Types of Histone Post-Translational Modifications

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Contributor: Madhvi Sharma , Amanpreet K. Sidhu , Mahesh Kumar Samota , Mamta Gupta , Pushpendra Koli , Mukesh Choudhary

Abiotic stresses profoundly alter plant growth and development, resulting in yield losses. Plants have evolved adaptive mechanisms to combat these challenges, triggering intricate molecular responses to maintain tissue hydration and temperature stability during stress. A pivotal player in this defense is histone modification, governing gene expression in response to diverse environmental cues. Post-translational modifications (PTMs) of histone tails, including acetylation, phosphorylation, methylation, ubiquitination, and sumoylation, regulate transcription, DNA processes, and stress-related traits.

histone ubiquitination methylation stress tolerance post-translational modifications

1. Introduction

Plants face formidable challenges when confronted with abiotic stresses, necessitating precise adjustments across various physiological pathways. These adaptive responses encompass critical functions, such as photosynthesis, antioxidant regulation, water uptake, ion homeostasis, and osmolyte synthesis [1][2][3][4][5][6]. In the face of environmental constraints, these morphophysiological adaptations are underpinned by an intricate network of post-translational modifications (PTMs), orchestrated by multifaceted molecular mechanisms [7].

Plant adaptation to abiotic stresses hinges on the dynamic regulation of gene expression, encompassing a multitude of genes controlled by an array of transcription factors (TFs) and chromatin-associated factors. While substantial attention has been devoted to elucidating the roles of TFs, enzymes catalyzing covalent histone modifications, and chromatin remodeling complexes, the contribution of histone chaperones remains less explored, and their significance in this context remains enigmatic. Notably, protein phosphorylation serves as a well-established mechanism for transmitting stress signals, whereas emerging modifications, like S-nitrosylation, are still in their infancy. In the realm of PTMs, ubiquitin and SUMO conjugations emerged as central regulatory processes in eukaryotes [8][9]. These modifications, however, exert distinct effects contingent upon the transcriptional or translational stage at which the targeted transcript or protein is situated. Consequently, the interplay of these diverse PTMs collectively dictates the ultimate impact on the associated cellular processes and phenotypic outcomes.

Chromatin regulation emerges as a pivotal player in governing gene expression, with DNA methylation, histone modifications, and other genome activities intricately intertwined with adaptive responses to environmental challenges in plants [10][11][12]. An array of epigenetic mechanisms, including DNA methylation, histone modifications, ATP-dependent chromatin remodeling, incorporation of histone variants, and regulation by noncoding RNA, orchestrate the structure and function of chromatin [13][14]. Specifically, methylation, acetylation, phosphorylation, ubiquitination, and sumoylation represent a subset of PTMs occurring on the N-terminal tails of histone proteins. These modifications, collectively referred to as the “histone code,” are pivotal in establishing and perpetuating epigenetic memory, profoundly influencing chromatin structure and gene expression [15][16].

Within the intricate world of chromatin, the configuration significantly influences genome expression, largely regulated by the interplay of DNA methylation machinery and histone chaperones, also known as nucleosome assembly/disassembly factors. They facilitate nucleosome assembly and disassembly, impacting replication-dependent and replication-independent processes and collaborate with free histones to prevent indiscriminate histone–DNA interactions. Hence, histone chaperones play a critical role in modulating histone availability and the incorporation into nucleosomes [17][18].

In summary, this multifaceted interplay of plant responses to abiotic stresses, encompassing diverse pathways, PTMs, and chromatin dynamics, underscores the intricate web of adaptations crucial for plant survival in challenging environments (**Figure 1**).

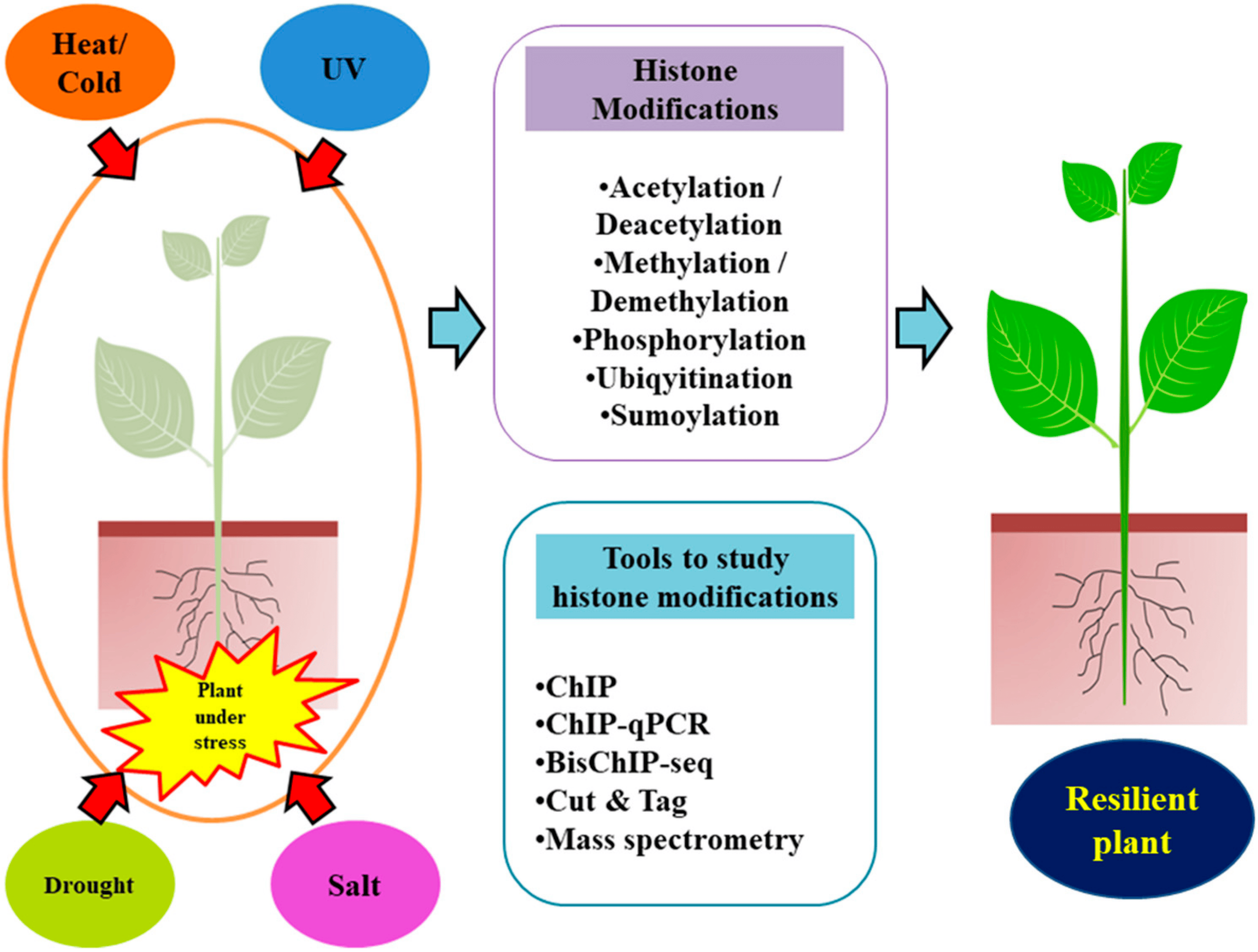

Figure 1. Plants are exposed to many abiotic stresses due to unpredictable climate changes, including cold and hot temperatures, drought, salinity, and ultraviolet radiation, all of which affect their productivity. Dynamic changes in histone modifications are important for the regulation of genes during environmental stress.

2. Epigenetic Memory and Chromatin Dynamics in Plant Stress Responses

Plants often experience unfavorable environmental conditions in growing habitats. Depending on the stress response, plants can retain information for a time after a previous stress (known as stress memory), so they can adapt more quickly to the same adversity in the future [19]. Epigenetic regulation is closely associated with the development of stress memories [19][20][21]. Research showed that stress treatment can alter the chromatin status of genes that respond to stress, and these changes persist after recovery and even in progeny [22][23][24]. Several factors play a role in regulating gene expression in eukaryotic cells, including the dynamic environment of chromatin. Epigenetic mechanisms, including covalent modifications to DNA and histone tails, are crucial for inducing favorable chromatin states that enable gene expression in response to stress and hence bestowing the plants with better adaptation. Several epigenetic factors cause chromatin modifications on exposure to various abiotic stresses in plants [25]. Each nucleosome contains a basic core histone octamer composed of four types of histone proteins, namely H2A, H2B, H3, and H4. In addition to these core histones, many histone variants are also reported. To date, only one variant is observed for H4, whereas several variants are encountered for H2A, H2B, and H3. These variants are believed to enhance the dynamics of nucleosome, diversity and play a crucial role in epigenetic genome regulation (**Figure 2**). The study of these variants can provide various clues in understanding the mechanism behind epigenetic genome regulation.

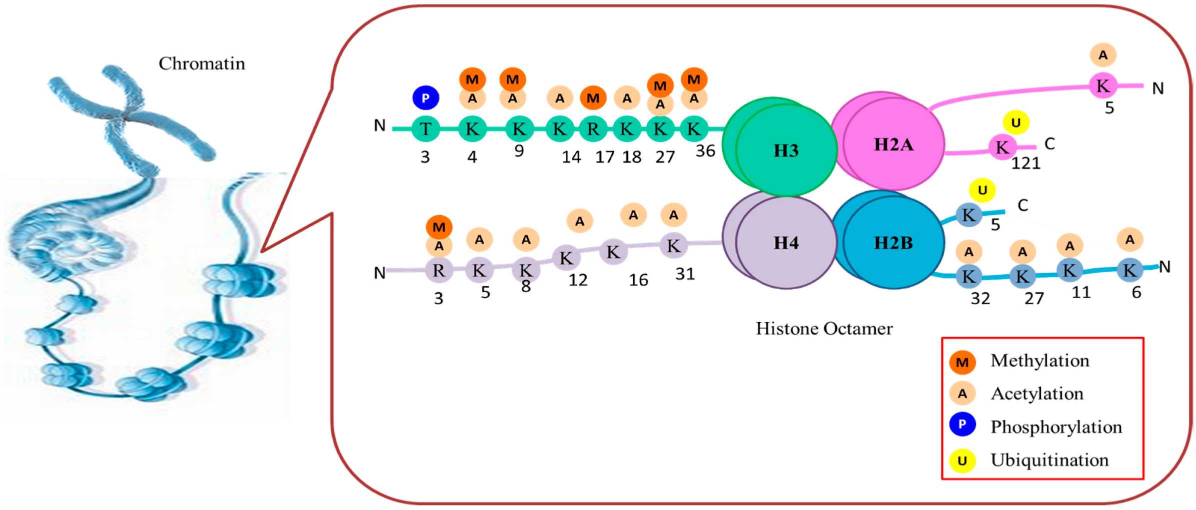

Figure 2. Histone modifications at different polypeptide amino acid residue locations and the group added by the different enzymes.

The majority of histone modifications take place at the N-terminal coil known as the histone tail rather than the globular C-terminal domain. Many basic amino acid residues, such as arginine and lysine, can be found in high concentrations in histones. The amino acid residues in histone tails can change chemically through acetylation, methylation, phosphorylation, and ubiquitination. The aforementioned modifications are believed to influence the functioning of genes located in proximity to core histones. Most histone-modifying enzymes are remarkably conserved across the plant realm, including well-researched and defined histone modifiers, such as histone methyltransferases (HMTs), histone demethylases (HDMs), histone deacetylases (HDACs), and histone acetyltransferases (HATs). Other less-studied enzymes include kinases, arginine deiminases, lysine- and arginine-specific methyltransferases, ubiquitinates, lysine and arginine-specific demethylases, and deubiquitinases. While there are studies on histone modifications and stress response in plants, this research seems to delve into the specific mechanisms and examples of how histone modifications influence stress tolerance in different plant species.

3. Molecular Sculptors: Types of Histone Post-Translational Modifications

3.1. Acetylation and Deacetylation

Histone acetylation involves a covalent alteration that enables the transfer of acetyl groups from acetyl CoA to the ε-amino group of lysine residues within histone molecules. This modification leads to the neutralization of lysine's positive charge, subsequently diminishing the binding affinity between the modified histone and DNA [26][27]. Conversely, histone deacetylation is associated with a "closed" chromatin structure and the repression of gene activity [28]. Histone acetyltransferases and histone deacetylases are responsible for the reversible acetylation of histones (**Table 1**). At the outset, attention centered on identifying enzymes responsible for the introduction ("writers") and removal ("erasers") of these modifications [28]. Among these enzymatic agents, there are those that add chemical groups to histone tails or core domains, such as HATs, kinases, methyltransferases, and ubiquitinases. In contrast, there are enzymes that eliminate these modifications, including HDMs, phosphatases, deubiquitinases, and HDACs. Histone acetylation and deacetylation are critical regulators of plant stress tolerance. In *Arabidopsis thaliana*, a model plant, the HD2-type histone deacetylase HD2C has been found to negatively regulate drought tolerance. HD2C represses the expression of drought-responsive genes by deacetylating histones in their promoter regions, leading to reduced gene expression and impaired drought response in the plant [29]. Conversely, in Arabidopsis, certain genes positively regulate salt stress tolerance by enhancing the expression of salt-responsive genes. As an example, HD2C and HDA6 (histone deacetylase) work in tandem to govern the reaction to salt stress by controlling the expression of ABA-responsive genes including *ABSCISIC ACID INSENSITIVE1* and *ABSCISIC ACID INSENSITIVE2*. The heightened expression of HDA705, a counterpart of Arabidopsis' HDA6 or HDA7, led to diminished ABA levels and reduced salt stress tolerance in Arabidopsis seedlings [30]. Histone acetylation patterns also impact heat stress responses in wheat (*Triticum aestivum*). *TaHAG1* is a gene that encodes a histone acetyltransferase that is orthologous to Arabidopsis *AtHAG1/GCN5,* and rice *OsHAG702* promotes heat stress tolerance in wheat [31]. Moreover, histone acetylation can also modulate plant defense responses against pathogens. In Arabidopsis, the histone acetyltransferase *HAG1* (HISTONE ACETYLTRANSFERASE OF THE GNAT FAMILY 1) is involved in activating defense genes against bacterial pathogens. HAG1 acetylates histones in the promoters of these genes, promoting their expression and enhancing the plant's resistance to bacterial infection [32]. Furthermore, epigenetic memory and priming have been observed in maize (*Zea mays*), where exposure to brief drought stress induces changes in histone acetylation patterns, leading to improved drought tolerance upon subsequent stress [33][34].

Table 1. Histone modifications occurring under different abiotic stresses in plants. Special attention is given to the proteins acting as substrates for modifications, encompassing both histone and nonhistone proteins.

Modification Type	Regulator Name	Crop	Stress Type	References
Acetylation Acetyltransferase	*GCN5*, *AtHAC1*	Arabidopsis and Poplar	Heat, salinity, and drought (Chimeric dCas9 HAT)	[35][36][37]
Acetylation Acetyltransferase	HAT, AREB	Poplar	Drought	[36]
Deacetylation (Deactylase)	HDAC, IDS1	Rice	Salinity	[38]
Deactylation (Deactylase)	HDAC, MYB96	Arabidopsis	Drought	[39]
Deactylation Deacetylase	HDA9, HDA15, HDA705, BdHD1, HD2C	Arabidopsis, Rice, and Brachypodium	Drought, salinity cold, and heat	[28][39][40][41][42]
H3K9 acetylation	HAT, *GCN5*, *ZmEXPANSIN-B2*	Maize	Salinity	[43]
H3 hyperacetylation	*HAT* genes, *OsHAT* genes	Rice	Drought	[44][45]
Deactylation (Deactylase)	HDA9, CYP707A1, CYP707A2	Arabidopsis	Drought	[46]
Deactylation (Deactylase)	BdHD1, WRKY24	Purple False Brome or Stiff Brome	Drought	[47]
Acetylation	*AtHAC1*	Arabidopsis	Heat	[48]
Acetylation	MYST, ELP3, *GCN5*	Barley	Drought	[49]
Acetylation	*OsHAC703*, *OsHAG703*, *OsHAF701*, *OsHAM70*	Rice	Drought	[50]
Deacetylation (Deactylase)	84KHDA903	Tobacco	Drought	[51]

Modification Type	Regulator Name	Crop	Stress Type	References
Deacetylation (Deactylase)	HD2C, HSFA3, HSFC1, HSP10	Arabidopsis	Heat	[42]
Acetylation	*GCN5*, PtrNAC006,	Black Cottonwood Tree	Drought	[52]
Recruiter	MYB96, IDS1, AREB1	Arabidopsis, Rice, and Poplar	Drought and salinity	[38][39][52]
Methylation Methyltransferase	ATX1, ATX4/5	Arabidopsis	Drought	[53][54]
Demethylation Demethylase	JMJ17	Arabidopsis	Drought	[55]
Trimethylation	HMT	Arabidopsis	Gamma irradiation	[56]
Ubiquitination Ubiquitinase	HUB1/2, AtHUB2, OsHUB2	Arabidopsis, Cotton, and Rice	Salinity and drought	[57][58][59][60][61]
Phosphorylation Kinase	MLK1/2	Arabidopsis	Drought and salinity	[62][63][64]
Ubiquitinase and deubiquitinase	H2B	Rice	Drought	[61]
Sumoylation	SUMO E3 ligase (AtSIZ1, OsSIZ1)	Arabidopsis and Rice	Heat	[65][66][67]
Ubiquitination	*SNAC1* gene	Wheat	Salt and drought	[68]

interplay e methyl yl groups, respectively. Histone lysine methylation occurs primarily at Lys4, Lys9, Lys27, and Lys36 of H3 in Arabidopsis [69][70][71]. Overall, histone methylation at H3K9 and H3K27 is connected with gene silencing, whereas methylation at H3K4 and H3K36 is tied to gene activation. Based on the number of methyl groups added to histone molecules, methylation is classified as mono-, di-, or trimethylation, and gene expression varies depending on the level of modification [26]. For instance, in Arabidopsis, the trimethylation of Lys27 (H3K27me3) leads to gene expression repression, while the trimethylation of Lys4 (H3K4me3) leads to the activation of gene transcription [72]. These methylation marks can be eliminated by histone demethylases (HDMs) with the assistance of various cofactors in plants, including lysine-specific demethylase 1 (LSD1) and the Jumonji C domain-containing protein (JMJ) [73][74][75] (as shown in **Table 1**). Methylation occurs on lysine and/or arginine amino acids within histones, altering their interaction with reader proteins and consequently influencing chromatin structure, which in turn determines whether transcription is activated or repressed. In Arabidopsis, repressive histone methylation modifications, such as H4R3me2, H3K9me2/3, and H3K27me3, are observed, whereas active histone methylation modifications, such as H4R3me2, H3K4me3, and H3K36me2/3, are evident [76][77]. Unlike acetylation, which damages the electrostatic properties of histone proteins, histone methylation preserves the electron charge of lysine. The histone methylation mark's mode of action (Tran's effects) is presumably coordinated through hydrophobicity; however, this assertion is not absolute, and other hypotheses have been put forth. Moreover, a variety of histone H3 lysine residue methylation holds significance in plants, encompassing repressive dimethylation at Lys9 (H3K9me2) and trimethylation at Lys27 (H3K27me3), along with permissive trimethylation at Lys4 (H3K4me3) and Lys36 (H3K36me3) [78]. Additionally, plants exhibit two arginine methylation sites (H3R17 and H4R3) and five lysine methylation sites (H3K4, H3K9, H3K27, H3K36, and H4R20), each potentially holding a distinctive role in the orchestration of transcriptional regulation [76]. For instance, Polycomb Repressive Complex 2 (PRC2) having an HMT unit mediates the histone modification H3K27me3, which was reported to be associated with gene repression in eukaryotes [79][80]. The identification of these PRC2 complexes originally occurred in Drosophila as Hox gene regulators, subsequently revealing homologous PRC2 subunits within plants and animals [81][82].

Histone demethylation involves the removal of methyl groups from specific lysine or arginine residues on histone proteins. This modification can have a profound impact on chromatin structure and, subsequently, on the transcriptional regulation of genes involved in plant abiotic stress tolerance. Histone demethylation can either activate or suppress the transcription of stress-related genes [83]. The specific effect depends on the histone residue being demethylated and the enzyme responsible for the demethylation. For example, the removal of methyl groups from histone H3 lysine 4 (H3K4) is associated with gene activation, while the demethylation of histone H3 lysine 9 (H3K9) or histone H3 lysine 27 (H3K27) is linked to gene repression [84]. The demethylation of histone H3K4 and histone H3 lysine 36 (H3K36) near the promoter regions of stress-responsive genes can lead to their activation [85]. This allows plants to mount a rapid response to abiotic stress conditions by increasing the expression of genes involved in stress tolerance, such as those encoding heat shock proteins, antioxidant enzymes, and osmoprotectants.

3.3. Phosphorylation

Phosphorylation, the process of adding a phosphate group (PO_4^{3-}) to a molecule, is orchestrated by specific protein kinases, while phosphatases facilitate phosphate group removal [86]. Within this complex landscape, histones, the proteins around which DNA is wound in chromatin, are subject to dynamic phosphorylation events that primarily target threonine (Thr), serine (Ser), and tyrosine (Tyr) residues [87]. Histone phosphorylation often responds to signals, such as DNA damage, extracellular cues, or cell division progression. In the context of histone modifications, phosphorylation on histone H3 is of particular interest, with prominent sites including Ser 10, Ser 28 (H3S10ph and H3S28ph), Thr 3, and Thr 11 (H3T3ph and H3T11ph) [88]. The importance of these modifications is underscored by observations in Arabidopsis where a mutant deficient in closely related Ser/Thr protein kinases (At3g03940 and At5g18190) displayed heightened sensitivity to osmotic and salt stress, along with dwarfism. Intriguingly, this mutant exhibited a significantly reduced level of phosphorylated histone H3 at Thr 3 (H3T3ph). Genome-wide assessments unveiled an elevation in H3T3ph at Thr 3 within pericentromeric regions of Arabidopsis thaliana under osmotic stress conditions [89][90][91].

This phosphorylation of histone H3 plays a crucial role in various cellular processes, including chromosome segregation, chromatin condensation, and transcriptional regulation [92]. Additionally, histone H2AX phosphorylation at Ser 129, known as γH2AX, is a pivotal player in the DNA damage response and repair. Rapid phosphorylation of H2AX occurs at sites of double-strand DNA breaks, catalyzed by PI3K kinases. This modification represents one of the earliest and most discernible post-translational signals triggered by DNA damage [93][94][95]. The Arabidopsis genome houses an extensive array of over 1000 protein kinases, including calcium-dependent protein kinases (CPKs), mitogen-activated protein kinases (MAPKs), receptor-like kinases (RLKs), and sucrose nonfermenting-related kinases (SnRKs). Alongside these, it hosts approximately 150 protein phosphatases, encompassing type 1 (PP1) and type 2A phosphatases, the protein tyrosine phosphatase family, and the metal-dependent protein phosphatase family [96]. Specific MAPKs, such as MPK3, MPK4, and MPK6, have been identified as key players in the phosphorylation of HSFA4A at Ser-309. This intricate regulatory mechanism serves to modulate the activity of the heat-activated factor HSFA4A. Elevated temperatures and increased salinity both trigger HSFA4A activation, and their combined action influences the accessibility of HSFA4A-binding sites within the promoters of target genes, like *ZAT12*, *HSP17.6A*, and *WRKY30*. This finely tuned orchestration governs the plant’s response to abiotic stresses [97]. Histone phosphorylation, influenced by the activity of MAPKs and the action of transcription factors, like HSFA4A, can further modulate gene expression. It can make the chromatin structure more permissive or restrictive for the transcription of the genes involved in heat stress response. Overall, the connection among MAPKs, HSFA4A, and histone phosphorylation lies in the signaling pathway activated by heat stress in plants. MAPKs are involved in the early signaling events of heat stress response, phosphorylating HSFA4A, which, in turn, activates the transcription of stress-responsive genes. Histone phosphorylation can then act as an additional layer of regulation, ensuring that the right genes are expressed in response to heat stress, contributing to the plant’s adaption and survival under adverse conditions.

Furthermore, rising temperatures induce the nuclear translocation of the BR-regulated transcription factor, brassinazole-resistant 1 (BZR1). In the nucleus, BZR1 binds to the promoter of PIF4 (phytochrome-interacting factor), leading to cell elongation [98][99]. Notably, histone H2A phosphorylation at Ser 95 in Arabidopsis, catalyzed by MuTP9-like kinases, such as MLK4 and MLK3, has been shown to promote flowering time and enhance the deposition of H2A.Z [92].

In summary, histone phosphorylation is a dynamic and finely regulated process involving a delicate balance between kinases and phosphatases. These kinases engage diverse targets to orchestrate distinct temperature-signaling pathways, thereby governing the plant’s responses to a range of temperatures from elevated to exceedingly high. This intricate regulatory network underscores the pivotal role of histone phosphorylation in plant stress tolerance.

3.4. Ubiquitination

The enzymatic process involving the transfer of one or more ubiquitin monomers to the protein substrate is termed ubiquitination (or ubiquitylation) [100]. Monoubiquitination brings about alterations in the subcellular localization, biochemical properties, or molecular functions of target proteins. In contrast, polyubiquitination serves as a signal for proteasome-mediated degradation [101]. This modification occurs specifically on lysine residues 119 of H2A and 120 of H2B. The ubiquitination process primarily encompasses three stages: ubiquitin protein activation, ubiquitin conjugation, and ubiquitin ligation. These steps necessitate the addition of ubiquitin to the target protein and are executed by their respective ubiquitin-activating enzymes (E1s), ubiquitin-conjugating enzymes (E2s), and ubiquitin ligases (E3s) [102]. Among the ubiquitination enzymes, the most abundant are E3 ubiquitin ligases. In rice and arabidopsis, a drought stress tolerance cascade involving 3 ubiquitin ligase OsPUB67 and its target protein OsDIS1 and OsRZP34 has been well explored. OsPUB67 positively regulates drought tolerance by promoting improved scavenging of ROS and closure of stomata under drought, whereas OsDIS1 and OsRZP34 are negative regulators that open the stomata under drought stress. OsPUB67 ubiquitinates the targets OsRZFP34 and OsDIS1 for proteolysis-mediated degradation, leading to an increased level of stomatal closure [103][104][105].

In a study conducted by Tripathi et al. [106], researchers delved into the physiological role of OsNAPL6, a putative rice NAP superfamily histone chaperone responsive to stress. This nuclear-localized histone chaperone possesses the ability to form nucleosome-like structures. Through a combination of overexpression and knockdown strategies, they unveiled a positive connection between OsNAPL6 expression levels and the plant’s ability to adapt to diverse abiotic stresses. Their investigation, involving comparative transcriptome profiling and promoter recruitment analyses, highlighted OsNAPL6′s role in stress response by influencing the expression of various genes associated with diverse functions. Many ubiquitin ligases were discovered in stress-related mutants, accounting for regulatory roles in abiotic stress tolerance, particularly drought tolerance, in Arabidopsis and crop species [107]. For example, a small regulatory protein (E3 ubiquitin ligase RING FINGER 1) imparts drought tolerance in durum wheat [1]. Furthermore, H2A (H2Aub) and H2B (H2Bub) monoubiquitination affect transcription in eukaryotes both actively and repressively. In Arabidopsis, H2AK121 monoubiquitination occurs independently of H3K27me3, but it does not cooperate with PRC2, which is required to maintain H3K27me3 [108][109].

In addition to DNA methylation, histone H3 heterochromatic methylation is required for H2B deubiquitination. H2B monoubiquitination, in more detail, activates transcription via the presence of H3K4me3 [110]. The experimental study in Arabidopsis observed a direct link between H2B monoubiquitination and plant immunity because they found that pathogen infection increases the H2B monoubiquitination at R-gene *SNC1* [111]. Likewise, in tomatoes, the presence of the histone H2B monoubiquitination enzymes HUB1, HUB2, SlHUB1, and SlHUB2 has been identified as a contributor to resistance against *B. cinerea*. Their role is likely centered on maintaining a balance between the signaling pathways governed by SA and JA/ethylene. The expression of the gene governing the SA (salicylic acid)-mediated signaling pathway was significantly upregulated, while the expression of genes in the JA (Jasmonic acid)/ethylene pathway were critically downregulated. This interaction establishes a crucial connection between plant immunity and the process of ubiquitination [112]. According to research on wheat’s histone modification, TaHUB2 (the second histone H2B monoubiquitination enzyme) interacts with TaH2B in vernalization pathways and may be necessary for wheat heading [113][114]. TaHUB2 serves as a ubiquitin RING-type E3 ligase. In Arabidopsis, the HUB1 (histone monoubiquitination 1, gene encoding E3 ligase) mediated H2Bub1 (histone H2B monoubiquitination) has been proven as a mechanism regulating auxin biosynthesis [115]. A recent investigation revealed that GhUbox8, an E3 ligase of the U-box-type, collaboratively modulates histone monoubiquitination of H2A and H2B in conjunction with GhUBC2L, an E2 enzyme. This concerted action governs the expression of genes associated with cell cycle progression and organ development [116]. This discovery reinforces the significance of histone monoubiquitination in orchestrating the regulation of organ size within the context of cotton.

3.5. Sumoylation

The Small Ubiquitin-like Modifier (SUMO) protein family engages in a process of attaching to and detaching from various proteins within the cell, thereby modulating the functionality of these proteins. In the research conducted by Shiio et al. [117], it was demonstrated that SUMO can modify H4, leading to the recruitment of HDAC and HP1 proteins. This recruitment subsequently results in the suppression of transcriptional activity through competitive interactions with other active marks, such as methylation, acetylation, and ubiquitination. In Arabidopsis, there are instances of SUMOylated chromatin modifiers and components, such as HDA19, H2B, and GCN5, and the deubiquitinating enzyme UBP26, which functions to remove ubiquitin attached to H2B. As an illustration, exposure to heat stress (37 °C for 30 min) induces a reduction in H2B SUMOylation while simultaneously increasing SUMOylation in GCN5 HAT [118]. This phenomenon plays a pivotal role in modulating DNA methylation patterns during heat stress within Arabidopsis, as the SUMOylation of histone acetylases/deacetylases facilitates the conversion of euchromatic regions into heterochromatic ones [119]. In the Arabidopsis context, SUMOylation associated with chromatin serves as a pivotal switch, regulating the transcriptional balance between plant development and the response to heat stress. These SUMO-mediated changes in chromatin signals lead to the upregulation of heat-responsive genes and the downregulation of growth-related genes. Notably, the inactivation of the SUMO ligase gene *SIZ1* resulted in reduced SUMO signals on chromatin and a corresponding attenuation of rapid transcriptional responses to heat stress [120][121].

Through a comprehensive approach encompassing proteomic and interactome analyses, a total of 350 SUMO targets and SUMO-interacting proteins were unveiled in Arabidopsis. This exploration extended to those entities that exhibited accumulation subsequent to subjecting plants to conditions of heat and oxidative stress, employing three distinct research methodologies [118][122]. The majority of SUMO substrates control nuclear activities, such as DNA methylation, DNA repair, RNA processing, chromatin remodeling, and gene transcription [123][124]. Genes, such as *COP1* and *SIZ1,* serve as typical examples of proteins that dynamically regulate high-temperature-induced growth responses via SUMOylation or ubiquitination. Alternatively, SUMO can be subjected to controlled proteolysis via the generation of poly-SUMO chains mediated by SUMO ligases like PIAL1/2. This process is paralleled by the regulation of SUMO through the activity of SUMO ligases, such as PIAL1/2, which orchestrate the assembly of poly-SUMO chains. This polymeric configuration serves as a docking site for STUbLs, facilitating the conjugation of polyubiquitin chains to both SUMO and the target protein. Consequently, this orchestrated interaction primes the 26S proteasome for targeted degradation. This intricate interplay elevates the scope of transcriptional control to a greater level [125].

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