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Advancements in Understanding Histone Modification Regulation Mechanisms and Their Applications in Breeding for Plant Responses to Abiotic Stress

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Abstract: Abiotic stresses such as drought, salinity, extreme temperature, and heavy-metal toxicity are among the principal constraints on global crop productivity, and their impact is intensifying under climate change. Beyond changes in DNA sequence, plants rely heavily on reversible chromatin modifications to rapidly and flexibly adjust gene expression in response to fluctuating environments. Among these, histone acetylation, methylation, phosphorylation, and ubiquitination act as an interconnected regulatory layer, often described as the histone code that governs whether stress-responsive genes are activated, repressed, or kept in a poised state for rapid future induction. This review synthesizes current understanding of the molecular writers, erasers, and readers that establish and interpret histone marks in plants, examines how these marks are dynamically remodeled during drought, salinity, temperature extremes, and heavy-metal exposure, and considers the phenomenon of chromatin-based stress memory mediated by bivalent H3K4me3–H3K27me3 domains. We further evaluate how this mechanistic knowledge is being translated into breeding practice, including epiallele-based selection, genome-wide epigenomic profiling, and CRISPR/dCas9-based epigenome editing that directly installs or removes histone marks at target loci without altering the underlying DNA sequence. Representative case studies in Arabidopsis, rice, wheat, cotton, poplar, soybean, and common bean illustrate measurable gains in stress tolerance achieved through manipulation of histone-modifying enzymes such as HDA6, HDA9, HD2C/D, OsHDT701, GCN5/ADA2, and HUB2. We conclude by outlining remaining challenges, including incomplete understanding of crosstalk between histone marks and other epigenetic layers, the stability and heritability of engineered epialleles, and regulatory pathways for non-transgenic epigenome-edited crops, and we propose priority directions for integrating chromatin biology into climate-resilient breeding pipelines.

Keywords: histone modification; chromatin regulation; abiotic stress; epigenetics; histone acetylation; histone methylation; CRISPR/dCas9 epigenome editing; stress memory; crop breeding

1. Introduction

Plants are sessile organisms that cannot escape unfavorable environmental conditions and must therefore rely on highly plastic molecular mechanisms to survive fluctuations in water availability, salinity, temperature, and soil chemistry. Drought, salinity, and temperature extremes alone are estimated to account for a substantial share of global yield losses in major staple crops, and the frequency and severity of these stresses are projected to increase under ongoing climate change. Traditional breeding and transgenic approaches that target single stress-responsive genes have delivered important gains, but they do not fully capture the layered, reversible, and often rapidly reprogrammable nature of plant stress responses.

Chromatin, the complex of DNA wrapped around histone octamers, provides an additional and highly dynamic regulatory layer above the DNA sequence itself. Post-translational modifications of histone tails, including acetylation, methylation, phosphorylation, ubiquitination, and sumoylation, alter chromatin accessibility and

recruit specific reader proteins, thereby determining whether a given stress-responsive gene is transcriptionally active, poised, or silenced. Because these marks are enzymatically reversible, they allow plants to respond quickly to an oncoming stress and, in some cases, to retain a form of chromatin-based memory that primes a faster or stronger response to a recurring stress.

Recent advances in chromatin immunoprecipitation sequencing (ChIP-seq), assay for transposase-accessible chromatin sequencing (ATAC-seq), and single-cell epigenomic profiling have considerably expanded the catalogue of histone marks associated with abiotic stress responses across model and crop species. In parallel, the maturation of CRISPR/dCas9-based epigenome editing tools now allows researchers to install or remove specific histone marks at defined loci without altering the DNA sequence, opening a path toward non-transgenic, precisely targeted improvement of stress tolerance. This review integrates mechanistic findings on histone modification regulation with emerging breeding applications, aiming to provide a consolidated reference for researchers working at the interface of plant epigenetics and crop improvement.

2. Molecular Mechanisms of Histone Modification

Histone modification refers to the enzymatic addition or removal of chemical groups on the N-terminal tails (and, in some cases, globular domains) of core histones H2A, H2B, H3, and H4. These modifications are installed by 'writer' enzymes, removed by 'eraser' enzymes, and interpreted by 'reader' proteins that contain specialized recognition domains such as bromodomains, chromodomains, and PHD fingers. The combinatorial pattern of marks at a given locus, often referred to as the histone code, integrates multiple upstream signaling inputs to produce a coherent transcriptional outcome.

2.1 Histone Acetylation and Deacetylation

Acetylation of lysine residues on histones H3 and H4 neutralizes their positive charge, weakening histone–DNA contacts and generally producing a more open, transcriptionally permissive chromatin state. This mark is installed by histone acetyltransferases (HATs), including GCN5-related and CBP/p300-type enzymes, and removed by histone deacetylases (HDACs). Plant HDACs fall into three structurally distinct families: the RPD3/HDA1 family (e.g., HDA6, HDA9, HDA19), the plant-specific HD2 family (HD2A–HD2D), and the SIR2 family. Members of the RPD3/HDA1 family, particularly HDA6, HDA9, and HDA19, have been repeatedly linked to salt, cold, and drought responses in Arabidopsis, generally acting as repressors that must be relieved for full stress-gene induction. In rice, the HD2-type deacetylase OsHDT701 positively regulates salt and drought tolerance as well as disease resistance; whereas OsHDA705 appears to act antagonistically during seed germination under salt and ABA treatment, illustrating that the direction of an HDAC's effect can be locus- and context-dependent rather than uniformly repressive or activating.

2.2 Histone Methylation

Histone methylation can be either activating or repressive depending on the specific lysine residue and degree of methylation. Trimethylation of histone H3 at lysine 4 (H3K4me3) and methylation at H3K36 are generally associated with active transcription and are installed by SET-domain methyltransferases such as ATX1/ATX2 and SDG8. In contrast, H3K9 methylation (installed by SUVH-family enzymes) and H3K27me3, deposited by the Polycomb Repressive Complex 2 (PRC2, including CURLY LEAF and SWINGER), are associated with transcriptional silencing. A particularly important regulatory motif is the bivalent co-occurrence of H3K4me3 and H3K27me3 at the same locus, which places a gene in a poised rather than fully active or fully silenced state. Recent work indicates that dynamic switching of these bivalent marks at specific stress-responsive loci allows plants to fine-tune the amplitude and timing of gene induction across drought, salinity, temperature, and nutrient stress, and that this switching contributes to short-term chromatin-based stress memory.

2.3 Histone Phosphorylation, Ubiquitination, and Other Modifications

Beyond acetylation and methylation, several additional histone marks contribute to abiotic stress regulation. Phosphorylation of H3 serine residues (e.g., H3S10, H3S28) links kinase-signaling cascades, including mitogen-activated protein kinase pathways activated by osmotic and temperature stress, to chromatin condensation states,

and it frequently acts in combination with adjacent acetylation marks. Monoubiquitination of histone H2B (H2Bub1), catalyzed by E3 ubiquitin ligases such as HUB1 and HUB2, promotes downstream deposition of activating methylation marks including H3K4me3 and H3K36me3. In cotton, overexpression of the Arabidopsis HUB2 gene raised H2Bub1 and H3K4me3 levels at drought-responsive DREB loci and improved field-level drought performance, illustrating a direct mechanistic link between ubiquitination, subsequent methylation, and an agronomically relevant stress phenotype.

2.4 The Histone Code and Crosstalk with Other Epigenetic Layers

Histone modifications rarely act in isolation. They interact extensively with DNA methylation, ATP-dependent chromatin remodeling complexes, small RNA pathways, and, as increasingly recognized, RNA N6-methyladenosine (m6A) modification. For instance, the RNA methyltransferases METTL3 and METTL14 have been shown to cooperate with chromatin-modifying proteins, forming feedback loops that sustain appropriate gene expression during prolonged stress exposure. Likewise, histone methylation and DNA methylation frequently reinforce one another at silenced stress loci, and their combined removal is often required for full transcriptional activation. This multi-layered crosstalk means that manipulating a single histone mark can have context-dependent effects, underscoring the need for integrated, locus-specific characterization before such marks are used as breeding targets.

Table 1. Major classes of histone modifications relevant to plant abiotic stress responses, their writer/eraser enzymes, and general regulatory roles.

Modification	Key Residues	Writer Enzymes	Eraser Enzymes	Chromatin Effect	General Role in Stress
Acetylation	H3K9, H3K14, H3K27, H4K5/8/12/16	HATs (GCN5, HAT1, CBP/p300-type)	HDACs (RPD3/HDA1: HDA6, HDA9, HDA19; HD2-type: HD2A–D; SIR2-type)	Neutralizes lysine charge; loosens nucleosome contacts; opens chromatin	Generally activates stress-responsive genes; HDACs fine-tune magnitude/ timing of induction
Methylation (activating)	H3K4me1/2/3, H3K36me2/3	SET-domain methyltransferases (ATX1/2, SDG8)	Demethylases (JMJ-family, LDL1/2)	Recruits reader proteins that stabilize active transcription complexes	Marks poised/active stress genes; supports rapid re-induction on repeated stress
Methylation (repressive)	H3K9me2, H3K27me3	SUVH-family (H3K9me2); PRC2 complex (H3K27me3: CLF, SWN, MEA)	IBM1, JMJ demethylases (H3K9); REF6, ELF6 (H3K27)	Compacts chromatin; recruits Polycomb-repressive machinery	Silences stress genes under non-stress conditions; removed/ redistributed upon stress onset
Bivalent H3K4me3–H3K27me3	H3K4 + H3K27 on same nucleosome/ locus	Combined COMPASS-like + PRC2 activity	JMJ + REF6/ELF6	Poised chromatin state, neither fully active nor silent	Enables rapid, reversible switching of stress genes; basis of short-term stress memory
Phosph-orylation	H3S10, H3S28	Mitogen-activated/AUR kinases	Phosphatases (e.g., PP2C-related)	Alters higher-order chromatin condensation;	Integrates rapid kinase-signaling cascades (e.g., MAPK) with

				crosstalks with adjacent acetylation	chromatin state during stress
Ubiquitination	H2Bub1 (K143 in Arabidopsis)	E3 ligases (HUB1, HUB2) with E2 conjugases	Deubiquitinases (UBP26)	Facilitates nucleosome disassembly; promotes downstream H3K4/H3K36 methylation	Positively regulates drought- and ABA-responsive gene transcription

3. Regulatory Mechanisms Linking Histone Modifications to Abiotic Stress Responses

The following sections summarize how histone modification dynamics are integrated into the regulatory networks governing plant responses to the major classes of abiotic stress.

3.1 Drought Stress

Drought responses in plants are tightly linked to abscisic acid (ABA) signaling, and several histone-modifying enzymes directly intersect with this pathway. HDA9 forms a repressive complex with the transcription factor ABI4 that silences the ABA-catabolic genes CYP707A1 and CYP707A2, thereby maintaining ABA levels needed for stomatal closure and drought tolerance; loss of HDA9 reduces ABA content and increases drought sensitivity despite reduced ABA sensitivity. HD2C and HD2D, both HD2-type deacetylases, positively regulate drought and salt tolerance by modulating ABA-responsive gene networks. At the chromatin-activation end of the spectrum, the histone acetyltransferase AtHAT1 promotes transcriptional activation of the drought-responsive transcription factor AREB1, and targeted recruitment of AtHAT1 through CRISPR/dCas9-based activation substantially improves survival after severe water-deficit stress, as detailed in Section 4.

3.2 Salinity Stress

Salt stress responses similarly involve dynamic histone acetylation. HDA6 loss-of-function mutants display heightened sensitivity to ABA and salt, implicating HDA6 in the negative regulation of stress-gene repression that must be reversed for adaptive responses to proceed. In rice, OsHDT701 overexpression enhances salt tolerance, while OsHDA705 overexpression reduces tolerance during germination, again reflecting locus- and developmental-stage-specific outcomes. Chromatin accessibility profiling (e.g., single-cell ATAC-seq) has additionally revealed that chromatin opens preferentially at sodium and metal transporter loci such as NRAMP and IRT1 in salt-tolerant genotypes, linking chromatin state directly to ion homeostasis under salinity stress.

3.3 Temperature Stress: Cold and Heat

Cold stress tolerance in Arabidopsis depends on proper histone deacetylation at cold-regulated (COR) loci; the WD40 protein HOS15 is required, together with associated HDACs, to repress cold-tolerance genes under non-stress conditions, and hos15 mutants show elevated H3 acetylation and altered cold responses. Conversely, mutations in the HAT complex components GCN5 and ADA2 alter expression of COR genes and reduce freezing tolerance, indicating that a properly balanced acetylation/deacetylation cycle, rather than acetylation alone, is required for optimal cold adaptation. Under heat stress, RNA m6A methylation accelerates turnover of stress-related transcripts and interacts with chromatin-modifying machinery to help maintain gene expression equilibrium during prolonged high-temperature exposure, indicating that thermomorphogenic responses are shaped jointly by histone- and RNA-level epigenetic marks.

3.4 Nutrient Deficiency and Heavy-Metal Stress

Heavy-metal stress, such as cadmium exposure, induces deposition of activating H3K9ac and H3K4me3 marks at detoxification loci including phytochelatin synthase (PCS1), glutathione S-transferase (GST), and metallothionein genes. Basal repression of these loci under non-stress conditions is maintained by HDA6 and HDA19, and mutants lacking these deacetylases accumulate more metal, indicating that HDAC-mediated repression must be relieved for effective detoxification. Small RNA pathways acting on auxin receptor transcripts further modulate root architecture to limit metal uptake, illustrating that histone-based and small-RNA-based regulation act in a coordinated fashion during metal stress.

3.5 Stress Memory and Bivalent Chromatin Domains

A distinguishing feature of chromatin-based stress regulation is the capacity to establish a form of transcriptional memory that primes plants for improved responses to recurring stress episodes. Bivalent H3K4me3–H3K27me3 domains at specific stress-responsive loci can be dynamically resolved toward either mark depending on stress history, allowing genes to be re-induced more rapidly upon repeated exposure. This chromatin-based memory operates alongside DNA methylation and non-coding RNA mechanisms to establish multi-generational or within-generation priming effects, and it represents one of the most promising, though still incompletely understood, targets for breeding crops with enhanced resilience to recurrent environmental extremes.

4. Applications in Breeding for Abiotic Stress Tolerance

Translating mechanistic knowledge of histone modification into breeding practice is proceeding along several complementary tracks: selection on naturally occurring epialleles, genome-wide epigenomic profiling to guide marker-assisted selection, direct transgenic manipulation of histone-modifying enzymes, and, most recently, targeted CRISPR/dCas9-based epigenome editing.

4.1 Epigenetic Breeding and Epiallele Selection

Natural populations and germplasm collections harbor heritable epialleles, chromatin or DNA methylation states that alter gene expression without changing the underlying DNA sequence. When such epialleles are stably transmitted across generations, they can be selected in a manner analogous to conventional genetic markers. Genome-wide profiling approaches modeled on the ENCODE project, including ChIP-seq for histone marks, ATAC-seq for chromatin accessibility, and bisulfite sequencing for DNA methylation, are increasingly used to map regulatory regions associated with stress tolerance, disease resistance, and yield stability in horticultural and field crops. By correlating specific epigenetic marks with expression of stress-response genes, breeders can identify demethylated or appropriately acetylated variants suited to arid, saline, or thermally extreme production environments, and select for these variants without introducing transgenes.

4.2 CRISPR/dCas9 Epigenome Editing

The catalytically inactive Cas9 protein (dCas9) can be fused to histone-modifying domains and guided to specific loci by single guide RNAs, enabling precise, sequence-targeted installation or removal of histone marks without cutting the DNA. In a widely cited proof-of-concept, a dCas9–AtHAT1 fusion was directed to the promoter of the drought-responsive transcription factor AREB1 in Arabidopsis. The resulting CRISPR-activation (CRISPRa) lines showed higher AREB1 and RD29A expression, improved stomatal regulation under water deficit, and markedly improved survival after severe drought stress followed by rehydration compared with control plants. Related dCas9-based strategies have targeted H3K27me3 removal (via KRAB-domain or TET1 fusions) and DNA methylation writers (DNMT3A fusions) to modulate stress-responsive loci such as OsDREB1 in rice and TaNHX1 in wheat, with reported improvements in drought and salinity tolerance, respectively. Because these edits do not alter the DNA sequence, epigenome-edited lines may in some jurisdictions face a distinct regulatory pathway from conventional transgenic or DNA-edited crops, although this regulatory landscape is still evolving and varies by country.

4.3 Multi-Omics-Assisted Breeding

Because histone modifications interact extensively with DNA methylation, small RNAs, and RNA modifications, breeding programs are increasingly integrating multiple omics layers, genomic, transcriptomic, epigenomic, and metabolomic, to identify robust, pleiotropy-aware targets for improvement. This is particularly relevant in polyploid crops such as wheat and soybean, where multiple gene copies and complex regulatory redundancy complicate single-locus editing strategies. Multi-omics integration also helps distinguish causal epigenetic variation from marks that are merely correlated with a stress-tolerant phenotype, reducing the risk of selecting non-heritable or environmentally unstable epialleles.

4.4 Case Studies Across Crop Species

In soybean, genome-wide surveys have documented histone acetylation and methylation changes responsive to temperature shifts, and these findings are being incorporated into molecular breeding pipelines aimed at counteracting climate-driven yield declines, which have been projected to reduce soybean production by roughly one-fifth under open-air warming experiments. In poplar, genome-wide identification of HDAC and HAT gene families under drought has expanded the catalogue of candidate loci for woody perennial stress breeding, and heterologous expression of the poplar deacetylase gene 84KHDA909 in Arabidopsis improved root growth, raised proline accumulation, and lowered malondialdehyde levels under both drought and salt stress. In cotton, overexpression of the Arabidopsis ubiquitin ligase gene HUB2 improved boll-setting rate and reduced boll abscission under field drought conditions through altered H2Bub1 and H3K4me3 marks at DREB loci. Collectively, these case studies demonstrate that histone-modification-based interventions, whether through natural variation, transgenic overexpression, or direct epigenome editing, can produce measurable, agronomically relevant improvements in stress tolerance across both model and crop species.

The chart below compiles representative, literature-reported quantitative outcomes from studies that manipulated histone modifications to improve abiotic stress tolerance, spanning a CRISPR/dCas9 histone-acetyltransferase fusion in Arabidopsis, CRISPR-based epigenome activation in rice, and a proposed epigenetic breeding target for heavy-metal detoxification across legume, cereal, and Brassica crops. These examples illustrate the practical magnitude of trait improvement that histone-modification-based strategies can achieve, while also highlighting that reported metrics differ across studies (survival/recovery rate versus relative tolerance gain) and should be interpreted within their original experimental contexts rather than compared as a single standardized measure.

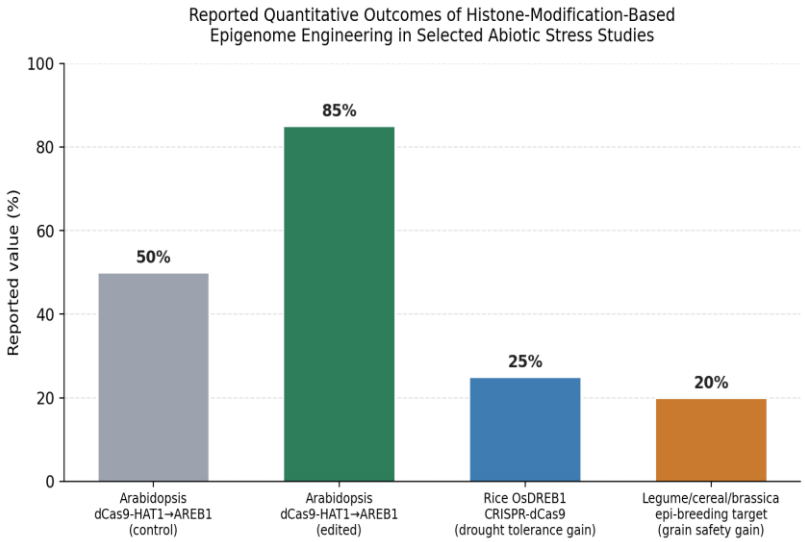

Figure 1. Reported quantitative outcomes from histone-modification-based epigenome engineering. Sources: Roca Paixão et al. (2019), Scientific Reports; Frontiers in Plant Science epigenetic stress-adaptation review (2026).

5. Challenges and Future Perspectives

Despite substantial progress, several challenges constrain the routine application of histone-modification knowledge to breeding. First, the same histone mark or histone-modifying enzyme can have opposite effects on stress tolerance depending on the target locus, tissue, developmental stage, or genetic background, as illustrated by the contrasting roles of OsHDT701 and OsHDA705 in rice salt tolerance. This context-dependence complicates the design of universally beneficial interventions and calls for locus-resolved, tissue-specific characterization before deployment. Second, the heritability and long-term stability of engineered or selected epialleles across generations and environments remains incompletely characterized; epigenetic marks are, by definition, more labile than DNA sequence changes, and some may revert or become unstable under field conditions or during meiosis.

Third, crosstalk among histone modifications, DNA methylation, chromatin remodeling complexes, and RNA modifications means that single-mark interventions may trigger compensatory changes elsewhere in the epigenome, with uncertain net effects on whole-plant physiology and yield. Fourth, most mechanistic studies remain concentrated in Arabidopsis and a small number of major crops; translating findings to under-studied but regionally important species, and to polyploid genomes with duplicated regulatory machinery, will require expanded genomic and epigenomic resources. Finally, regulatory frameworks for epigenome-edited, non-transgenic crops are still under development in most countries, and clearer guidance will be needed before such crops can move efficiently from laboratory demonstration to field deployment.

Looking forward, priority directions include: (i) systematic, genome-wide mapping of histone marks across diverse stress conditions and germplasm panels to build predictive models linking chromatin state to phenotype; (ii) refinement of CRISPR/dCas9 epigenome-editing tools, including next-generation SunTag and split-effector systems, to improve targeting precision and reduce off-target chromatin effects; (iii) multi-generational field trials to establish the heritability and environmental robustness of candidate epialleles; and (iv) closer integration of histone-modification data with conventional genomic selection pipelines so that chromatin-based traits can be incorporated alongside DNA-sequence markers in mainstream breeding programs.

6. Conclusion

Histone modifications constitute a fast, reversible, and highly integrative regulatory layer that allows plants to sense and respond to drought, salinity, temperature extremes, and heavy-metal stress. Advances in understanding the writers, erasers, and readers that establish this regulatory layer, together with the discovery of bivalent chromatin domains underlying stress memory, have substantially deepened mechanistic insight over the past decade. Equally important, this knowledge is now translating into practical breeding tools, from epiallele-based marker-assisted selection to direct CRISPR/dCas9 epigenome editing, that have already produced measurable gains in drought and salinity tolerance in model and crop species alike. Continued progress will depend on resolving context-dependent and crosstalk-related complexities, establishing the field-level stability of engineered epigenetic states, and building the regulatory and genomic infrastructure needed to bring histone-modification-based breeding into mainstream agricultural practice, an outcome that could meaningfully contribute to global food security under accelerating climate change.

References

[1] Yu, M.-H., Liao, W.-C., & Wu, K. (2025). Histone methylation in plant responses to abiotic stresses. Journal of Experimental Botany, 76(17), 4771–4786.

[2] Frontiers in Plant Science. (2026). Epigenetic modifications in plant abiotic stress adaptation: Towards climate-resilient and sustainable crop improvement. Frontiers in Plant Science.

[3] Zeng, Y., Muhammad, A., Wan, X., Gao, Y., Zhao, W., & El-Sappah, A. H. (2025). Epitranscriptomic modifications for enhancing abiotic stress resistance in plants. Frontiers in Plant Science.

[4] Discover Plants (Springer Nature). (2025). Epigenetic mechanisms regulating plant responses to abiotic stress and their role in developing climate-resilient crops.

[5] Kumar, M., & Rani, K. (2023). Epigenomics in stress tolerance of plants under the climate change. Molecular Biology Reports, 50(7), 6201–6216.

[6] Roles of microRNAs and histone modifications in enhancing stress tolerance in soybean and their applications in molecular breeding. (2025). [Review article]. PMC12203253.

[7] Roca Paixão, J. F., Gillet, F. X., Ribeiro, T. P., Bournaud, C., Lourenço-Tessutti, I. T., Noriega, D. D., de Melo, B. P., de Almeida-Engler, J., & Grossi-de-Sá, M. F. (2019). Improved drought stress tolerance in Arabidopsis by CRISPR/dCas9 fusion with a Histone AcetylTransferase. Scientific Reports, 9, 8080.

[8] Chen, L.-T., Luo, M., Wang, Y.-Y., & Wu, K. (2010). Involvement of Arabidopsis histone deacetylase HDA6 in ABA and salt stress response. Journal of Experimental Botany, 61(12), 3345–3353.

[9] Kim, J.-M., To, T. K., Ishida, J., Matsui, A., Kimura, H., & Seki, M. (2012/2016). Histone deacetylase HDA9 negatively regulates salt and drought stress responsiveness in Arabidopsis. Journal of Experimental Botany, 67(6), 1703–1713.

[10] Histone Deacetylase HDA9 With ABI4 Contributes to Abscisic Acid Homeostasis in Drought Stress Response. (n.d.). PMC7052305.

[11] Zhu, J., Jeong, J. C., Zhu, Y., Sokolchik, I., Miyazaki, S., Zhu, J.-K., Hasegawa, P. M., Bohnert, H. J., Shi, H., Yun, D.-J., & Bressan, R. A. (2008). Involvement of Arabidopsis HOS15 in histone deacetylation and cold tolerance. Proceedings of the National Academy of Sciences.

[12] Vlachonasios, K. E., Thomashow, M. F., & Triezenberg, S. J. (2003). Disruption mutations of ADA2b and GCN5 transcriptional adaptor genes dramatically affect Arabidopsis growth, development, and gene expression. Plant Cell, 15(3), 626–638.

[13] Han, Z., Yu, H., Zhao, Z., Hunter, D., Luo, X., Duan, J., & Tian, L. (2016). AtHD2D gene plays a role in plant growth, development, and response to abiotic stresses in Arabidopsis thaliana. Frontiers in Plant Science, 7, 310.

[14] Sridha, S., & Wu, K. (2006). Identification of AtHD2C as a novel regulator of abscisic acid responses in Arabidopsis. The Plant Journal, 46(1), 124–133.

Plant Responses to Abiotic Stress Regulated by Histone Deacetylases. (2017). Frontiers in Plant Science / PMC5737090.

[15] Zhao, X., Wang, H., Zhang, B., et al. (2022). Overexpression of histone deacetylase gene 84KHDA909 from poplar confers enhanced tolerance to drought and salt stresses in Arabidopsis. Plant Science, 324, 111434.

[16] Genome-wide identification and expression analysis of histone deacetylase and histone acetyltransferase genes in response to drought in poplars. (2024). BMC Genomics, 25(1), 657.

[17] An Arabidopsis E3 ligase HUB2 increases histone H2B monoubiquitination and enhances drought tolerance in transgenic cotton. (2019). Plant Biotechnology Journal / PMC6381789.

[18] HD2A and HD2C co-regulate drought stress response by modulating stomatal closure and root growth in Arabidopsis. (2022). PMC9727301.

[19] Molecular cloning and subcellular localization of six HDACs and their roles in response to salt and drought stress in kenaf (Hibiscus cannabinus L.). (2019). PMC6451785.

[20] Epigenetic crop improvement: Integrating ENCODE strategies into horticultural breeding. (2025). Horticulture Research, 12(11), uhaf213.

[21] Advancing crop resilience to environmental stresses: Insights from epigenetic modification and CRISPR/dCas9-based editing. (2026). ScienceDirect [journal article].