

Epigenetic Regulation of Stress Responses in Plants: Mechanisms, Dynamics, and Heritable Memory

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Abstract

Plants are continuously exposed to diverse abiotic and biotic stresses such as drought, salinity, extreme temperatures, oxidative stress, and pathogenic attacks. To adapt and survive under such challenging conditions, they employ sophisticated epigenetic regulatory mechanisms that modulate gene expression without altering the DNA sequence. This review synthesizes findings from Chinnusamy and Zhu (2009) and Abdulraheem et al. (2024), providing a comprehensive overview of the dynamic role of epigenetic regulation in plant stress responses. Key mechanisms include DNA methylation, histone modifications, small RNA-mediated gene silencing, and chromatin remodelling. DNA methylation, primarily at CG, CHG, and CHH contexts, can lead to stress-responsive gene activation or silencing and may be stably inherited, contributing to stress memory. Histone modifications such as acetylation and methylation adjust chromatin accessibility, with specific marks like H3K4me3 and H3K9ac enhancing transcription under stress. Small RNAs, including miRNAs and siRNAs, play dual roles in gene silencing and transcriptional regulation, particularly through RNA-directed DNA methylation (RdDM). Chromatin remodelers work in concert with these elements to reorganize nucleosomes and modulate gene accessibility in response to environmental cues. Notably, epigenetic changes can persist beyond immediate stress responses, influencing developmental traits and enabling transgenerational inheritance of stress tolerance. These insights highlight the adaptive advantage conferred by epigenetic plasticity in plants. As high-throughput sequencing and CRISPR-based epigenome editing tools advance, epigenetic regulation offers a promising frontier for developing climate-resilient and high-yielding crops to ensure sustainable agriculture in the era of global climate change.

Keywords: Abiotic and Biotic stress, epigenetics, gene expression, gene silencing, inheritance, climate resilience, high yield, sustainable agriculture.

Introduction

Plants constantly encounter abiotic and biotic stresses—such as drought, salinity, extreme temperatures, oxidative damage, and pathogen attack—that necessitate robust, dynamic mechanisms for adaptation. One of the most pivotal regulatory systems involves epigenetic

modifications, which modulate gene expression without altering DNA sequence. These modifications include DNA methylation, histone post-translational modifications, non-coding RNAs, and chromatin remodelling, all of which cooperatively determine chromatin accessibility and gene transcription patterns. While Chinnusamy and Zhu (2009) offered a foundational view into these epigenetic systems, highlighting the potential for epigenetic stress memory, Abdulraheem et al. (2024) provided updated insights by integrating high-throughput profiling and focusing on model and crop plants under varied environmental stresses. Together, these studies underscore epigenetics as a vital layer in plant stress biology with promising implications for crop improvement.

DNA Methylation: Mechanisms and Functional Roles

DNA methylation (DM), typically at the 5-carbon of cytosine residues in CG, CHG, and CHH contexts, is catalyzed by enzymes such as MET1, CMT3, and DRM1/2. It plays a fundamental role in transcriptional repression, particularly in heterochromatic regions and transposable elements. Under stress conditions, DM is dynamically reprogrammed. Chinnusamy and Zhu (2009) reported that cold stress in maize led to hypomethylation of the *ZmM11* promoter, correlating with its transcriptional activation and sustained expression even after the stress was relieved, suggesting a form of persistent memory. Similarly, in tobacco, multiple stresses (aluminum, salt, cold) induced demethylation in coding regions of the *NtGPDH* gene, promoting stress-responsive gene activation.

Abdulraheem et al. (2024) expanded on this by detailing how DNA methylation patterns shift globally under stress, especially in model plants like *Arabidopsis thaliana* and crops such as rice and apple. They described stress-specific methylation changes in the promoter regions of key regulatory genes, such as *ATDM1*, and noted their association with drought tolerance. Importantly, both reviews emphasized that DNA methylation is not always repressive; its impact depends on genomic context—methylation in gene bodies can stabilize expression, while promoter methylation typically silences transcription. Additionally, DNA methylation interacts with other epigenetic mechanisms. Histone deacetylation via HDA6 can promote DNA methylation, forming a feedback loop that reinforces gene silencing. Furthermore, methylation of

satellite DNA was linked to photosynthetic shifts under stress in *Mesembryanthemum crystallinum*, highlighting methylation's developmental consequences.

Histone Modifications: Orchestrating Transcriptional Plasticity

Histone modifications are critical determinants of chromatin structure and gene activity. The N-terminal tails of histones undergo modifications such as acetylation, methylation, phosphorylation, and ubiquitination. These modifications form a “histone code” that influences transcription. For example, trimethylation of H3K4 (H3K4me3) and acetylation of H3K9 (H3K9ac) are associated with active chromatin, whereas H3K27me3 and H3K9me2 are linked to gene repression.

Chinnusamy and Zhu (2009) highlighted how drought and submergence stress led to increased H3K4me3 and H3 acetylation at key loci like *ADH1* and *PDC1*, with expression patterns reverting after stress withdrawal, illustrating dynamic chromatin remodelling. They also documented the involvement of histone deacetylases (HDACs) such as HDA6 and HDA19 in silencing stress-responsive genes via chromatin compaction. HDA6, for example, is upregulated by ABA and jasmonic acid, and its loss of function results in hyperacetylation and inappropriate expression of silenced genes.

Abdulraheem et al. elaborated on how histone acetylation and methylation marks change in concert with transcriptional reprogramming in rice and maize. In *Oryza sativa*, drought tolerance is associated with H3K9ac and H3K4me3 enrichment at transcription factors like WRKYs and DREB family members. Moreover, the authors noted that histone modification patterns are conserved across species, suggesting broad functional relevance. This conservation is evident in studies showing that the same modifications that regulate heat shock proteins in yeast also regulate CBF1-controlled cold tolerance in *Arabidopsis*.

Small RNAs and RNA-Directed DNA Methylation (RdDM)

Small RNAs, particularly microRNAs (miRNAs) and small interfering RNAs (siRNAs), are integral to transcriptional and post-transcriptional gene silencing. These molecules guide the RNA-directed DNA methylation (RdDM) pathway, in which siRNAs direct DRM2 to methylate complementary DNA regions, establishing transcriptional silencing. Chinnusamy and Zhu (2009) illustrated how nat-siRNAs like *SRO5-P5CDH* regulate gene expression under salt stress, leading to increased proline accumulation—a known osmoprotectant. They also described the role of ROS1, a DNA demethylase, and its RNA-binding

cofactor ROS3 in reversing RdDM, thereby fine-tuning methylation at stress-regulated genes. Abdulraheem et al. showed that miR398, downregulated under oxidative stress, targets CSD1/2 (superoxide dismutases), enabling detoxification pathways. Other miRNAs, such as miR393, regulate auxin signaling during drought, while miR156 modulates developmental timing and stress resilience by repressing SPL transcription factors. The role of small RNAs is therefore both regulatory and adaptive, with potential transgenerational effects via RdDM.

Chromatin Remodelling and Stress-Induced Plasticity

Chromatin remodelling complexes use ATP hydrolysis to reposition nucleosomes and alter DNA accessibility. These complexes often work synergistically with histone modifiers and DNA methyltransferases to shape transcriptional landscapes during stress.

Chinnusamy and Zhu detailed the role of SNF2/BRAHMA-type remodelers like AtCHR12 in mediating growth arrest under drought and heat stress. Knockouts of these remodelers reduce stress sensitivity, indicating their importance in growth-stress trade-offs. Abdulraheem et al. showed that chromatin remodelling plays a central role in epigenetically activating transcription factors and defense-related genes. The interaction between SNF2 remodelers and flowering repressors like FLC under cold stress suggests that chromatin remodelling mediates developmental adjustments during environmental challenges.

Epigenetic Memory and Transgenerational Inheritance

One of the most intriguing aspects of plant epigenetics is stress memory, where previous exposure to stress leads to primed responses upon re-exposure. This memory may be short-lived (e.g., persistence of transcripts or proteins) or long-term, involving heritable epigenetic changes. Chinnusamy and Zhu provided compelling examples: progeny of *Tobacco mosaic virus*-infected plants displayed hypomethylated LRR loci and higher recombination rates, a clear case of transgenerational epigenetic inheritance. In rice, application of 5-azadeoxycytidine (a demethylating agent) led to hypomethylation of the Xa21G promoter and enhanced pathogen resistance in progeny.

Abdulraheem et al. noted that methylation changes at stress-responsive loci often persist into the next generation, and may influence traits like flowering time, seed dormancy, and root morphology. They also emphasized the adaptive value of such memory, although it may carry yield penalties if the stress is no longer present—a concept important for seed sourcing and breeding strategies.

Conclusions and Future Prospects

Together, these two works emphasize that epigenetic regulation is central to how plants perceive, respond to, and "remember" stress. DNA methylation, histone modifications, and small RNA networks collaborate to fine-tune gene expression across diverse stresses. The dynamic yet heritable nature of epigenetic marks provides an elegant mechanism for both immediate acclimation and long-term adaptation. Future efforts should focus on epigenetic engineering, using tools like CRISPR-dCas9-fused effectors to modify specific epigenetic marks at target loci. High-throughput technologies such as bisulfite sequencing, ChIP-seq, ATAC-seq, and small RNA profiling can now provide base-level resolution of epigenetic states across plant genomes. These advances, coupled with precision breeding, hold great promise for developing stress-resilient, high-yielding crops.

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