

Heritable Epigenetic Changes in Plant Stress Responses: Implications for Crop Resilience

Courage Humphrey Ojeilua¹; Atijosan Oluwabukola Eunice²; Damilola Elizabeth Fadipe³; Daizy Princess Abdulai⁴; Sunday Kaura⁵; Kehinde Clement Agbonyin⁶; and Godson Akpovwovwo Onophurhi¹

¹Department of Plant Biology and Biotechnology, University of Benin. ²Agronomy Department, Faculty of Agriculture, State University of Ponta Grossa, Parana, Brazil. ³Chemical Engineering Department, University of Arkansas, Fayetteville USA. ⁴Chemistry Department, Faculty of Pure and Applied Sciences, Fourah Bay College, University of Sierra Leone. ⁵Biochemistry Department, Faculty of Natural and Applied Science, Veritas University Abuja. ⁶Global Climate Smart Agriculture Youth Network, LAUTECH Centre of Excellence.

Corresponding author: ojeiluacourage@gmail.com

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Abstract

In many parts of the world, especially sub-Saharan Africa, farmers face tough environmental conditions that make cultivation difficult. Issues like unpredictable rainfall, poor soils, high temperatures, and salt buildup affect plant growth and reduce yields, adding pressure to already strained food systems. Although breeding programs and genetic engineering have improved stress tolerance in some crops, they do not fully explain how plants respond quickly to stress or pass those responses to the next generation. Recent research highlights epigenetic mechanisms, including DNA methylation, histone modifications, chromatin remodeling, and small RNAs, as key regulators that help plants adjust gene activity under stress. This review examines how these mechanisms influence plant responses to abiotic stress, focusing on stress memory, distinguishing between stable and temporary changes, and transgenerational inheritance. It draws on peer-reviewed studies from PubMed, Google Scholar, ScienceDirect, and Scopus, using targeted search terms related to plant epigenetics and stress adaptation. The review evaluates evidence from both model species and crops and considers how tools like epiRILs, epimutagenesis, CRISPR-based editing, and epigenome-wide association studies (EWAS) could be used in breeding. It also emphasizes the potential for underused crops and low-input farming systems. Despite recent progress, many epigenetic responses remain difficult to validate outside the laboratory. Efforts should focus on finding practical solutions to meet farmers' needs, especially in producing stress-resilient crops.

Keywords: Epigenetic Regulation, Abiotic Stress, DNA Methylation, Stress Memory, Crop Resilience, Epigenome Editing.

Introduction

The harm from abiotic stresses, including droughts, too much salt in the soil, heat waves, and poor soil conditions in farming, is as dangerous as the food scarcity found in developing countries. As a result of these uncertainties, plant growth slows down and photosynthesis, nutrient uptake, and efficient water use are all disrupted (Kul et al., 2021). As a result,

farming becomes less productive and regularly puts food security at risk in places frequently affected by stress (Arena et al., 2018). With weather and soil conditions more difficult to know, these challenges are happening more frequently and intensely (Lesk et al., 2016). It has led us to design plants that are capable of living in tough and unpredictable areas. (Varshney et al., 2021). This adaptive process is visualized in Figure 1, which outlines the progression from stress exposure to genetic and epigenetic responses.

There is a warning from the Intergovernmental Panel on Climate Change (IPCC, 2022) that extreme environmental conditions will likely grow more frequent and severe by the mid-21st century, especially in tropical and subtropical zones. These regions are projected to experience escalating effects of abiotic stress, occurrences that are detrimental to the food systems already grappling with limited resilience (Affoh et al., 2022). Salt stress alone impacts a significant portion of the world's irrigated farmland and will continue to limit plant resilience in many affected regions (Zörb et al., 2018). Soil nutrient loss is another major concern, particularly in some areas of Sub-Saharan Africa and South Asia where land degradation is prevalent (Sánchez, 2019). When certain crops like cereals and legumes are exposed to hot weather during flowering, the effects may reduce fertilization and result in an insufficient number of seeds produced (Zhao et al., 2017).

Although most biotic stresses are specific to only one crop, abiotic stresses sometimes affect various crops all at once, and their effects might add up and become stronger (Pandey et al., 2017). Knowing this is now crucial for managing plant stress and improving how crops handle stresses (Bailey-Serres et al., 2019).

Most of the work currently focused on enhancing plant resistance to stress has mainly targeted changes at the genetic and molecular levels. In doing so, scholars have discovered the roles of DREB, NAC, and WRKY transcription factors, as well as the involvement of abscisic acid and MAPK cascades in the plant stress response (Gupta et al., 2020). As part of the protein strategy, genes for heat shock proteins, aquaporins, and antioxidant enzymes have also been utilized (Hasanuzzaman et al., 2020). These findings have influenced how breeders implement marker-assisted selection and genetic modification methods (Varshney et al., 2021). Nevertheless, scientists now recognize that other factors are necessary to explain the rapid and instantaneous ways many plants cope with stress (Springer & Schmitz, 2017).

Such a gap in knowledge means epigenetics now acts as an extra level of regulation in plant stress biology. Changes in epigenetics do not influence the structure of a plant's DNA, but they can change how genes behave and can be passed to the next generation through reproduction in rare cases (Zhang et al., 2018). These mechanisms, which include DNA methylation, histone modification, chromatin remodeling, and small non-coding RNAs, cause these changes (Lämke & Bäurle, 2017). They help decide how much space DNA takes in the cell and activate or inactivate particular genes, helping plants cope with changes in their environment (Kumar, 2016). A new study shows that epigenetic regulation helps plants respond to stress and allows them to respond better if they are stressed a second time (Ashapkin et al., 2020).

Various stresses trigger epigenetic changes in plants to decide which genes will be active through DNA methylation, leading to the suppression of transposable elements and helping control stress-related genes (Zhang et al., 2018). Acetylated or methylated histones can restructure the nearby chromatin, influencing how adjacent genes are regulated (Sharma et al., 2023).

Also, chromatin remodeling separates nucleosomes to reveal or hide hidden genes, while small RNAs help regulate stress responses by either turning off certain genes or influencing DNA methylation effects (Kim et al., 2010). With this system in place, stress-related genes in plants can activate or deactivate quickly, without losing the ability to do so again. Sometimes, these epigenetic changes are not erased after the stress ends, so the plant continues to remember and respond more effectively if the event happens again.

Researchers call this stress memory because it explains how plants continue using previous information about stressful times (Avramova, 2015). The memory for stress management stays and lives with them thanks to stable parts of epigenetics such as DNA methylation and histone modifications (Crisp et al., 2016). Unlike genetic mutations, these changes do not alter the DNA sequence, but they can still influence traits over time, acting as a form of non-genetic inheritance (Heard & Martienssen, 2014). Whether these marks are temporary, reversible, or long-lasting depends on many factors, and their full role in helping plants adapt to abiotic stress is still being studied (Baulcombe & Dean, 2014).

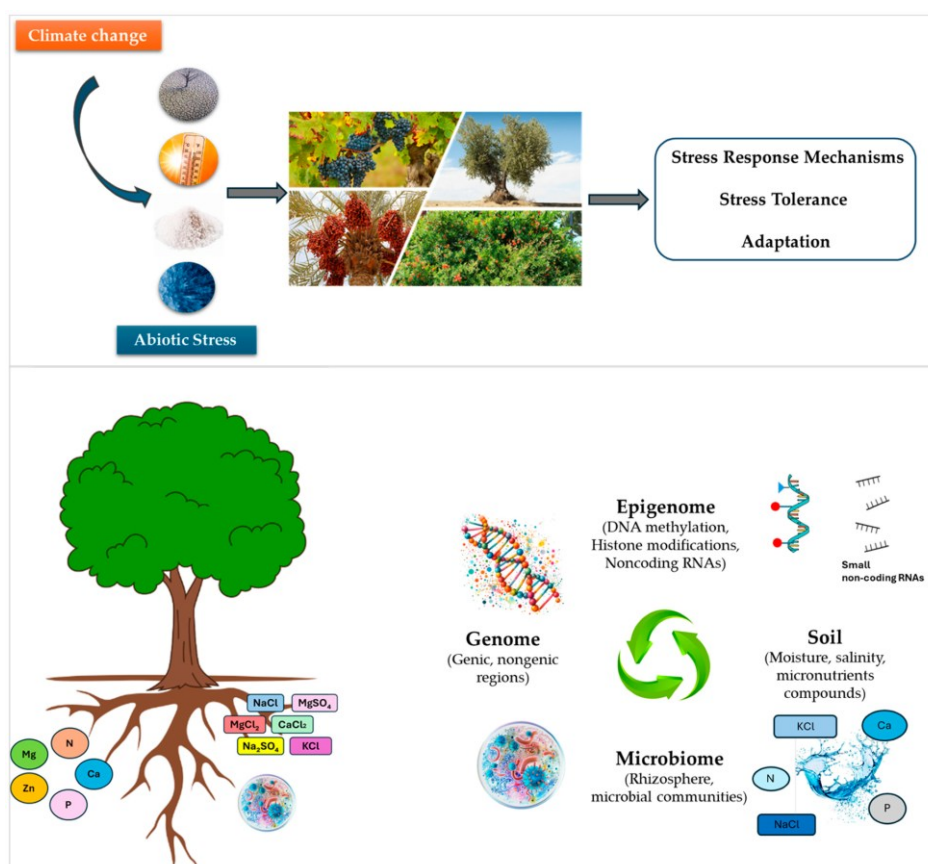


Figure 1: Plant stress, vulnerability, genetic intervention, and adaptive recovery.

Source: Adapted from Kapazoglou et al. (2025)

Statement of Problem

Epigenetic regulation has become a crucial layer in plant stress responses, yet its role in long-term adaptation remains poorly understood. A key challenge is differentiating short-term regulatory changes that disappear after stress recovery from those that persist and affect the plant's traits over time. It also remains unclear how some stress-induced epigenetic marks evade resetting during reproduction. While transgenerational inheritance has been observed, the results are inconsistent and vary depending on species, genotype, type of stress, and developmental stage. Most current knowledge comes from studies on model plants grown under controlled conditions, with limited evidence from real field environments or food crops. Additionally, there is no clear framework yet for how to utilize epigenetic markers in crop breeding. This gap continues to hinder the practical application of epigenetic tools for developing stress-resilient crops. It remains unclear how these stable marks can be translated into indicators that breeders can track and utilize, especially under real drought, salinity, or heat stress. Figure 2 illustrates how stress signals can trigger epigenetic regulation, leading to adaptive outcomes.

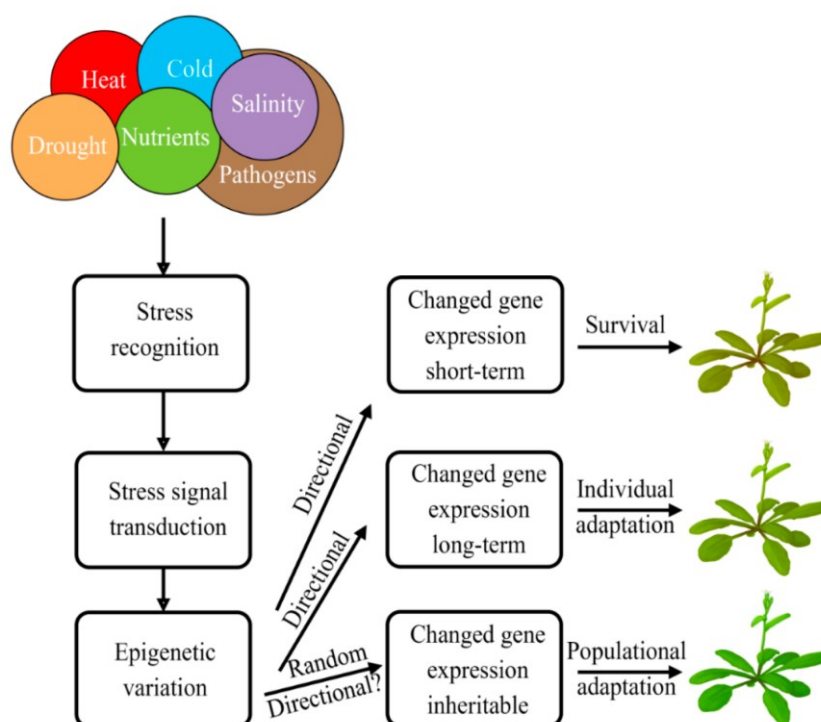


Figure 2: Model of stress-induced epigenetic regulation leading to plant adaptation.

Source: Adapted from Ashapkin et al. (2020).

Objective of the Review

Objectives of this review include:

- To examine how DNA methylation, histone modifications, chromatin remodeling, and small RNAs regulate plant responses to abiotic stress.

- To distinguish between short-term epigenetic responses and longer-term stress memory mechanisms.
- To evaluate the potential for transgenerational inheritance of stress-induced epigenetic changes.
- To explore how epigenetic regulation contributes to plant adaptation and crop resilience.
- To identify key research gaps and challenges in applying epigenetic knowledge to breeding and field-level solutions.

Methods

Peer-reviewed articles were collected to examine how plants regulate gene activity under abiotic stress using epigenetic mechanisms. Searches were conducted through databases including Google Scholar, PubMed, ScienceDirect, and Scopus, using combined terms such as "plant epigenetics," "abiotic stress," "DNA methylation," "histone modifications," "transgenerational inheritance," and "epigenetic memory." The search was carried out manually without automation tools, and papers were selected based on relevance to the molecular processes covered in this review.

Both original research articles and review papers were included. Review papers helped in establishing theoretical frameworks and summarizing existing models, while experimental studies were prioritized when describing stress-induced changes in methylation patterns, chromatin states, or gene expression under abiotic conditions. The dataset included a mix of open-access journals (e.g., *PLOS ONE*, *Plants*, *IJMS*, *Frontiers in Plant Science*, etc.) and subscription-based sources (e.g., *Nature Genetics*, *The Plant Cell*, *PNAS*, and others). Access to subscription-based articles was made possible through institutional login or publicly shared versions by authors.

Papers were retained if they presented experimentally supported insights into stress-induced epigenetic changes, either through methylome analysis, histone mark profiling, small RNA studies, or transcriptomic responses linked to chromatin changes. Studies that offered evidence of epigenetic persistence, within-generation memory, or inheritance through meiosis were especially prioritized. Relevance to food crops, trait expression, or environmental resilience guided inclusion, where multiple studies addressed similar pathways.

Over 150 papers were initially considered. After screening for redundancy and clarity of evidence, approximately 100 were selected and analyzed in full. Thematic grouping was done manually based on the type of mechanism discussed and the species involved. Preference was given to studies published after 2015, while earlier foundational works were retained when still relevant. Case studies and experimental examples were selected to reflect both model plant research and applied outcomes in crops. This review does not follow a meta-analytical format but instead applies a structured thematic synthesis that links mechanistic knowledge to stress resilience in crops.

Discussion

Regulatory Genes that Govern Abiotic Stress Adaptation

DNA Methylation: Stress-Responsive Patterns and Functional Targets

DNA methylation is one of the major epigenetic mechanisms that regulates gene expression without altering the underlying DNA sequence. It involves the addition of a methyl group to the fifth carbon of cytosine bases and occurs in three sequence contexts: CG, CHG, and CHH, where H represents A, T, or C (Zhang et al., 2018). These patterns are established and maintained by different enzymes: MET1 preserves CG methylation, CMT3 maintains CHG methylation, and DRM2 mediates de novo methylation via the RNA-directed DNA methylation (RdDM) pathway (Law & Jacobsen, 2010).

Certain regions within the DNA of regulatory elements and transposable elements, which affect how genes are expressed, can be affected by changes in DNA methylation triggered by abiotic stress conditions (Secco et al., 2015). Under drought, this plant shows both an increase and a decrease in methylation at given spots in the genome, mainly near transposons and stress regulators (Downen et al., 2012).

Through genome-wide analysis, it is apparent that at least 15% of genes that change their methylation in drought are near transposable elements, implying a way they may control stress-related gene activity (Kim et al., 2012).

Genes such as *RD29A* and *NCED3*, which are involved in the abscisic acid (ABA) signaling pathway, exhibit stress-induced changes in promoter methylation that correlate with shifts in gene expression (Ding et al., 2013). In *Arabidopsis thaliana*, drought triggers both gains and losses of promoter methylation. In contrast, *Oryza sativa* shows a more consistent pattern of promoter hypermethylation under drought and salt stress, pointing to species-specific differences in methylation-mediated stress regulation (Downen et al., 2012).

Salt stress in *Oryza sativa* causes more methylation in the promoter regions of ion transporter genes, including *OsHKT1;5*, which manages salt transport into plant shoots (Yun et al., 2024). Thanks to a change in epigenetic patterns, plants can tolerate more salt and their leaves have less sodium (Wang et al., 2016). There is evidence from bisulfite sequencing that methylation changes also occur in non-coding intergenic regions, which suggests their involvement in more than just the coding genes (Ferreira et al., 2015). The process involves an immediate burst of gene activity and then long-lasting methylation holds in place the genes important for coping with stress (Yin et al., 2024). This means that DNA methylation seems to control gene activity both immediately and long after a stress event in rice (Zhang et al., 2018).

As a result of heat stress, there is less methylation in the Euchromatin region, which causes chromatin to open up and makes it quicker for stress-related genes to turn on (Liu et al., 2020). In response to cold temperatures, the methylation in transposable elements and surrounding regulatory parts increases, which can help control their activeness and the stability of the genome through low energy use (Ramakrishnan et al., 2022). Not all methylation events silence genes; in some cases, they promote expression by blocking

small RNA-mediated silencing or stabilizing chromatin structures like enhancer-promoter loops (Zhang et al., 2018).

A key question in plant epigenetics is the reversibility of stress-induced DNA methylation. While many methylation changes are transient and return to baseline after stress recovery, others remain stable through mitotic divisions, suggesting within-generation stress memory (Wibowo et al., 2016). Evidence for transgenerational inheritance of such marks is also growing. Studies in *Arabidopsis thaliana*, *Zea mays*, and *Oryza sativa* show that some stress-induced methylation profiles can persist through meiosis and be passed to progeny, sometimes correlating with improved tolerance to drought, salinity, or heat (Crisp et al., 2016; Zheng et al., 2017). These effects, however, are not universal. The stability and inheritance of methylation marks depend on genotype, developmental stage, and tissue-specific patterns, indicating that epigenetic memory is conditional rather than deterministic (Heard & Martienssen, 2014).

Another significant limitation in the study of plant epigenetics is the challenge of linking large-scale methylation changes to observable phenotypic outcomes. While high-resolution methylome maps have become increasingly accessible, the functional interpretation of many stress-induced methylation events remains ambiguous, especially those occurring in intergenic regions or transposable element (TE)-rich domains, where regulatory roles are often indirect or poorly understood (Zhang et al., 2018; Eichten et al., 2014). Furthermore, a persistent causality dilemma complicates analysis: it is frequently unclear whether methylation changes serve as primary regulators of gene expression or whether they are downstream consequences of transcriptional shifts triggered by other regulatory pathways (Kawakatsu & Ecker, 2019).

The role of stress-induced methylation changes remains uncertain without direct evidence linking them to gene expression and plant traits. Future research should combine methylome, transcriptome, and phenotypic data under both controlled and field conditions to clarify how specific epigenetic states influence gene regulation and plant performance. A key priority is the functional validation of candidate loci, potentially through CRISPR/dCas9-based epigenetic editing, to assess whether particular methylation marks contribute to stress adaptation (Gallego-Bartolomé, 2020). Distinguishing between adaptive, neutral, and maladaptive epigenetic responses under variable stress combinations will be critical for applying these insights in breeding and crop improvement strategies.

Histone Modifications and Chromatin Remodeling in Stress Tolerance

Histone modifications form an important epigenetic layer that shapes gene expression in plants under abiotic stress. These chemical changes affect chromatin structure and gene accessibility without altering the DNA sequence. Key modifications include H3K4me3, H3K27me3, H3K9ac, and H3K9me2. H3K4me3 is linked to gene activation, while H3K27me3 is associated with stable repression (Nunez-Vazquez et al., 2022). Acetylation at H3K9 (H3K9ac) relaxes chromatin to support transcription, while dimethylation at the same site (H3K9me2) promotes heterochromatin formation and gene silencing (Wang et al., 2024).

These marks are involved in chromatin-level control of gene activity during stress and often interact with DNA methylation and nucleosome remodeling (Luo et al., 2012).

The enzymes that regulate these marks include histone acetyltransferases (HATs), deacetylases (HDACs), and methyltransferases (HMTs) (Wang et al., 2024). Under stress conditions such as drought, salinity, or extreme temperatures, these enzymes adjust chromatin states across the genome (Nunez-Vazquez et al., 2022). For instance, salinity stress increases H3K4me₃ and reduces H3K27me₃ at certain genes, boosting their expression (Nunez-Vazquez et al., 2022). In *Arabidopsis thaliana*, the demethylase REF6 removes H3K27me₃ marks under heat stress to activate thermotolerance genes (Cui et al., 2016). HDA6, a histone deacetylase, modulates H3K9ac levels to regulate ABA-responsive genes under salt and drought stress (Chen et al., 2010).

During times of stress, SWI/SNF family chromatin remodeling complexes are very important for gene regulation. OsCHR4 from *Oryza sativa*, a type of SWI/SNF ATPase protein, plays a part in salt and cold tolerance by arranging the nucleosomes at stress-related genes (Zhao et al., 2020). To manage access to DNA, these complexes move nucleosomes and frequently join with histone changes and DNA methylation to control the amount of transcription caused by environmental challenges (Clapier et al., 2017; Guo et al., 2019). Figure 3 illustrates that histone modifications and changes in chromatin structure cooperate with DNA methylation to oversee the way genes involved in stress are expressed. Despite new research on epigenetics linked to stress, some important details are yet to be found. Experts are still unsure exactly how histone marks and DNA methylation communicate together, especially during times of persisting stress (Chang et al., 2020). Researchers still do not know the complex nature of all these modifications in different tissues, and solid studies showing their effect on non-model crops are few.

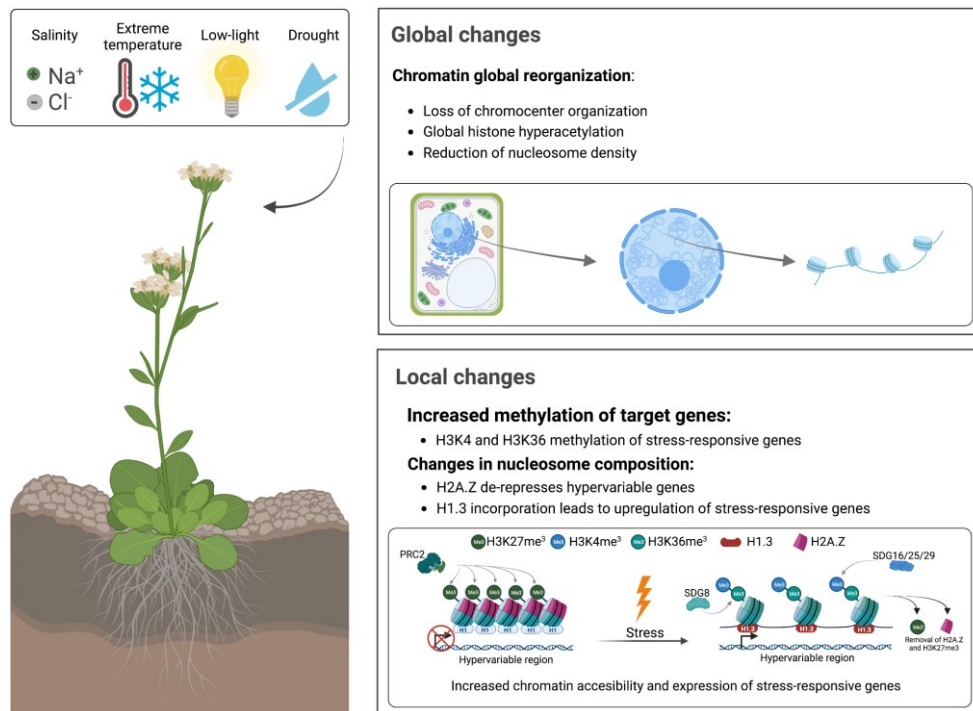


Figure 3: Overview of DNA Methylation and Histone Modification in Plant Abiotic Stress Response

Source: Adapted from Nunez-Vazquez et al. 2022

Small RNAs and RNA-Directed DNA Methylation (RdDM)

Small interfering RNAs (siRNAs) and microRNAs (miRNAs) among sRNAs are vital for how plants respond to different types of stress. The molecules achieve an exact shutdown of genes triggered by different environmental influences and conditions. In plants, they also take part in the complicated RNA-dependent DNA methylation pathway (RdDM) that leads to silencing of certain genes (Zhang et al., 2018).

By cutting double-stranded RNAs, DICER-like (DCL) proteins generate small interfering RNAs (siRNAs). These siRNAs are then loaded onto ARGONAUTE (AGO) proteins and guide DNA methylation of homologous DNA regions through the RNA-directed DNA methylation (RdDM) pathway (Matzke & Mosher, 2014). The system is important for preventing the action of transposable elements (TEs) and stress-responsive genes under non-living conditions such as drought, salinity, and excessive temperatures (Zhang et al., 2018). The main components of RdDM, such as RNA Polymerase IV and V, RDR2, DCL3, and DRM2, work together to maintain chromatin silencing and genome stability during stress (Borges & Martienssen, 2015).

Most miRNAs are 21-nucleotide units that reduce the expression of genes by either destroying target mRNAs or keeping them from being translated (Sunkar et al., 2012). Experts have found that several miRNAs can respond to stress in plants. A good example is miR393, which focuses on genes needed for sensing auxin and is triggered by high salt or water deprivation to mediate plant growth and hormones (Navarro et al., 2006). Similarly, miR398 downregulates Cu/Zn-superoxide dismutase (CSD) genes under oxidative stress,

fine-tuning the plant's antioxidant defense system (Sunkar et al., 2006). These miRNAs help balance energy and stress-response trade-offs in fluctuating environments (Khraiwesh et al., 2012).

While the roles of siRNAs and miRNAs in stress adaptation are increasingly evident, key challenges remain. There is limited understanding of how tissue-specific sRNA expression contributes to localized stress tolerance (Bartel, 2004). Moreover, the long-term persistence and heritability of sRNA-mediated silencing under repeated or prolonged stress are not well established (Bond & Baulcombe, 2014). Emerging evidence suggests that certain sRNAs may be mobile, moving between tissues to coordinate systemic responses, but the biological relevance and regulatory controls of such mobility are not yet fully understood (Kehr & Buhtz, 2007).

To effectively harness small RNA pathways for crop improvement, future research should prioritize multi-omics integration and detailed spatio-temporal profiling, especially under field conditions and across genetically diverse cultivars (Xie, 2009). Figure 4 provides an integrated model of how different epigenetic mechanisms, including sRNAs, contribute to short- and long-term stress adaptation.

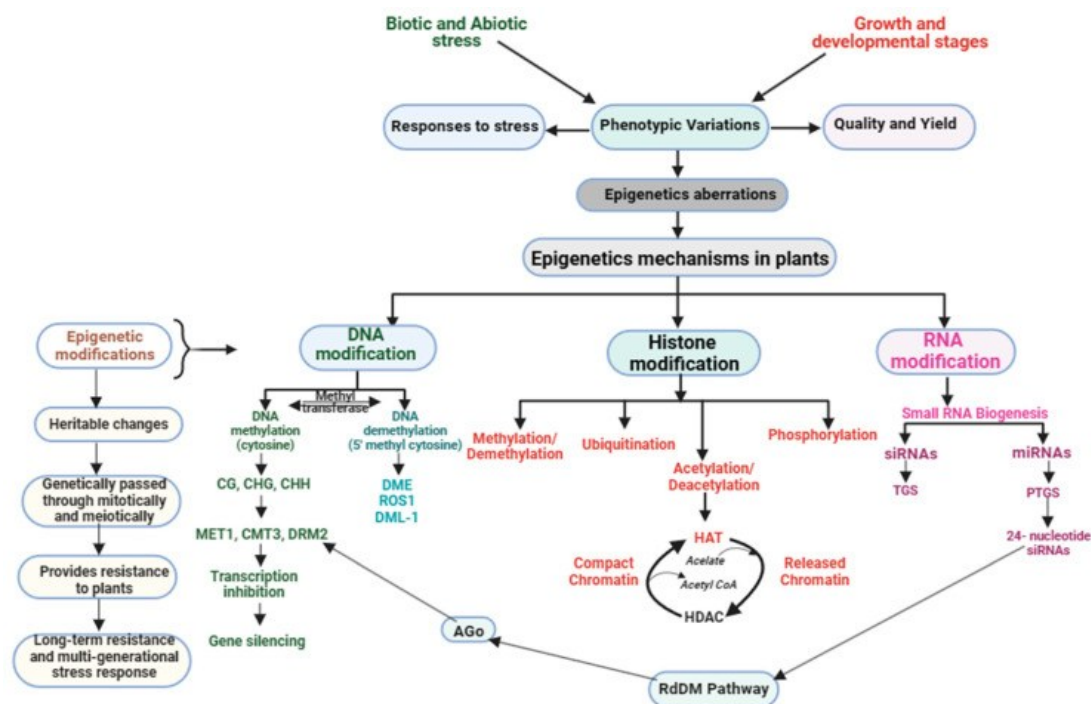


Figure 4: Conceptual model of epigenetic regulation in plant stress responses.

Source: Adapted from Abdulraheem et al., 2024

The figure illustrates a layered response to stress, beginning with recognition of abiotic and biotic stressors, followed by signal transduction and epigenetic variation. Three downstream outcomes of gene expression changes are depicted: short-term responses

supporting immediate survival, longer-term adjustments enabling individual adaptation, and stable, heritable changes that contribute to population-level adaptation.

Epigenetic Reversibility and Persistence

Transient vs. Stable Epigenetic Marks

Epigenetic marks in plants show varying levels of stability in response to abiotic stress. Some, like histone acetylation marks (e.g., H3K9ac), are short-lived and quickly induced by stress, allowing chromatin relaxation and rapid gene activation (Kim et al., 2015; Charron et al., 2009). Others, such as CG-context DNA methylation maintained by MET1, and histone trimethylation marks like H3K27me3, are more stable and linked to long-term gene silencing beyond the initial stress period (Zhang et al., 2006; Law & Jacobsen, 2010).

Repeated or prolonged stress can reinforce these stable marks, forming within-generation stress memory. In *Arabidopsis thaliana*, drought induces persistent hypomethylation at the RD29A promoter, a key gene in the ABA pathway, resulting in stronger gene activation during later stress (Kim, To, Ishida, et al., 2012). This process, known as “priming,” shows how earlier stress can leave a molecular imprint that shapes future responses without altering the DNA sequence (Crisp et al., 2016).

The stability of stress-induced epigenetic modifications in plants is influenced by factors such as genotype, developmental stage, and tissue specificity. At stages like when seeds germinate or meristems form, active mechanisms of DNA remover (ROS1) and histone remover (REF6) show that epigenetic reprogramming is controlled, not just something that occurs by chance (Sheldon et al., 2008; Qian et al., 2012; Cui et al., 2016).

It is still unclear if persistent epigenetic marks help or hurt our survival when facing future stresses. Certain research shows that retained marks could increase the body’s readiness to meet repeated stressors, but other studies believe they simply reflect the remains of old chromatin patterns.

Priming and Acquired Stress Tolerance

Research has found that plants can store memories of past environmental events, which is called priming (Crisp et al., 2016). Having undergone priming means that organisms will respond more strongly next time they face the same stressor, even if the response is not genetic (Hilker et al., 2015). Sessile organisms such as plants need this ability since they have to react to continual changes in their surroundings (Bruce et al., 2007).

Epigenetic changes take place at the molecular level during priming, shaping chromatin so genes can be turned on or off without modifying the DNA sequence (as Conrath explained in 2011). Part of the primed state involves reorganizing some chromatin into regions that remain dormant until stress occurs but are poised for rapid activation when stress reappears. These regions are often marked by both activating histone marks (e.g., H3K4me3) and repressive marks (e.g., H3K27me3), a bivalent pattern that preserves regulatory flexibility (Lämke & Bäurle, 2017). This dual marking encodes molecular memory at stress-responsive genes, enabling quicker and more efficient transcriptional responses upon re-exposure to similar stress (Ding et al., 2012).

After being slightly exposed to cold or slight dehydration, *Arabidopsis thaliana* promptly reactivates the expression of stress genes RD29A and COR15A, a well-known case of plant transcriptional memory (Ding et al., 2012). The process is faster and the effects are stronger in these genes when the stress is repeated than during the first time they were triggered. This represents a state brought about by previous stress, so that molecules left by the stress act quickly to promote new genes being turned on (Lämke & Bäurle, 2017).

Aside from histones, priming may also affect DNA by reducing methylation levels, which leads to the production of more small RNAs. Because of these tissue marks, cells can react sharply and better when they face another stressful event (Crisp et al., 2016). In many cases, these imprints remain through mitotic divisions, supporting within-generation memory and allowing plants to respond more quickly and effectively to repeated stress (Luna et al., 2011).

Stimulated plants typically produce more antioxidants, greater levels of osmoprotectants, and lower salts in their tissues, depending on the stress that affects the species (Fàbregas et al., 2018). Because of this, priming helps prevent more cellular injury and increases the chances of survival, all at a lower energy cost and without the need for constant protection (Sharma et al., 2022).

Even though priming can help plants cope with stress better, exactly how chromatin alterations and small RNAs are involved is not fully known (Bäurle & Trindade, 2020). How stable and effective primed states are depends on the type of tissue, how far along development is, the environment, and the plant's genotype (Hilker & Schmölling, 2019). Further research is needed to define the biological conditions that support priming, assess its consistency across species, and develop strategies for incorporating it into breeding and practical stress management in the field (Springer & Schmitz, 2017).

Stress-Type-Specific Epigenetic Dynamics

Different types of abiotic stress trigger distinct epigenetic changes in plants. Drought often causes locus-specific DNA hypomethylation in regulatory regions of stress-related genes like RD29A and NCED3, increasing their expression (Kim, To, & Seki, 2012). In contrast, salinity tends to cause promoter hypermethylation of genes involved in ion regulation, such as OsHKT1;5 in rice, potentially reducing expression to prevent sodium buildup (Zhang et al., 2018). Heat stress is commonly linked to a widespread decrease in CHH methylation and increased H3K9ac histone acetylation, especially in euchromatic regions. These changes loosen chromatin and support rapid activation of heat-responsive genes (Sadler et al., 2016).

Epigenetic changes induced by various stresses can be either stable or reversible in different ways. After drought stress subsides, these changes often persist, creating a type of within-generation memory (Sani et al., 2013). Unlike other varieties, heat marks typically disappear fairly quickly when the stress is relieved (Kim, To, & Seki, 2012). The aftermath of salinity stress may not be easily resolved, and some alterations remain long after the stress has ended (Chinnusamy & Zhu, 2009). Certain traits related to environmental stress can also

influence how a plant removes or rearranges these changes in chromatin (Kinoshita & Seki, 2014).

Studies indicate that each abiotic stress leads to different epigenetic responses in plants. They do not use a single approach, but target certain chromatin and DNA methylation that depend on the kind and strength of the stress (Lämke & Bäurle, 2017).

Evidence Across Model and Crop Systems

Research in model species and crop plants shows that abiotic stress can trigger epigenetic changes that may be inherited across generations. In *Arabidopsis thaliana*, stress-induced DNA methylation changes, particularly in transposable elements and promoter regions of stress-responsive genes, have been observed to persist even when subsequent generations are not exposed to stress (Wibowo et al., 2016). Offspring of drought-treated plants often carry distinct methylation patterns at loci involved in abscisic acid signaling and dehydration tolerance, which may contribute to improved resilience under non-stress conditions (Crisp et al., 2016; Secco et al., 2015).

In maize (*Zea mays*), a genetically diverse and widely cultivated crop, abiotic stresses such as drought and heat stress can induce heritable epigenetic modifications that influence key agronomic traits. These stresses lead to stable changes in DNA methylation and histone modifications at stress-responsive loci, particularly near transposable elements and small RNA clusters (Wang et al., 2016). Some of these epigenetic changes persist across generations without further stress exposure, indicating transgenerational epigenetic inheritance (Li et al., 2012). Such inheritance patterns have been linked to altered phenotypes in progeny, including shifts in flowering time, enhanced root system plasticity, and improved biomass production, traits that confer increased resilience to environmental fluctuations (Eichten et al., 2014).

Not all epigenetic modifications exhibit equal persistence across generations. DNA methylation changes in the CG context are often stably inherited, whereas non-CG methylation forms, such as CHH methylation, along with histone acetylation marks, are typically reset during gametogenesis or early embryonic development (Calarco et al., 2012; Martienssen et al., 2008). This differential retention reflects a selective regulatory mechanism that allows for the inheritance of stress-adaptive traits while minimizing the risk of perpetuating potentially deleterious stress-induced epigenetic states.

These findings demonstrate that both model plants and crop species can exhibit transgenerational inheritance of stress-induced epigenetic modifications. However, the stability of these marks, their phenotypic effects, and the molecular mechanisms governing their transmission vary substantially across species and stress types (Heard & Martienssen, 2014; Hauser et al., 2011). Investigating these dynamics under both controlled and field conditions is essential to determine the consistency, adaptive value, and applicability of epigenetic memory in crop improvement (Springer & Schmitz, 2017).

Case Study: Epigenetic Modulation of OsHKT1;5 in Rice under Salt Stress

OsHKT1;5 is found in rice (*Oryza sativa*) plants and helps the plant tolerate salinity by moving excess Na⁺ from its water xylem to the roots. It avoids a build-up of harmful ions in the shoots and controls the overall balance of ions during salt stress. Epigenetic analysis reveals that the mouth region of OsHKT1;5 is methylated differently in salt-resistant compared with salt-sensitive varieties of rice. In sensitive cultivars, a rise in CG and CHG methylation in their DNA lowers the amount of gene expression, resulting in lower ability to keep salt out of the cells and more injury from it. On the other hand, plants with tolerant genotypes have less methylation and thus can produce more OsHKT1;5 for superior stress tolerance.

Using both methylome and transcriptome analyses, some researchers (like Wang et al., 2016) have found that the differences in methylation are related to changes in leaf sodium, shoot growth, and stress response in the plants. Some altered epigenetic markers here are not reset after the stress is over, supporting the possibility that they help an organism withstand future stress.

This case illustrates how epigenetic regulation at a single gene can modulate stress responses in a trait-relevant way. As such, *OsHKT1;5* and its methylation profile represent a promising target for epigenome-assisted breeding or targeted editing aimed at improving salt tolerance in rice.

Table 1: Summary of Transgenerational Epigenetic Responses to Abiotic Stress in Model and Crop Plants

Species	Type of Epigenetic Change	Inheritance Outcome
<i>Arabidopsis thaliana</i>	DNA methylation at TEs and stress-responsive gene promoters	Enhanced drought tolerance in progeny
<i>Oryza sativa</i>	DNA methylation (CG, CHG); histone modifications	Improved salt tolerance and phosphorus uptake
<i>Zea mays</i>	DNA/histone methylation; small RNAs at TEs	Heritable changes in flowering, root traits

Mechanisms Supporting Inheritance

Germline Integrity of Epigenetic Marks

In plants, the germline arises from somatic cells during late development, allowing stress-induced epigenetic modifications to be transmitted to the next generation (Heard & Martienssen, 2014). Unlike in animals, DNA methylation marks in plants are not fully erased during gametogenesis, allowing certain modifications, particularly those in the CG context, to persist across generations (Li et al., 2024; Zilberman et al., 2006). This epigenetic stability plays a key role in maintaining gene expression patterns and silencing transposable elements, thereby safeguarding genome integrity in the offspring (Slotkin & Martienssen, 2007).

Small RNA-Mediated Inheritance Pathways

Small RNAs (sRNAs), including small interfering RNAs (siRNAs) and microRNAs (miRNAs), are very important as they guide and maintain epigenetic states across generations (Matzke et al., 2015). In plants, the RNA-directed DNA methylation (RdDM) pathway utilizes 24-nucleotide siRNAs to direct de novo DNA methylation at specific genomic loci, leading to transcriptional gene silencing (Calarco et al., 2012). These sRNAs move between cells and help silence transposable elements and regulate gene expression during development (Slotkin & Martienssen, 2007). sRNAs produced in companion cells can also be transported to gametes, contributing to the transmission of epigenetic information (Martienssen & Moazed, 2015).

Escape from Epigenetic Reprogramming

Although plants undergo epigenetic reprogramming during reproduction, it is less extensive than in animals (Calarco et al., 2012). Some loci, particularly those near transposable elements and imprinted genes, are not reset and retain their epigenetic marks across generations (Slotkin & Martienssen, 2007). This selective retention is reinforced by small RNAs and the RNA-directed DNA methylation (RdDM) pathway, which maintains methylation patterns during gametogenesis and embryogenesis (Martienssen & Moazed, 2015). As a result, stress-responsive epigenetic modifications can be stably inherited without altering the DNA sequence (Heard & Martienssen, 2014).

Table 2. Summary of Key Epigenetic Findings in Plant Abiotic Stress Response and Crop Resilience: A Critical Synthesis of Reviewed Literature

To synthesize the breadth of current research across plant species and stress conditions, Table 2 presents a critical comparative summary of key studies investigating epigenetic responses to abiotic stress. It highlights the underlying mechanisms, the presence or absence of heritable stress memory, and the potential applications of these findings in the context of crop improvement

Table 2. Summary of Key Epigenetic Findings in Plant Abiotic Stress Response and Crop Resilience: A Critical Synthesis of Reviewed Literature

Study / Source	Plant Species / System	Abiotic Stress Type	Epigenetic Mechanism	Critical Findings	Evidence of Memory or Inheritance	Context & Relevance to Crop Improvement
Wibowo et al. (2016)	<i>Arabidopsis thaliana</i>	Drought, osmotic stress	DNA methylation	Identified stress-specific hypomethylation sites that persisted through mitotic divisions but were restricted in the male germline.	Somatic memory confirmed; inheritance constrained to specific genomic loci.	Demonstrates the importance of locus-specific methylation plasticity in adapting to recurring stress; implications for within-generation priming.
Zheng et al. (2017)	<i>Oryza sativa</i> (rice)	Drought (multi-generation)	DNA methylation	Persistent DMRs observed after repeated drought exposure, linked to phenotypic improvements in offspring.	Transgenerational inheritance is confirmed across multiple generations.	Validates epimutagenesis as a breeding strategy for drought resilience in rice.
Ding et al. (2013); Crisp et al. (2016)	<i>Arabidopsis thaliana</i>	Dehydration	Histone modifications, DNA methylation	Classified four types of dehydration memory genes based on transcriptional reactivation patterns.	Stable chromatin marks at stress-responsive loci suggest memory within the somatic lineage.	Offers a functional classification model useful for predicting gene reactivation potential.
Zhang et al. (2018); Yin et al. (2024)	<i>Oryza sativa</i>	Salt, drought	DNA methylation (temporal dynamics)	Defined biphasic epigenetic response: early activation of genes followed by stable methylation to sustain adaptive expression.	Suggests stress memory with both transient and persistent phases.	Useful for designing temporal gene regulation systems in crops with complex stress profiles.
Cui et al. (2016)	<i>Arabidopsis thaliana</i>	Heat	Histone modification (H3K27me3 demethylation via REF6)	REF6 removes repressive marks at thermotolerance loci to activate gene expression rapidly.	Memory not tested transgenerationally, but mitotic stability implied.	Highlights the role of demethylases as potential targets for thermal resilience.
Guo et al. (2019); Zhao et al. (2020)	<i>Oryza sativa</i>	Salt, cold	Chromatin remodeling (SWI/SNF ATPase OsCHR4)	SWI/SNF chromatin remodelers modulate nucleosome positioning, influencing stress gene accessibility.	No direct inheritance tested; impact is somatic.	Promotes understanding of non-sequence-based regulation of stress gene networks.

Sani et al. (2013)	<i>Arabidopsis thaliana</i>	Salt (hyperosmotic priming)	DNA methylation, histone modification	Established that osmotic stress priming induces durable chromatin changes and transcriptional memory.	Epigenetic memory persisted across multiple cell divisions.	Model for developing primed crop lines without transgenic interventions.
Wang et al. (2016)	<i>Oryza sativa</i>	Drought	Whole-genome methylome profiling	Over 15% of drought-induced DMRs occurred near transposable elements and correlated with adaptive gene regulation.	Mixed: some marks reset, others persisted.	Points to the utility of TE-adjacent epialleles in breeding resilient rice varieties.
Quadrana & Colot (2016); Johannes et al. (2009)	<i>Arabidopsis</i> epiRILs	Developmental & stress responses	Stable epialleles from ddm1 mutants	Epialleles regulate complex traits (e.g., flowering time, pathogen resistance) independent of sequence variation.	Epigenetic differences stably inherited across generations.	Provides a foundation for epigenetic selection tools in breeding pipelines.
Navarro et al. (2006); Sunkar et al. (2006)	<i>Arabidopsis thaliana</i>	Salt, oxidative stress	miRNAs (miR393, miR398)	miRNAs fine-tune auxin signaling and antioxidant defense under stress.	Short-term regulation; inheritance not documented.	Useful for rapid stress mitigation; combinable with long-term epigenetic strategies.
Zhang et al. (2020)	Tomato, <i>Arabidopsis</i>	General developmental & stress	Stable natural epialleles	Identified stable, naturally occurring epialleles impacting fruit ripening and stress response.	Yes, shown to segregate independently of DNA mutations.	Promotes non-GMO trait development via epiallele-based selection.
Secco et al. (2015)	<i>Oryza sativa</i>	Phosphate starvation	DNA methylation	Stress-induced transcription drives temporary methylation changes near repetitive elements.	Transient changes reversed after stress.	Supports the concept of dynamic methylation marks tuned to environmental cycles.
Kim et al. (2012); Kim et al. (2015)	<i>Arabidopsis thaliana</i>	Heat, drought, and salinity	Chromatin, histone, methylation	Recovery from stress involves resetting of chromatin status, with poised states retained for rapid reactivation.	Partially retained chromatin states suggest preparatory memory.	Informs the development of "stress-ready" crop cultivars.

Incorporating Epigenetic Variation into Crop Breeding

Although there is more proof that epigenetic traits influence plant growth and survival under harsh conditions, these traits are not widely used in traditional plant breeding (Varotto et al., 2020). This situation mostly stems from worries about how stable and inheritable epigenetic marks are (Quadrana & Colot, 2016). Since epigenetic changes such as DNA methylation can be reversed and affected by external stressors, it is less certain how they will be passed down through generations (Springer & Schmitz, 2017).

The use of epigenetics in molecular breeding is limited, according to He et al. (2010), because the necessary platforms are still expensive and slow. Various technologies exist, but because they need a lot of effort and advanced bioinformatics tools, most of them are not practical in normal crop breeding activities (Kawakatsu & Ecker, 2019). Also, it is still difficult to distinguish functional changes from those that are merely noise or biologically irrelevant in epigenetic analysis.

Nonetheless, recent studies have shown the potential of epigenetic variation to improve complex traits and enhance stress resilience in crops (Springer & Schmitz, 2017). Persistent stress-induced modifications, including epigenetic memory, indicate that prior exposure can prime plants for stronger responses to recurring stress (Lämke & Bäurle, 2017). Stable epialleles affecting traits such as flowering time, biomass accumulation, and grain quality have been identified in several major crops, providing concrete targets for selection in breeding programs (Quadrana & Colot, 2016).

Integrating epigenetic information into breeding strategies will require revised frameworks for trait evaluation and selection (Pratap et al., 2019). This involves identifying stable epigenetic markers that correlate with target phenotypes and show reliable inheritance patterns (Gallusci et al., 2016).

Available Tools and Technologies

Recent technological advances have expanded the ability to study and manipulate epigenetic regulation in plants. Among these, epigenetic recombinant inbred lines (epiRILs) have become a key tool for investigating heritable epigenetic variation. EpiRILs are created by crossing wild-type plants with mutants lacking DNA methylation machinery, such as *met1* or *ddm1* (Johannes et al., 2009). These lines share nearly identical genetic backgrounds but carry stable, segregating epigenetic differences. In *Arabidopsis thaliana*, epiRIL studies have identified epialleles that affect traits like flowering time, biomass accumulation, and pathogen resistance, demonstrating the phenotypic effects of epigenetic variation independent of DNA sequence changes (Cortijo et al., 2014). Similar strategies have been applied to tomato and rice, where epiRIL-like populations are being explored for traits such as fruit ripening and drought resilience (Zhang et al., 2020; Quadrana & Colot, 2016).

Complementary to epiRILs is the method of epi mutagenesis, which artificially induces epigenetic alterations through chemical treatments or targeted disruption of epigenetic regulators (Springer & Schmitz, 2017). These approaches can generate novel heritable

epialleles and reveal cryptic variation that may otherwise be overlooked in traditional breeding pipelines (Li et al., 2014). For example, treatment with 5-azacytidine has been used in crops like sorghum and barley to reduce DNA methylation and uncover hidden phenotypic plasticity (Wang et al., 2009).

New CRISPR-based editing technologies have greatly changed the way plant genomics is studied (Gallego-Bartolomé et al. 2019). When attached to epigenetic enzymes, catalytically inactive dCas9 allows the location-specific addition or removal of epigenetic alterations, not DNA alterations. Thanks to this kind of manipulation, researchers can learn a lot about how regulators function and may help improve agricultural products by making controlled, reversible changes to epigenetics (Papikian et al., 2019). So far, both rice and maize have shown promise in research with dCas9, which can influence the timing of flowers and how genes are controlled by stress (Zhang et al., 2018).

Besides, more research groups are using epigenome-wide association studies (EWAS) to measure the links between traits and changes in epigenetic features such as cytosine methylation and histone modifications among various populations or breeding groups (Kawakatsu et al., 2016). If used together with high-throughput phenotyping and genomics, EWAS makes it possible to find epigenetic markers valuable for marker-assisted selection (Meng et al., 2016). Researchers make efficient use of MethGo, EPIC, and Integrative Genomics Viewer (IGV) to support their analysis and understanding of large-scale epigenomic datasets (Liao et al., 2015).

Application to Underutilized and Resilient Crops

Although epigenetic research has mainly been done on important crops, looking into epigenetics in understudied plants could have a big impact on the robustness of agriculture and the world's food supply (Gallusci et al., 2016). Many stressed ecotypes and landraces grown in difficult conditions have special properties formed by genetics and epigenetics (Varshney et al., 2017). Because of these crops, plants can have more epigenetic diversity, which helps them deal with drought, heat, and salinity (Springer & Schmitz, 2017).

Collecting detailed epigenomics data for millet, teff, pigeon pea, or fonio could play a big role in quickening their inclusion in breeding activities. If we explored DNA methylation, histone modifications, and RNA profiles in these species under various conditions, this would allow us to see additional, hidden, adaptive differences and their regulatory mechanisms (Zhang et al., 2018).

In situations where there are few inputs and the environment is always changing in agroecological systems, epigenetics is very important. Local adaptation is helped by epigenetics, which allows adjustments in a trait without changing the genes themselves (Richards et al., 2017). A focus on traditional farming and native crop plants may help detect local epigenetic reactions, which can lead to the development of a sustainable type of agriculture that thrives with biodiversity and relies little on chemicals (Latzel et al., 2016).

Translating Epigenetic Insights from Model Plants to Crops: Barriers and Opportunities

Although studies on *Arabidopsis thaliana* and *Oryza sativa* provide valuable insights into epigenetic regulation under abiotic stress (Pandey et al., 2016; Zhang et al., 2018), applying this knowledge to new types of crops remains challenging. Using findings from models in breeding programs is difficult because of a number of biological and translational hurdles.

The genome of several staple crops is one of the main challenges to growing them. In wheat (*Triticum aestivum*) and similar polyploid species, the presence of multiple homologs of chromosomes makes epigenetic effects harder to see or for them to affect gene expression (Kumar & Raju, 2021). Because of polyploidy, detecting these stress-induced epialleles becomes more challenging, which also makes epigenetic approaches unreliable.

Another challenge is the instability of stress-induced epigenetic marks under field conditions. While mitotic and even transgenerational memory have been demonstrated in controlled environments (Lämke & Bäurle, 2017), fluctuating abiotic stress, soil heterogeneity, and microbial interactions in the field often disrupt or reverse these marks. This limits the predictability and scalability of lab-based epigenetic strategies when applied in real-world agricultural systems.

A third barrier is the lack of comprehensive epigenomic data for underutilized crops. Many resilient species cultivated in low-input or marginal environments remain underexplored at the epigenetic level (da Costa et al., 2024). These crops may harbor valuable stress-responsive epialleles, yet few resources exist for methylome or chromatin profiling in these systems. Without such data, extending epigenetic breeding strategies beyond major crops is difficult.

Overcoming these barriers will require expanded epigenomic reference datasets across crop taxa, improved tools for functional epigenetic validation in polyploids, and increased field-based studies that connect epigenetic states with adaptive agronomic traits.

To enable the translational application of current epigenetic insights, it is critical to identify the outstanding challenges that constrain their effective deployment in crop stress resilience. Table 3 presents a structured synthesis of key unresolved questions in the field of plant stress epigenetics. The table integrates biological uncertainties with translational gaps, aligning each challenge with a specific research question, proposed methodological approach, and an assessment of both feasibility and crop relevance. This framework is intended to guide future research priorities and inform strategic investments in crop improvement through epigenetic mechanisms.

Table 3. Unresolved Questions in Plant Epigenetics for Stress Resilience

Challenge	Example Question	Suggested Approach	Priority / Feasibility	Notes / Crop Relevance
Inheritance consistency	Why are some methylation marks retained while others are reset after reproduction?	Longitudinal epigenomic profiling across developmental stages and generations	High / Medium	Especially relevant to crops with rapid reproductive cycles (e.g., rice, Arabidopsis)
Field validation	Do epialleles confirmed in controlled conditions maintain function under diverse environmental field conditions?	Multi-location field trials with phenotypic and epigenetic monitoring	High / High	Critical for translating lab findings into breeding programs
Editing tools	Can dCas9-epigenetic systems be used to introduce heritable, beneficial epigenetic changes?	Targeted CRISPR/dCas9-based modification of known stress-responsive loci	Medium / Experimental	Promising for targeted trait development in elite varieties
Epigenetic-environment interaction	How do multiple simultaneous or sequential stressors influence epigenetic states and memory?	Combined stress modeling and multi-omics integration (methylome transcriptome phenotype)	Medium / Challenging	Important for climate-adaptive strategies across crops (e.g., maize, millet)
Application to underutilized crops	How transferable are model crop findings to orphan or indigenous species in marginal environments?	Epigenome mapping and marker discovery in stress-adapted landraces and wild relatives	High / Feasible with investment	Prioritizes crops like fonio, pigeon pea, teff, and sorghum

Future Research Directions

Although major advances have clarified how plants use epigenetic mechanisms to respond to abiotic stress, applying these insights to crop improvement remains challenging. As emphasized throughout this review, future research must move beyond model species and controlled environments. A central goal is to validate these mechanisms under real agricultural conditions. This includes testing findings across a wide range of genetic backgrounds, environmental settings, and stress combinations. Field trials across multiple locations and environmental gradients will be critical to assess whether specific epigenetic modifications are consistent, stable, and functionally relevant in crop systems. Further research is needed to clarify the temporal and spatial dynamics of epigenetic regulation. The maintenance, resetting, and functional interaction of epigenetic marks across tissues and developmental stages under changing environmental conditions remain poorly understood. High-resolution, long-term datasets ideally spanning multiple generations are essential to track the persistence and inheritance of stress-induced epigenetic changes. Progress will also depend on interdisciplinary collaboration. Integrating epigenetic findings with insights from agronomy, plant physiology, climate science, and socioecology can support the development of systems-based approaches to crop adaptation. This is

especially important in agroecological and low-input systems, where phenotypic plasticity and local adaptation drive resilience.

Finally, the effective use of epigenetic technologies in agriculture requires transparent and equitable frameworks. Key issues, including access to epigenetic resources, fair benefit-sharing with farming communities, and clear communication of each tool's scope and limitations, must be addressed to ensure that research outcomes align with principles of fairness and sustainability.

Conclusion

Epigenetic regulation plays a key role in plant responses to abiotic stress by enabling dynamic and sometimes heritable changes in gene expression without altering the DNA sequence itself. Mechanisms such as DNA methylation, histone modifications, chromatin remodeling, and small RNAs have been shown to mediate not just immediate stress responses, but also stress memory and, in some cases, transgenerational inheritance, offering a flexible and reversible layer of control over gene activity. While this has been well-demonstrated in model species and is increasingly studied in crops, major gaps remain. The functional relevance, stability, and heritability of many stress-induced changes are still unclear, especially under field conditions where environmental variability complicates validation. There is also a lack of attention to underutilized crops and landraces that may carry useful epigenetic diversity. To move forward, research must go beyond profiling and begin to test how these mechanisms work under real-world scenarios, especially in low-input systems where traditional breeding falls short. Applying this knowledge in breeding programs, through epiRILs, EWAS, epimutagenesis, or CRISPR-based approaches, can help strengthen crop resilience in the face of climate uncertainty. But for epigenetics to become a true tool in agriculture, coordinated efforts are needed to close knowledge gaps, validate mechanisms in diverse species and environments, and develop scalable, farmer-relevant strategies that link discovery to real outcomes.

Recommendations

To make epigenetics more practical in the field, researchers need to test these stress-related markers in real-world conditions across various crop types and stress scenarios. Breeders should begin integrating epigenetic screening into their regular selection processes, especially for traits like drought, salt, and heat tolerance. Policymakers can support this effort by endorsing non-GMO tools and backing crop research that aligns with local farming systems. Ensuring that farmers and communities benefit equitably and clearly communicating the scope and limitations of these tools are also crucial.

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