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Epigenetic mechanisms regulating plant responses to abiotic stress and their role in developing climate resilient crops

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Abstract

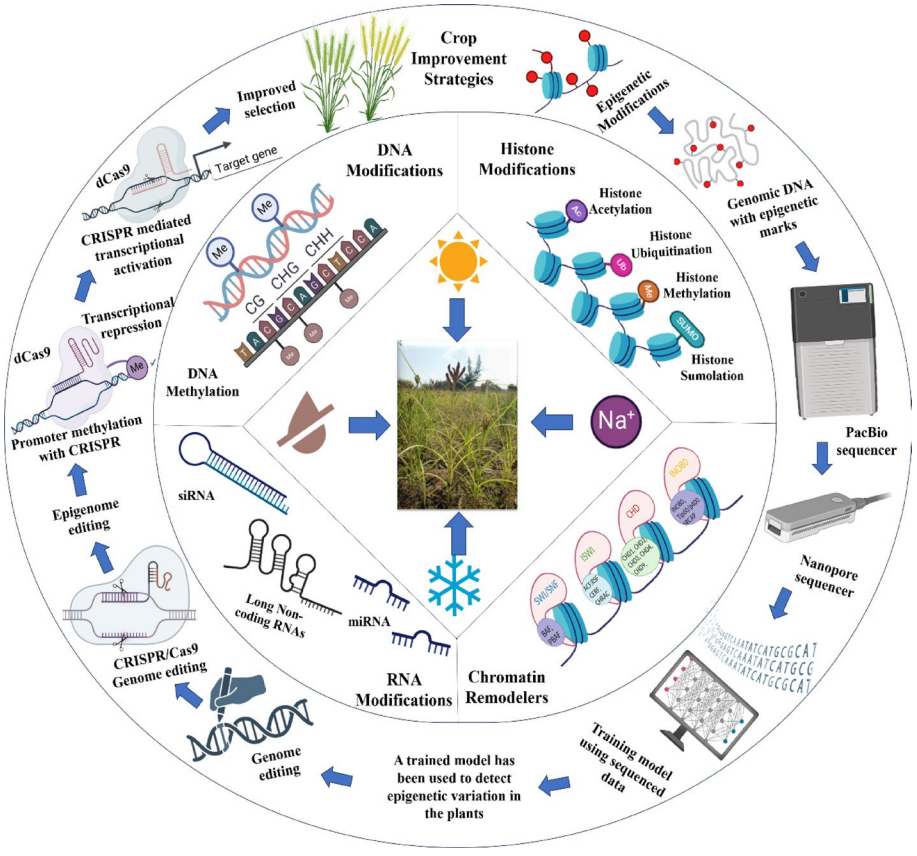
Abiotic stresses such as drought, salinity, and temperature extremes are major constraints to global crop productivity and food security. Plants respond to these factors through epigenetic modifications, chromatin remodelling, and transcriptional reprogramming that dynamically regulate gene activity and stress memory. This review synthesizes current knowledge on DNA methylation, histone modifications, non-coding RNAs, and chromatin remodelling, emphasizing the enzymes, protein complexes, and stress-responsive genes that illustrate their roles in abiotic stress adaptation. A comparative synthesis across model and crop species, including Arabidopsis, rice, maize, and wheat, reveals both conserved and species-specific patterns of epigenetic regulation, as well as major knowledge gaps. We also examine recent advances in genome and epigenome editing technologies, particularly CRISPR/dCas9 systems, and their application in crop stress resilience. Beyond molecular insights, the review highlights socio-economic and ethical considerations, contrasting regulatory landscapes in India and globally. By integrating molecular mechanisms with applied perspectives, this review provides a comprehensive resource to guide future research and crop improvement strategies for climate-resilient agriculture.

Keywords Stress priming, Epigenetic memory, CRISPR/dCas9, Non-Coding RNAs, Epigenetic modifications, Abiotic stress

1 Introduction

The concept of "Epigenetics" was first established by Conrad Waddington in 1942 to describe phenotypic changes that can be passed on to subsequent generations without a change in the genetic material [1]. Plant studies have been significantly advanced in the field of epigenetics, specifically how genes are regulated and how they can be inherited. One of the major concepts in this area is the distinction between euchromatin and heterochromatin, both of which are essential for the regulation of gene expression. Active gene transcription is often associated with euchromatin, gene silencing is often

Graphical abstract



associated with heterochromatin. This fundamental understanding has been supported by studies showing that chromatin structure regulates gene accessibility and expression in many plants [2].

Epigenetic alterations in plants are different from genetic mutations in terms of their reversible properties, which can lead to fast adjustment according to a changing environment. They are key players in tuning gene expression during abiotic stresses such as drought and salinity. For example, specific epigenetic marks can be changed to boost survival when plants are faced with stressful situations, by upregulating stress-responsive genes and downregulating non-essential genes and transposable elements [3]. This plasticity enables plants to modulate their phenotypic responses according to rapidly changing environmental challenges.

When the stress decreases, then the epigenetic switch will turn back, turning on regular gene expression and allowing for growth to resume. Such recovery requires the activity of mechanisms like demethylation and removal of repressive histone marks [4]. Such is the case for cold stress, where studies showed that cold stress results in long-lasting hypomethylation of cold-responsive genes, including COR15A in *Arabidopsis*, thus allowing rapid activation of these genes upon re-exposure to cold [5]. This phenomenon shows how epigenetic changes can provide plants with a form of "stress memory," allowing them to respond more efficiently to recurring stresses [6]. However, the increasing variability of climate, characterized by prolonged droughts, unpredictable rainfall,

and extreme temperatures, intensifies the frequency and severity of abiotic and biotic stresses, posing significant threats to plant survival and productivity [7].

A detailed overview of these mechanisms, their functions, key enzymes, and their specific roles in stress tolerance is presented in Table 1. Such adaptations allow for a rapid responses within hours to days and provide long-term acclimation through epigenetic memory that enables the plant to "remember" a prior stress event and respond more quickly to subsequent stress events [8]. Epigenetic memory and stress tolerance are promising targets for future research in agriculture with great prospects for developing climate change-resilient crops. Such improvements are needed for sustainably increasing and stabilizing productivity in the context of changing environmental conditions [9]. This review aims to consolidate recent advances in plant epigenetics, including DNA methylation, histone modifications, and RNA-mediated regulation, alongside developments in genome and epigenome editing. It further examines examples of stress-response mechanisms across major crops and discusses their socio-economic and ethical implications in modern crop improvement and climate-resilient farming. By integrating these perspectives, the review provides a timely resource to guide future research and application of epigenetic strategies for climate-resilient crop improvement.

2 Epigenetic mechanisms in plants

2.1 DNA methylation dynamics in plant stress responses

DNA methylation is a key epigenetic mechanism involving the addition of a methyl group to cytosine bases, occurring in three distinct contexts: CG, CHG, and CHH. CG methylation (Fig. 1), maintained by Writers - METHYLTRANSFERASE 1 (MET1), is symmetrical, heritable, and commonly found in gene bodies, often linked to moderately expressed genes [20]. CHG methylation, regulated by CHROMOMETHYLASE 3 (CMT3), is also symmetrical and plays a key role in silencing transposable elements and repetitive sequences [21]. CHH methylation, on the other hand, is asymmetrical and catalyzed by DOMAIN REARRANGED METHYLTRANSFERASES (DRM1/2) via the RNA-directed DNA Methylation (RdDM) pathway, primarily targeting promoter regions and transposable elements for de novo methylation [22]. DNA methylation modulates gene expression during stress, contributing to stress-induced silencing or recovery-related reactivation [23]. Stress-induced methylation silences non-essential genes and transposable elements to maintain genomic stability. H3K9me2-associated DNA methylation [24] silences genes under abiotic stresses like drought or salinity. Active demethylation mediated by enzymes which are called as Erasers like DEMETER (DME) and *REPRESSOR OF SILENCING 1 (ROS1)*, reverses these changes, reactivating critical genes necessary for growth and recovery, showing that stress recovery is associated with DNA demethylation in specific genes. Some methylation patterns provide plants with "stress memory," enabling faster responses to recurring stresses [25]. Readers, or methylation-binding proteins, such as MBDs (Methyl-CpG-binding domain proteins) and the SUVH family of histone methyltransferases, play a central role in interpreting DNA methylation marks. These proteins recognize methylated cytosines commonly at CpG sites and act as mediators, recruiting various chromatin-modifying complexes. This can lead to transcriptional repression or, in certain contexts, activation [26].

Table 1 Epigenetic mechanisms and their roles in plant stress responses

Epigenetic Mechanism	Description	Functions/mechanisms	Key enzymes/genes/proteins	Role in stress	References
DNA methylation	Addition of a methyl group (-CH3) to the cytosine base in DNA, primarily in CG, CHG, and CHH contexts (H = A, T, or C).	Silences transposable elements and repetitive DNA sequences to maintain genomic stability. Modulates gene expression by altering chromatin accessibility.	Establishment: RdDM pathway (DRM2) Maintenance: MET1, CMT2, CMT3, DRM2 Removal: ROS1, DME, DML2, DML3 (base excision repair pathway)	Stress-induced methylation silences non-essential genes during drought. Recovery-associated demethylation reactivates essential genes.	[10, 11]
Histone modifications	Post-translational modifications of histone proteins, such as acetylation, methylation, phosphorylation, and ubiquitination, which alter chromatin structure and gene expression.	- **Acetylation (e.g., H3K9ac)**: Associated with open chromatin and active gene expression. - **Methylation (e.g., H3K4me3, H3K27me3)**: Regulates chromatin activation or repression depending on the site.	Acetylation: Promotes transcription Methylation: Effects vary (e.g., H3K9me2 for silencing, H3K4me3 for activation) Enzymes: Histone acetyltransferases/ deacetylases, COMPASS, PRC2, Jumonji C, LSD1-like proteins	Acetylation activates genes involved in salinity tolerance. Repressive marks like H3K27me3 silence non-essential genes under cold stress.	[12, 13]
RNA interference (RNAi)	A process involving small RNAs, such as microRNAs (miRNAs) and small interfering RNAs (siRNAs), that regulate gene expression at transcriptional and post-transcriptional levels.	- **miRNAs**: Target mRNAs for degradation or repress translation to fine-tune gene expression. - **siRNAs**: Mediate RNA-dependent DNA methylation (RdDM) to silence transposable elements and repetitive sequences.	TIR1, Aux/IAA, GH3, and SAUR gene families RNA Polymerase IV (Pol IV), RNA-dependent RNA polymerase 2 (RDR2), Dicer-like 3 (DCL3), and ARGONAUTE 4 (AGO4)	miRNAs (e.g., miR393) regulate auxin signaling during drought. siRNAs silence transposable elements under heat stress to maintain genomic integrity.	[10, 14–16]
Long non-coding RNAs (lncRNAs)	RNA transcripts longer than 200 nucleotides that do not code for proteins but regulate gene expression through transcriptional and post-transcriptional mechanisms.	- Recruit chromatin-modifying enzymes to specific loci to alter histone marks and DNA methylation. - Act as miRNA sponges, preventing miRNA-mediated repression of target genes. - Modulate mRNA stability and splicing.	COLDAIR recruits chromatin-modifying enzymes, particularly the Polycomb Repressive Complex 2 (PRC2), which is essential for establishing repressive histone marks (H3K27me3) at the FLC locus	**COLDAIR** and **COOLAIR** in *Arabidopsis* regulate flowering during cold stress by modifying histone marks at the **FLC** locus. **DIR** in rice regulates ABA-responsive genes, enhancing drought tolerance.	[17–19]

Values in bold indicate key examples highlighted in the text for their central regulatory role and/or particularly well-characterized function in plant stress responses

Cold stress in *Arabidopsis thaliana* induces persistent hypomethylation (loss of methyl marks) and an upregulation of cold-responsive genes such as *COR15A*, allowing rapid reactivation upon re-exposure to cold stress [27]. Cold stress leads to increased cytosine methylation (hypermethylation) in *Prunus simonii* and Alpine plants, which in turn regulates the expression of cold-responsive genes by repressing non-essential pathways [28]. Under drought stress, *Arabidopsis* shows global hypomethylation and upregulation of stress-responsive genes such as *RD29A* and *RAP2.4*, while transposable elements become hypermethylated and repressed to maintain genome stability [29]. Similarly, in *Medicago sativa*, methylation levels decrease under drought, correlating with upregulation of stress-tolerance genes [30], while *Populus trichocarpa* experiences locus-specific hypomethylation and upregulation of drought-responsive genes [31]. In salinity stress, tolerant rice (*Oryza sativa*) varieties exhibit reduced CHH methylation and upregulation of ion transport genes like HKT1 and SOS1, enhancing their expression, whereas salt-sensitive varieties show hypermethylation and downregulation of these same genes [32]. Likewise, *Brassica napus* displays hypomethylation and upregulation in tolerant genotypes and hypermethylation in sensitive ones, influencing stress-adaptive pathways [33]. Some of the key enzymes and proteins that have their effect on stress tolerance are summarized in Table 2.

3 Histone modifications regulating stress-inducible genes

Histone modifications are critical regulators of chromatin structure and gene expression in plants, significantly influencing their responses to environmental stresses. These modifications are mediated by distinct groups of enzymes that act as writers, erasers, and readers. Writers such as histone acetyltransferases (HATs), including *GCN5* and HAT family members [34], and histone methyltransferases (HMTs) like the SDG and SUVH families [35], deposit activating or repressive marks on histones [36]. Erasers include histone deacetylases (HDACs), which remove acetyl groups, and Jumonji C (JMJ) domain proteins such as *REF6* and *JMJ14*, which demethylate histones to fine-tune transcriptional activity [37, 38]. Readers such as bromodomain-containing proteins (BRDs) interpret acetylation marks [39], while LIKE HETEROCHROMATIN PROTEIN 1 (LHP1) recognizes repressive marks like H3K27me3, stabilizing silenced chromatin states [40].

Together, these enzyme systems shape the balance between activation and repression of chromatin states and stress-responsive pathways, and their activity is reflected in specific modification patterns under stress. Acetylation, mediated by histone acetyltransferases (HATs) and reversed by histone deacetylases (HDACs) (Fig. 2), neutralizes histone charges, loosening chromatin structure and promoting transcription of stress-responsive genes like those marked with H3K9ac and H3K27ac [41, 42]. Methylation, catalyzed by histone methyltransferases (HMTs) and removed by demethylases, has variable effects depending on the site of modification; active marks like H3K4me3 promote gene activation, while repressive marks such as H3K27me3 and H3K9me2 compact chromatin into heterochromatin, silencing genes that may be de-repressed under stress [43]. Ubiquitination, involving the addition or removal of ubiquitin molecules by ubiquitin ligases or deubiquitinases, regulates transcription by signaling chromatin remodeling, as seen with H2B ubiquitination enhancing transcriptional activation [44]. These modifications collectively influence chromatin accessibility: acetylation promotes euchromatin and transcription, methylation fine-tunes gene expression, and ubiquitination recruits

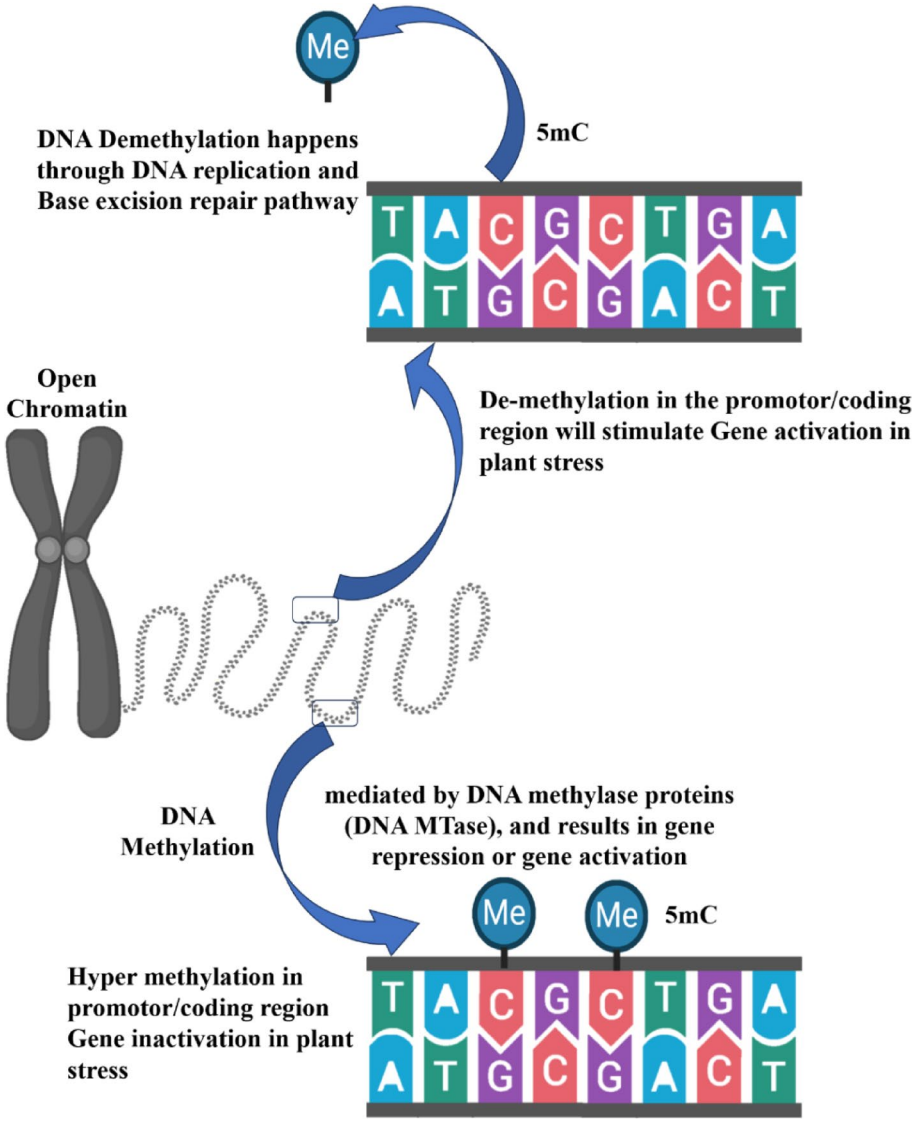


Fig. 1 Schematic representation of DNA methylation dynamics in plants under stress conditions. DNA methylation involves the addition of a methyl group to cytosine (C), forming 5-methylcytosine (5mC), primarily in CG contexts, and is catalyzed by DNA methyltransferases (MTases). Hypermethylation in promoter or coding regions typically leads to gene repression, while demethylation promotes gene activation. Passive DNA demethylation occurs via DNA replication, while active removal is mediated by base excision repair pathways. Open chromatin configuration promotes accessibility for transcription. Diagram created using BioRender. Me, methyl group; 5mC, 5-methylcytosine

chromatin remodelers, and their effects on stress tolerance are presented in Table 2. Case studies highlight their roles in stress adaptation—cold stress reduces repressive marks like H3K27me3 on genes such as *COR15A*, enabling faster activation and epigenetic memory [45]. Similarly, heat stress decreases H3K9me2 levels in rice and promotes histone acetylation in *Arabidopsis*, which are associated with improved heat tolerance [46]. These modifications are thus pivotal in regulating plant growth, development, and resilience to stress.

Table 2 Epigenetic mechanisms in heat, drought, and salt stress tolerance

Epigenetic level	Mechanism	Genes/proteins involved	Effect on stress tolerance	References
DNA methylation	Heterochromatin decondensation under heat stress	HD2B, HD2C	Limits histone hyperacetylation, DNA hypomethylation	[47, 48]
	DNA Cytosine Methylation Regulation	SDG25, ATX1	Mutations lead to increased DNA methylation and reduced heat stress-responsive gene expression, lowering tolerance.	[49]
	Differential methylation in tolerant vs. sensitive varieties	HKT genes	Regulates salt resistance	[50]
	Alternative Splicing (AS) Events	Intron retention (IR), alternative 3′ splice site (Alt3′SS)	Higher AS events in drought-tolerant Z141 and drought-sensitive NY-17 under drought stress	[51]
	Cytosine DNA Methylation	HvDME (DNA demethylase gene)	Influences its responsiveness to drought conditions.	[52]
	Reduced DNA methylation affects gene and TE expression	Respiratory chain enzymes in cotton	Promotes heat-responsive gene expression	[53]
	DNA Methylation Modulation	HcGLP3, HcDOF1.4, HcULP3, HcVHA, HcPP2C39, HcSRF6	Exogenous GSH increases DNA methylation levels, improving gene expression for salt stress adaptation.	[54]
Histone acetylation	H3K9/K14 acetylation activates heat-responsive genes	GCN5, ASF1a/b	Enhances heat tolerance	[55, 56]
	H3K9/K14 acetylation activates salt-tolerance genes	CTL1, PGX3, MYB54	Enhances salt stress tolerance	[57]
	Acetic acid reduces HDA6 binding to drought-responsive genes	HDA6, PDC1, ALDH2B7	Enhances ABA signaling and drought tolerance	[58]
	HDA710 represses salt tolerance genes	OsLEA3, OsABI5, OsbZIP72, OsNHX1	Reduces salt resistance	[59]
	HDA9 represses heat-responsive gene HSFA2	HSFA2	Negatively regulates salt tolerance	[60]
Histone methylation	H3K4 methyltransferase promotes gene expression	OsHKT1;5	Enhances salt resistance	[61]
	H3K27 demethylases promote drought-responsive gene expression	GmZF351	Enhances salt tolerance	[62]
	H3K4me2, H4K5ac regulated thermotolerance	GhHSFA1a, GhHSFA2	Positive for Thermotolerance	[63]
	Histone H3K4 Methylation	SDG25, ATX1	Enhancing heat-stress tolerance	[49]
	JMJ27 prevents H3K9me2 accumulation	GOLS2, RD20	Activates drought-response genes	[64]
	H2Bub1 activates salt-responsive genes.	HUB1/2, UBC1/2	Enhances gene activation under salt stress	[65]
	H3K4 demethylase represses negative regulators under salt stress	WRKY46, WRKY70	Enhances salt tolerance	[66]
	Loss of repressive H1.3 enhances the SOS pathway genes under salt conditions.	SOS1, SOS2, SOS3	Improves salt resistance	[67]
Chromatin architecture	Heat stress activates transposable elements (TEs)	ONSEN, HSFA1/HSFA2	TE activation enhances heat tolerance	[68, 69]
	Drought-induced chromatin accessibility increases gene activation.	OsCHR4	Improves drought resistance	[70]

Table 2 (continued)

Epigenetic level	Mechanism	Genes/proteins involved	Effect on stress tolerance	References
Chromatin remodeling	Loss of OsCHR4 enhances cuticular wax biosynthesis	OsCHR4	Improves drought resistance	[70]
	Chromatin remodeler H2A.Z modulates salt-responsive genes.	–	Promotes salt tolerance	[71]
	Heat negatively affects the strength of the compartmentation in constitutive heterochromatin, and positively affects it in euchromatin.	HSFA1a	The chromatin accessibility pattern was dynamically modified by heat stress.	[72]
	Chromatin Binding associated with target genes	ATX1	Influencing transcriptional memory during stress recovery.	[49]
Sumoylation	Sumoylation dynamics regulate transcriptional switches.	–	Slows transcriptional regulation under heat stress	[73]
	The SUMO system in sweet potato showed expression against abiotic stress	IbSCE1a/b/c	Improved salt and drought tolerance.	[74]

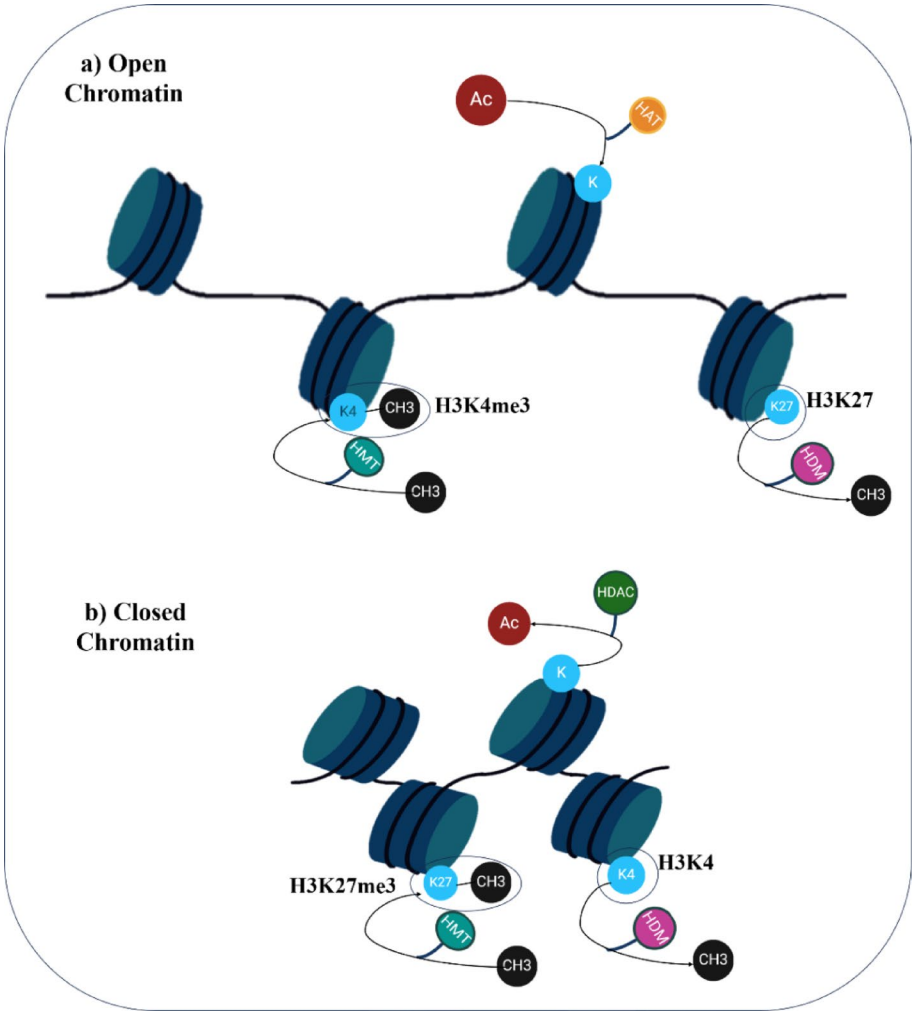


Fig. 2 Role of histone modifications in chromatin remodelling and gene expression regulation. **a** Open chromatin state is maintained by acetylation of histone tails via histone acetyltransferases (HATs), enhancing gene activation. **b** Closed chromatin results from histone deacetylation (HDACs) and methylation, leading to gene silencing. Methylation at H3K4 (H3K4me3) activates gene expression, while H3K27me3 is associated with repression. Ac, acetylation; Me, methylation; CH3, methyl group. Figure constructed using BioRender

4 ATP-Dependent chromatin remodeling in stress tolerance

Chromatin remodeling is a pivotal epigenetic process involving the dynamic alteration of chromatin structure to regulate DNA accessibility for transcription, replication, and repair. This process is essential for plant stress responses, allowing adaptation to abiotic stresses such as drought, heat, and salinity, as well as biotic stresses like pathogen attacks. ATP-dependent chromatin remodeling complexes play a central role in this process by utilizing energy from ATP hydrolysis to reposition, eject, or restructure nucleosomes, thereby modifying chromatin architecture [75]. These modifications enable or restrict access to regulatory DNA regions, influencing stress-responsive gene expression. Mechanisms include nucleosome sliding, which exposes promoters or enhancers; nucleosome ejection, providing direct access to stress-responsive genes; and histone variant exchange, which alters chromatin's structural and functional properties [76]. Key ATP-dependent remodeling complexes in plants include SWI/SNF, ISWI, CHD, and INO80 (Fig. 3). For instance, the SWI/SNF complex, with subunits like BRAHMA

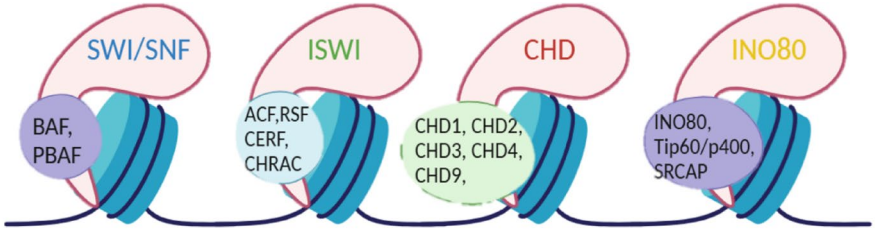


Fig. 3 Four major families of chromatin remodelers—SWI/SNF, ISWI, CHD, and INO80—regulate nucleosome positioning and chromatin accessibility. Each complex contains distinct subunits that use ATP hydrolysis to slide or evict nucleosomes, thereby modulating access to regulatory DNA. These remodelers are involved in transcriptional regulation, histone exchange, and repair processes. The figure shows the interaction of remodelers with nucleosomes. Abbreviations: BAF, BRG1-associated factor; CHRAC , chromatin accessibility complex; SRCAP, SNF2-related CREBBP activator protein. Created using BioRender

(BRM) and SWI3, facilitates transcriptional activation under stress conditions, while the INO80 complex aids in DNA repair during stress [77]. In pathogen defense, *Arabidopsis thaliana* activates the SWI/SNF complex upon infection by *Pseudomonas syringae*, promoting pathogenesis-related gene expression through nucleosome repositioning [78]. Similarly, NPR1-mediated systemic acquired resistance (SAR) depends on chromatin remodeling to remove repressive histone marks, activating salicylic acid-responsive genes [79]. In abiotic stress responses, chromatin remodeling enables the activation of stress-tolerant pathways. During drought stress, the SWI/SNF complex regulates ABA-responsive genes like *RD29A* and *RAB18* by sliding nucleosomes, while DDM1 protects heterochromatin structure to ensure genome integrity [80]. In response to heat stress, BRM-mediated remodeling facilitates heat shock protein expression by enabling transcription factor binding at heat shock elements [81]. Chromatin remodeling interacts with other epigenetic mechanisms such as histone modifications and DNA methylation. Remodeling complexes collaborate with histone acetyltransferases (HATs) or deacetylases (HDACs) to regulate chromatin accessibility [82]. For example, during drought stress, increased histone acetylation (H3K9ac) at stress-responsive loci is facilitated by remodelers [83]. In the RNA-directed DNA methylation (RdDM) pathway, chromatin remodelers ensure DNA methylation is maintained at repetitive elements, contributing to genomic stability under stress [84]. The significance of chromatin remodeling lies in its ability to enable rapid and dynamic gene regulation, crucial for adapting to environmental fluctuations. Moreover, it contributes to stress memory, allowing plants to respond more effectively to recurring stresses, and ensures genomic stability by silencing transposable elements. These functions make chromatin remodelers vital targets for developing stress-tolerant crops [85].

5 The role of Non-coding RNAs in stress regulation

Non-coding RNAs (ncRNAs) represent a diverse group of regulatory molecules that fine-tune gene expression in plants during growth, development, and stress adaptation. They are broadly classified into microRNAs (miRNAs), small interfering RNAs (siRNAs), and long non-coding RNAs (lncRNAs), each contributing unique and overlapping functions in stress regulation. Small RNAs (sRNAs) are short, non-coding RNA molecules, typically ranging from 20 to 24 nucleotides in length, that play critical roles in regulating gene expression at both transcriptional and post-transcriptional levels [86].

These molecules are involved in diverse biological processes, including developmental regulation, stress responses, and the maintenance of genome stability.

In plants, sRNAs are categorized into two main classes: microRNAs (miRNAs) and small interfering RNAs (siRNAs). miRNAs are derived from single-stranded RNA precursors that form hairpin structures and are processed by the enzyme DICER-LIKE 1 (DCL1) into mature miRNAs [87]. These miRNAs are then incorporated into the RNA-Induced Silencing Complex (RISC), where they guide the complex to target mRNAs based on sequence complementarity, leading to mRNA degradation or translational repression.

Several small RNAs have been identified as being regulated in response to drought stress in recent studies. Novel_105 miRNA was upregulated under drought stress in *Solanum tuberosum* [88], Sto-miR159n was downregulated under drought in *Sophora tonkinensis* [89], and miR408 in *Cajanus cajan* was induced by salinity stress [90]. Additionally, miR398 and miR862 were identified in *Pennisetum glaucum* and miR398 was downregulated under oxidative stress, leading to upregulation of its targets copper/zinc superoxide dismutases (CSD1 and CSD2), while miR862 was upregulated under drought stress [91]. For instance, miR398 targets copper/zinc superoxide dismutases (CSD1 and CSD2), modulating oxidative stress responses [92]. In contrast, siRNAs originate from double-stranded RNA (dsRNA) precursors, which can arise from transposable elements, viruses, or overlapping transcripts. They are processed by DICER-LIKE 3 (DCL3) and other DCL proteins and play significant roles in RNA-directed DNA methylation (RdDM) and post-transcriptional gene silencing. siRNAs are essential for heterochromatin formation, transposable element silencing, and antiviral defense [93]. Additionally, siRNAs are crucial in maintaining genomic stability by silencing transposable elements through the RdDM pathway, which recruits DNA methyltransferases like DRM2 to mediate de novo methylation [94].

Non-coding RNAs (ncRNAs) are RNA molecules that do not code for proteins but play vital roles in regulating gene expression and stress responses in plants. Among these, long non-coding RNAs (lncRNAs) have emerged as key players in various biological processes [95]. lncRNAs, typically longer than 200 nucleotides and lacking significant open reading frames, regulate gene expression at both transcriptional and post-transcriptional levels [96]. They function by recruiting chromatin-modifying enzymes to specific genomic loci, influencing histone modifications and DNA methylation, as seen in *Arabidopsis thaliana*, where the antisense lncRNA COOLAIR promotes histone methylation at the *FLOWERING LOCUS C* (FLC) gene to regulate flowering time [97]. They can also interfere with transcription by blocking RNA polymerase II progression or by modulating mRNA stability, decay, or alternative splicing [98]. For instance, ELENA1 enhances the stability of pathogenesis-related (PR) gene transcripts in *Arabidopsis*, boosting immunity, while IPS1 acts as a decoy for miR399, regulating phosphate homeostasis [99]. Additionally, lncRNAs contribute to nuclear architecture, scaffolding chromatin and regulatory proteins to affect chromatin structure and gene expression. These regulatory mechanisms enable lncRNAs to play critical roles in plant stress responses [76].

In abiotic stress, lncRNAs show distinct regulation patterns. For instance, *DIR* is upregulated under drought stress, enhancing ABA signaling and improving tolerance. In contrast, certain salinity- and heat-responsive lncRNAs are induced under stress and

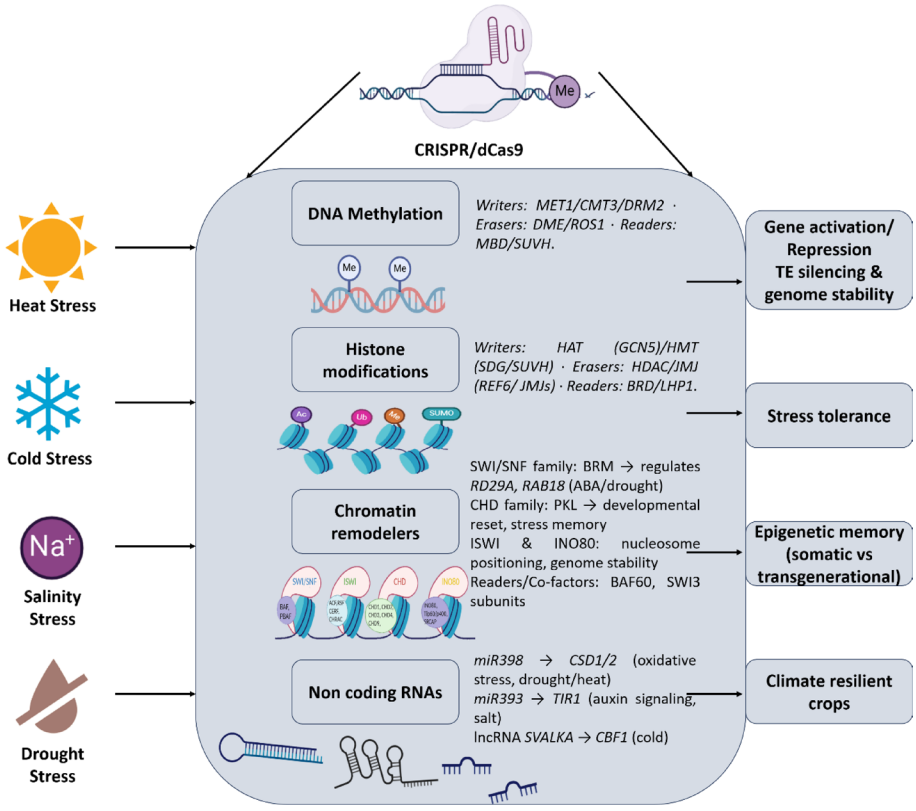


Fig. 4 Integrated epigenetic pathways in plant stress adaptation. Environmental stresses (heat, cold, salinity, drought) trigger signaling cascades (ROS, Ca^{2+}, MAPK, ABA/SA) that converge on four regulatory layers: DNA methylation (writers: MET1/CMT3/DRM2; erasers: DME/ROS1; readers: MBD/SUVH), histone modifications (writers: HATs/HMTs; erasers: HDAC/JMJs; readers: BRD/LHP1), chromatin remodelers (SWI/SNF, CHD, ISWI, INO80 complexes), and non-coding RNAs (miR398 → *CSD1/2*; miR393 → *TIR1*; lncRNA *SVALKA* → *CBF1*). These mechanisms regulate stress-responsive genes (*RD29A*, *RAB18*, *HSFA2*, *COR15A*), silence transposable elements, and establish both somatic and transgenerational epigenetic memory. Together they enhance stress tolerance and contribute to the development of climate-resilient crops. CRISPR/dCas9-based epigenome editing provides a targeted overlay to modulate these pathways for crop improvement

interact with chromatin modifiers to activate stress-responsive genes [100]. COLDAIR is upregulated during cold stress, recruiting Polycomb Repressive Complex 2 (PRC2) to deposit repressive marks at the *FLC* locus, thereby regulating flowering after vernalization [97]. Furthermore, lncRNAs integrate with hormonal pathways and interact with small RNAs to fine-tune stress-responsive gene expression and their regulatory effects, as provided in Table 3.

Taken together, these mechanisms form an integrated regulatory network that links environmental perception to gene regulation and stress adaptation (Fig. 4). This synthesis highlights the interplay between DNA methylation, histone modifications, chromatin remodeling, and non-coding RNAs, while also underscoring the potential of CRISPR/dCas9 to precisely modulate these pathways.

6 Technological advances in epigenetic studies

Epigenetics has experienced remarkable technological advancements, enabling researchers to unravel how plants regulate gene expression and adapt to environmental stresses. These breakthroughs have provided a comprehensive understanding of the dynamic

mechanisms underpinning plant resilience, revealing how epigenetic modifications such as DNA methylation, histone modifications, and chromatin accessibility contribute to gene regulation in response to changing environments. High-throughput sequencing technologies, innovative epigenome editing tools, and advanced bioinformatics platforms are at the forefront of these developments, paving the way for transformative applications in crop improvement [124].

High-throughput sequencing methods, such as bisulfite sequencing, reduced representation bisulfite sequencing (RRBS), and whole-genome bisulfite sequencing (WGBS), have revolutionized epigenetic research by offering genome-wide insights into DNA methylation patterns [125]. Bisulfite sequencing, a cornerstone technique, allows for single-base resolution mapping by converting unmethylated cytosines into uracil while preserving methylated cytosines. This method has been instrumental in identifying stress-induced differentially methylated regions (DMRs) in plants [126]. For instance, studies have employed bisulfite sequencing to investigate methylation changes in rice under salt stress, uncovering key genes involved in ion transport and osmotic regulation [127]. RRBS, a cost-effective alternative, targets specific genomic regions to reduce sequencing costs while maintaining resolution [128]. WGBS provides an exhaustive view of the methylation landscape, enabling comprehensive studies that link methylation patterns with gene expression and environmental responses. These sequencing technologies have been vital in revealing how methylation contributes to stress tolerance and adaptability in plants.

Advances in chromatin analysis techniques, such as Chromatin Immunoprecipitation (ChIP) and Assay for Transposase-Accessible Chromatin Sequencing (ATAC-Seq), have deepened our understanding of histone modifications and chromatin accessibility. ChIP, a widely used method, isolates DNA-protein complexes using specific antibodies to map histone modifications and transcription factor binding sites [129]. By targeting marks like H3K4me3 (active chromatin) and H3K27me3 (repressed chromatin), ChIP has uncovered the regulatory roles of histone modifications in plant stress responses [130]. For example, it has been utilized to study heat-induced histone acetylation in *Arabidopsis* and transcription factor binding during plant defense [131]. ATAC-Seq identifies open chromatin regions by leveraging transposases to insert sequencing adapters into accessible DNA. This technique has been pivotal in mapping chromatin accessibility changes in response to stress, such as the activation of drought-responsive genes in sorghum, and discovering regulatory elements involved in environmental stress tolerance [132].

Complementing experimental advancements, bioinformatics and computational tools play a critical role in analyzing and interpreting vast epigenomic datasets. Tools like Bismark and MethPipe facilitate the analysis of bisulfite sequencing data, enabling the mapping of methylation patterns and identification of DMRs linked to phenotypic traits under stress [133]. ChIP-Seq analysis tools, such as MACS2 and HOMER, identify peak calling. Machine learning techniques further enhance this field by analyzing large datasets to predict stress-responsive genes and epigenomic patterns. For instance, AI-based models have been employed to predict drought tolerance in maize by integrating epigenomic and transcriptomic datasets, demonstrating the potential of computational tools in advancing crop resilience research [134].

Table 3 Role of long non-coding RNAs (lncRNAs) in plant stress responses: mechanisms, targets, and effects

Epigenetic Level	Mechanism	Genes/proteins involved	Effect on stress tolerance	References
Post-transcriptional	Interaction of lncRNAs as eTMs for miRNAs	lncRNAs TCONS_00048391, TCONS_00010856, bra-miR164a	Facilitates response to heat stress	[101]
Transcriptional	Expression of novel banana HS-lncRNAs and interaction with miRNAs	lncRNAs as precursors for miRNAs like miR8007b, miR414, miR2083, miR847	Regulates transcriptional and post-transcriptional responses to heat stress	[102]
Transcriptional	Heat-responsive lncRNAs in *B. juncea* as eTMs of miRNAs	lncRNAs TCONS_00051908, TCONS_00088973	Contributes to tolerance against heat and drought stress	[103]
Transcriptional	Interaction network of heat-responsive lncRNAs and target genes in rice	lncRNAs like TCONS_00092993; osa-miR1850	Enhances heat stress tolerance in tolerant and susceptible varieties	[104]
Post-transcriptional	Regulatory network prediction of heat-responsive lncRNAs in maize	Heat shock proteins, spliceosome, late embryogenesis abundant protein genes	Regulates stress-response pathways and increases heat tolerance	[105]
Transcriptional	Cold acclimation via inhibition of CBF1 transcription	CBF1, SVALKA, cryptic antisense CBF1 (asCBF1)	Enhances cold acclimation	[106]
Transcriptional and Post-Transcriptional	Activation of MAF4 via NAT lncRNA_2962 under cold stress	NAT lncRNA_2962, MADS AFFECTING FLOWERING4 (MAF4), WDR5a	Suppresses flowering under cold stress	[107]
Transcriptional	Regulation of flowering through FLC paralogs	FLC2, NATs at the FLC2 locus	Repression of flowering under cold stress in B. rapa	[108]
Transcriptional	Regulation of stress-responsive genes and transcription factors	CBF4, LEA, WRKY	Cold stress tolerance in Vitis vinifera	[109]
Alternative splicing	Regulation of TAS1a lncRNA by splicing under cold stress	TAS1a, AT2G27400.1, miR173	Modulates cold stress response via tasiRNA biogenesis	[110]
Transcriptional and post-transcriptional	Discovery of lncRNAs and miRNAs regulating stress responses in tomato	Various lncRNAs and miRNAs	Enhances abiotic and biotic stress resilience, including cold stress	[111]
Transcriptional and post-transcriptional	Regulation of gene expression via lncRNAs induced or suppressed under drought stress	lncRNA77580	Enhances drought tolerance but increases salinity sensitivity	[112]
Post-transcriptional	Interaction with miRNAs regulating the chlorophyll biosynthesis pathway	lncRNA MSTRG.28732.3, miR171, Os02g0662700, Os02g0663100, Os06g0105350	Modulates drought tolerance	[113]
Transcriptional	Drought-responsive transcriptome in wild rice	1655 novel lncRNAs	Improved drought adaptation	[114]
Transcriptional	Mechanisms related to oxidoreductase activity, water binding, and electron carrier activity	653 lncRNAs in maize	Improved drought tolerance	[115]
Post-transcriptional	Drought-responsive regulatory network via calcium signaling and ABA metabolism	1405 high-confidence lncRNAs (185 DE)	Enhanced drought tolerance	[116]

Table 3 (continued)

Epigenetic Level	Mechanism	Genes/proteins involved	Effect on stress tolerance	References
Transcriptional	Regulation through sucrose and starch metabolism pathways	DN33069_c1g1 in alfalfa	Drought stress regulation	[117]
Post-transcriptional	Regulation of pollen development-related genes	3053 drought-responsive lncRNAs in tomato anthers	Improved pollen development under drought stress	[118]
Transcriptional regulation	Differential expression of salt-responsive lncRNAs	Transcription factors (AP2, NAC, bZIP, ERF, MYB, WRKY); Potassium transporters, Aquaporins (TIP1-2, PIP2-5)	Enhances transcriptional regulation of salt-responsive genes, improving ion balance, and maintaining osmotic stress regulation.	[119]
Transcriptional regulation	lncRNA MSTRG.8888.1 alters bHLH protein levels and binds promoters of salt-tolerant transcripts (trans-acting)	bHLH transcription factors	Enhances salt tolerance by regulating transcription of salt-responsive genes.	[120]
Differential expression	LncRNAs in wild and cultivated tomato show differential expression under salinity stress	Genes in ABA, BR, and ETH signaling pathways	Enhances molecular understanding of stress pathways and responses, improving salt tolerance.	[121]
Transcriptional regulation	LncRNAs like TCONS_00292946 and TCONS_00176941 show time-dependent expression under salinity stress.	Target genes related to salt stress in groundnut	Time-specific expression of lncRNAs regulates salt stress responses.	[122]
Differential expression	Differential expression of lncRNAs in Chenopodium quinoa under salinity stress	4,460 differentially expressed lncRNAs, transcription factors	Highlights regulatory roles in quinoa's salinity tolerance.	[123]

These technological innovations have transformed the field of plant epigenetics, enabling a deeper understanding of the complex regulatory mechanisms that govern responses to environmental stresses. By combining high-throughput sequencing, cutting-edge editing tools, and advanced computational platforms, researchers can uncover key epigenetic drivers of stress tolerance and adaptability. This knowledge has significant implications for agriculture, particularly in the development of climate-resilient crops capable of withstanding environmental challenges such as drought, salinity, and temperature extremes. The integration of these technologies into plant breeding programs offers new avenues for enhancing crop productivity and sustainability in the face of global environmental change.

The advancements in epigenetic research have provided powerful tools to dissect the intricate molecular mechanisms underlying plant resilience. High-throughput sequencing technologies reveal the genome-wide patterns of epigenetic modifications, while chromatin analysis techniques and epigenome editing tools enable detailed studies of chromatin dynamics and targeted interventions. Bioinformatics platforms and machine learning algorithms further facilitate the integration and interpretation of complex datasets, linking epigenomic changes to phenotypic outcomes. Collectively, these innovations are transforming plant epigenetics into a promising field with far-reaching applications, driving efforts to improve crop performance and ensure agricultural sustainability in an era of climate uncertainty.

7 Epigenetics and crop improvement

7.1 Translating epigenetic insights into breeding strategies

Epigenetic breeding strategies are emerging as innovative approaches to enhance crop resilience and productivity in the face of environmental challenges. Two key strategies in this domain include inducing beneficial epigenetic changes via stress priming and screening for epigenetically diverse cultivars [135]. Inducing beneficial epigenetic changes via stress priming refers to the pre-exposure of plants to mild stress conditions, which can enhance their ability to withstand subsequent, more severe stress events [136]. This process is mediated by epigenetic modifications that allow plants to "remember" the initial stress and respond more effectively later, as shown in Fig. 5 [137]. Yadav et al., demonstrated that multigenerational exposure to heat stress in *Arabidopsis thaliana* leads to phenotypic resilience and both genetic and epigenetic variations in offspring. These stress-associated epigenetic variations, such as differentially methylated positions (DMPs) and regions (DMRs), can be stably inherited and utilized in epigenetic-assisted breeding programs to develop superior stress-tolerant crops [138]. This flexibility is crucial for developing crops that can adapt to rapidly changing environments. Additionally, Kakoulidou et al., discussed the potential applications of epigenetic strategies in crop improvement, highlighting the need for identifying epigenetically regulated traits that can be harnessed for breeding [139]. By identifying and selecting cultivars with beneficial epigenetic variations, breeders can enhance the resilience of crops to abiotic stresses. Villagomez-Aranda et al., noted that potentiating the natural defensive strategies of plants through epigenetic mechanisms can provide novel directions for plant breeding [140]. This approach allows for the selection of cultivars that exhibit enhanced phenotypic plasticity and adaptability to environmental perturbations. Verkest et al., highlighted that integrated breeding strategies that consider both genetic

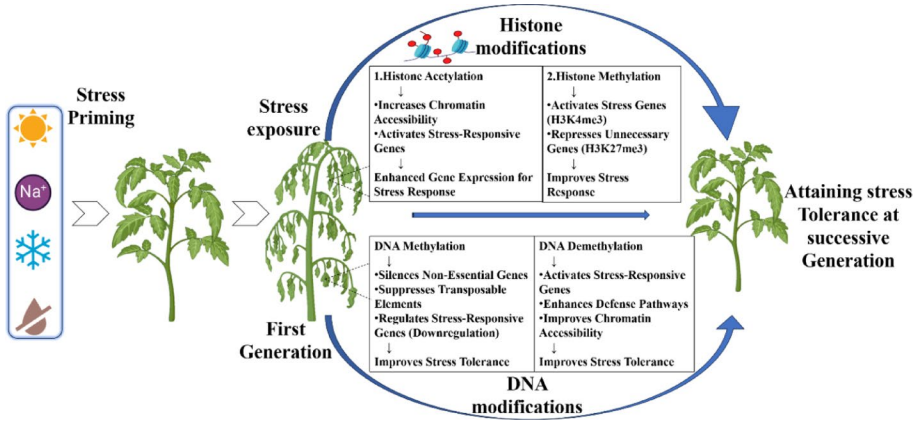


Fig. 5 Illustration of stress priming and transgenerational epigenetic memory in plants. Initial exposure to abiotic stress (e.g., drought, salinity, temperature) induces transcriptional and epigenetic changes such as DNA methylation and histone modifications. These result in transcriptional reprogramming and enhanced stress tolerance. Upon re-exposure, primed plants exhibit improved resilience. Histone acetylation and demethylation activate gene expression, while DNA methylation and H3K27me3 repress non-essential pathways. Diagram created using BioRender

and epigenetic factors can lead to significant improvements in traits such as drought tolerance and energy use efficiency in canola [141]. In addition to these approaches, future epigenetic breeding efforts will benefit from the systematic identification of stable epialleles and epigenetic quantitative trait loci (epiQTLs), which can be integrated into marker-assisted selection and genomic selection pipelines [142]. This integration would allow breeders to track epigenetic variants with agronomic relevance in the same way that DNA-based markers are currently used. Seed priming techniques that induce transgenerational stress memory provide an accessible, low-cost application for enhancing resilience, particularly in smallholder farming systems [143]. Additionally, advances in CRISPR/dCas9-based epigenome editing offer the possibility to fine-tune chromatin states at stress-responsive loci in elite cultivars without introducing foreign DNA, thereby aligning with regulatory and consumer preferences [144]. Together, these strategies illustrate a practical continuum from near-term field applications (seed priming) to long-term breeding innovations (epigenome editing), strengthening the pathway toward climate-resilient crop development.

7.2 Crops enhanced through epigenetic (e.g., rice and maize)

Epigenetics has led to significant advancements in crop improvement, particularly in rice and maize, through the application of epigenetic breeding strategies. These strategies leverage the dynamic nature of epigenetic modifications to enhance stress tolerance and overall agronomic performance. One important aspect is the development of salt-tolerant rice varieties, particularly the 'Pokkali' variety. Research by Ferreira et al., demonstrated that 'Pokkali' exhibits rapid relaxation of DNA methylation levels in response to salinity stress, which is crucial for its salt tolerance [145]. The dynamic adjustment of DNA methylation helps 'Pokkali' to retain stress resistance gene expression, providing an evolutionary context under which epigenetic modifications can be utilized for enhancing the variety of crops. Additionally, Karan et al., illustrated that differential DNA methylation patterns among rice genotypes affected gene expression in the context of salt stress, thereby affecting stress tolerance [146]. Such a diversity in epigenetic

response points toward the possibility of selecting rice cultivars with favorable epigenetic traits that can adapt to saline conditions, and opt to breed for epigenotype. Zheng et al., highlighted the importance of transgenerational epimutations in the adaptation of rice to drought. The study showed that prolonged exposure to drought induces stable epigenetic changes that increase the resilience to multiple generations [147]. Such findings illustrate the potential of epigenetic mechanisms to facilitate long-term adaptation in rice, making it a valuable model for breeding programs aimed at improving stress tolerance. In maize, the understanding of epigenetic regulation has also paved the way for developing hybrid varieties with superior traits. Duarte-Aké discussed how epigenetic mechanisms, particularly histone modifications, can enhance heterosis—the phenomenon where hybrid offspring exhibit improved or superior qualities compared to their parents [25]. By using epigenetic markers and artificial epigenome editing techniques, breeders can create novel hybrid maize varieties that are better equipped to handle environmental stresses and improve agricultural productivity. Moreover, the application of epigenetic knowledge in maize breeding has been linked to enhanced adaptability to climate change.

7.3 Use of epigenome editing tools like CRISPR-dCas9 to modify stress-related genes

The use of epigenome editing tools, particularly CRISPR-dCas9, has revolutionized the ability to modify stress-related genes in plants, enhancing their resilience to environmental challenges. This technology allows for precise and targeted modifications of the epigenetic landscape, enabling researchers to manipulate gene expression without altering the underlying DNA sequence (Fig. 6) [148, 149]. Unlike conventional Cas9, dCas9 lacks endonuclease activity due to mutations in the RuvC1 (D10A) and HNH (H840A) domains, making it ideal for gene repression (CRISPRi) or activation (CRISPRa) when fused to transcriptional effectors such as KRAB, SRDX, or VP64 [150]. This capability can be harnessed to recruit various epigenetic modifiers to target genes, thereby influencing their expression. Thakore et al., demonstrated that by fusing dCas9 with KRAB repressor domains, they could effectively silence distal regulatory elements, enhancing the specificity and efficiency of epigenome editing also recruits histone deacetylases to silence gene expression [151]. This approach allows for the targeted repression of genes associated with stress responses, which can be crucial for developing stress-tolerant crops. Vojta et al., expanded the functionality of the CRISPR-dCas9 system by repurposing it for targeted DNA methylation. They fused the DNMT3A catalytic domain to

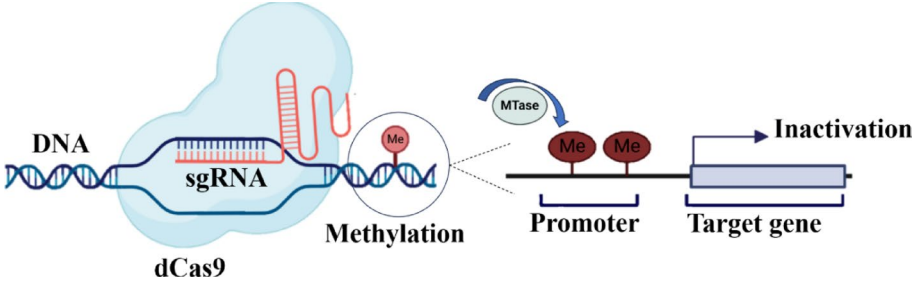


Fig. 6 Targeted DNA methylation using the CRISPR/dCas9 epigenome editing system. The catalytically inactive Cas9 (dCas9) is directed by a guide RNA (sgRNA) to specific promoter regions, where it recruits a fused DNA methyltransferase (MTase). This leads to deposition of methylation marks (Me) and subsequent gene repression or silencing without altering the DNA sequence. This approach enables precise control of gene expression in plants. MTase = methyltransferase; Me = methyl group. Diagram created using BioRender

dCas9, enabling the precise addition of methyl groups to specific loci, which can silence genes involved in stress responses [152]. Advanced multi-effector constructs, such as dCas9-SunTag (Multiplies activation domains to boost expression by tethering VP64 copies to dCas9 using a GCN4 peptide array) and CRISPR-Act2.0, have significantly improved gene activation in model plants by recruiting multiple activator domains (e.g., VP64, p65, EDLL) to a single promoter region [150]. For instance, Papikian et al. demonstrated up to 100-fold activation of the *FWA* gene in Arabidopsis using a SunTag-based dCas9 complex [153]. Delivery of dCas9 fusion constructs in plants is typically accomplished through Agrobacterium-mediated transformation, viral vectors, or nanoparticle-based carriers. Recent advances have enhanced tissue-specific and inducible expression systems to reduce off-target effects and fine-tune gene regulation in a spatiotemporal manner. By targeting specific promoters and enhancers, they can modulate the expression of genes that confer resilience to drought conditions, thereby improving the overall stress tolerance of the crop [154]. Taken together, CRISPR/dCas9 systems provide powerful tools for epigenome modulation in plants. However, only a small subset of applications has been validated under stress conditions (notably AREB1/ABF2 and AVP1 under drought), whereas most studies remain proof-of-concept demonstrations. Future work should prioritize extending these tools to field-relevant stress assays to realize their full potential for crop resilience. Several case studies have demonstrated the potential of dCas9-based epigenome editing in plants (Table 4).

Despite the promising applications of CRISPR-dCas9 in crop improvement, challenges remain in optimizing delivery methods and ensuring specificity to avoid off-target effects. Johnston et al., pointed out that the activation of stress genes can occur as a side effect of CRISPR component expression, highlighting the need for careful design and validation of gRNAs to minimize unintended consequences [160]. As the technology

Table 4 Case studies in crops using CRISPR/dCas9

Crop	Target gene	Effector used	Modification type	Observed outcome	References
Arabidopsis	*AREB1/ABF2*	dCas9-AtHAT1	Activation (Histone Acetylation)	Drought tolerance, survival, chlorophyll	[155]
Arabidopsis	*AVP1*	dCas9-VP16-p65-HSF1	Activation	Ion accumulation, improved drought response	[156]
Maize	*PDS1*	dCas9 (repressor/activator)	Activation/ Repression	60% repression and 2.5× activation using dual sgRNAs	[157]
Rice	*OsER1*	dCas9-TV	Activation	62× fold transcriptional activation	[158]
Arabidopsis	*AtCLAVATA3*	dCas9-SunTag	Activation	100× activation; sustained effect in T2 generation	[153]
N. benthamiana	*PDS*	dCas9-EDLL	Activation	3.4× fold activation	[159]

continues to evolve, the integration of CRISPR-dCas9 with other genomic and epigenomic tools will likely enhance its efficacy and precision. The potential for CRISPR-dCas9 to facilitate rapid advancements in crop resilience to abiotic stresses underscores its significance in modern agricultural practices.

8 Field applications and economic relevance of epigenetic modifications

Recent translational research has demonstrated that epigenetic regulation can directly contribute to improved climate resilience in crops. For example, targeted activation of stress-related genes such as *AVP1* and *ABI1* using CRISPR/dCas9-VP64 or VP16-p65-HSF1 complexes in *Arabidopsis* has been shown to enhance drought tolerance and ion accumulation, confirming the potential of epigenome modulation without introducing permanent DNA alterations (Park et al., 2017). In rice, stress-adaptive varieties such as *Pokkali* exhibit promoter methylation of *OsHKT1;5* and *OsDREB2A*, contributing to enhanced salinity tolerance and improved physiological performance under abiotic stress (Baek et al., 2011). These examples validate the application of molecular epigenetic mechanisms in enhancing real-world plant traits. While full commercialization of epigenetically engineered hybrids is still in early phases, preliminary reports suggest that the strategic use of such tools in crops like maize and soybean could offer yield stabilization under stress with minimal genetic disturbance. Continued research, particularly field-level validation and integration with breeding programs, is necessary to fully harness the economic and agronomic potential of epigenome editing.

8.1 Comparative analysis and critical interpretation

Epigenetic responses to abiotic stress show considerable variation across plant species due to differences in genome organization, chromatin structure, and the abundance of transposable elements (TEs). For example, in *Arabidopsis thaliana*, histone acetylation marks such as H3K23ac and H3K27ac are rapidly deposited in response to drought and heat stress, facilitating short-term transcriptional activation of stress-inducible genes. These changes are moderately heritable and often persist for 2–3 generations [161]. In contrast, *Oryza sativa* (rice) primarily employs DNA methylation changes, particularly at CG and CHH sites in promoter regions, to regulate gene expression under drought and salinity conditions. However, these methylation patterns are mostly somatic and rarely inherited across generations [84]. *Zea mays* (maize) displays a dominance of histone methylation, particularly H3K4me3 and H3K27me3, in response to drought stress [162]. In polyploid species like *Triticum aestivum* (wheat), stable DNA methylation changes in stress-responsive loci such as *TaDREB1* and *TaHSP26* have been documented under drought conditions [163]. These changes are often associated with high TE activity, contributing to more stable transgenerational epigenetic memory compared to diploid species. These comparisons not only reveal the diversity of epigenetic regulatory mechanisms across plant species but also underscore the importance of context-specific approaches to epigenetic engineering. For instance, leveraging histone-based modulation may be more effective in short-generation crops like *Arabidopsis*, whereas methylation-targeted strategies could be optimized for polyploid crops like wheat, where stability and heritability are desirable. However, the variable transgenerational potential of these modifications poses a key challenge. Further research is essential to elucidate

how environmental stress signals are perceived, processed, and stably encoded epigenetically across generations in diverse crop systems.

8.2 Epigenetic technologies in Indian agriculture and ethical considerations

India's agriculture is highly vulnerable to climate-induced abiotic stresses, with more than 50% of cultivable land prone to drought, heat, and salinity. Given this context, epigenetic technologies such as CRISPR/dCas9-based tools offer a non-transgenic, precise, and rapid alternative for developing climate-resilient crops [164]. Many key Indian crops such as rice, wheat, groundnut, chickpea, and finger millet exhibit stress-responsive epigenetic plasticity. For example, rice cultivars in Eastern and Southern India have demonstrated stress memory via promoter methylation of genes. These traits make them excellent candidates for targeted epigenome editing using tools like dCas9-SunTag or CRISPR-Act systems, especially in polyploid species like wheat and groundnut. Additionally, such interventions align with India's crop diversification policies, including the International Year of Millets 2023 initiative, by enabling epigenetic enhancement of underutilized traditional crops. On the regulatory front, India's Department of Biotechnology (DBT) and Genetic Engineering Appraisal Committee (GEAC) have introduced guidelines in 2022 that exempt site-directed nuclease-1 and nuclease-2 (SDN-1 and SDN-2) based edits, including epigenetic changes—from stringent GMO regulations, provided no foreign DNA is incorporated. Ethically, this raises crucial considerations regarding accessibility, farmer autonomy, and biosafety. Epigenetically edited crops must remain affordable and accessible to smallholder farmers, ideally through public sector breeding programs. Off-target epigenetic modifications must be transparently monitored, and participatory models involving farmers, scientists, and policy makers should be encouraged to ensure societal acceptance. In this context, epigenome editing represents not only a technological advancement but also a potential tool for democratizing crop improvement in India's diverse and resource-limited farming systems.

Beyond the Indian context, international perspectives further highlight the socio-economic implications of epigenetic interventions. In the European Union, strict GMO-equivalent regulations pose challenges for rapid adoption, whereas the United States and China are advancing more quickly with supportive frameworks for genome and epigenome editing in crops. This divergence underscores the importance of harmonizing global policies to ensure equitable access and trade compatibility. From a food security standpoint, epigenetic technologies could play a critical role in stabilizing yields under climate extremes, reducing input dependency, and enhancing resilience in orphan crops such as millets, sorghum, and legumes that are vital to smallholder farmers across Asia and Africa. Ethical considerations extend beyond regulation: biodiversity conservation, transparent communication of potential risks, and public engagement will be key to societal acceptance. Addressing these socio-economic and ethical dimensions ensures that epigenome editing contributes not only to technological progress but also to inclusive, sustainable, and equitable agricultural development.

9 Future directions: epigenetics for climate-resilient agriculture

9.1 Unexplored epigenetic mechanisms

The role of non-coding RNAs (ncRNAs) in orchestrating complex stress responses in plants is a burgeoning area of research. Non-coding RNAs, including microRNAs

(miRNAs) and long non-coding RNAs (lncRNAs), have been shown to play critical roles in regulating gene expression during abiotic and biotic stress conditions. For instance, miRNAs are involved in post-transcriptional regulation of gene expression, which is crucial for plant adaptation to environmental stresses. Furthermore, lncRNAs have been implicated in modulating chromatin states and epigenetic modifications, thereby influencing stress resilience and phenotypic plasticity in plants. Future research should address whether ncRNA-mediated regulation is stable across generations and under field conditions, and whether stress-responsive lncRNAs can serve as biomarkers or targets for breeding programs. Investigating cross-talk between ncRNAs and DNA methylation/histone modifications during combined stresses (e.g., drought + heat) remains a critical knowledge gap.

9.2 Synthetic biology applications

The application of synthetic biology in designing synthetic promoters with stress-inducible epigenetic regulation represents a promising frontier in plant biotechnology. By engineering synthetic promoters that can respond to specific stress signals, researchers can potentially control the expression of genes associated with stress tolerance more precisely [165]. This approach could facilitate the development of crops that are not only more resilient to environmental challenges but also exhibit improved agronomic traits. For example, the integration of epigenetic markers into breeding programs could streamline the selection of hybrid varieties that are better adapted to climate change [25]. To translate these insights into practice, synthetic biology tools must be validated in diverse crop species beyond Arabidopsis and rice. Integrating epigenetic markers into marker-assisted selection could accelerate breeding, while epigenetic seed priming strategies offer near-term applications for enhancing resilience in smallholder farming systems.

9.3 Challenges

Despite the potential benefits of epigenome editing and synthetic biology applications, several challenges and ethical considerations must be addressed. One significant concern is the risk of unintended effects resulting from epigenome editing, which could lead to unpredictable changes in gene expression and plant phenotype. The complexity of epigenetic regulation means that even minor alterations could have cascading effects on plant development and stress responses. Additionally, ensuring equitable access to epigenetically enhanced crops is crucial to prevent disparities in agricultural productivity and food security. From a food security perspective, equitable deployment is essential: epigenetic technologies should be made accessible for orphan crops such as millets, sorghum, and legumes that sustain smallholder farmers in climate-vulnerable regions. Field-scale testing of epigenetically enhanced varieties, alongside robust regulatory frameworks, will be crucial for translating molecular advances into agricultural impact. As these technologies advance, it is imperative to establish regulatory frameworks that promote responsible research and equitable distribution of benefits derived from epigenetic innovations in crop breeding.

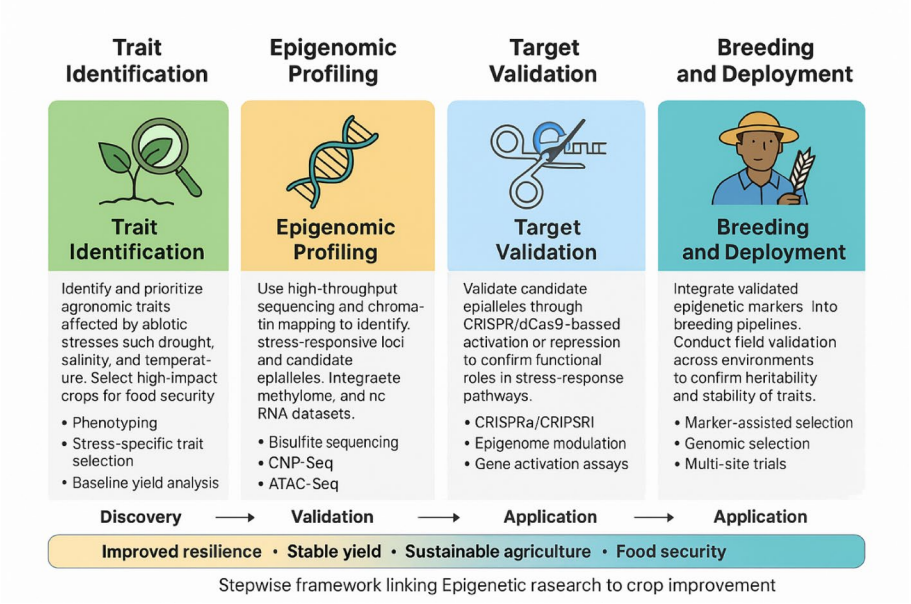


Fig. 7 Stepwise framework for integrating epigenetic knowledge into crop improvement

10 Conclusion

This review consolidates current understanding of how epigenetic mechanisms such as DNA methylation, histone modifications, chromatin remodeling, and non-coding RNAs regulate plant responses to abiotic stresses including drought, salinity, and temperature extremes. These molecular processes play a central role in modulating gene expression, maintaining genomic stability, and enabling plants to develop both short-term acclimation and long-term stress memory.

To make these insights more actionable for crop improvement, a stepwise framework is proposed to guide researchers and breeders in translating epigenetic knowledge into practical outcomes (Fig. 7):

Step 1. Trait identification Prioritize key agronomic traits most affected by abiotic stress, such as drought tolerance, salinity resistance, and thermal stability. Target crops with significant yield and food security relevance.

Step 2. Epigenomic profiling Utilize high-throughput sequencing, methylome mapping, and histone mark profiling to identify stress-responsive loci and candidate epialleles. Integrate transcriptomic and metabolomic datasets to correlate epigenetic signatures with phenotypic variation.

Step 3. Target validation Employ CRISPR/dCas9-based epigenome editing to functionally validate the causal role of candidate epialleles in regulating stress-responsive pathways. Focus on reversible, non-transgenic edits to ensure regulatory compliance and field applicability.

Step 4. Breeding and deployment Incorporate validated epigenetic markers into breeding programs through marker-assisted or genomic selection pipelines. Conduct multi-location field trials to assess trait stability, heritability, and performance under real-world stress conditions.

This multi-step pathway bridges molecular research with applied breeding, providing a roadmap for the development of climate-resilient crop varieties. Moving forward, future research should emphasize underexplored regulatory layers such as non-coding RNAs

and chromatin remodelers, alongside stress-validated CRISPR/dCas9 applications. Integrating these molecular insights with breeding innovations and field-level validation can accelerate the transition from discovery to sustainable agricultural practice, ensuring food security in an era of climate uncertainty.

Author contributions
Bevin Nishanth—Conceptualization, Software; Babu Rao—Project administration; Suji—Conceptualization, Supervision; Rifa Fathima—Original draft preparation; Premkumar—Original draft preparation; Balasankar Iyyappan and Sorna Kumar—Validation; Yuvaraj Dinakarkumar—Review and editing.

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Declarations

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