Epigenetic adaptation to drought and salinity in crop plants

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Review paper

Abstract: The severe impact of drought and salinity on plant productivity presents a significant threat to worldwide food security. Plants exhibit the capacity to sense stimuli in their environment and adjust defense mechanisms through diverse regulatory networks to cope with abiotic stress. The complexities of drought and salinity tolerances can be deconstructed into contributing factors and mechanisms, classified under two categories: genetics and epigenetics. Epigenetic mechanisms play a role in partially attributing crop adaptation to the most formidable drought and salinity stresses. Plants respond to stress in part by undergoing stable alterations in gene expression, a process that involves the physical "marking" of DNA or its associated proteins, commonly called epigenetics. Plants utilize various epigenetic mechanisms to refine gene expression, vital for adaptation and phenotypic plasticity. These include DNA methylation, histone modifications, chromatin remodeling, epitranscriptomics, and gene silencing mediated by small RNAs. Notably, epigenetic modifications can be inherited or erased. Enhanced knowledge of epigenetics complements genetics and will aid in developing strategies to integrate them into crop improvement programs aimed at addressing adaptation to abiotic stress. This review highlights the latest and noteworthy findings regarding crop epigenetic responses to abiotic stress signals, particularly those pertinent to drought and salinity tolerance.

Keywords: drought tolerance, CpG island, epigenomics, osmotic stress, salt tolerance, water stress.

Introduction

The productivity of plants is directly reliant on their growth and development, with their ability to adapt to drought and salinity serving as crucial factors, given these are among the most impactful environmental stresses. Drought stress induces numerous adverse effects on plants, subjecting them to common stressors like osmotic and oxidative stresses, similar to those associated with salinity. Drought and salinity stress cause osmotic stress, leading to subsequent dehydration in plant cells. Plant response to osmotic stress involves modifications to constitutively expressed TFs, triggered by both ABA-independent and -dependent mechanisms (Zhu, 2002; Li et al., 2014). With escalating salt concentration, plants experience two primary impairments: osmotic stress and specific ion toxicity, leading to secondary stresses like nutritional disorders and oxidative stress. These effects contribute to a reduction in plant growth, disrupting physiological and metabolic functions, including reduced water and nutrient absorption, membrane dysfunction, and critical process impairments like protein synthesis, respiration, and photosynthesis (Arzani et al., 2023). Various research studies indicate that plants are unable to ignore the onset of challenging environmental conditions, and they demonstrate a form of "stress memory" (Bruce et al., 2007; Lämke and Bäurle, 2017; Gallusci et al., 2023). They guide or supervise their adaptation to recurring, chronic, and combined abiotic stresses by reorganizing their genomic and biochemical architecture (Walter et al., 2013). Cellular response and adaptation to environmental stress depend on a diverse array of tightly controlled regulatory mechanisms, operating at the transcriptional and post-transcriptional tiers. Generally, drought and salinity stimuli can induce different epigenetic mechanisms for regulating the key gene expressions such as inward rectifying K+ channel (*AKT1*), pyrroline-5-carboxylate synthetase (*P5CS*), high-affinity potassium transporters (*HKTs*), and ABA biosynthesis genes (*i.e.*, *NCED1*, *NCED3*, *ABA1*, *ABA2*, *ABA3*, *ABF2, ABF4, ABI3, ABI4*, and *ABI5*) (Arzani and Ashraf, 2016).

Epigenetics is a term with various definitions currently employed across the literature.

Nevertheless, a more frequently employed definition, pertinent to the role of epigenetics in plant defense responses, asserts that epigenetics is the mechanism responsible for the persistent changes in the expression of genes. There are two fundamental epigenetic modifications: the covalent alteration of DNA through methylation and modifications of histones at the post-translational for the modulation of chromatin structure. Broadly speaking, these dynamic mechanisms control the capacity of DNA and chromatin to undertake transcription of the gene. These processes entail marking DNA or its related histones physically, allowing cells that are genotypically identical to manifest distinct phenotypes (Felsenfeld, 2014). In addition, several noncoding RNAs, such as micro RNAs, and long noncoding RNAs are also altered, influencing many biochemical pathways. In recent years, notable progress has been made in our comprehension of the role played by epigenetic mechanisms in plant responses to environmental stimuli, particularly in the context of stress (Mladenov et al., 2021). Hence, these heritable chemical changes in covalent DNA and histones, which control the expression of genes without modifying the underlying nucleotide sequence, constitute a group of regulators influencing plant response and resilience to stress (Li et al., 2021b; Singroha et al., 2022).

DNA methylation

Methylation of DNA is a vital process in gene expression regulation and the plant's responsiveness to abiotic stress (Kumar and Mohapatra, 2021). In plants, DNA methylation primarily involves a methyl group addition at the 5′ position of cytosine resulting in 5-methylcytosine (5mC), or at the N6 position of adenine resulting in N6-methyladenine (6mA) (Li et al., 2020). DNA methylation more frequently happens on cytosines adjacent to guanine nucleobases (CpG) and is commonly regarded as a transcriptional repression marker for genes. It interferes with the transcriptional machinery binding to regulatory sites and recruits transcriptional repressors to facilitate the establishment of a heterochromatin state. DNA methyltransferases (DNMTs) are specific enzymes that transfer methyl groups to the 5-position of the pyrimidine ring of DNA cytosine

nucleotides (Quadrana and Colot, 2016; Li et al., 2020) (Quadrana and Colot, 2016).

Besides the sequence and quantity of methylation, the genomic locations of DNA methylation, such as gene bodies, regulatory elements, transcriptional start sites, transposable elements, and repeat sequences have varying functional consequences. In plants, gene body methylation (GBM) pertains to genes where, in contrast to the absence of methylated cytosine at the start and termination of transcriptional sites, CG methylation of DNA occurs inside the coding regions (Bewick and Schmitz, 2017). DNA methylation within gene bodies may influence diverse processes, including differential promoter usage, transcription elongation, and alternative splicing (Jones, 2012). GBM-associated genes, unlike other epigenetic modifications leading to transcriptional repression, are essentially expressed and are linked to constitutive genes exhibiting moderate to high expression levels (Bewick and Schmitz, 2017; Muyle and Gaut, 2019).

Thus, in addition to contributing to phenotypic diversity (Quadrana and Colot, 2016; Noshay and Springer, 2021), changes in methylation patterns can prompt significant plastic responses to abiotic stress. Disruptions in the enzymes responsible for DNA methylation result in varied survival outcomes in the plant's stress response, emphasizing the crucial function of DNA methylation in responses to stress (Wibowo et al., 2016; Kumar et al., 2024). Consequently, methylation of DNA, going beyond a binary on-off switch, imparts a diverse and nuanced spectrum of "different meanings of gene expression," contingent on the underlying sequence and its genomic position (Niederhuth and Schmitz, 2017). Unlike highly variable gene expression, the plasticity of DNA methylation in genic regions appears to be minimally affected by environmental changes. Its associations with differential gene expression vary across tissues, species, and environmental conditions (Okitsu and Hsieh, 2007; Colak and Karadayi, 2022; Hämälä et al., 2022). For instance, in pigeonpea (*Cajanus cajan* L. Huth), genes with high gene body methylation (GBM) had the lowest expression, while those with moderate GBM showed the highest expression (Junaid et al., 2022). In *Eutrema salsugineum* (Muyle and Gaut, 2019), rice

(Rajkumar et al., 2020), and *Populus euphratica* (Su et al., 2018), the loss of GBM was linked to decreased gene expression levels. However, in maize, drought stress-induced gene body DNA methylation was negatively correlated with gene expression (Wang et al., 2021).

Plant studies have demonstrated the significant role of GBM in the regulation of AS (Hu et al., 2014). Alternative splicing (AS) is a mechanism conserved throughout evolution that enhances the complexity of transcriptome and proteome. Consequently, a single gene generates multiple mRNA isoforms, thereby increasing phenotypic diversity (Reddy et al., 2013). Genes encoding AS factors are typically down-regulated at the transcription stage but often undergo alternative splicing themselves (Reddy et al., 2013), a process influenced by changes in DNA methylation (Wang et al., 2016). Analysis of RNA-seq and BS-seq data from identical tissue (seedling) in rice isogenic lines reveal the impact of cytosine methylation loss in regions of the gene body through AS changes in plants (Hu et al., 2014). In maize, DNA methylation in the gene body positively correlates with exon splicing events under drought stress (Wang et al., 2021).

The various reports that adenine nucleotides in DNA are also methylated by adding a CH_3 group at the N1 or N6 position although at very lower rates than cytosine, introduce an additional complexity layer to the epigenetic phenomena influencing genomic DNA in the plant cell (Kumar et al., 2018; Liang et al., 2018). The first position (N1) and the sixth position (C6) of the purine ring of adenine are methylated to form N1-methyladenine and N6-methyladenine (6-mA), respectively (Sedgwick et al., 2007). The effects of 6-mA vary depending on the location in the genome, encompassing transcriptional silencing and activation, transgenerational chromatin regulation, as well as the source and severity of stress. 6mA in the gene body is related to actively expressed genes in *Arabidopsis thaliana* (Liang et al., 2018) and rice (Zhou et al., 2018). In general, DNA N6-methyladenine, unlike 5-methylcytosine in the gene promoter, does not play a definitive role in repression but leads to divergent modulation of gene expression. In rice, an increase in density of 6 mA is associated with an increase in salt and heat

resistance and a decrease in cold resistance (Zhang et al., 2018).

The regulation of gene expression during a plant's response to abiotic stress is significantly influenced by DNA methylation (Kumar and Mohapatra, 2021). The association between DNA methylation and drought stress tolerance has been established in rice cultivars, particularly in IR20, a drought-sensitive cultivar. When exposed to drought stress, IR20 exhibits hypomethylation, while tolerant cultivars display hypermethylation (Gayacharan and Joel, 2013). DNA methylation under drought stress is expected to be genotypic and growth stage-dependent, and it also appears to be organ/tissue-dependent. Drought induces 12.1% methylation alteration in Indica rice (*Oryza sativa* L.), spanning various genotypes, tissues, and growth stages. Notably, the DNA methylation in leaves was higher than that in roots during similar developmental stages, suggesting a pivotal role for roots in responding to water deficiency (Suji and Joel, 2010). Salinity stress induces opposing effects on methylation or demethylation of 5mC in the regulation of transcription in various species of plants, thereby differentially modulating the downstream expression of salinity-related genes. Salinity stress triggers 5mC demethylation at the promoter of certain transporters, leading to improved salinity tolerance through higher expression of the transporter genes in soybean (Zhang et al., 2020) and rice (Zhu et al., 2015). Conversely, salinity stress causes higher turnover rates of 5mC, potentially influencing the ion transporter gene expressions (such as HKT2;1 and HKT2;3) or miRNA and thereby enhancing tolerance to salinity (Ganie et al., 2016; Kumar et al., 2017).

The alterations in methylation/demethylation are largely durable even after recovery of the plant, suggesting the potential to establish stress memory. Numerous studies have sought to elucidate the mechanism of establishing memory for stress in crops, spanning biochemical and physiological perspectives, as well as epigenome modification, to enhance stress tolerance in crops. Evidence suggests that induced stress memory in Arabidopsis, after salt stress treatment, is accomplished by modulating the transcription level of the light-induced *P5CS1* gene involved in proline synthetase (Feng et al., 2016).

Histone modifications and histone post-transcriptional modifications

The organization and modification of chromatin have pivotal roles in shaping how plants respond to environmental shifts, such as salinity (Nguyen et al., 2019) and drought (Peirats-Llobet et al., 2016), by regulating the accessibility of genes to TFs. In certain instances, the memory of stress exposure can be transmitted to successive generations through mechanisms of epigenetic inheritance (Sun et al., 2021). The fundamental functional unit of chromatin, known as the nucleosome, comprises an octamer of histones consisting of H2A, H2B, H3, and H4 histones two copies each. This octamer is wrapped around 147 base pairs of DNA. In response to abiotic stress, such as drought and salinity stress, plants exhibit transcriptional induction in target genes. This response is attributed to the rapid and dynamic removal of the H2A.Z variant from stress-related genes. In contrast, under non-stress conditions, the existence of H2A.Z nucleosomes within gene bodies safeguards the repression of drought and salinity stress-responsive genes (Nguyen and Cheong, 2018).

Moreover, post-translational covalent alterations of histones have the potential to modify chromatin structure, thereby influencing the cis-regulatory element accessibility to TFs (Zhang et al., 2020). Out of numerous histone post-translational modifications (HPTMs) documented (Zhu et al., 2015), methylation, acetylation, phosphorylation, and ubiquitination have garnered more attention in the context of plant stress response. These marks on the histone are produced by complexes of histone "writer" including histone methyltransferases (HMT), acetyltransferases (HAT), ubiquitinases, and kinases, and excluded by "erasers" such as demethylases (HDM), deacetylases (HDA), de-ubiquitinases, and phosphatases, (Maeji and Nishimura, 2018).

Histone acetylation: Histone lysine acetylation and deacetylation serve as widespread epigenetic regulators in nearly all eukaryotes, influencing multiple cellular processes by modifying chromatin structure and function (Ma et al., 2013). The

acetylation of lysine residues (K) on histones H3 and H4, notably at K9, K14, K18, K23, K27, and K36 positions for H3, and K5, K8, K12, K16, and K20 positions for H4, diminishes the binding strength between histones and DNA. This occurs through the neutralization of the positive charge of histones, ultimately resulting in a looser structure of chromatin. Conversely, deacetylation has the opposite effect, causing chromatin compaction and restricting the access of TFs to DNA (Berger, 2007). The antagonism between HATs and HDACs (histone deacetylases), that write and erase the histone acetylation mark respectively, results in dynamic regulation of the structure of chromatin (Boycheva et al., 2014). In addition to altering the chromatin structure, histone acetylation modifies the surface of nucleosomes, influencing their configuration for binding proteins essential in gene transcription (Berger, 2007). Consequently, histone acetylation serves as a pivotal factor in regulating the extent of chromatin folding, thereby modulating the homeostatic gene program and gene expression in plants responding to stress. This regulation occurs through alterations in the quantity and/or arrangement of acetylated histones (Hu et al., 2019). The gene activations in response to drought and salinity are mainly governed by alterations in histones and nucleosome density within the promoters, with less frequent occurrences in the open reading frames (ORFs) of these genes. Under drought stress, alterations in histones, such as H3K9ac and H3K4me3, were observed within the regions of Rd20 and Rd29A in comparison to conditions optimal for growth (Kim et al., 2008). Research indicates that moisture stress triggers heightened expression of HAT genes in rice (Hou et al., 2021), Chinese cabbage (Eom and Hyun, 2018), and *Brachypodium distachyon* (Tan et al., 2019). HAT genes (*TaHAC2*, *TaHAG2*, and *TaHAG3*) exhibited up-regulation under drought stress in a wheat cultivar with higher drought tolerance, but not in other drought-sensitive cultivars (Li et al., 2021a). The acetylation of H3K9/14 contributes to salinity tolerance in Arabidopsis by modulating the expression of *MYB54*, *PGX3*, and *CTL1* (Wang et al., 2019). In maize, the expression of cell wall-associated genes, *ZmXET1* and *ZmEXPB2*, increases during salt stress due to H3K9 hyperacetylation in the promoter region (Li et al., 2014). Another

instance involves the upregulation of ABA-responsive genes and salt stress, including *OsLEA3*, *OsbZIP72*, *OsABI5*, and *OsNHX1* in rice. This upregulation correlates with the promoter regions, which exhibit increased acetylation of histone H4 under salt stress and ABA treatment (Ullah et al., 2021). The overexpression of gene 9-cis-epoxy carotenoid dioxygenase, producing the enzyme involved in the biosynthesis of ABA, was notably enhanced by HMT (Ding et al., 2011).

Histone methylation: The modification of histone is a dynamic process that involves addition, removal, recognition, and interpretation by distinct writer enzymes, eraser enzymes, and reader proteins, respectively. Methylation occurring at single, double, or triple sites on histone tails, specifically at lysine (K) or arginine (R), modifies the hydrophobicity properties of side chains of histone, thus influencing their binding with the transcriptional machinery and reader proteins. K and R methylation affects the organization of chromatin and gene expression, exhibiting variations based on the specific amino acid position of the modification (Lämke and Bäurle, 2017).

Research studies suggest that DNA methylation, whether hyper or hypo, holds a pivotal significance in modifying gene functions under adverse environments. In the context of salinity stress, methylation of gene bodies and promoters is instrumental in modulating gene expression genotypically in a manner specific to the organ. Numerous investigations into histone methylation dynamics and the response to effective mutations in HMT/HDMT activities emphasize the significance of histone methylation in development and stress responses(Ueda and Seki, 2020).

Importantly, findings indicate that under certain stressful environments, active expression of stress-related genes necessitates eliminating repressive methylation marks and the addition of active methylation marks (Sun et al., 2019). For instance, salinity stress results in the reduction of suppressive histone marks including H3K27me and 3H3K9me2, coupled with the accrual of functional methylation marks such as H3K4me3 on salt-tolerance genes (Song et al., 2012; Paul et al., 2017). In soybean, the deactivation of genes in salt-exposed plants firmly correlates with the H3K27me3 establishment under *de novo* conditions in the coding regions or

promoters not present in control plants (Sun et al., 2019).

A diminished quantity of H3K27me3 within the drought-responsive TF loci is associated with increased tolerance to stress in Arabidopsis (Ramirez‑Prado et al., 2019). In rice, H3K4me3 modification of 4837 genes was observed under moisture stress, with the status of methylation affecting the activation of a limited set of drought-responsive genes (Zong et al., 2013). Additionally, during salinity stress in Arabidopsis, the reduced amount of H4R3sme2 (histone4 arginine3 symmetric dimethylation) induces the expression of the flowering gene FLC and stress-responsive genes (Zhang et al., 2011). Under drought stress, H4R3sme2-type histone methylation in the ANAC055 region of promoter results in increased expression of *P5CS1* and elevated proline levels in wild-type Arabidopsis ((Fu et al., 2017).

Histones ubiquitylation: Ubiquitination is a form of post-translational alteration of proteins, wherein the selective degradation of proteins in the cell through the post-translational addition of ubiquitin for their breakdown by proteases (March and Farrona, 2018). This process not only influences protein stability but also has the potential to alter protein localization, transcriptional activity, or functional activity within a cell (March and Farrona, 2018; Chen et al., 2020). Multi-ubiquitination on target proteins often leads to degradation by 26S proteasome, while mono-ubiquitination regulates the function and localization of protein independently of proteolysis (Chen et al., 2020). Mono-ubiquitination of histones is a significant type of HPTM occurring at lysine 121 (K121) for histone H2A and lysine 143 (K143) for histone H2B (March and Farrona, 2018).

The mono-ubiquitination of histone lysine H2B (H2Bub1) is viewed as an active transcriptional mark participating in defense response, flowering timing, seed dormancy, and regulation of salinity and drought stress (Chen et al., 2019; Chen et al., 2020). The downregulation of MPK4 and MYB42 under salinity stress was accompanied by lower levels of H3K4me3 and H2Bub1 in hypersensitive mutants of *A. thaliana* (Sun et al., 2020). It has been indicated that ubiquitination changes of H2A.Z contribute to the regulation of the stress-responsive genes in Arabidopsis under drought stress (Sura et al., 2017).

Histone phosphorylation: Histone H3 can undergo phosphorylation at arginine and threonine. While the putative role of this epigenetic change has been extensively investigated within the framework of the cell cycle (Houben et al., 2007), its response to environmental stress in plants remains not well-understood. In addition to the rapid response to stresses, histone post-translational modifications (HPTMs), such as histone methylation, also function as an environmental memory, aiding plant adaptation to environmental changes. This memory mechanism enables previously stressed plants to better cope with the same stress in subsequent exposures (Lämke and Bäurle, 2017).

Chromatin remodeling complexes

The contribution of chromatin remodeling complexes to epigenetic regulation of the expression of genes, especially in the context of plant stress responses is vital (Eichten and Springer, 2015; Pandey et al., 2016; Tonosaki et al., 2022). These complexes are responsible for altering chromatin structure, influencing the accessibility of DNA to regulatory proteins and transcriptional apparatus (Pandey et al., 2016). Amid biotic and abiotic stress, chromatin remodeling complexes contribute to altering the expression of stress-related genes, shaping the plant's ability to withstand and thrive in challenging environments (Kim, 2019). Chromatin remodeling complexes reprogram gene expression patterns in plants responding to stress. These complexes facilitate structural alterations to either repress or activate the responsive genes, securing precise regulation of gene expression and ensuring survival ((Wang and Qiao, 2020).

In the context of plant stress responses, chromatin remodeling complexes modify gene expression through the ATP hydrolysis-derived energy, sliding, evicting, or changing nucleosome composition (He et al., 2023). Enzymes that modify histones catalyze posttranslational changes in histone proteins, either inhibiting or stimulating gene transcription. Highly condensed chromatin hinders the access of polymerases, TFs, and other nuclear proteins to DNA. Chromatin undergoes structural alterations in response to stress signals,

enabling DNA to be rendered accessible (Bhadouriya et al., 2021).

Noncoding RNAs

Noncoding RNAs, which lack an open reading frame, critical for translation, are abundantly present and contribute to various cellular processes. This category encompasses short non-coding RNAs shorter than 200 nucleotides (e.g., siRNAs and miRNAs), long non-coding RNAs (lncRNAs) comprising over 200 nucleotides, and circular RNAs. Research indicates that a substantial fraction of noncoding RNAs, including lncRNAs and miRNAs, have diverse biological functions in cellular processes including the modulation of replication of DNA, transcription, translation, and stability (Ma et al., 2022). While noncoding RNAs are not traditionally regarded as epigenetic factors, they actively participate in epigenetic modifications. The miRNAs and siRNAs, a group of single-stranded RNAs with a length ranging from 21 to 24 nucleotides, represent one of the more prevalent categories of molecules involved in gene regulation. Also known as small RNAs (sRNA) or RNA interference (RNAi), this group of RNAs is prevalent in both plant and animal genomes, influencing growth, cellular behavior, gene expression regulation, genome protection against endogenous and extrinsic threats, and conveying adaptation to biotic and abiotic stress. The varied category of small RNAs demonstrates variability in their specific functions, including adaptation to abiotic stress, like drought in plants (Ferdous et al., 2015). These small non-coding RNAs have appeared as crucial regulators of essential genomic activations, like modifications in chromatin structure, transcription, and translation (Borges and Martienssen, 2015). Double-stranded RNAs are synthesized during their processing as intermediates by RNA-dependent RNA polymerases (RDRs) to originate the small interfering RNAs (siRNAs) (Song et al., 2019). The activities of small RNAs, like miRNA, induced by abiotic stress, such as drought, cold, salinity, and oxidative stress are documented (Sunkar and Zhu, 2004), underscoring the function of intrinsic endogenic pathways of small RNAs in combating these stresses. Transgenic approaches contribute to improvements at various degrees in modern crop-improvement schemes, ensuring plasticity and increased yield under environmental stress conditions. RNAi has been instrumental in addressing abiotic stresses in various crops. For instance, RACK1 genetically modified RNAi rice, (Younis et al., 2014), exhibited an improved tolerance to drought compared to wild types (non-transgenic lines).

Table 1 provides a summary of studies investigating epigenetic modifications in crop plants in response to drought and salinity stress, employing the aforementioned methodologies. Furthermore, Figure 1 depicts the significant contribution of plant epigenetic responses in conferring tolerance to drought and salinity stresses, overcoming environmental challenges, and evolving.

Epitranscriptomics

Post-transcriptional modification is an additional epigenetic alteration, extending beyond those induced by histone modifications and DNA methylation. These modifications occur in diverse RNAs including mRNA, tRNA, rRNA, and lncRNA, introducing a new layer of regulatory mechanisms in plants (Rajkumar et al., 2020). Among these, N5-methylcytidine (m5C) and N6-methyladenosine (m6A) are prevalent, and ample internal modifications are identified in mRNAs. Numerous investigations have observed that covalent RNA modifications contribute to regulating the quantity and quality of eukaryotic transcripts. These modifications influence the secondary structure, stability, translatability, degradation, and functionality of RNA molecules (Yang et al., 2019; Kumar and Mohapatra, 2021).

Studies have demonstrated that these epitranscriptomic signals have broad effects on the plant's response to salinity stress through the regulation of RNA fate (Hu et al., 2021; Zheng et al., 2021; Wang et al., 2022). When the plant was exposed to drought stress, there was an elevation in m6A levels within the 5'UTR region, facilitating the translation of transcripts that exhibit resistance (Shoaib et al., 2022). Consequently, stress induces a reorganization of m6A across the transcriptome, resulting in a heightened presence of mRNAs with 5' UTR m6A.

Table 1. The epigenetic modifications in response to drought and salinity stress in crop plants

| Species	Stress condition	Epigenetic modification			Reference
		Histone modification	DNA modification	RNA modification	
Zea mays	Drought	H3K4me3, H3K9ac			(Forestan et al., 2020)
Gossypium hirsutum	Drought	H2Bub, H3K4me3			(Chen et al., 2019)
Oryza sativa	Drought			Non-coding RNA (mir162b)	(Tian et al., 2015)
O. sativa	Drought			Non-coding RNA (mir164)	(Feng et al., 2016)
O. sativa	Drought	H2Bub1			(Ma et al., 2013)
Glycine max	Drought			Non-coding RNA (miR169g)	(Ni et al., 2013)
Nicotiana tabacum	Drought	HDAC			(Ma et al., 2017)
Hordeum vulgare	Drought	H3K9ac, H3K14ac, H3K27ac			(Papaefthimiou et al., 2010)
Z. mays	Drought		Hypermethylation		(Wang et al., 2021)
O. sativa	Drought		Promoter Hypomethylation (CLT1 and PSBP gene)		(Ding et al., 2011)
O. sativa	Drought		Hypermethylation		(Kou et al., 2022)
Triticum aestivum	Drought		Hypermethylation		(Duan et al., 2020)
T. aestivum	Osmotic (PEG)		Hypermethylation		(Li et al., 2020)
Medicago sativa	Salinity	H3K9Ac			(Deng et al., 2018)
G. max	Salinity	HDAC		miR482bd-5	(Cadavid et al., 2020)
G. hirsutum	Salinity			LncRNA973	(Zhang et al., 2019)
G. hirsutum	Salinity			lnc_388, lnc_973, lnc_253	(Deng et al., 2018)
Solanum lycopersicum	Salinity			miR156, miR398	(Çakır et al., 2021)
Ipomoea batatas	Salinity			nta-miR156a_R + 3, farmiR159_L + 2_1ss22T, mes-MIR319ep5_2ss12GC19 GA	(Yang et al., 2020)
O. sativa	Salinity			miR171b, miR167f	(Parmar et al., 2020)
T. aestivum	Salinity			TaemiR408	(Bai et al., 2018)
Z. mays	Salinity			miR164s, mir-36	(Fu et al., 2017)
Z. mays	Salinity		Hypomethylation		(Sun et al., 2018; Shams et al., 2020)
Capsicum annuum	Salinity		Hypermethylation		(Shams et al., 2020)
Beta vulgaris	Salinity		Hypomethylation		(Skorupa et al., 2021)
T. aestivum	Salinity		Coding region hypermethylation (TaHKT2;1 & TaHKT2;3)		(Kumar et al., 2017)
T. aestivum	Salinity		hypomethylation		(Hosseinpour et al., 2022)
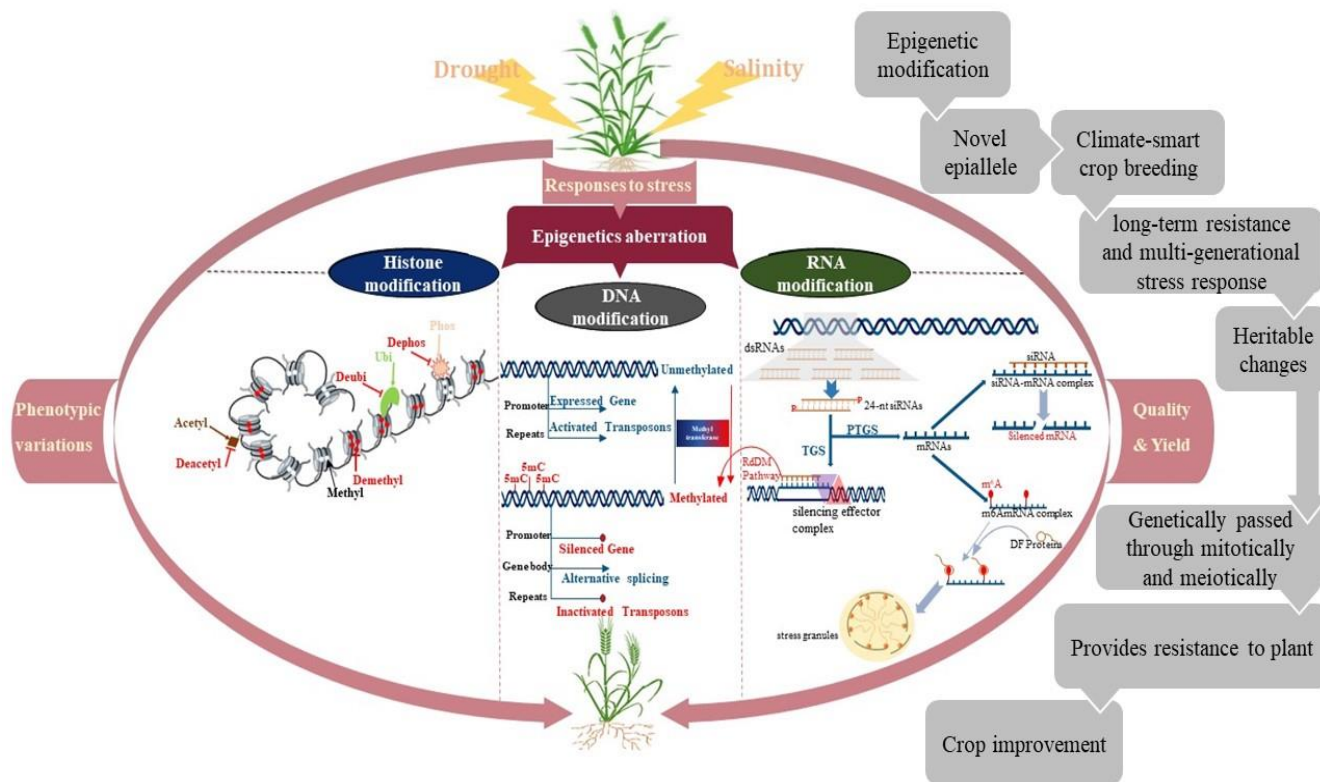
Figure 1. The vital role of plant epigenetic responses for tolerance of drought and salinity stresses, overcoming environmental challenges, and evolution over time. These changes modifications include histone modifications such as methylation (Methyl), acetylation (Acetyl), phosphorylation (Phos), and ubiquitination (Ubi), DNA modifications, and RNA modifications of the two pathways of transcriptional gene silencing (TGS) and post-transcriptional gene silencing (PTGS).

These findings suggest that the redistribution of m6A on mRNAs remains consistent across organisms, both under stress and normal conditions.

The long-distance transport of RNA information molecules, including siRNAs, miRNAs, tRNAs, rRNAs, and mRNAs, which exhibit systemic signaling functions in vascular tissues, contributes to facilitating the adaptation of plants to abiotic stress (Thieme et al., 2015; Zhang et al., 2018)

Conclusion

Losses in crop production due to drought and salinity stresses pose a significant challenge for staple food crops, and the issue is expected to be exacerbated by the global warming scenario in the future. The use of epigenetic technologies bears great potential for developing novel crop cultivars, particularly in enhancing stress tolerance through the generation of new epialleles. Epigenetic

alterations can result in modified gene transcription, facilitating better adaptation to abiotic stresses. Additionally, acting as "plant stress memory," these modifications enable plants to respond effectively to challenges in their environment, providing resilience for future generations to withstand environmental stresses. The intricate cross-talk between various epigenetic regulation levels contributes to shaping stress responses, fostering resilience, and enhancing adaptability in plants.

Substantial advancement has been achieved in comprehending the function of epigenetic modulation in plant responses to various stressful environmental conditions. Transitioning from epigenetics to potential breeding applications and shifting from an "experimental" to a "conventional" methodology in plant improvement requires overcoming key challenges. This involves enhancing technology, refining data workflow

systems, advancing information about plant species across all epigenetic levels, and better integrating data of epigenomic studies with other "omics" datasets.

Supplementary Materials
No supplementary material is available for this article.

Author contributions
Conceptualization; M.H. and A.A., writing original draft, investigation, reviewing and editing; A.A.,

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سازگاری اپی ژنتیکی به خشکی و شوری در گیاهان زراعی

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چکیده: تأثیر شدید تنش خشکی و شوری بر عملکرد گیاهان، تهدیدی مهم برای امنیت غذایی در سراسر جهان است. گیاهان دارای توانایی درک محرک‌های محیطی خود هستند و مکانیسم‌های دفاعی مقابله با تنش غیرزنده را از طریق شبکه‌های تنظیمی متنوع تنظیم می‌کنند. پیچیدگی‌های تحمل به خشکی و شوری را می‌توان به مشارکت دو عامل و مکانیسم ژنتیک و اپی‌ژنتیک تفکیک کرد. مکانیسم‌های اپی‌ژنتیکی در سازگاری گیاهان به شدیدترین تنش‌های خشکی و شوری نقش دارند. گیاهان تاحدی با انجام تغییرات پایدار در بیان ژن از طریق فرآیند «علامت‌گذاری» فیزیکی DNA یا پروتئین‌های مرتبط با آن که معمولاً اپی‌ژنتیک نامیده می‌شود به تنش پاسخ می‌دهند. گیاهان از مکانیسم‌های اپی‌ژنتیکی مختلف که برای سازگاری و انعطاف‌پذیری فنوتیپی حیاتی است برای تغییر بیان ژن استفاده می‌کنند. این مکانیسم‌ها شامل متیلاسیون DNA، تغییرات هیستون، بازسازی کروماتین، اپی‌ترانسکریپتومیکس و خاموش کردن ژن به واسطه RNAهای کوچک است. قابل ذکر است که تغییرات اپی‌ژنتیکی می‌توانند وراثتی یا غیر وراثتی و ناپایدار باشند. دانش پیشرفته اپی‌ژنتیک مکمل ژنتیک است و به توسعه استراتژی‌ها برای ادغام آن‌ها در برنامه‌های اصلاح گیاهان در جهت سازگاری با تنش غیر زنده کمک می‌کند. این بررسی جدیدترین یافته‌های قابل‌توجه در مورد پاسخ‌های اپی‌ژنتیکی گیاهان زراعی به سیگنال‌های تنش غیرزنده به‌ویژه تحمل به خشکی و شوری را ارائه می‌کند.

کلمات کلیدی: تحمل به خشکی، نواحی CpG، اپی ژنومیک، تنش اسمزی، تحمل به شوری، تنش آبی.