Harnessing Epigenetic Mechanisms for Crop Resilience: A Comprehensive Review of Plant Responses to Biotic and Abiotic Stresses

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ABSTRACT

Climate change is leading to significant biotic and abiotic stresses, which is alarming for the future of sustainable crop production and improvement. Global agriculture faces mounting challenges. Understanding epigenetic mechanisms can help improve crops. Exploring plant epigenetic mechanisms can enhance crop resilience, productivity, and stress tolerance, ensuring food security for the growing global populations. Epigenetic mechanisms often involve heritable modifications in organisms without any direct changes in the DNA. Epigenetics is essential for making plants adaptive to different stressed conditions. Abiotic and biotic stresses are major limiting factors for plant growth, development, and survival. Epigenetic mechanisms, such as DNA methylation, histone tail modifications, and RNA-directed pathways, regulate gene expression and allow plants to develop memory against these stresses. This memory is crucial for plants to respond effectively to uncertain stresses in the future. These epigenetic modifications are heritable to the next generations. Researchers have shown that plants use epigenetic memory to adapt to a rapidly changing environment, particularly harsh biotic and abiotic challenges, enabling plants to enhance their ability to adapt to diverse environments and withstand abrupt changes in their surroundings. A thorough understanding of these mechanisms can help us develop safer and more efficient methods of crop improvement to make crops more resilient and create a food-secure future for generations. The mechanisms of RNA-directed pathways, DNA methylation, and histone tail modifications are critical in modulating plant responses to diverse stressors, as they directly take part in the expression and suppression of targeted genes.

Keywords: Epigenetic mechanisms, DNA methylation, Histone tail modifications, RNA-directed pathways, Stress tolerance

Introduction

"An epigenetic trait is a stably heritable phenotype resulting from changes in a chromosome without alterations in the DNA sequence." (Definition first proposed by Conrad Waddington)

Living organisms face continuous environmental stresses, which can trigger different protective adaptive mechanisms. These stresses can negatively impact the growth, development, and reproduction of organisms.[1] Climate change can expose plants to abiotic stresses like heat and cold stress, drought, and salinity. The epigenetic mechanisms help the plants in regulating gene responses to stress.[2] Moreover, biotic factors such as herbivores, pathogens, and other strong competitors can adversely impact a plant's performance, with the severe impact being different across plant species due to genetic influences.[3] Waddington was the first to define epigenetics as the interactions between genes and their products that shape the overall phenotype of an organism.[4]

DNA methylation, micro RNAs, and post-translational histone modifications (epigenetic factors) are essential regulators for plant response to stress.[5] Plants adapt to stress by using genetically determined mechanisms like DNA methylation and histone modifications, giving plants an evolutionary advantage by enabling short-term memory responses without permanent alteration in the genome.[6] RNA-directed DNA methylation (RdDM) pathway is a crucial pathway in gene regulation of gene expression under abiotic stress.[7] Stress memory in the plants, which is transferred from one generation to another, is controlled by histone modifications.[8] Epigenomic configurations are important in evolutionary responses that can be used for accurate crop predictions to changing climate.[9] The research has been primarily focused on the epigenetic consequences of the interactions instead of the possible role of plant epigenetic framework in the quality of stress response.[10] Genetically identical individuals can exhibit differences in DNA methylation in response to similar stress.[11]

With the growing global population (10 billion expected by 2050), the drastic effects of climate change, and the shift in Earth's rainfall pattern and seasons, the agriculture sector is vulnerable.[12] Epigenetics can be used as a significant tool in plant breeding.[13] This review provides a comprehensive insight into the epigenetic responses of a plant to stress, emphasizing mechanisms such as DNA methylation and histone modifications to develop naturally evolved adaptive strategies that enhance resilience to biotic and abiotic stresses (Figure 1).

A Brief Overview of the Mechanisms

Epigenetic changes are not direct alterations in the DNA of an organism, but these are often heritable modifications that can affect the phenotype.[14] Epigenetic marks consist of chemical modifications to DNA, including methylation and various post-translational modifications of histone proteins, such as acetylation, methylation, ubiquitination, sumoylation, and phosphorylation. These changes generally occur at the

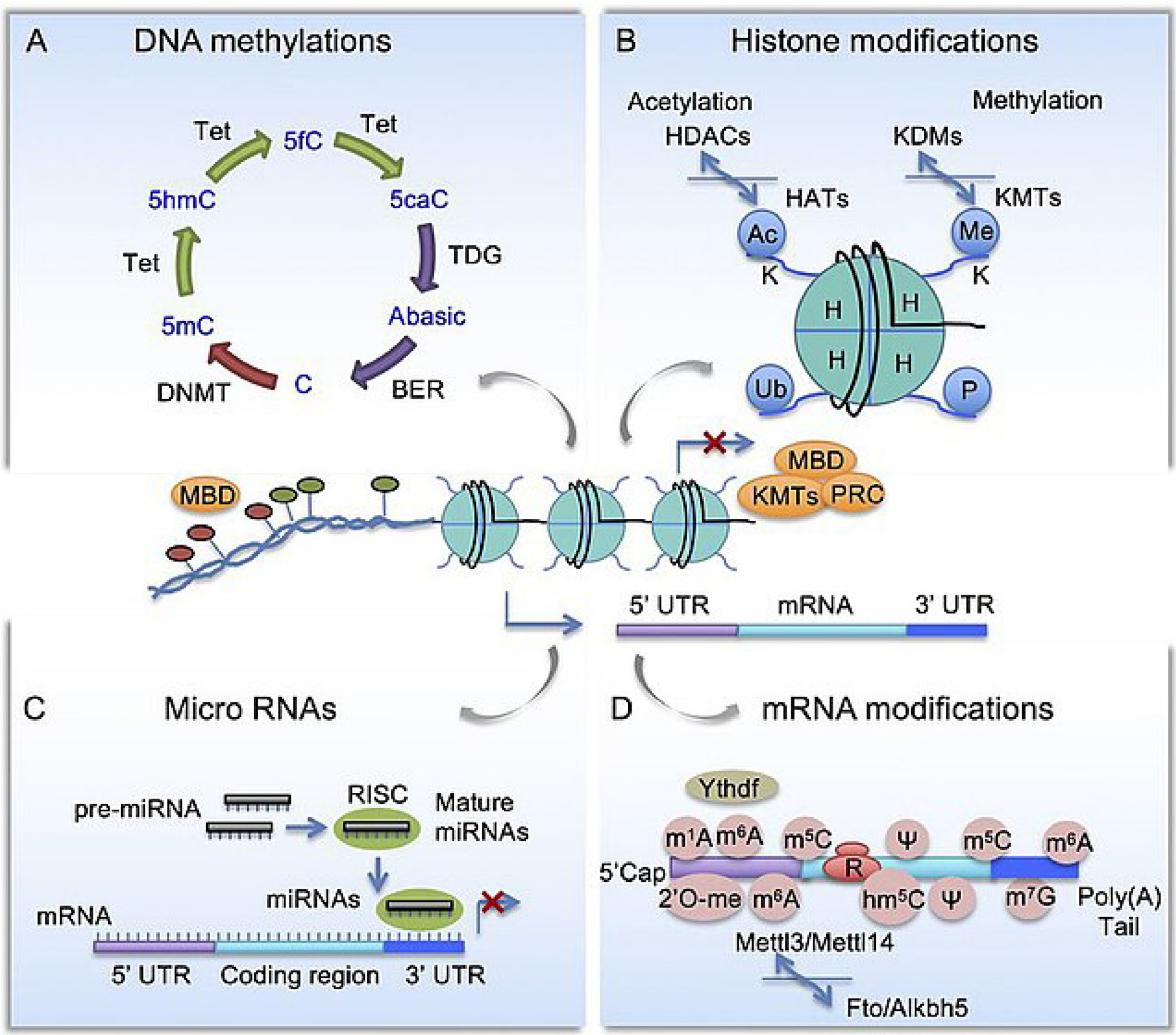

Fig 1 | Comprehensive schematic representation of epigenetic mechanisms highlighting DNA methylation, histone modification, and chromatin remodeling interactions influencing gene expression
Attribution: Wahane S, Halawani D, Zhou X and Zou H

histone N-terminal,[15] which can control gene expression and change the accessibility of the genomic regions, leading to phenotypic plasticity.[16]

DNA methylation is one of the most researched epigenetic mechanisms.[16] It is a genomic modification that regulates gene expression and modulates chromatin structure. Methylation is a key mechanism that directly influences a plant's development and evolution.[17] Plant DNA methylation is accomplished by a family of enzymes known as DNA methyltransferases, which link a methyl group (-CH3) at cytosine in symmetric, CG, and CHG contexts as well as asymmetric, CHH contexts (where H is any nucleotide other than G).[5] The degree of DNA methylation influences other molecular processes such as gene expression, transposon mobility, chromosome interaction, circRNA biogenesis, and RNA methylation.[17] Furthermore, miRNAs are the key components of the RNA interference process; they regulate gene expression in plants by translation repression (mRNA degradation) and play crucial roles in the development and biotic stress responses of plants.[18] miRNAs also modulate abscisic acid (ABA)-dependent and ABA-independent pathways, crucial regulators in drought stress.[19] Furthermore, histone methylation, which involves the addition of methyl groups to lysine and arginine residues of H3 and H4 and is catalyzed by histone methyltransferases, is considered a key regulator in epigenetic stress response in plants (Figure 2).[19]

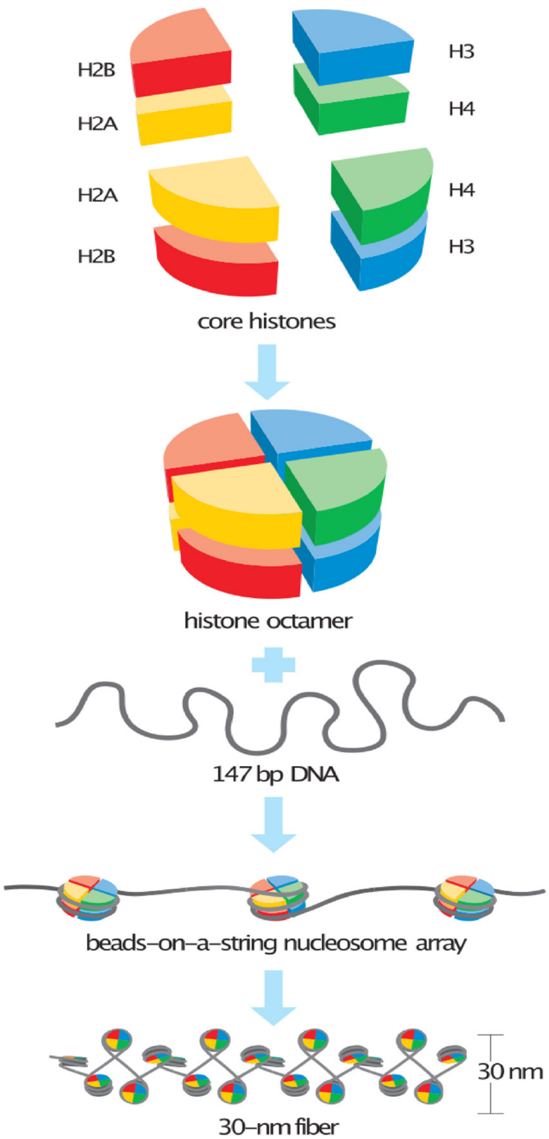

Fig 2 | Illustrating histone modifications and their role in regulating chromatin structure and gene expression dynamics"
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Epigenetic Stress Memory

Plants rely on epigenetic adaptive strategy mechanisms, such as DNA methylation changes. These changes regulate stress-responsive genes without altering the DNA sequence. These changes can create a stress memory in that individual, where they can remember the previous stress and act more effectively to the future stress. This memory can be passed down to future generations, strengthening their response to the stressor.[20] Stress priming is a phenomenon that helps plants respond to recurring stress. Prolonged exposure to stress helps the plant to retain the information, enabling it to adapt quickly and efficiently.[21] Stress priming is a strategy used by plants to capitalize on existing abiotic stress signals to create a more rapid, robust, and effective coping response to future stressors.[22]

In one analyzed study, Arabidopsis was used to treat dehydration stress, demonstrating a high diversity of memory-type responses. Some genes maintained expression levels similar to those before and during each stress treatment, whereas others showed increased expression levels, named stress memory genes. These genes were called "stress memory genes," while others were stress-responsive non-memory genes. During the recovery period, high levels of H3K4me3 and a stalled form of RNA polymerase II–Ser5P PolII were found in memory genes. The study also found that 1963 dehydration-responsive genes exhibited different transcript levels after the third stress, termed "memory genes." About a quarter of memory genes in the first category were implicated in cold/heat acclimation and responses to salt and ABA.[23]

Beyond short-term epigenetic memory (priming), changes in epigenome may be transmitted through plant generations. Naturally occurring and artificially induced instances of these transgenerationally inheritable epigenetic alterations, or epimutations, were reported.[24] The emergence of stress-induced transgenerational memory certainly benefits the plant progeny to become more resilient to stress.[25] ONSEN is a retrotransposon in Arabidopsis activated by heat stress producing extrachromosomal DNA. In siRNA-deficient mutants, ONSEN undergoes heritable transgenerational retrotransposition during flower development, marking an epigenetic change. siRNAs in wild-type plants prevent stress-triggered retrotransposition, ensuring genomic stability across generations.[26]

Abiotic Stresses and Epigenetics

Heat Stress

Heat stress is a primary environmental element that poses a great danger to food security as global warming develops.[27] In high altitudes, extreme temperatures have been found to affect plant growth, development, crop yield, and nutritional quality.[28] Differences in the levels of cytosine methylation patterns were recorded between heat-tolerant and heat-sensitive genotypes.[29] Under heat stress, methylation increased in the heat-sensitive genotype compared to the tolerant genotype.[30] Epigenetic mechanisms, including DNA methylation, histone modifications, and non-coding RNAs, play a pivotal role in regulating the expression of genes in response to heat stress, safeguarding plants from extreme temperature damage.[31] Extensive studies have been done on DNA methylation in response to heat stress using *Arabidopsis thaliana* as a base model.[32] A plastic response was identified to climate variation, revealing a genome-wide CHH methylation pattern influenced by seasonality. A correlation between chromomethylase 2 (CMT2) and temperature seasonality was observed, with certain mutants of CMT2 showing reduced sensitivity to temperature, suggesting that epigenetic changes may drive natural adaptation.[32] Heat stress in *A. thaliana* increases genome methylation under heat stress by upregulating key DNA methylation genes like MET1, CMT3, and DRM2. This upregulation is directed by small RNAs, RdDM, using RNA polymerases POIIV and POIV, which are important plant-specific RNA polymerases.[33] The famous heat shock proteins (HSPs), such as HSP12, HSP20, and HSP70, which are known to protect plants against extreme conditions like high temperatures, enhance heat tolerance by accumulating histone modifications such as H3K9 acetylation and H3K4 trimethylation.[34] Histone modifications and methylation through the RdDM pathway assist plants in heat tolerance.[35] Heat Shock Transcription Factors A1 (HsfA1) are considered master regulators in a plant's heat shock response, activating essential plant genes, and it is found that plants lacking HsfA1s are more sensitive to heat stress.[36] The SDC gene in *A. thaliana* is silenced under normal conditions but becomes active under heat stress to regulate gene expression.[37] While working with epigenetic mutants in *A. thaliana*, it was discovered that transcriptional response to heat stress relies on the RdDM pathway and Rpd3-type histone HDA6 and even the nearby transposable elements (TEs) influence heat-dependent gene expression.[7]

Drought Stress

Drought affects a plant's phenotype on molecular, cellular, physiological, and morphological levels.[38] It was discovered in a comparative study that the plants (*Z. mays and A. thaliana*) that were subjected to drought showed improved water retention in the next generations.[39] It is now established that repeated exposure to stress leads plants to respond more effectively to future challenges.[40] DNA methylation helps crops like *Oryza sativa* to adapt to drought stress with significant changes occurring at specific genome sites.[41] Another study on rice cultivars under drought stress revealed significant differences in methylation levels in regions linked to stress-related gene expression.[42] ABA is a phytohormone that is upregulated in response to drought stress.[43] ABA plays a key role in regulating multiple drought stress-related genes, and ABA-induced gene upregulation was reported by exposure to drought.[44] Histone modifications are found to be crucial in ABA responses during the seedling stage; the BR-activated BES1-TPL-HDA19 complex silences ABI3 chromatin by facilitating histone deacetylation, suppressing ABA signaling.[45] Furthermore, the guard cell-specific memory contributes to maintaining partially closed stomata during the recovery period.[41] In summary, changes in chromatin, histone modifications, and DNA methylation are essential in the drought tolerance response of plants.[46]

Cold Stress

Cold stress is a significant environmental factor restricting agricultural expansion and crop productivity in hilly terrains.[47] The study of the epigenomic landscape in plants exposed to cold stress is still a rapidly emerging field.[48] Cold acclimation is an ability in plants that allows them to tolerate freezing conditions (to some extent) after exposure to low temperatures.[16] Plants have many well-established cold-stress pathways, including the C-repeat binding factor (CBF)-cold-responsive (COR) pathway. The COR genes are upregulated when cold stress increases the levels of CBF transcription factors.[49] The PICKLE (PKL) gene was found to be involved with the CBF-dependent cold stress response against cold stress in Arabidopsis.[50] PKL mutants had lower expression of CBF3 (key cold-tolerance regulator) and its target genes COR (COR15B and RD29A).[51] PKL is also a key regulator of the RdDM pathway and helps in the disposition of H3K27me3.51 H3K27me3 decreases with cold stress, and this change persists even after things get normal, suggesting its role in the plant's stress memory.[51] Epigenetic changes are also involved in low-temperature induced dormancy in plants and reduced methylation due to cold stress results in subsequent fruit setting.[52]

Salinity Stress

High salt accumulation in soil constitutes a significant constraint on crop production, impacting 20% of the global cultivated area and markedly influencing the distribution and abundance of plant species.[53] Salinity stress adversely affects plant life due to sodium ion toxicity, osmotic stress, and secondary stresses, including oxidative damage.[16] Epigenetic modifications exert a multifaceted influence on stress-inducible genes and regulate the expression of transcription factors.[54] DNA methylation modulates the expression of genes that respond to salt stress. In one study comparing salt-tolerant and salt-sensitive rice varieties, DNA methylation in promoter and gene body regions plays a significant role in controlling gene expression in a genotype- and organ-specific manner under salinity stress. The research also found that DNA methylation decreases in response to high salinity, particularly linked to the upregulation of the DRM2 gene, which was more pronounced in salt-sensitive rice but not in salt-tolerant varieties. The results suggest that changes in DNA methylation patterns could affect how plants tolerate salt stress.[54]

The high-affinity K^+ channel1 (HKT1) is a transporter that controls Na^+ influx in plants and interacts with the salt overly sensitive (SOS) pathway to build resistance against salt.[55] HKT1 mutation may inhibit SOS plants' salt-hypersensitive phenotype.[55] Salinity stress induces the expression of the HKT1 gene, characterized by high levels of H3k27me3. The RdDM mutants in Arabidopsis showed reduced DNA methylation, which enhanced the expression of HKT1, suggesting that RdDM acts as a repressor of HKT1.[56] A different study on salt stress treatment found distinct DNA methylation patterns in salt-tolerant wheat cultivars and its progenitors, these patterns were thought to be related to the varying levels of HKTs which are controlled by epigenetic mechanisms.[57] Salt stress has a direct impact on genome-wide DNA methylation and histone modifications, which are crucial for plant's salt tolerance mechanisms.[58]

Biotic Stresses and Epigenetics

Plants are sessile; therefore, they cannot escape biotic stressors such as pathogens and herbivores. Plants have developed extremely complex defense regulatory systems to protect themselves from pests and diseases.[59] Research on epigenetics and biotic interactions could address plant adaptation, phenotypic plasticity, and crop improvement. However, biotic interactions are context-dependent, making comparisons challenging, and a trait-oriented approach is proposed for studying interferences in multiple biotic interactions. According to increasing research, epigenetic regulation is essential for determining plant immunity and phenotypic changes during plant-microbe interaction.[61] Plants do not have specialized cells for immune response or an adaptive immune system. Plants can identify conserved pathogen-associated molecular patterns (PAMPs) through the host plasma membrane-associated pattern recognition receptors (PRRs). PAMP-triggered immunity refers to the general, nonspecific immune responses triggered by this recognition.[62,63]

Viral Pathogens

Plants recognize pathogens, activating signaling pathways that trigger defense responses; growing evidence indicates that epigenetic mechanisms directly participate in plant immune memory. The initial evidence for epigenetic regulation of plant tolerance to biotic factors was the modulation of viral virulence through post-transcriptional gene silencing.[64] Plants defend against RNA viruses by transforming their genomes into double-stranded RNA, degraded into small interfering RNAs by DCL2 and DCL4. They also defend against DNA viruses through RNA-directed DNA methylation-mediated transcriptional gene silencing, while RNA methylation furthermore modulates viral infections such as Alfalfa mosaic virus in Arabidopsis.[65]

Microbes and Pests

The present research revealed that during *Pseudomonas syringae* infection in *Arabidopsis*, DNA demethylation of TEs activates immune-response genes. The pathogen-induced changes in DNA methylation patterns are crucial for regulating plant defense, emphasizing the importance of methylation in transcriptional control during bacterial infection.[66] DNA methylation, regulated by NRPE1 and ROS1, impacts *Arabidopsis* immunity. A decrease in methylation showed enhanced resistance to *Hpa* and altered SA gene expression, whereas the increase in methylation showed more susceptibility. This research highlights DNA methylation's role in regulating defense genes, influencing pathogen resistance, and transcriptional control.[67] Pathogen infection activates specific genes in tomatoes, focusing on the oxylipin pathway genes (DES, DOX1, LoxD) and the stress-responsive gene WRKY75. *Botrytis cinerea* and *Pseudomonas syringae* infections triggered increases in histone marks H3K4me3 and H3K9ac, with B. cinerea showing stronger modifications. These research results suggest histone modifications regulate gene activation in response to different pathogens.[68]

Conclusion

Epigenetic mechanisms such as DNA methylation, histone tail modifications, and micro RNA directional pathways are crucial for regulating the expression of the genes under stress conditions, thereby enhancing plant resilience to deal with biotic and abiotic stresses. These epigenetic stress response memories are often heritable to the next generations, helping the next progenies of the plants to effectively adapt to uncertain stresses. Thus, understanding these mechanisms, especially RNA-directed pathways can help for sustainable improvement in crops for resilience to drought, salinity, heat, cold, and pathogenic threats. These epigenetic mechanisms provide phenotypic plasticity. The variations are the foundation for plant breeding and genetic engineering to improve crop quality. Hence, epigenetics has emerged as an emerging field of study, and understanding these epigenetic mechanisms can help us to make a food-secure world for future generations through sustainable protection and improvement in crop improvement.

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