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Review Paper

The role of epigenetic modifications in plant responses to stress

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ABSTRACT:
Epigenetics is the study of hereditary changes in gene expression under the premise that the nucleotide sequence is not changed. Such hereditary changes mainly involve DNA methylation, histone modification, and chromatin remodeling. These covalent modifications play indispensable roles in regulating gene expression; DNA replication, recombination, and repair; and cell differentiation. Epigenetic modifications can be partially inherited by daughter cells during mitosis and meiosis and influenced by external factors, such as environmental stresses and supply deficits. In this review, we summarize the current knowledge regarding epigenetic factors, such as DNA methylation, histone acetylation, and regulation by non-coding RNAs, in the development and stress response of plants.

Keywords:
DNA methylation, environmental stress, epigenetics, histone acetylation, non-coding RNAs

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INTRODUCTION

Although epigenetics was originally proposed by Waddington in 1939, almost no one recognized this concept until the twenty-first century since what carried the genetic information was unknown at the time (Villota-Salazar *et al*. 2016). In the 1980s, epistemology was widely recognized after the publication of "apparent mutations" (Haig 2004). The concept of epigenetics has evolved in the study of many genetic phenomena that are incompatible with classical genetic laws (Holliday 2006). Classical genetics dictates that genotypes determine phenotypes and any phenotypic changes in organisms are caused by genetic mutations, which can be stably passed on to the next generation. Thereby, future generations are also expected to exhibit the same phenotype. In contrast, epigenetics refers to the regulation of gene expression to influence the phenotype without changing any genetic information, so as to better cope with environmental changes (Dowen *et al*. 2012).

Plant development is influenced by both hormones and environmental factors. It is determined by the interactions between genotypes and environmental factors. Such developmental processes include cell division, cell expansion, as well as the differentiation and maturation of cells and tissues (Ljung 2013). Gene expression varies at different stages of plant development, and only a specific set of genes is expressed at each stage while others are suppressed (Tian *et al*. 2005). Cell differentiation is accompanied by differential gene expression. Plant development, like any other organismal development, requires controlled organogenesis. Such control is mediated by the spatiotemporal expression of specific genes, which is epigenetically mediated at the transcriptional and post-transcriptional levels (Finnegan *et al*. 1996). Whereas the formation of certain tissues or organs in plants can be affected by mechanisms of genetic perturbation resulting from mutations, environmental stimuli can also influence these developmental processes.

Plants are subject to unpredictable environmental conditions, such as temperature, light intensity, nutrients, moisture, and various biological factors. In order to survive, plants have to adapt to environmental changes by reacting quickly. Therefore, plant development has high plasticity. Plants have been found to initiate a range of strategies, such as modifications of key regulatory pro-

teins, and epigenetic changes, to cope with environmental stresses (Pastor *et al*. 2013). Epigenetic information can modulate plant development and various physiological responses by controlling spatiotemporal gene expressions. In plants, mutations in several key epigenetic regulatory genes can cause pleiotropic phenotypes, including delayed or accelerated floral transformation, morphological changes, and abnormal abiotic or biotic stress responses (Mirouze & Paszkowski 2011; Huff *et al*. 2012), indicating that epigenetic regulators play an important role in maintaining genomic stability and regulating plant growth and development. Under stress, epigenetic mechanisms initiate dynamic changes in chromatin structure to respond to external stimuli (Talbert & Henikoff 2014). Although the chromatin structure returns to its original state after a few seconds, some epigenetic modifications in chromatin remodeling may persist (Gapp *et al*. 2014). In addition, some genetic markers can be inherited across generations to accommodate long-term environmental stress (Heard & Martienssen 2014). In general, epigenetic mechanisms regulate spatiotemporal gene expression so as to enable plants to adapt to external stress, it is thus important to study how epigenetic modifications affect chromatin structure and gene expression. In this review, we discuss the role of epigenetic responses to environmental stresses.

DNA METHYLATION

DNA methylation refers to the transfer of a methyl group from S-adenosylmethionine to carbon 5 of a cytosine on DNA by DNA methyltransferase (DNMT) families, thereby forming 5-methylcytosine (m5C) (Sahu *et al*. 2013). In plants, m5C DNA glycosylases are critical enzymes that directly excise m5C and initiate its replacement with an unmethylated cytosine during the active DNA demethylation pathway and are thus often referred to as DNA demethylases (Parrilla-Doblas *et al*. 2019) (Fig. 1). In 1925, m5C was first discovered in the hydrolysate of the tuberculin of *Mycobacterium tuberculosis* (Johnson & Coghill 1925). Subsequently, higher levels of m5C were found in plants (Vaniushin & Belozerskii 1959). Cytosine methylation modifications on DNA mainly consist of asymmetric (mCpHpH) and symmetric (mCpG and mCpHpG) methylations. For example, in *Arabidopsis thaliana*, the methylation levels of CG, CHG, and CHH are 24%, 6.7%, and 1.7%, respectively, and genome-wide DNA methylation sites and levels differ by tissue type and developmental stage (Dhar *et al*. 2014). In plants, DNMTs have evolved to exert *de novo* methylation at unmethylated sites or maintain methylation upon DNA replication (Feng & Michaels 2015). *De novo* DNA methylation is established mainly by the RNA-directed DNA methylation (RdDM) pathway (Fig. 1), which relies on complex transcriptional machineries comprising two plant-specific, RNA polymerase II (Pol II)–related RNA polymerases known as Pol IV and Pol V (Matzke *et al*. 2015). In addition, sequence-specific pairing between small interfering RNAs (siRNAs) and scaffold RNAs, as well as protein interactions between Argonaute 4 (AGO4), DNA-directed RNA polymerase V subunit 1 containing AGO hook (motif containing Gly–Trp or Try–Gly repeats), and RDM3 (RNA-directed DNA methylation 3), are also required for RdDM (Zhang *et al*. 2018). Moreover, the maintenance of DNA methylation relies on the cytosine sequence context. The maintenance of methylation depends on methyltransferase 1 (MET1) and variant in methylation 1-3 (VIM 1-3) in the CG context, whereas it depends both on the RdDM pathway and chromomethylase 2 (CMT2) activity in the CHH context (Gallusci *et al*. 2016). The CHG context is catalyzed by the plant specific CMT3, via a self-reinforcing loop between CMT3 and the heterochromatic dimethylation of lysine 9 of the histone H3 subunit (H3K9me2) (Lindroth *et al*. 2001; Zhang *et al*. 2018). In the *Arabidopsis* ecotype Col-0 genome, approximately 20% of the genes show a certain degree of cytosine methylation, but > 90% of methylation occurs in genomic repeat and transposon regions, and this epigenetic modification is also the key to regulating gene expression (Genger *et al*. 2003).

DNA methylation is a major modification mechanism for gene silencing (Cortellino *et al*. 2011). Dynamic regulation of gene expression by DNA methylation levels and location is a very effective means for the establishment of cell function and the coordination of plant development (Dowen *et al*. 2012). It has been found that 5mC methylation of 5S rDNA is significantly increased during early seedling development in *Arabidopsis*, and this modification is often accompanied by changes in heterochromatin structure (Mathieu *et al*. 2003; Teyssier *et al*. 2008). In many plants (including *Arabidopsis*, tomato, and tobacco), high levels of CG methylation occur in CG-rich regions. Similarly, the hypomethylation of plant genomes can also have an effect on gene expression. Flowering locus C (*FLC*) is an important gene which controls the flowering time in *Arabidopsis*, and the expression of *FLC* inhibits the flowering of plants. The level of *FLC* expression is subject to epigenetic control, and this control is affected by environmental factors. In the vernalization-sensitive *Arabidopsis* ecotype, a decrease in DNA methylation downregulates the expression of *FLC*, thereby promoting flowering (Michaels & Amasino 2001), suggesting that cold-induced epigenetic modifications, including histone methylation and DNA methylation, require epigenetic silencing of *FLC* (Yang *et al*. 2014).

Changes in plant DNA methylation often occur in certain specific situations, such as environmental changes. Cold stress induces rapid and large-scale DNA methylation changes in *Chorispora bungeana* (Table 1), a perennial alpine subnival plant, and this observation suggests that rapid modification in cytosine methylation can potentially serve as a rapid and flexible regulatory mechanism for *C. bungeana* to adapt to intricate cold stress in nature

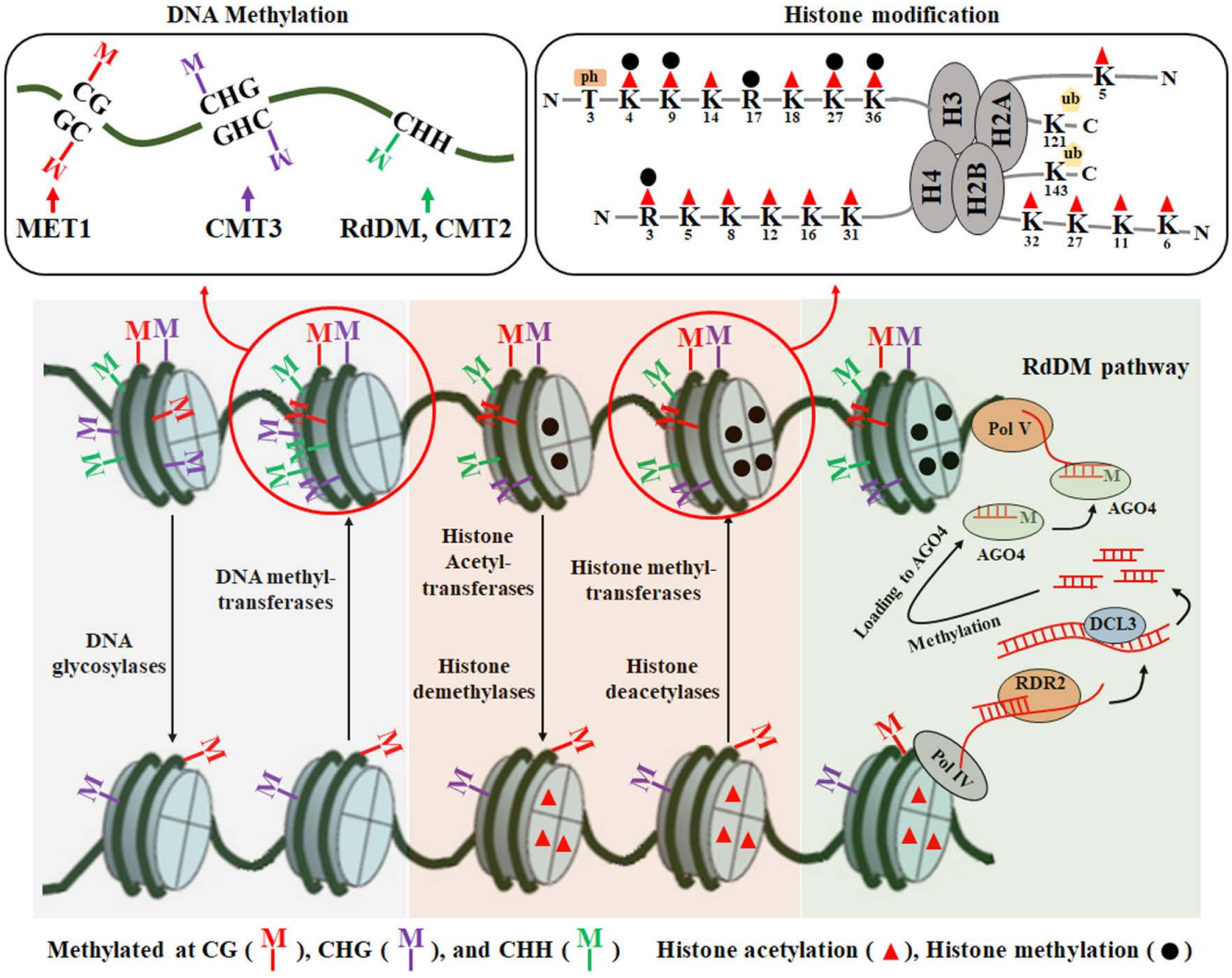

Fig. 1. Plant Epigenetic mechanisms, DNA methylation, histone modification, and RNA-directed DNA methylation (RdDM) in plants. Maintenance of DNA methylation at CG, CHG, or CHH site requires the activity of methyltransferase 1 (MET1), variant in methylation 1-3 (VIM 1-3), chromomethylase 3 (CMT3), RdDM, or CMT2. The histone modifications include acetylation (red triangle), methylation (black circle), phosphorylation (ph), and ubiquitination (ub). Two plant-specific RNA polymerases (Pol IV and Pol V) are essential to RdDM, which also requires activities from RNA-dependent RNA polymerase (RDR2), Dicer-Like 3 (DCL3, an enzyme that cleaves double-stranded RNA), the Argonaute family RNA-binding protein (AGO4). This model has been modified from Fedoroff (2012), Grimanelli & Ingouff (2020), and Ueda & Seki (2020).

(Song *et al.* 2015). Rapid alteration of DNA methylation may be a powerful strategy for plants to adapt to environmental changes, and understating DNA methylation dynamics may facilitate increasing crop tolerance against global climate change. DNA methylation also plays a role in plant immunity against pathogenic bacteria. In *Arabidopsis*, enhanced resistance against *Pseudomonas syringae* pv. tomato DC3000 is observed when the genes involved in DNA methylation and demethylation are mutated (Yu *et al.* 2013; Le *et al.* 2014). In addition, the resistance of rice to *Xanthomonas oryzae* is enhanced by the treatment of DNA-demethylating agent 5-azadeoxycytidine (Table 1; Akimoto *et al.* 2007). High-resolution DNA methylation profiling provides a genome-wide insight into biotic stress-responsive genes. The expression of these genes is modulated by DNA methylation and demethylation (Dowen *et al.* 2012), suggesting that pathogen-induced variation of DNA methylation can dramatically change to alter gene expression. In conclusion, DNA methylation is widely present in the plant genome, with plant-specific

Table 1. Epigenetic regulation of plant responses to different stress factors.

Epigenetic factors	Treatments	Epigenetic responses	References
DNA methylation	Vernalization	Low DNA methylation induced by vernalization reduced the expression of Flowering locus C (*FLC*), and promoted flowering	Michaels & Amasino 2001
	Cold	Large-scale DNA methylation changed in *Chorispora bungeana*	Song *et al.* 2015
		Increased DNA methylation in tomato	Zhang *et al.* 2016
	DNA-demethylating agent	Enhancing rice resistance to *Xanthomonas oryzae*	Akimoto *et al.* 2007
	Pseudomonas syringae	Reduced DNA methylation in *Arabidopsis*	Yu *et al.* 2013
Non-coding RNAs	Knock out of miR169a	Enhanced drought tolerance in *Arabidopsis*	Zhao *et al.* 2016b
	Cold	COOLAIR enhanced the cold-induced down-regulation of *FLC* expression	Csorba *et al.* 2014
		COLDAIR recruited PRC2 to promote H3K27me3 accumulation at *FLC*	Tian *et al.* 2019
	Drought	Up-regulation of miR408 and miR156	Kantar *et al.* 2010 Mutum *et al.* 2013 Arshad *et al.* 2018
Histone acetylation	Heat	Enhancing acetylation levels of H3K9 and H3K14 in the promoter regions of Heat Shock Transcription Factor A3 (HSFA3) and Ultraviolet Hypersensitive 6 (UVH6)	Hu *et al.* 2015
	Salt	Up-regulation of cell-wall–related genes by elevated H3K9 acetylation in promoter and coding regions	Li *et al.* 2014
	Drought	HDA6 (histone deacetylase) reduced the expression of pyruvate decarboxylase *PDC1* and acetaldehyade dehydrogenase *ALDH2B7*	Kim *et al.* 2017
	Ky-2 (Histone deacetylase inhibitor)	Enhancing salt tolerance via increasing expression of *AtSOS1* (encoding a Na^+/H^+ antiporter) and *AtSOS3* (EF-hand Ca^{2+} -binding protein)	Sako *et al.* 2016
	SAHA (Histone deacetylase inhibitor)	Inducement of histones H3 and H4 hyperacetylation and the increasing expression of genes involved in phytohormone biosynthesis pathways	Patanun *et al.* 2017

developmental stages showing different methylation patterns, and plays a very important role in all stages of plant development. Additionally, plants also have stable methylation patterns that are involved in maintaining their genomic stability.

NON-CODING RNAS AS EPIGENETIC REGULATORS

Non-coding RNAs (ncRNAs), which do not translate into peptides, perform their biological functions at the RNA level (Axtell 2013). They are generally divided into small (< 200 nucleotides) or long (> 200 nucleotides) ncRNAs. The first group includes small interfering RNAs (siRNAs), microRNAs (miRNAs), PIWI-interacting RNAs (piRNAs, animals only), and transfer RNA-derived small RNAs (tsRNAs) (Wang *et al*. 2019); whereas the latter includes sense, antisense, intergenic, intronic, and bidirectional long non-coding RNAs (lncRNAs) (Ma *et al*. 2013).

In plants, miRNAs predominantly act as post-transcriptional regulators of the mRNAs they target, whereas siRNAs regulate gene silencing at either the transcriptional (TGS) or post-transcriptional (PTGS) level (Wang *et al*. 2019). miRNA precursors encoded in the nuclear genome are cleaved by a complex consisting of Dicer-like 1 (DCL1), the double-stranded RNA-binding protein Hyponastic Leaves 1 (HYL1), and the zinc-finger protein Serrate (SE), with the assistance of the nuclear cap-binding complex (Miskiewicz *et al*. 2017), and are further processed by Dicer 1 to produce a miRNA/miRNA* duplex. RNA silencing complexes containing miRNAs and Argonaute proteins interact with target mRNAs by partial sequences matching to lead the mRNA degradation or repression of the translation process (Miskiewicz *et al*. 2017). The genome of the model plant *Arabidopsis thaliana* has been estimated to give rise to a total of 427 miRNAs (Li & Zhang 2016). However, only a small number of them have been experimentally characterized, and it has been suggested that stress-responsive miRNAs respond to environmental conditions in a stress-, tissue-, and genotype-dependent manner (Zhang 2015). During embryogenesis, miR160 negatively represses the expression of auxin response factors (ARF) 10 and 16 (Liu *et al*. 2010), which are required for the maintenance of ABSCISIC ACID INSENSITIVE 3 (ABI3) expression, a key regulator in the abscisic acid-mediated seed dormancy (Liu *et al*. 2013). In addition, miR156/miR157 are responsible for the temporal expression pattern of most SQUAMOSA PROMOTER BINDING PROTEIN-LIKE (SPL) transcription factors including *SPL9* and *SPL13*, which are essential for the expression of adult vegetative traits (He *et al*. 2018). miR165/166 target class III HOMEODOMAIN-LEUCINE ZIPPER (HD-ZIP III) family transcription factors, which are mainly involved in plant development, such as shoot apical meristem (SAM) maintenance, polarity of lateral organs, xylem patterning, and embryo formation (Song *et al*. 2019). Interestingly, miR165/166 interact with their complementary sequences in the transcripts of HD-ZIP III transcription factors, PHABULOSA and PHAVOLUTA, to effect the methylation of downstream coding sequences on the template chromosome (Bao *et al*. 2004). Furthermore, some 24-nt-long miRNAs direct cytosine DNA methylation at their own loci in cis and at their target genes in trans in rice (Wu *et al*. 2010). In *Physcomitrella patens*, miRNAs induced DNA methylation under ABA treatment (Khraiwesh *et al*. 2010), indicating that miRNA-directed DNA methylation triggered the epigenetic gene silencing. To survive under stress, plants alter miRNA expression resulting in modulating target gene expression to restore cellular homeostasis (Ahmed *et al*. 2020; Asefpour Vakilian 2020). Therefore, stress-response–related miRNAs have become potential targets for improving stress tolerance by using genome-editing technologies. For example, miR169a acts as a negative regulator of ABA-dependent pathways (Li *et al*. 2008), and knocking out this miRNA by using a dual-sgRNA CRISPR/Cas9 system induces drought tolerance in *A. thaliana* (Table 1; Zhao *et al*. 2016b). In addition, negative factors in stress tolerance, such as rice miR393 (negative regulator of two rice auxin receptor genes, OsTIR1, and OsAFB2) and rice miR812q (negative regulator of Calcineurin B-Like protein interacting protein kinase 10 expression), can contribute to enhancing stress tolerance (Xia *et al*. 2012; Shriram *et al*. 2016). Furthermore, the prediction and identification of miRNA targets should be a critical initial step in understanding the function of miRNAs in plants.

During viral infections in plants, double-stranded RNAs produced by viral- or cellular-encoded RNA-dependent RNA polymerases are processed into 21-24 nt siRNAs by DICER-LIKE endonucleases (Vaucheret 2006). siRNAs can systemically relocate to neighboring cells via plasmodesmata and phloem and are used to control various biological processes (Hyun *et al*. 2011) including plant epigenetic modification through the RdDM pathway (Xie & Yu 2015) (Fig. 1). As the components of a conserved *de novo* DNA methylation mechanism, siRNAs are loaded onto AGO4, 6, or 9 complexes to target Pol V-dependent nascent scaffold transcripts and recruit the DNA methyl transferase DOMAINS REARRANGED METHYLTRANSFERASE 2 to catalyze de novo cytosine methylation (Zhao *et al*. 2016a). These small RNAs can be divided into trans-acting siRNAs (ta-siRNAs), heterochromatin siRNAs (hc-siRNAs), and natural antisense siRNAs (nat-siRNAs) based on their biogenesis and functions (Guleria *et al*. 2011). Among siRNAs, 24nt hc-siRNAs derived from intergenic and/or repetitive genomic regions are associated with RdDM and TGS (Axtell 2013). In addition to the canonical RdDM-mediated hc-siRNAs, several experimental lines of evidence have identified non-canonical RdDM pathways that involve ta-siRNA- and 21-22 nt siRNA (Xie & Yu 2015). In *Arabidopsis*, some RDR6 (a homolog of RDR2)-dependent siRNAs (21-22 nt) initiate

de novo DNA methylation at transposable sites (Nuthikattu *et al*. 2013). During the defense response in *Arabidopsis* to the biotrophic pathogen *Pseudomonas syringae* pv. tomato DC3000, salicylic acid-induced differentially methylated regions at transposons are associated with the upregulation of 21-nt siRNAs (Dowen *et al*. 2012).

In plants, lncRNAs are involved in diverse biological processes, including tissue development, sexual reproduction, and responses to external stimuli, such as drought, salinity, heat stress, and infections (Eom *et al*. 2018). Recently, it has been shown that lncRNAs transcribed by plant-specific Pol V are involved in the function of RdDM (Chekanova 2015). In addition, plant lncRNAs interact with chromatin-modifying complexes by lncRNA-mediated chromatin modifications. For example, in cold-stressed *Arabidopsis* plants, the expression of *FLC* is controlled by COLD ASSISTED INTRONIC NONCODING RNA (COLDAIR) and COOLAIR. COLDAIR is known as an intronic lncRNA and is necessary for the recruitment of PRC2 to promote H3K27me3 accumulation at *FLC* (Table 1; Tian *et al*. 2019), and COOLAIR, antisense lncRNA, decreases *FLC* transcription via the synchronized replacement of H3K36me3 with H3K27me3 at intragenic *FLC* nucleation sites (Table 1; Csorba *et al*. 2014). Taken together, compelling evidence supports the involvement of ncRNAs in the epigenetic regulation of particular genes. However, our understanding of epigenetic regulation by plant ncRNAs is still in its infancy, with many outstanding questions awaiting further investigation. Thus, unraveling the complexity, biogenesis, and action of plant ncRNAs in epigenetics remains an outstanding challenge in plant biology.

HISTONE ACETYLATION IN RESPONSE TO ENVIRONMENTAL STRESSES

In eukaryotes, histone modifications, including acetylation, methylation, phosphorylation, ubiquitination, and glycosylation are covalent post-translational modifications of histone proteins and play essential roles in chromatin-associated processes, such as gene regulation and epigenetic inheritance (Eom & Hyun 2018). Among these modifications, histone acetylation by histone acetyltransferases (HATs) and deacetylation by histone deacetylases (HDACs) are the major epigenetic modifications, which involve either the conjugation or removal of acetyl groups to/from the lysine residues of histones, thereby up- or down-regulating transcription levels, respectively (Boycheva *et al*. 2014) (Fig. 1). In *Arabidopsis*, 12 HATs are divided into four families, namely the general control non-repressible 5-related N-terminal acetyltransferase (GNAT) family; the MOZ, Ybf2/Sas3, Sas2, and Tip60 (MYST) family; the p300/CREB (cAMP-responsive element-binding protein)-binding protein (CBP) family; and the TATA-binding protein-associated factor (TAF) $_{II}$250 family (Ueda & Seki 2020). Recent studies have indicated that histone acetylation plays a pivotal role in environmental stress responses. The *Arabidopsis* histone acetyltransferase General control non-repressed protein 5 (GCN5) appears to positively regulate thermotolerance through enriching the acetylation levels of H3K9 and H3K14 in the promoter regions of Heat Shock Transcription Factor A3 (*HSFA3*) and Ultraviolet Hypersensitive 6 (*UVH6*) genes (Table 1; Hu *et al*. 2015). Under salt stress, acetylation of H3K9 and H3K14 is mediated by GCN5 in association with transcriptional activation of chitinase-like gene 1 (*CTL1*), polygalacturonase involved in expansion-3 (*PGX3*), and MYB domain protein-54 (*MYB54*), which are the downstream components of the GCN5-dependent salt tolerance pathway in *Arabidopsis* (Zheng *et al*. 2019). In addition, in maize, cell-wall–related genes, such as the β-expansin *ZmEXPB2* and xyloglucan endotransglucosylase *ZmXET1*, are upregulated by elevated H3K9 acetylation in promoter and coding regions, which is thought to be necessary for high-salinity responses (Table 1; Li *et al*. 2014). In *Populus trichocarpa*, GCN5-mediated histone acetylation to enhance H3K9 acetylation allows the enhanced recruitment of RNA polymerase II specifically at *PtrNAC* gene promoters for the development of drought tolerance (Li *et al*. 2019). The *Arabidopsis* CBP/p300-like protein HAC1 has been shown to exhibit HAT activity (Bordoli *et al*. 2001), and tomato HAC1 interacts with the heat stress transcription factor CLASS B HEAT SHOCK FACTOR B1 (HsfB1) (Bharti *et al*. 2004). In *hac1* mutant, the acetylation levels in the promoter regions of *FLC* is increased after UV-B exposure, and this epigenetic modification results in late-flowering (Fina *et al*. 2017). In addition, environmental stress-response alteration in the expression patterns of *HATs* and histone 3 acetylation patterns has been detected in rice and Chinese cabbage (Fang *et al*. 2014; Eom & Hyun 2018). In the case of histone deacetylases, three families of HDACs have been found in plants; the reduced potassium dependency 3 (RPD3/HDA1) superfamily, the HD2-like family, and the silent information regulator 2 (SIR2) family. (Luo *et al*. 2017). When plants are exposed to environmental stresses, HDAC genes exhibit diverse responses. For example, HDA6 (the RPD3-like family), HD2C (the HD2-like family), and HD2D (the HD2-like family) positively regulate the salt response, unlike HDA9 (the RPD3-like family) and HDA19 (the RPD3-like family) (Ueda & Seki 2020). Under drought stress, HDA6 downregulates the expression of pyruvate decarboxylase *PDC1* and acetaldehyade dehydrogenase *ALDH2B7*, which are involved in the acetate biosynthesis pathway (Table 1; Kim *et al*. 2017). In addition, chemical inhibition of histone deacetylation provides an effective approach to investigate the roles of histone acetylation in controlling many biological processes. For example, Ky-2 [Cyclo (-L-2-amino-8-hydroxamido-suberoyl-aminoisobutylyl-L-phenylalanyl-D-prolyl-)] increases global histone acetylation and the transcription of many genes, including *AtSOS1*

(encoding a Na^+/H^+ antiporter) and *AtSOS3* (an EF-hand Ca^{2+} -binding protein) by inhibiting HDAC, thereby resulting in enhanced salt tolerance in *Arabidopsis* (Table 1; Sako *et al*. 2016). In salt-treated cassava, SAHA (suberoylanilide hydroxamic acid, HDAC inhibitor) treatment induces hyperacetylation of histones H3 and H4 and the transcription of genes involved in phytohormone biosynthesis pathways (Table 1; Patanun *et al*. 2017). Collectively, genetic and chemical approaches indicate that histone acetylation plays a fundamental role in plant responses to various environmental stresses.

CONCLUSION

The field of epigenetics has become the frontier of biological studies where great progress has been made. DNA methylation, histone modification, and the non-coding-RNA-mediated regulation of gene expression are important epigenetic modifications in plants involved in the regulation of plant growth and development. Therefore, the relationship between epigenetics and metabolism is particularly important in deepening our understanding of epigenetic phenomena in plants, whereby epigenetics can be rationally linked to the principles of life, production, and agriculture for the benefit of society. Although our knowledge of epigenetic regulation in plants is very limited, the identification and functional characterization of plant epigenetic modulators should be an important endeavor that continues to disclose the hidden wonders of plant life.

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REZIME

Botanica SERBICA

Uloga epigenetičkih modifikacija biljaka u odgovoru na stres

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Epigenetika je proučavanje naslednih promena u ekspresiji gena pod pretpostavkom da se nukleotidna sekvenca ne menja. Takve nasledne promene uglavnom uključuju metilaciju DNK, modifikaciju histona i preoblikovanje hromatina. Ove kovalentne modifikacije igraju neophodnu ulogu u regulisanju ekspresije gena; replikacija, rekombinacija i popravka DNK, kao i diferencijacija ćelija. Epigenetske modifikacije mogu se delimično preneti ćerkama ćelijama tokom mitoze i mejoze, i pod uticajem spoljnih faktora, poput stresa izazvanih sredinskim uslovima i deficita snabdevanja. U ovom preglednom radu sumiramo trenutno znanje o epigenetskim faktorima, kao što su metilacija DNK, acetilacija histona i regulacija nekodirajućim RNK, u razvoju i odgovoru biljaka na stres.

Ključne reči: DNK metilacija, sredinski stres, epigenetika, acetilacija histona, nekodirajuća RNK