Plant Stress 19 (2026) 101144

Contents lists available at ScienceDirect

Plant Stress

journal homepage: www.sciencedirect.com/journal/plant-stress

Review

A review of the advances and perspectives in sequencing technologies for analysing plant epigenetic responses to abiotic stress

Siqing Fan, Hua Yang, Yufang Hu, Ling Zhang *, Mingkun Huang *

Jiangxi Provincial Key Laboratory of Ex Situ Plant Conservation and Utilization, Lushan, Jiangxi Key Laboratory for Sustainable Utilization of Chinese Materia Medica Resources, LushanBotanical Garden, Chinese Academy of Sciences, 9 Zhiqing Road, Jiujiang, Jiangxi 332900, China

ARTICLE INFO

Keywords:
Plant abiotic stress
Epigenetic regulation
Multi-omics
Sequencing technologies

ABSTRACT

Abiotic stresses, such as drought, salinity, heat, and cold constrain plant growth and productivity by influence plant internal regulatory networks. Transcriptional/epigenetic regulation, which encompasses mechanisms such as DNA methylation, histone modifications, chromatin accessibility, non-coding RNAs, and RNA modifications, orchestrates rapid transcriptional reprogramming and stress memory and provides key adaptive capacity for plants to resist stress. Recent sequencing breakthrough system-level mapping of these layers, including ATAC-seq (accessibility), CUT&Tag/ChIP-seq (histone marks), Hi-C (3D genome), WGBS (methylomes), lncRNA/small-RNA profiling (regulatory RNAs), and Nanopore direct RNA sequencing (RNA modification). This review summarizes the application of these methods to capture the landscape of dynamic DNA methylation, chromatin conformation changes, non-coding RNA regulation, and RNA modification under abiotic stress conditions, and addresses current technical challenges in multi-omics research and explores future perspectives.

1. Introduction

In the context of global climate change, abiotic stresses such as drought, salinity, heat, and cold are becoming increasingly frequent and intense, posing a serious threat to plant development and crop yield (Eckardt et al., 2022; Terán et al., 2024; Varshney et al., 2024; Y. Wu et al., 2024). Such environmental adversities are estimated to cause yield losses exceeding 50 % major crops (Zhang et al., 2025). As sessile organisms, plants cannot escape unfavorable conditions and have evolved intricate adaptive strategies involving metabolic reprogramming, hormonal signaling, and physiological adjustments. Among these, epigenetic regulation is a key mechanism that modulates gene activity in response to stress (Chang et al., 2020; Hemenway and Gehring, 2023). Epigenetic processes enable rapid, reversible, and sometimes heritable changes in gene expression, contributing to stress-induced transcriptional reprogramming and, in some cases, the establishment of stress memory (Gallusci et al., 2022; Oberkofler et al., 2021; Wibowo et al., 2016). Mechanistic dissection is complicated by transposable element-rich plant genomes, tissue heterogeneity, and multi-scale dynamics that can obscure enhancer-promoter logic and cell-type-specific responses (Maher et al., 2017; Tourdot and Grob, 2023).

Under abiotic stresses, multiple epigenetic layers act in concert to reshape transcriptional programs (Fig. 1). DNA methylation adjusts in context-specific ways, from promoter demethylation to transposon-proximal CHH changes, sometimes contributing to memory-like states (Wibowo et al., 2016; Zhang et al., 2018). Histone modifications and chromatin accessibility are redistributed at stress-responsive loci, and three-dimensional (3D) genome architecture can be rapidly rewired under heat or cold, with selective effects on enhancer-promoter communication (Hemenway and Gehring, 2023; Huang et al., 2023).

Recent advances in high-throughput and integrative omics now enable fine-grained interrogation of these layers (Jiang et al., 2023; Zagorščak et al., 2025; Zhang et al., 2025). Adopting a method-first perspective, this review surveys complementary sequencing readouts of the plant epigenome under stress. Assay for Transposase-Accessible Chromatin sequencing (ATAC-seq) profiles promoter- and enhancer-proximal accessibility and transcription factors (TFs) footprinting; Cleavage Under Targets and Tagmentation (CUT&Tag) and chromatin immunoprecipitation sequencing (ChIP-seq) map activating and repressive histone landscapes and factor occupancy; chromosome conformation capture (Hi-C) and Micrococcal nuclease-based 3D genome mapping technology (Micro-C) resolve higher-order genome architecture. Whole-genome bisulfite sequencing (WGBS) quantifies cytosine methylation at single-base resolution, small RNA sequencing

* Corresponding authors.
E-mail addresses: linzh00@126.com (L. Zhang), huangmk@lsbg.cn (M. Huang).

https://doi.org/10.1016/j.stress.2025.101144
Received 4 August 2025; Received in revised form 16 November 2025; Accepted 18 November 2025
Available online 19 November 2025

and long non-coding RNA (lncRNA) sequencing capture regulatory RNAs, and Nanopore direct RNA sequencing (DRS) for native base-modification and full-length isoform continuity (Kaya-Okur et al., 2019; Maher et al., 2017).

We integrate DNA methylation, histone states and chromatin accessibility, 3D genome architecture, and regulatory RNAs (including RNA modifications) into a unified view of plant responses to abiotic stress, and emphasize stress-focused signals that link these layers.

2. Sequencing technologies for decoding plant epigenetic responses to abiotic stress

Interrogating epigenetic regulation under abiotic stress relies on a suite of sequencing assays that resolve chromatin accessibility, histone landscapes, 3D genome architecture, DNA methylation, and regulatory RNAs. Here we emphasize what each assay measures and how these measurements inform stress biology; comparative characteristics are summarized in Table 1, layer-specific signatures in Table 2, and schematic overviews Figs. 2–6.

2.1. ATAC-seq

ATAC-seq is a powerful technique for genome-wide mapping of open chromatin regions. Developed by Buenrostro et al. in 2013, ATAC-seq utilizes a hyperactive Tn5 transposase that preferentially inserts sequencing adapters into nucleosome-depleted or loosely packed chromatin regions, thereby marking accessible chromatin sites for high-throughput sequencing (Fig. 2) (Buenrostro et al., 2013). Compared to traditional DNase I hypersensitive sites sequencing (DNase-seq), ATAC-seq requires minimal input material, avoids complex enzymatic digestion and purification steps, and offers a rapid and efficient workflow.

2.2. CUT&Tag and chip-seq

Developed by Henikoff and colleagues in 2019 (Kaya-Okur et al., 2019). CUT&Tag is a recently developed technique for profiling histone modifications and DNA-binding proteins. Conceptually serving as a more efficient alternative to ChIP-seq in concept, CUT&Tag offers substantial advantages, including higher resolution, lower input requirements, and compatibility with single-cell applications. The method uses a fusion protein consisting of protein A and a hyperactive Tn5 transposase (pA–Tn5), which binds to antibodies that are specific to histone modifications or DNA-binding proteins. Once tethered to target loci, the transposase performs in situ tagmentation, simultaneously cleaving and tagging adjacent DNA fragments, without the need for chromatin fragmentation by sonication or immunoprecipitation, as required in traditional ChIP-seq workflows. This streamlined protocol allows CUT&Tag to be completed in a single day, using significantly less input material (Fig. 3) (Kaufmann et al., 2010; Kaya-Okur et al., 2019).

2.3. Hi-C

Hi-C is a genome-wide chromosome conformation capture technique designed to investigate the 3D organization of the genome, which plays a critical role in regulating gene expression, dynamic chromatin reorganization, and the coordination of distal regulatory elements. Hi-C quantifies spatial contact frequencies between genomic loci by cross-linking DNA–protein and protein–protein interactions with formaldehyde, followed by chromatin digestion, proximity ligation, and high-

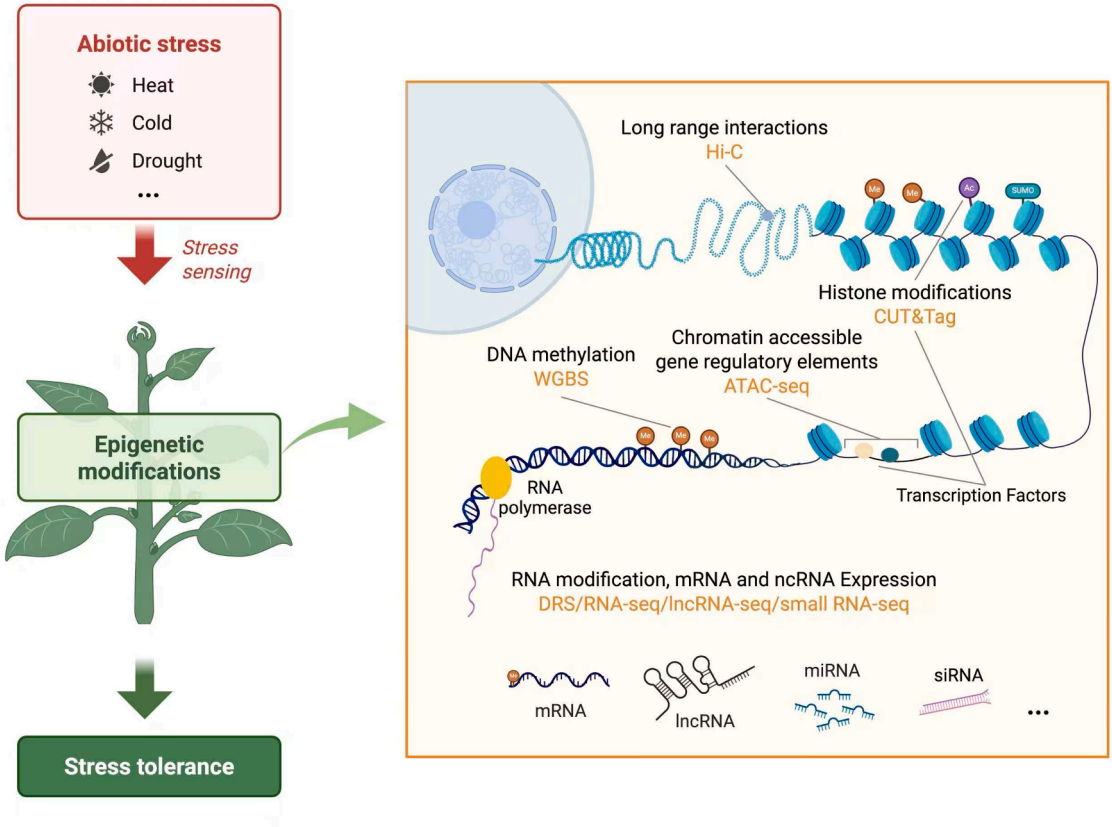

Fig. 1. The application of multi-omics sequencing technology in understanding the epigenetic regulation and responses to abiotic stress in plants. Plants usually fine-tune gene expression by changing the state of epigenetic modifications (e.g. DNA methylation, chromatin modifications, RNA modification and non-coding RNA expression) in response to abiotic stress, such as heat, cold and drought. Sequencing technologies such as WGBS, ATAC-seq, CUT&Tag and Hi-C have been developed to detect these epigenetic changes and reveal the underlying mechanisms.

Table 1
Comparison of major sequencing technologies for plant abiotic stress epigenetics.

Technique	Resolution	Sample requirements	Primary readout	Limitations	Promise in stress biology
ATAC-seq	~50–200bp	5k-50k nuclei or 10–50 mg tissue	ACRs/OCRs; TF footprints	Chloroplast reads; nuclei isolation bias; phenolics; batch sensitivity	Rapid capture of stress-induced ACRs; promoter/enhancer priming; footprinting of TFs hubs
CUT&Tag	sub-kb around epitopes	≤10 mg tissue / low-input	Histone marks & near-target TF binding	Antibody specificity; permeabilization efficiency; enzyme/buffer background	Sensitive mapping of H3K27ac/H3K4me3 gains or H3K27me3 loss; suited to time-course & scarce tissue
ChIP-seq	kb–sub-kb	50–200 mg tissue	Genome-wide histone marks/TF occupancy	Crosslinking/extraction bias; antibody quality; higher background	Broad historical baseline; robust for repressive marks and TF occupancy comparisons
Hi-C	kb–Mb (depth-dependent)	50–200 mg tissue	Compartments, TAD-like domains, loops	Restriction-site bias; repeats/ploidy; high depth & normalization needed	Detect stress-induced compartment/TAD rewiring and loop loss/formation
WGBS	single-base (CG/CHG/CHH)	≥200–500 ng DNA	Whole-genome methylome; DMRs	Conversion damage; GC bias; cost; cannot separate 5mC/5hmC	Quantifies stress DMRs and memory-like methylation; TE silencing dynamics
Small RNA-seq	18–30 nt classes	≥1 μg RNA	miRNA/siRNA (24-nt hc-siRNA), phasiRNA	Adapter dimers; size-selection; rRNA; repeat-mapping ambiguity	Identifies RdDM cues and regulatory modules targeting TFs; TE control under stress
lncRNA-seq	kb transcripts (strand-specific)	≥1 μg RNA	lncRNAs (cis/trans), NATs, eRNAs	Low abundance; incomplete annotation; coding-potential misclassification	Discovers lncRNA–chromatin bridges and stress-induced regulatory lncRNAs
Nanopore (Direct RNA)	Long reads + base-mod signals	≥500 ng RNA (HMW)	5mC/6 mA calls; full-length isoforms; haplotypes	Signal noise; model calibration; input quality; error rates	Single-molecule methylome–isoform co-profiling; phasing stress real-time modification dynamics

Table 2
Layer-specific stress-responsive signatures.

Epigenetic layer	Stress-responsive signatures
Chromatin accessibility	Emergent ACRs near stress-TF motifs (e.g., HSF/NAC/WRKY); TF footprint changes
Histone modifications	Activation-mark gains at induced loci; repressive-mark erosion at de-repressed loci
3D genome architecture	Compartment/TAD reorganization; loop loss/formation at responsive loci
DNA methylation	Promoter/TE-proximal DMRs; context-specific CG/CHG/CHH shifts; memory-lie patterns
Regulatory RNAs	miRNA/siRNA modules; context-dependent phasiRNAs; lncRNA-chromatin links
RNA modification	m^6A redistribution on stress-responsive transcripts/isoforms; occasional m^5C changes

Notes: Single-cell/spatial implementations are modalities (e.g., scATAC-seq, scCUT&Tag, spatial RNA) applicable across layers to resolve cell-type and in-tissue context.

throughput sequencing (Fig. 4) (Dekker et al., 2013). Hi-C data enable the characterization of genome architecture at multiple hierarchical levels, including chromosome territories, A/B compartments, topologically associating domains (TADs), and long-range chromatin loops, each contributing to the spatial organization of gene activity (Akgol Oksuz et al., 2021). For example, TADs serve as regulatory units that constrain enhancer-promoter interactions, whereas compartment switching can indicate large-scale changes in transcriptional potential under stress. Long-range chromatin loops facilitate communication between distant elements such as enhancers and their target promoters. Disruptions to these structures have been linked to altered gene expression in response to environmental cues.

2.4. WGBS

WGBS is widely regarded as the gold standard for mapping DNA methylation patterns at single-base resolution. The method relies on the chemical conversion of unmethylated cytosines to uracils using sodium bisulfite, while 5-methylcytosines remain unchanged. Sequencing the bisulfite-treated DNA and aligning it to a reference genome enables the precise identification of methylated cytosines across all sequence contexts (CG, CHG, and CHH) and the quantification of methylation levels (Fig. 5) (Li et al., 2017).

2.5. Sequencing of non-coding RNAs and direct RNA

Small RNA sequencing enumerates 18–30-nt species, including microRNAs (miRNAs), 24-nt heterochromatic small interfering RNAs (hc-siRNAs; RNA-directed DNA methylation, RdDM), and 21/24-nt phased small interfering RNAs (phasiRNAs), whereas lncRNA-seq profiles transcripts >200 nt using rRNA-depleted libraries and stringent annotation filters (Fig. 6). DRS threads native poly(A)-selected RNA molecules through a biological nanopore, while an adapter-motor complex anchored at the 3′ end enforces controlled 3′ to 5′ translocation. This process generates nucleotide-dependent ionic current traces that can be computationally decoded into sequence and, by bypassing reverse transcription and amplification, preserving endogenous RNA modification and poly(A)-tail features (Fig. 7) (Garalde et al., 2016; Zhu et al., 2024).

3. Dynamic regulation of DNA methylation under abiotic stress

DNA methylation is a key component of plant epigenetic regulation and exhibits remarkable plasticity during environmental stress responses (Liu et al., 2022; Zhang et al., 2018). It primarily occurs at cytosine (C) residues within three sequence contexts: CG, CHG, and CHH (where H represents A, T, or C). This modification is catalyzed by distinct families of DNA methyltransferases: METHYLTRANSFERASE 1 (MET1) maintains CG methylation; CHROMOMETHYLASES (CMT3/CMT2) establish CHG/CHH methylation in heterochromatin; and DOMAINS REARRANGED METHYLTRANSFERASE 2 (DRM2) mediates de novo methylation via RdDM pathway. Active DNA demethylation is carried out by ROS1/DME-family DNA glycosylases through a base-excision repair mechanism (Gallego-Bartolomé, 2020; Law and Jacobsen, 2010; Matzke and Mosher, 2014; Zhang et al., 2018). Under stress conditions, the expression or activity of these enzymes can change, shifting the balance between methylation and demethylation across genomic contexts (Naydenov et al., 2015).

In general, promoter or enhancer hypomethylation correlates with gene de-repression and can facilitate rapid induction of stress-responsive genes (e.g., HSF/HSP and drought-inducible factors), whereas hypermethylation contributes to silencing of negative regulators and transposable elements (TEs) to preserve genome stability. The regulatory outcome, however, is context-dependent: promoter-proximal methylation is typically repressive; TE-proximal CHH methylation is linked to RdDM and TE control; and gene-body CG methylation shows species- and locus-dependent associations with expression (Bewick and Schmitz,

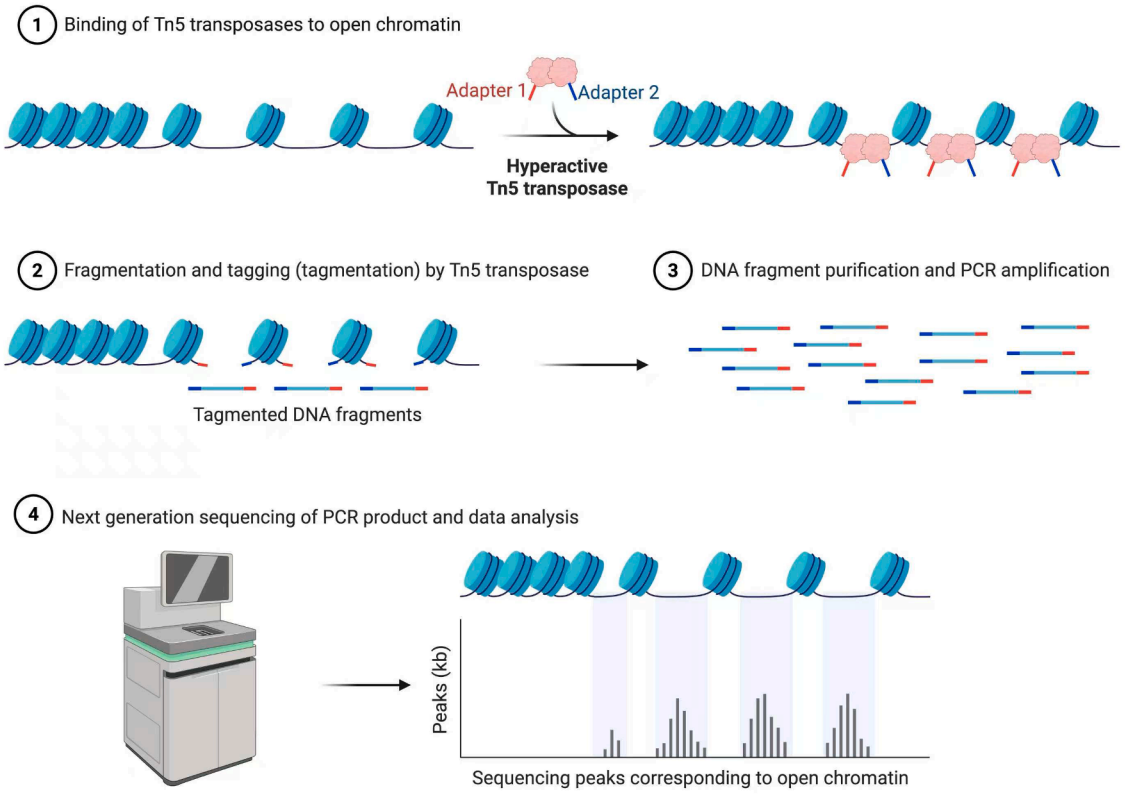

Fig. 2. The principle of ATAC-seq experiments. Incubation of the Tn5 transposase and nuclei enables tagmentation and fragmentation of open chromatin regions. The resulting DNA can then be amplified for sequencing, enabling the open chromatin regions to be detected through the enrichment of the sequencing reads.

2017; Zhang et al., 2018; Zilberman, 2017). These principles help interpret stress-induced methylome changes without over-generalizing across species or tissues.

Numerous studies have demonstrated that abiotic stresses can induce widespread alterations in methylation patterns across the genome. For instance, drought stress often correlates with a general trend of demethylation. In *Medicago ruthenica*, a close relative of *Medicago sativa*, drought treatment resulted in a ~4.41 % decrease in global 5-methylcytosine (5mC) levels, indicating a broad loss of methylation (Zi et al., 2024). In rice, up to 70 % of drought-induced methylation sites undergo demethylation. Interestingly, decreased DNA methylation associated with yield loss has been observed when drought stress occurs during the reproductive stage, suggesting a critical link between epigenetic changes and reproductive development (Gayacharan and Joel, 2013; Wang et al., 2010). Notably, such global trends are species-, tissue- and time-point-specific, and localized hypermethylation can also occur at particular genomic features (e.g., TE edges), underscoring the need for matched designs and careful interpretation (Bewick and Schmitz, 2017; Zhang et al., 2018).

Stress-induced demethylation is often associated with the transcriptional activation of stress-responsive genes. In *Arabidopsis*, genome-wide methylation levels declined markedly following heat stress and recovery, with targeted demethylation observed at specific loci, including those of heat shock proteins (HSPs). This pattern suggests active site-specific demethylation, likely mediated by DNA demethylases, rather than passive loss, enabling precise activation of heat-responsive genes (Korotko et al., 2021). In response to salt stress, DNA methylation changes have been linked to epigenetic "stress memory". In *Arabidopsis*, recurrent high-salinity treatments induced heritable methylation alterations, predominantly transmitted maternally; these marks gradually reverted in non-stressed progeny, indicating transient but adaptive memory. Mechanistically, some stress-induced differentially methylated regions (DMRs) regulate antisense lncRNAs, which in turn modulate their cognate genes, mediating memory formation (Wibowo et al., 2016).

The RdDM pathway also participates in stress responses. Stress-induced 24-nt small interfering RNAs (siRNAs) can guide DRM2-dependent methylation to specific loci, shaping CHH methylation and nearby gene/TE activity (Matzke and Mosher, 2014; Zhang et al., 2018). Recent studies in wheat have identified drought-responsive lncRNAs potentially regulated by 24-nt siRNAs, highlighting the crosstalk between non-coding RNAs and methylation machinery under stress conditions (Jin et al., 2024).

Collectively, abiotic stress modulates the activity and deployment of DNA methyltransferases and demethylases, leading to dynamic and context-specific changes in promoter-, gene-body- and TE-proximal methylation. These changes can repress or activate gene expression as needed, providing a flexible regulatory mechanism that enables plants to adjust transcriptional programs under stress. In certain contexts, such modifications contribute to adaptive memory-like states that influence subsequent responses and, occasionally, the next generation.

4. Histone modifications and higher-order chromatin remodeling in abiotic stress responses

In addition to DNA methylation, changes in chromatin conformation and covalent histone modifications constitute another fundamental layer of epigenetic regulation in plant responses to abiotic stress. Environmental cues frequently alter the expression and activity of histone-modifying enzymes, thereby reshaping chromatin accessibility and transcriptional activity at a genome-wide scale (Nunez-Vazquez et al., 2022; Yu et al., 2025). For instance, drought stress markedly increases levels of histone H3 lysine 4 trimethylation (H3K4me3) and H3 lysine 9 acetylation (H3K9ac) at the promoters of stress-responsive genes in *Arabidopsis* (e.g., *RD29A, RD29B*), and these active marks are closely associated with transcriptional upregulation during stress (Kim et al.,

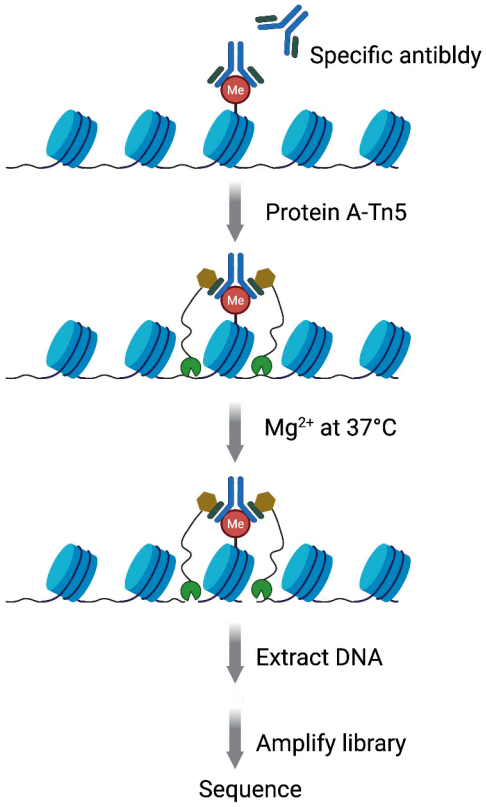

Fig. 3. Key experimental steps of CUT&Tag. The engineered Protein A-Tn5 fusion protein binds to the specific antibody (e.g. methylated histones) and cuts the specific DNA regions when Mg^{2+} is added at 37 °C. The resulting DNA can then be extracted and amplified for sequencing.

2008). Genome-wide analyses have revealed large-scale shifts in H3K4 methylation under drought, including widespread remodeling of *Arabidopsis* genome (van Dijk et al., 2010) and differential levels of H3K4me3 at >4800 genes in rice seedlings (Zong et al., 2012). Conversely, repressive marks such as H3K27me3 can be reduced or redistributed under stress, facilitating activation of stress-related loci; for example, long-term osmotic stress lowers H3K27me3 at specific genes (Sani et al., 2013). Histone acetylation is likewise dynamic: abiotic stresses modulate histone acetyltransferases (HATs) and deacetylases (HDACs), leading to global acetylation changes (Cui et al., 2023). In *Arabidopsis*, HDA6 contributes to deacetylation on the histone variant H2A.Z, enhancing ABA-signaling gene expression and improving drought/salt tolerance (Chen et al., 2010). under heat, HDA9 mediates eviction of H2A.Z-containing nucleosomes at the *YUC8* locus, lifting repression to enable thermomorphogenic growth (Tasset et al., 2018). These findings illustrate that dynamic histone marks and variants are integral to stress signaling.

Chromatin accessibility, defined as the openness of DNA to TFs and regulators, provides an early readout of regulatory priming. Accessible chromatin regions (ACRs) are enriched at promoters and enhancers and can undergo rapid, stress-induced remodeling. In tomato, high temperature induces stress-specific enhancer-promoter contacts accompanied by increased accessibility and active marks at heat-responsive genes; the heat shock TF, HSFA1a is required for establishing these ACRs and contacts, and its loss disrupts both accessibility and gene activation (Huang et al., 2023). In practice, ACR gains often precede or coincide with increases in activating histone marks (e.g., H3K27ac, H3K4me3) at the same loci, supporting a sequential model from accessibility to marking to transcriptional induction.

The 3D organization of chromatin represents a higher-order regulatory layer that is also responsive to abiotic stress (He et al., 2024; Lopes et al., 2024). Under normal conditions, plant chromatin exhibits hierarchical organization chromosome territories to A/B compartments, TAD domains and chromatin loops, which help coordinate gene expression. Abiotic stress can induce large-scale reorganization of these features. High-resolution Hi-C in *Brachypodium distachyon* under cold stress revealed widespread restructuring, including switching between active A and inactive B compartments, reduced compartmentalization strength, TAD shrinkage, and extensive loss of long-range loops (Zhang et al., 2023). Not all spatial changes immediately translate into transcriptional differences: some genes without major expression shifts remain in A compartments, whereas TAD boundary reorganization shows tighter links to transcription. In the same systems, dynamics of TAD domains correlate with shifts in H3K27me3 (repressive) and H3K27ac (activating), underscoring cross-talk between 3D architecture and histone landscapes.

Together, these observations highlight a coordinated cascade in which stress cues remodel accessibility, redistribute histone marks and, at selected loci, rewire 3D contacts to enable or stabilize transcriptional programs. Causality can be context- and time-dependent-accessibility changes often precede expression, whereas long-range loop loss or formation may reflect both regulatory control and downstream chromatin dynamics-emphasizing the value of time-resolved and integrative assays when interpreting stress responses.

5. Non-Coding RNAs as emerging epigenetic regulators in stress responses

Non-coding RNAs (ncRNAs), including miRNAs, siRNAs and lncRNAs, from a multilayered regulatory system that shapes plant responses to abiotic stress (Borsani et al., 2005; Heo and Sung, 2010; Shengjun Li et al., 2017; Y. Li et al., 2020; Oberkofler et al., 2021; Swiezewski et al., 2009). In plants, a canonical PIWI-piRNA pathway has not been established; instead, hc-siRNAs and phasiRNAs fulfill chromatin-linked and developmental functions (Borges and Martienssen, 2015; Fang and Qi, 2016; Juliano et al., 2011; Kakrana et al., 2018; Watanabe and Lin, 2014; Zaratiegui et al., 2007; Zhan and Meyers, 2023).

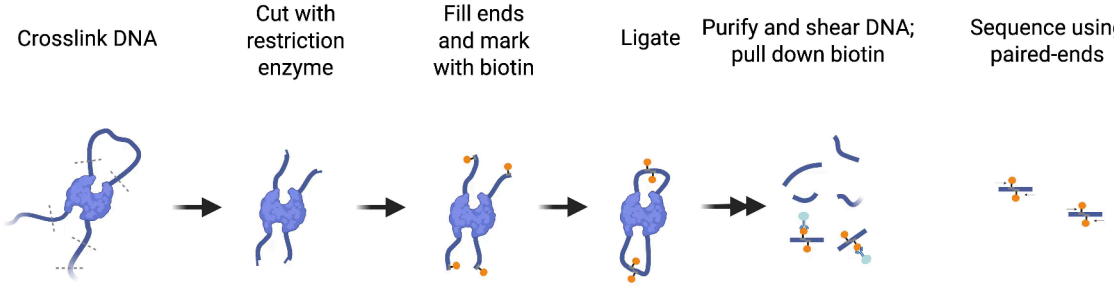

Fig. 4. Schematic diagram of the main steps in Hi-C experiments. Cross-linked DNA is cut with a restriction enzyme (e.g. DpnII), the sticky ends are filled in and marked with biotin-labelled bases. After ligation, the purified DNA is sheared into fragments, and the biotin-labelled DNA is extracted for sequencing.

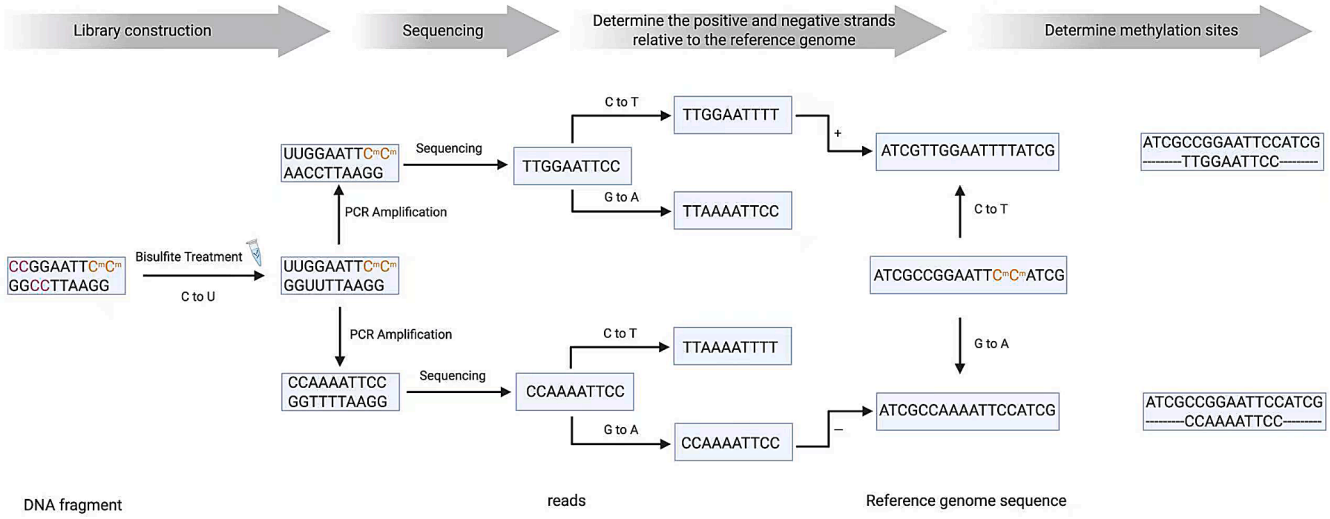

Fig. 5. Experimental Principle of the WGBS. The experimental principle of WGBS relies on sodium bisulfite converting unmethylated cytosines to uracils, while 5-methylcytosines remain unaltered. After sequencing and alignment to the reference genome, methylated cytosines in CG, CHG, and CHH contexts are identified at single-base resolution, quantifying methylation levels.

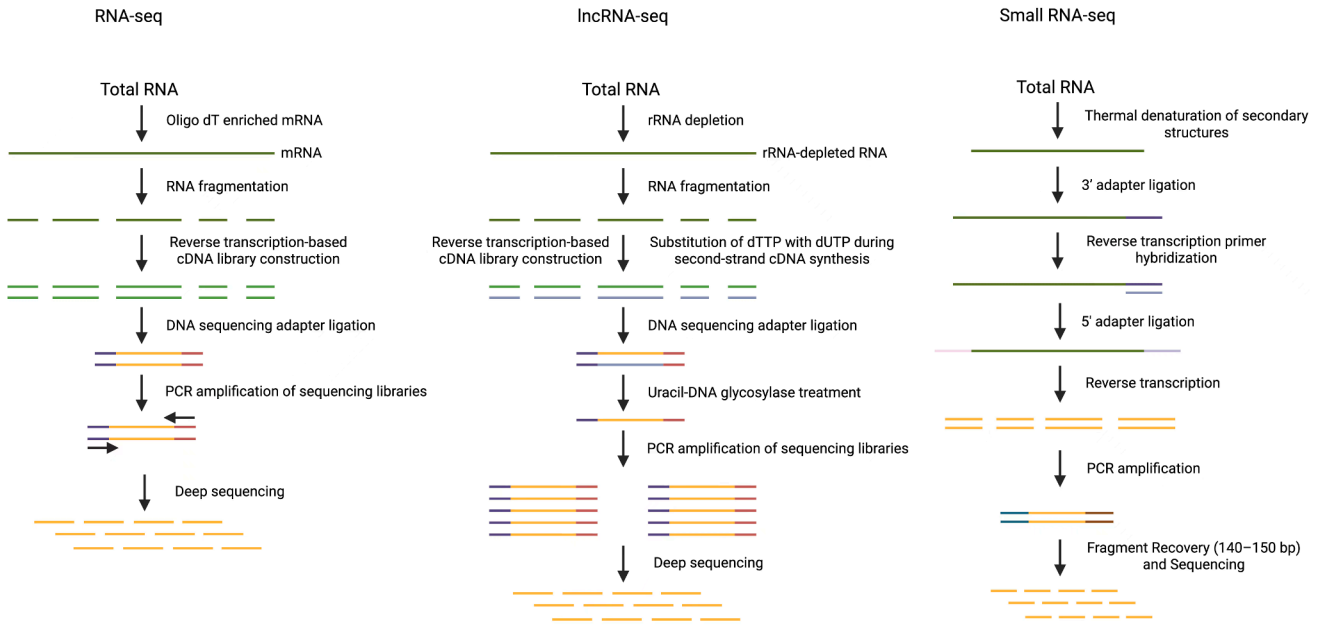

Fig. 6. Schematic diagram of RNA and non-coding RNA sequencing. RNA-seq typically employs strand non-specific library construction, with mRNA enrichment often achieved using oligo dT. lncRNA-seq adopts strand-specific library construction and enriches RNA by removing rRNA. Small RNA-seq requires heating to disrupt secondary structures and specifies the recovery of fragments within the 140–150 bp range.

5.1. miRNAs: post-transcriptional tuning of stress pathways

Plant miRNAs (~20–24-nt) direct sequence-specific mRNA cleavage or translational repression, thereby modulating key nodes of stress signaling (Reinhart et al., 2002; Yu et al., 2017). Under drought, miR159 and miR169 exemplify stress-responsive miRNAs targeting upstream regulators: miR159 constrains MYB factors, and miR169 targets NF-YA subunits. Downregulation of these miRNAs alleviates repression on their targets, promoting ABA-dependent transcription and enhancing drought tolerance; conversely, constitutive miR169c overexpression impairs stomatal closure and reduces drought resistance (Ji et al., 2023; Yu et al., 2019). miR398 overexpression diminishes peroxidase capacity and attenuates ROS scavenging, consistent with reduced drought tolerance (Zhou et al., 2020). By contrast, salt-induced miR393 represses auxin receptors, shifting resource allocation from growth to defense (Iglesias et al., 2014). Collectively, the miRNA network acts as a fine-tuning layer in which many miRNAs target transcription factors, establishing amplification and feedback motifs that balance growth and stress adaptation (Aravind et al., 2017; Jiang et al., 2023; Y. Li et al., 2020).

5.2. siRNA classes in chromatin-linked regulation: hc-siRNAs, phasiRNAs, nat-siRNAs

hc-siRNAs guide RdDM to TEs and nearby sequences, reinforcing heterochromatin and influencing expression of adjacent stress-

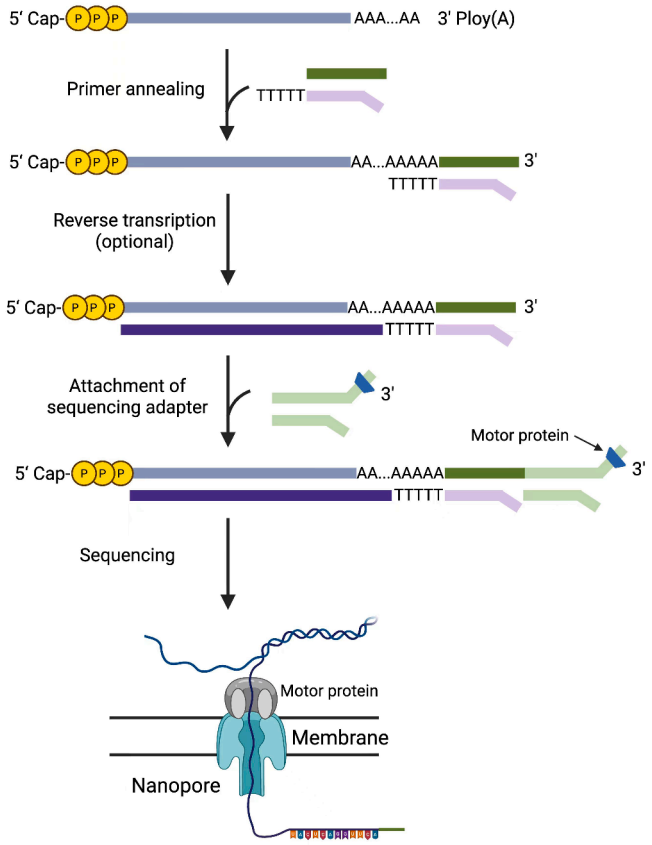

Fig. 7. Overview of the direct RNA sequencing (DRS). Library preparation protocol for DRS.

responsive genes (Matzke and Mosher, 2014; Zhang et al., 2018). Abiotic cues such as phosphate starvation or drought are associated with altered hc-siRNAs accumulation around TEs and corresponding localized methylation changes (Fan et al., 2022). phasiRNAs (21/24-nt), generated from PHAS loci, add context-dependent regulatory capacity; notably, temperature stress perturbs reproductive phasiRNA biogenesis and function in rice anthers, contributing to temperature-sensitive male sterility (AGO1d-dependent), which connects small-RNA pathways to stress-impacted fertility (Shi et al., 2022). In addition, natural-antisense siRNA (nat-siRNAs) can be induced under stress; the salt-responsive nat-siRNA pathway originally characterized in *Arabidopsis* illustrates how antisense transcription triggers targeted silencing during environmental changes (Borsani et al., 2005).

5.3. *lncRNAs: cis/trans regulation and chromatin interfaces*

lncRNAs (>200 nt) show stress- and tissue-specific expression and act through diverse mechanisms (Jin et al., 2024; Oberkofler et al., 2021). As natural antisense transcripts (NATs), they can modulate adjacent gene expression in cis; as competitive endogenous RNAs (ceRNAs), they sequester miRNAs to relieve repression of target mRNAs. A heat-responsive lncRNA in *Brassica rapa* acts as a decoy for miR159/miR172, mitigating their inhibition of heat-shock genes and transcription factors to enhance thermotolerance (Wang et al., 2019). lncRNAs also engage chromatin directly by recruiting epigenetic complexes. In *Arabidopsis*, COOLAIR and COLDAIR coordinate histone demethylation and H3K27 methylation at FLC during vernalization (Csorba et al., 2014; Heo and Sung, 2010; Swiezewski et al., 2009). Under drought, DANA1 interacts with DIP1 to recruit HDA9 to *CYP707A1/A2* promoters, reducing H3K9ac/H3K27ac and promoting tolerance (Jing Cai et al., 2024).

5.4. *An emerging interface with RNA modifications*

Epitranscriptomic marks intersect ncRNA circuits and stress regulation. In *Arabidopsis*, the m^6A "writer" MTA installs m^6A on pri-miRNAs to promote miRNA biogenesis, linking the m^6A pathway to small-RNA output (Bhat et al., 2020). The m^6A reader ECT8 acts as an abiotic-stress sensor that accelerate decay of target mRNAs by recruiting a decapping, illustrating how m^6A-readout modulates transcript stability during stress (Jingjing Cai et al., 2024). Writer component FIONA1 (FIO1) contributes to salt-stress tolerance by shaping the m6A methylome of stress-responsive transcripts (Hu et al., 2024). RNA 5-methylcytosine (m^5C) is widespread in *Arabidopsis* mRNAs and lncRNAs; the m^5C methyltransferase TRM4B controls a subset of mRNA m^5C sites and influences oxidative-stress phenotypes and transcript stability, underscoring a second modification layer with stress relevance (Cui et al., 2017; David et al., 2017). Recent syntheses further outline m6A-miRNA crosstalk and RNA-modification dynamics in plant stress adaptation (Cai et al., 2024; Hu et al., 2024).

Collectively, ncRNA pathways constitute coordinated regulatory modules in stress adaptation: miRNAs modulate key signaling hubs and their downstream effectors; hc-siRNAs reinforce TE-proximal chromatin states and influence adjacent gene activity; phasiRNAs extend small-RNA control into reproductive and stress-affected contexts; and lncRNAs interface RNA regulation with chromatin-associated mechanisms. Emerging evidence that m^6A, and in specific cases m^5C, modulates pri-miRNA processing, lncRNA stability, and the fate of stress-responsive mRNAs, establishing RNA modification as an adjustable layer within these networks. Together, these interdependent circuits enable rapid reallocation between growth and defense under fluctuating environments and underlie much of the epigenetic plasticity observed during abiotic stress.

6. Application of multi-omics approaches for decoding epigenetic complexity under abiotic stress

Understanding the intricate epigenetic mechanisms underlying plant stress adaptation requires a holistic integration of diverse high-throughout "omics" technologies. In recent years, multi-omics approaches combining chromatin accessibility assays, histone modification profiling, 3D genome mapping, DNA methylation sequencing, and transcriptome analysis (including coding and non-coding RNAs) have provided valuable insights into plant stress responses (Varadharajan et al., 2025). By decoding gene regulatory networks across these layers, integrative omics techniques can reveal critical mechanisms of abiotic stress tolerance that might remain hidden in single-omics studies (Varadharajan et al., 2025). Importantly, these technologies are increasingly applied in combination rather than isolation, as their complementary strengths enable cross-validation of results and provide a more integrated view of how distinct epigenetic layers interact during stress conditions. Below, we outline key sequencing-based omics techniques and emphasize how their integration helps decode the epigenetic complexity of plant responses to abiotic stress.

6.1. *Chromatin accessibility dynamics and transcriptomic integration*

In an integrative context, ATAC-seq is frequently combined with RNA-seq to link chromatin accessibility changes with gene expression output. For example, in drought-stressed apple (*Malus domestica*), ATAC-seq identified ~23,466 regions gaining accessibility and 2447 regions losing accessibility genome-wide. When these data were integrated with transcript levels, 240 genes showed both increased promoter accessibility and upregulated expression under drought, including key transcription factors like ATHB7, HAT5, WRKY26 (Wang et al., 2022). Such multi-omics analysis pinpointed stress-inducible regulatory elements and their target genes, suggesting that chromatin opening at specific enhancers/promoters facilitates the activation of downstream

drought-responsive genes. Similarly, ATAC-seq applied to cold-treated tea plants (*Camellia sinensis*) was combined with transcriptome and translatome profiling to construct stress-responsive regulatory networks. This integrative study revealed that chilling stress altered thousands of genes at both the transcriptional and translational levels and led to identification of distal transposase-hypersensitive sites (dACRs) linked to key cold-responsive transcription factors (Wang et al., 2021). These examples illustrate that coupling chromatin accessibility maps with mRNA expression data allows researchers to connect epigenomic changes (e.g. nucleosome eviction at regulatory sites) with functional outcomes in gene activity. Because ATAC-seq requires low input and minimal processing, it can be applied across developmental stages or cell types, making it ideal for time-course or cell-specific integration with transcriptomes to capture dynamic stress responses. Overall, profiling open chromatin and transcripts in tandem provides a foundational layer of multi-omics insight into how stress-triggered chromatin remodeling correlates with and potentially drives gene expression reprogramming (Wang et al., 2022).

6.2. Mapping histone modification landscapes in combination with other omics

Integrating histone modification maps with other omics datasets greatly enriches our understanding of stress-induced chromatin state dynamics. For instance, CUT&Tag or ChIP-seq of histone marks can be analyzed alongside ATAC-seq and RNA-seq data to determine how changes in chromatin modifications coincide with accessibility and transcriptional output. A recent application of CUT&Tag in rice and rapeseed demonstrated its ability to capture inducible histone mark changes under stress, which can then be correlated with gene expression changes (Ouyang and Li, 2023; Sharma et al., 2023). Because many histone marks either facilitate or hinder transcription, their integration with transcriptomic data can highlight which stress-responsive genes are likely regulated by chromatin-level mechanisms (e.g. gaining H3K4me3 or losing H3K27me3 at promoters). Moreover, combining multiple chromatin assays provides a more complete picture: open chromatin regions identified by ATAC-seq can be further characterized by the presence or absence of activating marks (like histone acetylation) via CUT&Tag, confirming their status as active enhancers, while regions with increased repressive marks would hint at stress-induced silencing. Such multi-omics cross-validation was exemplified in a study of *Arabidopsis* GCN5, a histone acetyltransferase: researchers integrated ATAC-seq with ChIP-seq for H3 acetylation in *gcn5* mutants, linking loss of H3K14ac to reduced chromatin accessibility at immunity genes, and thereby connecting a histone modification enzyme to chromatin accessibility and pathogen response (Kim et al., 2020). In summary, histone mark profiling methods like CUT&Tag, especially when combined with complementary assays, allow researchers to pinpoint the chromatin modifications associated with stress-responsive genes and to dissect the epigenetic signatures that distinguish active vs. repressed chromatin states during stress adaptation.

6.3. 3D genome architecture and regulatory network integration

Beyond linear chromatin features, the 3D organization of the genome (chromosome conformation) is a crucial epigenetic dimension influencing gene regulation. Hi-C sequencing and its variants (e.g. capture Hi-C) enable genome-wide mapping of physical chromatin contacts, revealing structures such as A/B compartments, TADs, and long-range enhancer-promoter loops (Zhang et al., 2023). Integrating 3D genome data with other omics is shedding light on how spatial chromatin reorganization under abiotic stress correlates with changes in gene expression and chromatin state. A striking example comes from *Brachypodium distachyon* under cold stress: high-resolution Hi-C maps (~1.5 kb resolution) showed that cold treatment globally disrupted chromatin architecture, inducing switches from active (A) to inactive (B) compartments, weakening overall compartmentalization, shrinking or abolishing many TADs, and markedly depleting long-range loops (Zhang et al., 2023). When these 3D changes were integrated with transcriptomic data, researchers found that cold-responsive genes largely remained in active (A) compartments regardless of compartment switches, suggesting that broad compartment changes had limited direct impact on transcription. Instead, gene expression changes were more closely associated with finer-scale architectural reorganization: many cold-upregulated genes lay in regions that lost or restructured TAD boundaries and chromatin loops, implicating these local 3D changed in gene activation. Interestingly, the loss of loops (disruption of pre-existing enhancer-promoter contacts) correlated with transcriptional alterations more than the formation of new loops. This multiscale integration, further combined with histone mark profiling, revealed that dynamic TAD and loop changes under cold stress were linked to histone modification changes (e.g. gained H3K27ac or lost H3K27me3), reinforcing the interplay between 3D genome structure and chromatin state (Zhang et al., 2023).

Another illustrative case in heat stress in tomato. Capture Hi-C analysis showed that within minutes of heat exposure, the chromatin undergoes rapid spatial reorganization: new promoter-enhancer loops form at heat-responsive loci, presumably to drive swift activation of heat-inducible genes (Huang et al., 2023). Integrative analysis revealed that this looping depends on the master heat-responsive TF HSFA1a in wild-type plants, heat shock rapidly triggered looping and strong transcription of HSFA1a-target genes, whereas HSFA1a-knockout plant failed to establish these enhancer contacts and showed attenuated gene induction (Huang et al., 2023). This finding highlights how a specific TF can orchestrate 3D genome changes, linking an environmental signal (heat) to physical chromatin restructuring and gene expression output. Together, such studies demonstrate that Hi-C data, when combined with transcriptomic and epigenomic information, unravel an additional layer of stress regulation: changes in nuclear architecture can either permit or constrain interactions between regulatory elements and genes, thus modulating transcriptional programs under stress. As high-resolution and single-cell 3D genomics become more accessible, integrating those with other omics (e.g. mapping chromatin loops alongside accessibility, histone marks, and expression in the same system) will provide even deeper insight. Spatial genome reorganization under abiotic stress is now recognized as an important facet of epigenetic complexity, and only through multi-omics integration can we discern its functional consequences in the orchestration of stress-responsive gene networks.

6.4. DNA methylation profiling integrated with gene expression

By integrating methylome data with transcriptomic and other epigenomic datasets, researchers can identify how changes in DNA methylation status under stress correlate with gene activity and other regulatory modifications. Interestingly, global DNA methylation responses to abiotic stress can vary dramatically by species and context, underscoring the need for comparative multi-omics analyses. For example, drought stress in mulberry (*Morus alba*) was found to increase overall genomic methylation levels, with WGBS revealing approximately 8.64 % higher methylation in drought-treated plants compared with well-watered controls (R. Li et al., 2020). This hypermethylation (particularly in the CG context) was hypothesized to contribute to drought adaptation by stabilizing the genome and regulating stress-related genes, possibly aiding osmotic adjustment and reactive oxygen species scavenging. In contrast, an integrative methylome/-transcriptome study in *Medicago ruthenica* showed the opposite trend: plants subjected to recurrent drought exhibited an ~4.4 % decrease in global DNA methylation (Zi et al., 2024). By overlaying gene expression data, the authors found that the majority of drought-induced differentially methylated regions were associated with gene upregulation, especially for genes involved in abscisic acid signaling and proline biosynthesis (key pathways for drought tolerance) (Zi et al., 2024). In

other words, stress in *Medicago* triggered active DNA demethylation at specific loci, particularly within promoters or gene bodies of stress-responsive genes. This process alleviated transcriptional repression and enhanced the expression of adaptive genes (Zi et al., 2024). This kind of integrative analysis (methylome + transcriptome) supports a model wherein targeted DNA demethylation is part of the plant's regulatory toolkit to activate stress-protective genes, often mediated by DNA glycosylase enzymes like ROS1/DME that remove methylcytosine.

Comparative multi-omics studies across species reinforce these insights. In sugar beet (*Beta vulgaris*), for instance, exposure to cold stress caused a pronounced reduction in DNA methylation, levels, most significantly at CHH sites (the non-symmetric context often targeted by the RdDM pathway) (Kroupin et al., 2023). This epigenetic change coincided with transcriptional shifs, including upregulation of DNA demethylase genes and activation of cold-responsive targets, suggesting an active epigenetic reconfiguration during cold acclimation (Gutschker et al., 2022; Kroupin et al., 2023). Likewise, analysis in soybean under drought found that demethylation of certain gene promoters correlated with their increased expression, implicating active DNA demethylation as a prerequisite for induction of some stress-response genes (Varadharajan et al., 2025). On the hand, some cases show increased methylation dampening stress gene expression: for example, methylome profiling in rice and wheat has identified loci where hypermethylation under stress correlates with gene repression, potentially as a means of reallocating resources by suppressing growth-related genes during stress (Sinha et al., 2025). Taken together, WGBS coupled with transcriptomics (and often small data to capture the RdDM pathway) provides a powerful integrative approach to link DNA methylation dynamics with gene regulatory outcomes under stress. It reveals whether epigenetic gene activation (via demethylation) or epigenetic gene silencing (via de novo methylation) is at play, and pinpoints which pathway are under epigenetic control. As multi-omics case studies accumulate, a unifying theme merges: DNA methylation changes under abiotic stress are highly context-dependent yet consistently function to fine-tune gene activity, thereby optimizing plant survival under adverse conditions (Guarino et al., 2022).

6.5. *Transcriptomic and epitranscriptomic profiling of non-coding RNAs and RNA modifications*

The transcriptional landscape, encompassing non-coding RNAs and covalent RNA modifications, represents another critical layer of epigenetic complexity that can be decoded through sequencing approaches and integrated with other omics datasets. High-throughput RNA sequencing not only profiles mRNA changes but also can be tailored to capture lncRNAs and small RNAs (e.g. miRNAs, siRNAs) that orchestrate post-transcriptional regulation under stress. By depleting rRNA and focusing on longer transcripts, lncRNA-seq has uncovered hundreds of novel lncRNAs in various plants, many of which show differential expression under drought, salinity, or temperature stresses (Bao et al., 2025; Yang et al., 2022). Integrating lncRNA expression data with mRNA profiles and other omics has proven useful for inferring lncRNA functions. For example, co-expression network analyses often reveal lncRNAs that are co-regulated with neighboring stress-responsive genes, hinting at cis-regulatory roles. In several species (cotton, rice, cassava, etc.), stress-induced lncRNAs have been predicted to act as miRNA target mimics or interact with chromatin modifiers, thereby modulating gene expression indirectly (Chen et al., 2021; Lu et al., 2016; Suksamran et al., 2020). A study in xerophyte *Chrysopogon* (*C.songorica*) identified 52 lncRNAs under drought that likely sequester miR397 and miR166, which in turn would elevate the expression of the miRNAs' target genes involved in lignin and auxin pathways (Yan et al., 2019). In cassava, 682 lncRNAs responsive to cold/drought stress were linked through integrative network analysis to hormone signaling and metabolism genes (Shuxia Li et al., 2017). Such multi-omics integration (lncRNA, small RNA, mRNA, and even DNA methylation data) has revealed that lncRNAs can coordinate with other epigenetic layers. For instance, in cotton, certain drought-induced lncRNAs were found to be associated with DNA methylation changes and histone modifications at fiber development genes, suggesting a complex cross-talk between lncRNA expression and chromatin state (Lu et al., 2017).

Small RNA-seq provides a parallel view of the epigenetic regulatory network by capturing miRNAs and siRNAs that guide gene silencing mechanisms. When integrated with transcriptome data, small RNA profiles help delineate miRNA-mRNA regulatory modules under stress. A clear example is seen in rice during drought: sequencing identified dozens of drought-responsive miRNAs, and overlaying QTL and mRNA data pinpointed Osa-miR2919 as a negative regulator of drought tolerance. This miRNA was upregulated in drought-tolerant varieties and was found to target a suite of genes (19 targets) within known drought-yield QTL regions, including those in cytokinin and brassinosteroid signaling pathways. The integrated analysis suggested that miR2919 helps fine-tune hormonal signals to curb growth and save resources under drought, consistent with its role in modulating hormone-related genes (Kumar et al., 2023). Another illustrative study in oil-tea (*Camellia oleifera*) combined miRNA-seq and mRNA-seq to compare a drought-tolerant vs. sensitive cultivar. The resulting miRNA-mRNA network identified specific miRNAs whose up-regulation or down-regulation under drought had opposite expression patterns to their target genes, forming putative stress-regulatory pairs (He et al., 2022). By repressing these targets, the miRNAs likely mitigate excess reactive oxygen or defense signaling, thereby improving drought tolerance via crosstalk with other stress pathways. Such findings, validated by qPCR, demonstrate how integrating small RNA and transcript data can reveal post-transcriptional regulatory circuits critical for stress adaptation (He et al., 2022).

A burgeoning frontier in multi-omics integration is the epitranscriptome, which encompasses chemical modifications on RNA (such N^6-methyladenosine, 5-methylcytosine on RNA, pseudoruidine, etc.) that influence transcript fate. Technologies like DRS now allow mapping of RNA modifications transcriptome-wide (Bharti et al., 2024; Dhingra et al., 2023). These data can be integrated with standard transcriptomics and proteomics to understand how RNA modifications modulate gene expression under stress. Emerging evidence indicates that m6A in particular is dynamically reprogrammed by stresses and plays a regulatory role in mRNA stability and translation. For example, under heat stress, plants exhibit elevated m6A on certain mRNAs, which was found to accelerate the decay of those transcripts, presumably to clear transcripts for proteins that are non-decay of those transcripts, presumably to clear transcripts for proteins that are non-essential under heat and to prioritize the synthesis of HSPs. Consistently, m6A "writer" enzymes (like MTA in *Arabidopsis*) and "eraser" demethylases are stress-responsive, and mutants in these often show altered stress phenotypes. Under drought conditions, m6A profiling revealed selective methylation changes that suppress the accumulation of specific drought-responsive mRNAs, tuning down their translation or stability to help plants conserve energy. In one case, the loss of an m6A methyltransferase led to hyper-inducible genes, indicating that m6A normally restrains their expression to prevent overreaction to stress. The epitranscriptomic layer thus intersects with transcriptional and post-transcriptional regulation; multi-omics studies are beginning to "fit" this layer into the larger regulatory network.

7. Current challenges and future prospects

Despite significant progress in multi-omics research on plant responses to abiotic stress, several technical challenges remain to be addressed, and new directions for future development are emerging.

7.1. *Emergence of single-cell and spatial epigenomics*

Conventional omics approaches are typically based on bulk cell

populations, which obscure the heterogeneity inherent to plant tissues. However, abiotic stress responses often exhibit strong cell type specificity. For example, the epigenetic response in root apical meristem cells may differ substantially from that in mesophyll cells. Recently, single-cell omics technologies have begun to emerge in plant research, including single-cell ATAC-seq, single-cell RNA sequencing, and single-cell CUT&Tag (Denyer et al., 2019; Dorrity et al., 2021; Ouyang et al., 2021).

Although the presence of rigid cell walls has historically complicated plant single-cell isolation, recent studies have successfully applied single-cell ATAC-seq to *Arabidopsis* protoplasts and single-nucleus CUT&Tag to both *Arabidopsis* and rice, generating high-resolution maps of chromatin accessibility and histone modifications at the single-cell level (Dorrity et al., 2021; Ouyang et al., 2021). These approaches offer new opportunities to dissect how epigenetic states vary across individual cell types and how stress signals are perceived and propagated within heterogeneous tissues.

In parallel, spatial omics technologies are gaining momentum in plant systems. Methods such as spatial CUT&Tag can now map histone modifications at near-cellular resolution directly on tissue sections (Deng et al., 2022). This opens the door to visualizing chromatin dynamics in situ under stress, such as differential epigenetic responses between root epidermal and stele cells. By preserving the spatial context of tissues, these tools promise to significantly deepen our understanding of the localization and coordination of epigenetic regulation during environmental responses.

7.2. AI-assisted integrative modeling

Artificial intelligence (AI), especially deep learning, has emerged as a powerful approach for integrating multi-omics data to decipher complex stress responses. For example, a recent rice study developed a nine-layer convolutional neural network to integrate ATAC-seq chromatin accessibility and RNA-seq transcriptomic data under drought stress, successfully identifying ~15 key transcription factor-target gene modules associated with stress tolerance (Liu et al., 2025). In maize, combining diverse omics features (e.g. genomic markers, metabolite profiles, and high-throughput phenotypic traits) using machine learning significantly improved trait prediction accuracy. For example, one multi-omics model raised grain yield predictive R^2 from 0.32 to 0.43 (C. Wu et al., 2024). Building on such successes, one can envision next-generation models that incorporate even more data layers, including DNA methylation, histone modification landscapes, 3D genome architecture, non-coding RNAs, to uncover molecular signatures predictive of enhanced stress tolerance. These integrative AI models could not only reveal mechanistic regulatory networks but also forecast stress-responsive genes and optimal gene combinations for crop improvement, thus guiding multiplex genome editing and accelerated breeding.

Despite this promise, several challenges remain in applying AI to multi-omics integration. Different omics platforms and experiments introduce substantial data variability, so rigorous normalization and cross-platform standardization are needed to ensure that heterogeneous datasets can be reliably integrated (Thingujam et al., 2025). Model interpretability is another concern: deep neural networks often operate as “black boxes”, making it hard to extract biological insights. To address this, researchers are incorporating interpretable AI strategies. For instance, attention mechanisms or feature-attribution tools like SHAP (SHapley Additive Explanations) can highlight influential input features, helping to identify which epigenomic or transcriptomic signals drive a model’s predictions (Thingujam et al., 2025). Ultimately, the reliability of AI-generated predictions hinges on the quality and breadth of training data as well as prudent modeling strategies. Close collaboration between plant biologists and computational scientists is therefore essential to ensure that AI predictions are biologically meaningful and testable in the context of stress tolerance.

8. Conclusion

Recent advances in sequencing and multi-omics technologies have transformed our ability to dissect the epigenetic architecture of plant responses to abiotic stress. Integrative studies of DNA methylation dynamics, histone-modification reprogramming, 3D chromatin reorganization, and non-coding RNA-mediated regulation are revealing how these interconnected layers coordinate stress-responsive transcriptional programs. Complementary insights arise from the epitranscriptome, which encompasses RNA chemical modifications that tune mRNA fate, as well as from the emergence of single-cell and tissue-localized regulatory states. Crucially, AI-assisted integrative modeling is beginning to bridge high-dimensional datasets, enabling predictive frameworks that link chromatin features to transcriptional output and phenotype. Despite persistent challenges in data standardization, cross-platform integration, causal inference and functional validation, a technology-driven perspective is accelerating both mechanistic understanding and translational opportunities. In sum, while this review emphasizes sequencing and methodological advances, these tools collectively offer a powerful roadmap for decoding and engineering plant stress resilience, representing an imperative for sustainable crop improvement under escalating climate pressures.

CRediT authorship contribution statement

Siqing Fan: Writing – review & editing, Writing – original draft. **Hua Yang:** Writing – review & editing, Validation. **Yufang Hu:** Writing – review & editing, Validation. **Ling Zhang:** Writing – review & editing, Validation. **Mingkun Huang:** Writing – review & editing, Writing – original draft, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no competing interests.

Acknowledgments

This work was supported by the National Natural Science Foundation of China (82260745) and Jiangxi Provincial Natural Science Foundation (20232BAB205015, China).

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.stress.2025.101144.

Data availability

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

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