regulating the metabolic flux leading to SAM production that is directly linked to DNA and histone methylation. Apart from *S*-nitrosylation, tyrosine nitration of METS1 (at tyrosine 287), SAM1 and 2, and S-adenosyl homocysteine hydrolase has been also reported (Chaki et al., 2009; Lozano-Juste et al., 2011). Incubation of sunflower hypocotyls with different concentrations of the peroxynitrite-generating agent (3-morpholinosydnonimine) resulted in a dose-dependant inhibition of extractable *S*-adenosyl homocysteine hydrolase activity (Chaki et al., 2009). The effects of S-nitrosylation and tyrosine nitration on enzymatic activity and/or protein stability remains to be further elucidated and confirmed especially *in planta*. Site-directed mutagenesis of putative redox-active amino acid residues identified in high-throughput screening approaches or in vitro studies will be especially revealing.

Overexpression of METS1 promoted genome-wide DNA methylation and repressed plant immunity (Gonzalez and Vera, 2019). METS1 activity is dependent on folate which is supplied by the folate biosynthetic pathway. Interestingly, disruption of the folate biosynthetic pathway in Arabidopsis that supplies one-carbon (C1) units essential for major metabolic pathways incl. methionine biosynthesis led to activation of a primed immune state (Gonzalez and Vera, 2019). Taken together, these findings suggest a mechanism of fine tuning of DNA methylation by the metabolic flux of folate biosynthesis that shapes an effective response to pathogen attack. The link between folate metabolism and DNA methylation is further corroborated by findings that treatment of *Arabidopsis* with sulfamethazine, an inhibitor of folate biosynthesis that depletes the folate pool, decreases DNA methylation (Zhang et al., 2012). Moreover, in line with the role of SAM as a methyl-donating substrate for histone methyltransferases, reduced levels of H3K9me2 were also observed after impairing folate synthesis. Intriguingly, folate metabolism has been linked to the cellular redox pool via its production of NADPH released by the enzyme methylenetetrahydrofolate dehydrogenase (MTHFD). Similar mechanism exists in animal cells where depletion of MTHD leads to oxidation of the NADPH and GSH pools and increased sensitivity to oxidative stress (Fan et al., 2014). While the importance of folate metabolism for producing one-carbon units essential for cellular metabolism has long been recognised, its function as a nexus between epigenetic modulation and redox homoeostasis merits further investigation.

1.5.2 | NAD+ metabolism

Many fundamental metabolic processes in plants depend on the pyridine nucleotides NAD(H) and its derivative NADP(H). They serve as primary electron carries in myriad redox reactions playing central roles in plant growth, development, and defence. The ratio between their reduced and oxidised forms is a major determinant of the cellular redox homoeostasis and is tightly intertwined with the antioxidant machinery. NAD+ is used as a substrate by poly ADP-ribose polymerases (PARPs) that catalyse the addition of ADP ribose to their targets among which are DNA and histone proteins. PARPs have been extensively studied in mammals where they have been implicated in DNA repair, chromatin remodelling, protein degradation, and cell death, but their roles in plants have also attracted attention (Perina et al., 2014). Plant histones rich in lysines (H1, H2A, and H2B) are preferred targets of PARPs (Willmitzer, 1979). The involvement of the three canonical PARPs in *Arabidopsis* have been predominantly studied in DNA damage response pathways. In particular, AtPARP1 and AtPARP2 are activated following treatment with DNA damaging agents, whereas AtPARP3 might not be involved in the process (Gu et al., 2019). Intriguingly, *AtPARP3* transcriptions peaks during ROS accumulation in embryo development and seeds of plants lacking PARP3 activity display low viability after aging (Rissel et al., 2014). It is tempting to speculate that the levels of poly(ADP-ribose) marks deposited during seed germination are orchestrated by ROS levels. The involvement of AtPARP3 in poly(ADP-ribosyl)ation, its targets, and related molecular mechanisms are still to be explored.

In humans, deposition of DNA methylation by the DNA methyltransferase DNMT1 is modulated by the activity of PARP1 with activation of ADP-ribosylation preserving the unmethylated status of discrete genomic regions (Caiafa et al., 2009). This functional interplay is likely to be fine-tuned by the cellular redox homoeostasis since DNA methylation is redox-dependent as described above. Interestingly, treatment of *Pisum sativum* (garden pea) cell cultures with nicotinamide, which acts as a PARP1 inhibitor, had a global DNA hypomethylating effect (Berglund et al., 2017).

The NAD+ pool is rapidly consumed by the PARP activity under stress conditions and rewiring cellular metabolism for *de novo* synthesis and activation of the NAD+ salvage pathway depletes the cellular ATP content and disrupts energy homoeostasis (Noctor et al., 2006). Maintaining stable NAD+ levels upon stress exposure by blocking PARP activity either pharmacologically or genetically and by overproduction of NAD+ results in increased (a)biotic stress tolerance (Block et al., 2005; Pétriacq et al., 2016; Schulz et al., 2012). NAD+ acts as a substrate for a class of evolutionary conserved NAD+ -dependent histone deacetylases and their activity is dependent on the NAD+ levels and NADH/NAD+ ratio. In rice, sirtuin OsSRT1 represses glycolysis by removing H3K9ac found of glycolytic genes but also by deacetylating and thus controlling the nuclear accumulation of the glycolytic enzyme glyceraldehyde-3-phosphate dehydrogenase (GAPDH) that is enriched on glycolytic genes promoters and stimulates their expression as a part of its moonlight function (Zhang et al., 2017). Interestingly, the enzymatic activity of GAPDH in Arabidopsis is inhibited by NO in crude cell culture extracts (Lindermayr et al., 2005). The interconnectedness and dependency on common substrates (NAD+ and acetyl-CoA) makes disentangling the interplay between glycolysis, NAD+, and redox metabolism on one hand, and epigenetic modifiers on the other hand, especially challenging. As a result, perturbations of individual components are likely to have broad, systemic effects propagated at the metabolic and epigenetic levels.

1.6 | Impact of chromatin dynamics on ROS homoeostasis

Transcriptional reprogramming following exposure to adverse environmental conditions reflects the coordinated activity of myriad signalling cascades that ultimately promote or suppress gene expression through the combined activity of TFs and epigenetic components. Transcriptional coactivator complexes, such as the evolutionary conserved SAGA complex, are important regulators of gene expression that recognise and alter the epigenetic landscape and interact with TFs. The SAGA complex regulates transcription of thousands of genes, and in *Arabidopsis* has been proposed to integrate developmental and stress programs (Kim et al., 2020). Intriguingly, the histone acetyltransferase TaHAG1 in bread wheat, a putative ortholog of the SAGA subunit GCN5 in *Arabidopsis*, binds to genomic regions situated near the transcriptional start sites (TSSs) of three out of the four respiratory burst oxidase genes responsible for H_2O_2 production (Zheng at al., 2021). Salt stress treatment significantly enriched the occupancy of TaHAG1 at the TSSs regions and led to accumulation of histone marks H3K9ac and H3K14ac. The stress-induced changes of *TaHAG1* occupancy and deposition of acetylation marks at H3 exemplify a potential mechanism for control of ROS homoeostasis via transcriptional activation of H_2O_2 producing genes that operates at the epigenetic level. The elevated H_2O_2 levels were positively associated with increased tolerance to salt stress in wheat accessions with varying ploidy. Modulation of the redox homoeostasis was not limited to enhanced H_2O_2 content but was also reflected at the level of the major antioxidant enzymes superoxide dismutase (SOD), ascorbate peroxidase (POD), and catalase (CAT). Salt-triggered increase of their enzymatic activities was significantly higher in lines overexpressing *TaHAG1* and in hexaploid wheat that displays elevated TaHAG1 transcripts in comparison to the tetraploid accession. Given that SAGA associates with thousands of genes, it is not unlikely that other important players involved in ROS scavenging or production could be similarly regulated at the epigenetic level.

TaHAG1 has also been shown to modulate the levels of H_2O_2 during powdery mildew infection on wheat plants (Song et al., 2022). Both *TaHAG1*-RNAi and *TaHAG1* knockout lines accumulated significantly lower H_2O_2 and SA amounts upon pathogen attack, whereas their levels were much higher in plants overexpressing *TaHAG1*. The enhanced ROS content during infection was attributed to increased expression of *TaPAD4*, a crucial component of plant immunity required for H_2O_2 and SA accumulation (Bernacki et al., 2019). TaHAG1 physically interacts with TaPLATZ5, a plant-specific zinc-binding protein, and together they target the promoter of *TaPAD4* and increase its acetylation. The above examples demonstrate that epigenetic regulation of both direct players in ROS production or crucial regulatory hubs can contribute to fine-tuning of the cellular redox homoeostasis.

Epigenetic regulation of H_2O_2-producing NADPH oxidase NOX4 has been also described in senescing animal cells (Sanders et al., 2015). Increased transcript levels of NOX4 correlate with enrichment of the activation histone mark H4K16ac and depletion of the repressive histone mark H4K20Me3, suggesting an active chromatin conformation. Silencing of the histone acetyltransferase Mof, which deposits H4K16ac, resulted in decreased levels of NOX4 (Sanders et al., 2015). Regulation of NADPH oxidases by histone methylation marks and DNA methylation has also been shown in animal models, but currently there is no experimental evidence for such regulation in plants (Brewer, 2021). Taken together, these examples point toward an evolutionary conserved epigenetic mechanism for control of ROS production.

2 | CONCLUSIONS

Oxidative posttranslational modifications alter the functions of various plant proteins and play major regulatory roles. Yet the functional consequences of oxidative posttranslational modifications on most proteins that have been discovered in large-scale screening approaches remain largely unknown. Among those proteins are various epigenetic players whose impact on gene expression is likely to be fine-tuned at the posttranslational level by oxidative modifications. Indeed, emerging evidence from animal systems and plants suggest that the dynamics of the epigenetic landscape are intrinsically intertwined with the cellular redox homoeostasis. Alterations of the cellular redox pool can have a direct effect on the enzymatic activity, localisation, or stability of histone and DNA modifying enzymes through modifications of redox-sensitive

amino acid residues. Additionally, Fe-S clusters that are highly sensitive to oxidation and are present in some epigenetic enzymes can also be subjected to a redox control. The main challenge will lie in understanding whether such oxidative posttranslational modifications have a truly functional role or represent a stochastic noise. Direct redox control of epigenetic players is a common regulatory mechanism described in various animal systems. Given the evolutionary conservation of many epigenetic enzymes, their redox regulation in plants can be more widespread that currently thought. The links between primary metabolism and epigenetic regulation are also increasingly viewed in light of redox signalling because major metabolic fluxes are affected by, or contribute to, the cellular redox homoeostasis. Ultimately, the epigenetic landscape integrates information that reflects a multitude of cellular activities and understanding the impact of redox signalling will help us obtain a more holistic picture of how gene expression is regulated at the epigenetic level. A systematic characterisation of the effect of ROS on the epigenetic landscape will be crucial to discover redox-sensitive histone marks and deepen our understanding of the molecular mechanisms underlying redox signalling under unfavourable environmental conditions.

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