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Epigenetic regulation in plant salt stress response

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Abstract. As sessile organisms, plants have evolved sophisticated regulatory systems because they must respond to a variety of environmental stimuli. Salt stress, in particular, affects the growth of crop plants and limits crop yield in many saline regions around the world. Therefore, developing salt-tolerant crop cultivars has great significance in global food security. Epigenetic regulation, which contributes to phenotype plasticity without altering the genotype, have important roles in how plant respond to salt stress. Moreover, the heritable nature of epigenetic modifications makes it possible to maintain the information and pass it down to the next generation as stress memory, thus enables the plant and its progeny to cope with recuring stress more efficiently. This paper provides an overview of major achievements in this field by analyzing previous studies, and concludes that major epigenetic regulatory pathways, including histone modifications, DNA modifications and small RNAs, are essential in plant salt stress response, and further insights into these mechanisms are of great value.

Keywords: epigenetics, salt stress, histone modification, DNA methylation, small RNAs.

1. Introduction

Plants are sessile organisms that cannot move, which exposes them to constantly changing environmental conditions. In order to adapt to unpredictable climate changes, including extreme temperatures, high salinity and drought, plants have developed a variety of sophisticated mechanisms in reaction to these abiotic stresses. The study of heritable phenotypic changes that do not involve DNA sequence alternations, termed as epigenetics, has been proven to have a significant influence on changing the general profile of plants' gene expression to help plants become more tolerant to abiotic stresses.

Salt stress, as a serious environmental stress that poses a severe threat to plant growth and development, massively reduced crop productivity. Salt stress causes dehydration, the accumulation of ions to toxic levels and the imbalances of phytohormones, all of which ultimately lead to gene expression alternation and metabolism failure [1]. Previous studies have identified three levels of epigenetic reprogramming that occur in plants in response to high salinity, including histone modification, DNA modification, and small RNA [2]. This article will give a summary of key epigenetic regulatory systems controlling plant salt stress response, which includes histone modification and chromatin remodeling, histone variants, DNA modification, small RNA and long non-coding RNA (lncRNA), and RNA methylation. This article will also discuss stress memory, which helps the plant and its descendants to perform more effective responses to external stimuli when it is exposed again. This can be achieved

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through the reservation of epigenetic marks modified and the transmission of these marks to the next generation.

Epigenetic regulations could result in phenotype plasticity, which enables the development of salt-tolerant crop cultivars, thus increasing crop yield in saline soils across the world and providing a solution to global food insecurity. Therefore, understanding the epigenetic mechanisms of plants' salt response has great significance.

2. Regulatory pathways of plant salt stress response

2.1. Histone modification and chromatin remodeling

A histone is a protein that binds to DNA to form the nucleosome, the structural component of chromatin, through which the eukaryotic genome can be epigenetically modified with heritable epigenetic marks [3]. The N' terminal tails of core histone proteins that stick out of the nucleosome are locations for histone modifications, including acetylation, methylation, phosphorylation and ubiquitination, which subsequently changes the affinity of DNA and histones to alter gene activity. In the past decades, it has been proven that histone modification is essential for controlling gene expression during salt stress in different species of plants [2].

2.1.1. Histone methylation. At various histone tail locations, lysine and arginine are marked with histone methylation, which results in either gene activation or gene repression. Histone lysine methyltransferases (HKMTs) add methyl group to lysine, while protein arginine methyltransferases (PRMTs) methylate arginine. In plants, many histone methylation sites, including H3K4, H3K9, H3K27, H3K36 on lysine, H3R8, H3R17, H3R26, H4R4 on arginine, have been identified [4]. These methylation marks have a function in many processes from maintaining genome stability to regulating plant development [4]. Typically, the methylation marks of H3K4me3 and H3K9me2 are usually considered antagonist, for the former one is responsible for the activation of the marked gene, while the latter one results in repression. A previous study in soybean has identified three salinity-responsive transcription factors Glyma11g02400, Glyma20g30840, and Glyma08g41450, whose up-regulation was linked with an elevation of H3K4me3 and a decreased level of H3K9me2, implying that histone modifications can be the target of dynamic change under salt stress [5]. In the oilseed crop castor bean which can successfully grow in saline soils, the expression level of the gene RSM1 (RASIALIS-LIKE SANT), a transcription factor participating in salt stress signalling, has been found in relation with H3K4me3 and H3K27me3 histone methylations [6]. Moreover, it has been revealed that over expression of the gene JMJ15, which codes for Arabidopsis H3K4 demethylase, could increase salt tolerance in gain-of-function mutants, while the loss-of-function mutants are more salt sensitive [7]. Constitutive and overexpressed JMJ15 repressed many salt responsive genes marked by H3K4me2/3, which further supports the importance of H3K4me3 in high salinity response [7].

Overall, dynamic histone methylation at different sites has an important role for plants to adapt to high salinity. Although many associations between histone methylation and phenotypic responses have been discovered, the molecular mechanisms through which histone methylation alters transcription activity still need to be further identified.

2.1.2. Histone acetylation. Histone acetylation usually adds a negatively charged acetyl group to lysine in H3 and H4 tails, reducing the affinity between DNA and histones, thus modifying the chromatin architecture from compact, transcriptionally repressed region to open, transcriptionally active region, resulting in the activation of the marked gene. Acetylation marks are added through histone acetyltransferases (HATs) and erased through histone deacetylases (HDACs).

There have been many studies associating histone acetylation and deacetylation with plants' response to salt stress, where acetylation improves gene accessibility and deacetylation result in gene suppression.

It has been revealed in maize that salt-induced up-regulation of the histone acetyltransferase genes ZmHATB and ZmGCN5 elevates the levels of H3K9 acetylation on the cell wall related genes

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ZmEXPB2 and ZmXET1, which modulate cell wall extensibility to adapt a positive response in high salinity situations [8]. Similarly, the histone acetyltransferase General control non-repressed protein 5 (GCN5) activates the cellulose synthesis genes chitinase-like gene CTL1, polygalacturonase involved in expansion-3 (PGX3) and MYB domain protein-54 (MYB54) through H3K9 acetylation and H3K14 acetylation in Arabidopsis, thus maintaining cell wall integrity and contributing to salt tolerance [9].

On the other hand, the transcription factor INDETERMINATE SPIKELET1 (IDS1), which weakens salt tolerance in rice, physically interacts with TPR1 and histone deacetylase HAD1, leading to the repression of salt stress-responsive genes LEA1 and SOS1 [10]. Overexpression of AtHD2C, a plant-specific histone deacetylase in Arabidopsis, could reduce transpiration and enhance salt tolerance [11].

2.1.3. Chromatin remodeling interplay with histone modifications. It is important to understand that histone modifications sometimes interact with one another to control gene expression at the chromatin level. For example, the core histone deacetylase complex HDA9-PWR-HOS15 in Arabidopsis, which represses a subset of environmental stress response genes including Salt Tolerance Zinc finger, mediates changes in both histone acetylation and histone methylation [12]. H3 acetylation accumulated along with reducing hetero-chromatic H3K9me1/2/3, suggesting these histone modifications may associate with each other [12]. Another analysis in Arabidopsis also observed that the histone deacetylase HDA6, which is an important factor for transposon silencing and has a role in salt stress responses, can interact with histone methyltransferases SUVH4/5/6 to control transposon via methylation deacetylation on histone H3 [13].

Chromatin architecture can be changed as a result of histone modifications. Many chromatin remodeling proteins, such as AGO2 and the transcriptional repressors IDS1/TRP1 in rice, are associate with various histone marks like methylation and deacetylation to regulate response to salt stress as well as other abiotic stresses [14].

2.2. Histone variants

Histone variants are non-allelic variants of histone that substitute for the canonical histones. Histone variants, deposited by specific histone chaperones, often confer special structural and functional features, and have important roles in plant development. H3.3, H2A.Z, and H2A.X are linked to an open chromatin state and active transcription, while H2A.W and H1 histones favor compacted heterochromatin and silent genomic regions [15].

Histone variants have been found to function in response to many external stimuli, including drought, light and water deficiency, extreme temperatures, as well as other regulatory processes [15]. Particularly, the occupation of H2A.Z in Arabidopsis has been decreased during salt stress to activate a salt-induced transcription factor gene AtMYB44 [16]. Other research also reported the involvement of H3.3 accumulation in the eviction of H2A.Z [2]. In the future, more investigations of histone and histone variants deposition are needed to show how environmental stimuli trigger the response.

2.3. DNA methylation

In plants, DNA methylation happens on the cytosine nucleotide in different sequence contexts: CG, CHG, and CHH (H=A, T, or C). The methyltransferase MET1 maintains CG methylation, while Chromomethylase 3 (CMT3) and CMT2, plant-specific, are responsible for CHG and CHH methylation, respectively [17]. DNA methylation blocks gene expression and maintains the stability of genome by the interference of transcription factor binding and by the attraction of reader proteins. Methylation patterns can be retained after DNA replication, which permits stress memory to be passed down.

Many researches have proven that salt stress could change the general profile of methylation patterns and regulate gene activity. In the crop plant barley, it was observed that salt stress increased methylation in leaves but diminished methylation in roots, suggesting that salt-induced methylation is organ-specific [2]. Analysis of different natural accessions of Arabidopsis exposed to salt stress also revealed a dynamic pattern of methylation and suggested that methylation changes may have convergent functions across different genetic backgrounds [18].

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More insights into DNA methylation showed some of the mechanisms by which DNA methylation mediate salt stress response. A recent study in rice has found that DNA methylation reader OsSUVH7 interacts with the protein OsBAG4 and the transcription factor OsMYB106 to form a complex, which activates the gene OsHKT1;5 encoding a Na+ transporter and is responsible for Na+/K+ homeostasis under salt stress [19]. Elevated CHH and CHG methylation in OsHKT1;5 gene was observed under high salinity, linking DNA methylation to salt tolerance [19].

Moreover, the soybean transcription factor genes, Glyma11g02400, Glyma08g41450, Glyma16g27950 and Glyma20g30840, were shown to be up-regulated through the changes of methylation status induced by salinity stress [5]. This was supported by the observation that when treated with the demethylation agent 5-aza-2-deoxycytideline, the cytosine methylation of the four genes was substantially reduced [5]. Notably, in the case of Glyma11g02400 and Glyma20g30840, CG demethylation was accompanied by elevated H3K9me2 and decreased non-CG methylation, consistent with other studies in Arabidopsis, supporting the "two-step" hypothesis that CG methylation induces H3K9 methylation, which then recruits non-CG methylation [5]. This further indicates that the interactions between DNA methylation and histone modification may have significant functions in the transcriptional control of some of the salt-responsive genes.

2.4. Small RNA and RNA-directed DNA methylation

Non-coding RNAs (ncRNAs) function without being translated into proteins. Housekeeping ncRNAs are constitutively expressed and required for normal function and variability of cells. On the other hand, regulatory non-coding RNAs are divided into short ncRNAs and long ncRNAs (lncRNAs) according to their lengths. Plant small RNAs (sRNAs), which are 20-24 nucleotide (nt) short ncRNAs, categorized into microRNAs (miRNAs) and small interfering RNAs (siRNAs) based on their biogenesis, have been shown to be important epigenetic regulators for plant responses to and tolerance of salt stress [20].

MiRNAs, which are genomically encoded, are imperfectly complementary to their target mRNA to repress translation. miRNAs originate from single-stranded primary miRNA transcripts, which form the hairpin or stem-loop structured precursor RNAs and then get converted into miRNA-miRNA* duplex, where one strand gets degraded and the duplex unwinds to form single-stranded mature miRNA [20]. The miRNA then enters an RNA-induced silencing complex (RISC), which is directed to the target mRNA transcripts through a sequence complementary of the miRNA and the target mRNA.

SiRNAs are generated via processing of long double-stranded RNAs produced exogenously or from bidirectionally transcribed RNAs endogenously. siRNAs can form a perfect duplex with target mRNA and cause the degradation of mRNA.

SiRNA and miRNA are two main pathways that mediate RNA interference (RNAi), a process by which an mRNA is targeted for degradation, resulting in post-transcriptional gene silencing. siRNA is also involved in the RNA-directed DNA methylation (RdDM) pathway specific to plant, which adds methylation to the targeted DNA sequences and transcriptionally repress the genes [17].

Analysis in rice with different salt tolerance natures observed a higher enrichment of sRNAs in hypermethylated genes and reduction of sRNAs in hypomethylated genes, suggesting that abundant sRNAs function in inducing DNA methylation [20]. Different studies have confirmed that the Argonaut (AGO) proteins involved in post-transcriptional and epigenetic silencing pathways are regulated by miRNAs including miR403 and miR172, suggesting a general function of miRNAs in small RNA induced silencing [20]. In Arabidopsis, AGO1 associates with miRNA gene to control the expression level of miRNAs, and increased levels of miR61 and miR173 were also observed in plants treated with salt [20]. The interactions of DNA methylation, miRNAs, target genes and their products form a complex network to control the level of miRNA and consequently trigger proper response [20].

SiRNAs have also been proven as key regulators for salt stress response. 24-nt siRNAs in Arabidopsis were found to associate with stress-induced SRO5 gene and repress the expression of P5CDH (pyrroline-5-carboxylate dehydrogenase), thus increasing proline accumulation to adapt to high saline conditions [20]. A substantial decrease of different siRNA species under salt stress was also observed in wheat and maize [20].

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SiRNAs could also induce the RNA-directed DNA methylation pathway, which plays crucial role in plants. The majority of RdDM activity is canonical RdDM which could enhance existing DNA methylation patterns, while non-canonic RdDM, involving miRNAs, establishes initial DNA methylation at new target regions [17]. sRNA-induced RdDM pathway functions in biological processes ranging from transposon silencing, development and reproduction, signalling, to stress response [17]. RdDM is able to generate appropriate stress responses by silencing transposable elements which become activated under stress conditions, or directly control the expression level of stress responsible genes [17].

In one example, RdDM regulates the Arabidopsis gene AtMYB74, which became up-regulated under salt stress and served as a transcription factor in salt-signalling pathway [21]. Salt stress induced the RdDM pathway through repressing the level of 24-nt siRNAs that target the AtMYB74 promoter region, consequently reduced the DNA methylation level of AtMYB74 promoter and activated the gene, suggesting the function of RdDM as a repressive epigenetic modification in regulating salt tolerance [21]. Moreover, exogenous and artificial siRNAs can also target the AtMYB74 promoter region and direct DNA methylation in Arabidopsis, suggesting the possibility of enhancing plants' salt tolerance through sRNA regulation to develop salt-tolerant crop cultivars [21].

2.5. RNA methylation

N6-methyladenosine (m6A) methylation is a common mRNA modification. m6A methylation is a newly emerged research field that establishes a novel mechanism of epitranscriptomic modification, which can influence many mRNA processes including mRNA stabilization and translation efficiency [22]. Recent research has revealed the vital function of m6A methylation in different stages of plant development, but its role in stress responses is still largely unknown [22].

One study in Arabidopsis analyzed the mutant of virilizer (VIR), a component of m6A methylation writer, and found that the level of m6A in vir mutant was highly reduced under salt treatment, and the vir mutant plants showed hypersensitivity to salt [22]. The authors further demonstrated that VIR mediates the deposition of m6A in the 3' untranslated regions (3'-UTRs), regulates the length of 3'UTRs in the transcripts via alternative polyadenylation, thus suppresses the expression of some negative salt stress regulators, including ATAF1, EGR1, GI and GSTU17 [22]. This study has emphasized the importance of mRNA methylation in salt stress response and suggested the significance of further research in this field.

3. Stress memory

Epigenetic modifications are heritable through cell division and can be transmitted to the next generation, which enables the plant and its progeny to trigger more efficient responses to recurring environmental stimuli, thus epigenetic regulations have great significance to stress memories and plant evolution [23]. Many studies have reported histone modifications involved in transcriptional memory of genes responsible for stress reaction, including the active transcription mark H3K4me3 during repeated dehydration and the repressive mark H3K27me3 in salt stress memory [24].

In one case, the salt-induced transcriptional memory of Arabidopsis P5CS1, a gene for proline biosynthetic enzyme, was responsible for increasing proline accumulation as an adaptive mechanism in salt tolerance [24]. The expression of P5CS1, induced by primary salt stress, decreased to a basal level during the recovery stage, and was elevated to a higher level under reoccurring salt stress [24]. The transcriptional memory of P5CS1 was dependent on HY5, a light-responsive transcription factor, via its function of maintaining H3K4me3 level at P5CS1, and light exposure during the recovery stage was indispensable in this process [24]. Further studies in stress memory may provide valuable insights into plant adaptation and help us better design salt-tolerant plants.

4. Conclusion

This paper discusses the epigenetic regulatory systems of plant response to salt stress and summarizes currently identified pathways of plant epigenetic regulation in the process, including histone modifications, DNA methylation, small RNAs, and some less studied fields such as RNA methylation

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and stress memory. This article presents the results of several studies in each regulatory pathway to better illustrate the mechanisms, and provides an overview of major achievements in this field, emphasizing the indispensable function of epigenetic regulatory systems in salt stress reactions. This review focuses on the stress of high salinity, but plant responses to other environmental stimuli such as extreme temperatures and drought are also similar to this structure. Overall, this work demonstrates that epigenetic regulation in levels of histone modification, DNA modification and small RNAs and the dynamic changes of different epigenetic marks are crucial in plant salt stress response. In the future, more effort is needed to understand the mechanisms of stress memory more detailedly, which can make contributions to the development of salt tolerant crop cultivars.

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