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Review Paper

Plant histone modifications in response to cold stress

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ABSTRACT:
Cold stress is a major environmental factor limiting agricultural expansion and crop yields, and plants have developed diverse molecular mechanisms to cope with a lifetime of exposure to cold stress. Histone modifications play a fundamental role in regulating chromatin dynamics and transcriptional activation, either directly or through protein adaptors termed effectors. Growing evidence indicates that the chromatin remodeling caused by histone modifications, including acetylation, methylation, phosphorylation, and ubiquitination, is required for stress-responsive transcription, stress adaptation, and stress memory in plants. In this mini-review, I have summarized the current knowledge regarding the histone modifications associated with plant responses to cold stress, and discussed the roles of these modifications in improving plant cold tolerance.

Keywords:
Cold acclimation, epigenetic regulations, vernalisation, transcriptional reprogramming

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INTRODUCTION

Cold stress, which can be classified as chilling stress (< 20°C) and freezing stress (< 0°C), influences the plant life cycle by affecting plant growth, development, and flowering times (Chinnusamy *et al.* 2007). Chilling stress can suppress the kinetics of physiological and metabolic processes, resulting in a reduced seed-germination rate, growth rate, and leaf expansion (Hussain *et al.* 2018). On the other hand, in plants exposed to freezing stress, freeze-induced dehydration and extracellular ice crystal formation are major factors inducing drought stress syndromes and mechanical wounding of the plasma membrane (Yamazaki *et al.* 2009). To overcome these problems, plants exhibit natural low-temperature acclimation, which is termed cold acclimation (Vyse *et al.* 2019). These characteristics are mediated by a complex multigenic process regulated by numerous biochemical and physiological factors to induce cryoprotectant accumulation, alterations of lipid composition, and changes in the transcriptome and proteome (Ouellet 2002). In addition, increasing evidence suggests that epigenetic modifications play critical roles in mediating plant response to cold stress and cold acclimation via the regulation of gene expression.

Epigenetic regulations, which are defined as heritable alterations in gene expression which do not affect the DNA sequence, include DNA methylation, histone modifications, and non-coding RNAs (Tang *et al.* 2020; Lu & Hyun 2021), and play a fundamental role not only in the response to various environmental stresses, but also in plant growth and development (Pikaard & Mittelsten Scheid 2014; Liang *et al.* 2020; Lu & Hyun 2021). Among epigenetic regulations, histone modifications, which together represent the histone code, regulate the function of the nucleosome and ultimately determine gene expression based on conformational changes in the chromatin structure (Jenuwein & Allis 2001; Zhao *et al.* 2019). Various post-translational modifications of the N-terminal tails of histones by a wide range of writer or eraser enzymes define distinct epigenomes which serve either to promote active transcription or gene silencing (Zhao *et al.* 2019). There is increasing evidence indicating the essential functions of histone modifications in environmental responses as well as in the environmental memory of plants to adapt to environmental changes.

Thus, in this mini-review, I have provided a brief overview of the regulation of histone modifications in cold responses, and included a focused review of recent discoveries which highlight the potential molecular mechanisms involved in cold tolerance.

HISTONE METHYLATION IN RESPONSE TO COLD STRESS

Histone methylation refers to the addition of methyl groups to the lysine and arginine residues of histone proteins, and is associated with either the activation or silencing of gene expression, which depends on the methylated residues or the methylation levels (mono-, di-, and trimethylation) (Zhang *et al.* 2009). The methylation targets are lysine residues 4, 9, 27, 36, and 79 in histone H3 and lysine residue 20 in H4 (Black *et al.* 2012). In general, methylations of H3K9, K27, and H4K20 have been implicated in gene silencing, whereas methylations of H3K4, K36, and K79 have been shown to be involved in transcriptional activation (Black *et al.* 2012). In addition, cold stress selectively unsilences tandem repeats in heterochromatin associated with the accumulation of H3K9 acetylation (H3K9ac) and the reduction of DNA methylation and H3K9 dimethylation (H3K9me2) (Hu *et al.* 2012). In *Arabidopsis*, cold stress was shown to induce a reduction in H3K27 trimethylation (H3K27me3) at the promoter regions of two cold-responsive genes, cold-regulated 15A (*COR15A*) and galactinol synthase 3 (*ATGOLS3*), resulting in the upregulation of *COR15A* and *ATGOLS3* (Kwon *et al.* 2009). Interestingly, the cold-induced decrease in H3K27me3 does not contribute to the transcriptional induction of *COR15A* and *ATGOLS3* upon re-exposure to cold stress (Kwon *et al.* 2009), indicating that H3K27me3 possibly plays the role of a memory mark. During vegetative growth, FLOWERING LOCUS C (*FLC*) is in a transcriptionally active state marked by H3K4me3 and H3K36me3, whereas vernalisation induces COOLAIR (long non-coding RNA transcribed antisense from *FLC*) and H3K27me3 to repress *FLC* transcription for timely flowering (Fig. 1; Yang *et al.* 2014; Tian *et al.* 2019; Luo & He 2020). Recent studies have shown that H3K27me3-mediated silencing of *FLC* during vernalisation is reset in the next generation to influence transcriptional re-activation (Crevillén *et al.* 2014; Tao *et al.* 2017), indicating that H3K27me3 facilitates epigenetic memory in the context of nuclear reprogramming (Borg *et al.* 2020). In addition, a large number of active genes involved in stress response and developmental processes are associated with bivalent H3K4me3-H3K27me3 in the response to cold stress in potato tubers (Zeng *et al.* 2019). Furthermore, cold-induced WRKY70, which positively regulates salicylic acid-responsive genes, is correlated with the status of H3K4me3 (Miura *et al.* 2020). These findings indicate that histone methylation is involved in gene regulation during responses to cold stress, thus suggesting that an understanding of cold-induced histone methylation and its targets will facilitate the elucidation of the network of plant cold responses.

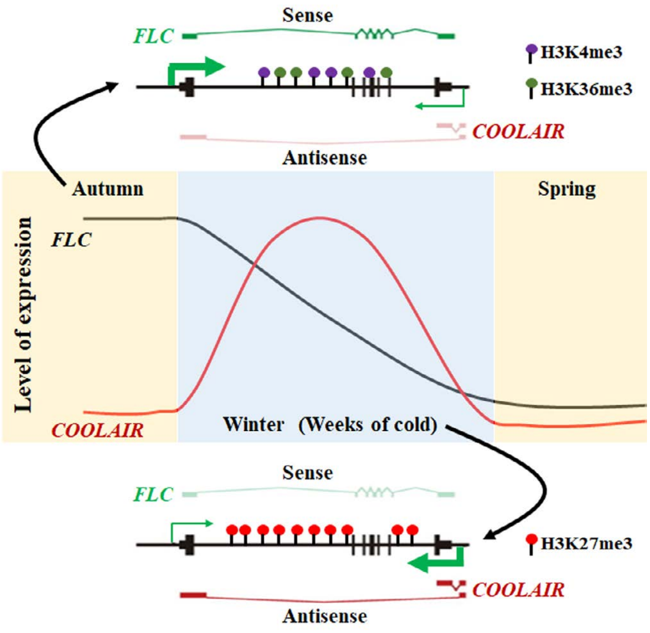

Fig. 1. An epigenetic switch for the repression of FLOWERING LOCUS C (FLC) during vernalisation. Before cold exposure (autumn), histone 3 methylation at lysine 4 and 36 (H3K4me3 and H3K36me3) contributed to the transcriptional induction of *FLC* sense mRNA. During winter, the increased histone 3 methylation at lysine 27 (H3K27me) and the induction of long non-coding RNA COOLAIR repressed *FLC* transcription.

ALTERATIONS OF HISTONE ACETYLATION DURING RESPONSE TO COLD STRESS

Reversible histone acetylation by histone acetyltransferases (HATs) and deacetylation by histone deacetylases (HDACs) at the histone N-terminal tails play a crucial role in gene repression (Pandey *et al.* 2002; Lu & Hyun 2021). Since the identification of 12 *HATs* and 18 *HDACs* in the *Arabidopsis thaliana* genome, several *HATs* and *HDACs* have been identified and isolated from several species (Aquea *et al.* 2010; Eom & Hyun 2021). Although very little is known about the detailed mechanisms regulated by HATs and HDACs, dynamic changes in global histone acetylation and deacetylation in response to stress indicate their role in reprogramming gene expression for plant responses or tolerance to stress (Hu *et al.* 2019). On exposure to cold stress, the hyper-acetylation of H3K9 promotes chromatin remodelling at the promoter and upstream region of the rice dehydration responsive element binding protein 1b, which functions in cold stress response (Roy *et al.* 2014), indicating that modifications in histone acetylation patterns are associated with the transcription of stress response genes. GENERAL CONTROL NON-REPRESSIBLE PROTEIN 5 (GCN5), a well-known plant histone acetyltransferase responsible for the lysine acetylation of histone H3 and H4, plays an important role in the responses to heat stress, cold stress, and nutrient element deficiency by regulating transcriptional activation to maintain the homeostasis of certain key metabolites (Gan *et al.* 2021). In cold acclimation, the C-REPEAT/DRE BINDING FACTOR (CBF)-dependent pathway has been recognized as a key factor which increases plant freezing tolerance by regulating the transcription of *COR* genes (Liu *et al.* 2019). In the *gcn5* mutant, the expression of *COR* genes (e.g. *COR15A*) is increased in response to chilling stress (5°C), but the rate of induction was delayed in comparison with that in wild-type plants, indicating that GCN5 plays a contributory role which enhances the transcriptional level of *COR* genes (Vlachonasios *et al.* 2003). Although the acetylation of histone H3 at the *COR* gene promoters increased on cold acclimation in the *gcn5* mutant to a degree similar to that observed for wild-type plants, the *gcn5* mutant showed delayed cold-induced acetylation of histone H3 at the *COR15A* promoter (Pavangadkar *et al.* 2010). Thus, delayed *COR15A* expression in the *gcn5* mutant is associated with the slow remodeling of chromatin at the *COR15A* promoter, thus indicating functional redundancy between HATs.

Similar to *HATs*, the expression pattern of *HDACs* is changed by environmental stresses (Eom & Hyun 2021), indicating that the functional interplay between HATs and HDACs is required for the dynamic balance in histone acetylation status during the response to environmental stresses. Under cold stress conditions (2°C), the overexpression of HD2D (also known as *HDT4*) in *Arabidopsis* exhibits a lower level of malondialdehyde than wild-type plants, yielding improved cold stress tolerance (Han *et al.* 2016). In contrast, *HD2C* (also known as *HDT3*)-overexpressing plants exhibit sensitivity to freezing stress in comparison with the wild-type plants (Park *et al.* 2018). The WD40-repeat protein HIGH EXPRESSION OF OSMOTICALLY RESPONSIVE GENES15 (HOS15) forms a complex with HD2C to repress *COR* gene expression by removing acetyl groups from *COR* chromatin under normal growth conditions. However, in response to cold stress, HOS15 recruits the CULLIN4-based E3 ubiquitin ligase to induce the ubiquitination and degradation of HD2C, resulting in increased levels of acetylated histone H3 on *COR* chromatin (Fig. 2; Park *et al.* 2018). In addition, the *hos15* mutant exhibits increased expression of stress-regulated genes, and is hypersensitive to freezing stress (Zhu *et al.* 2008). Thus, plant-specific HD2-type HDAC members play distinct roles in cold response processes, suggesting that an understanding of cold-induced HD2-type HDACs and their targets will facilitate the elucidation of the network of plant cold stress responses. In maize, histone hyperacetylation by treatment with the HDAC inhibitor trichostatin A results in hypersensitivity to freezing stress (Hu *et al.* 2011), indicating that the activity of HDACs is positively involved in plant responses to cold stress. Similarly, a loss-of-function mutation in *HDA6*, *Arabidopsis* histone deacetylase 6, resulted in low expression levels of those genes which influence lipid composition and cellular membrane fluidity, reducing the freezing tolerance (To *et al.* 2011). These findings indicate that HDACs facilitate the expression of cold-response genes by regulating histone modification, suggesting that clarification of the functional differences between HATs and HDACs will represent a significant challenge to our future understanding of plant cold responses and cold acclimation.

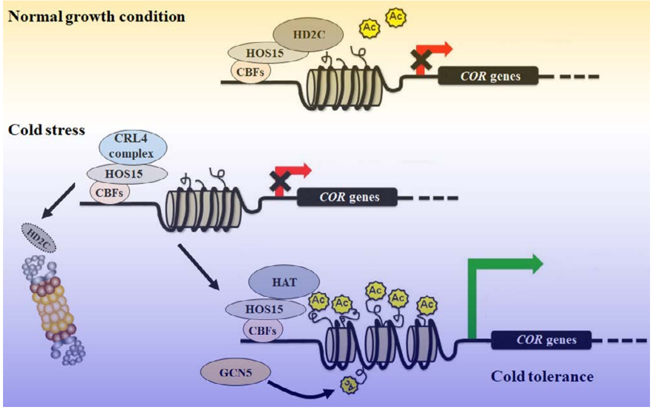

Fig. 2. Cold induces the expression of cold-regulated (*COR*) genes through the HOS15-mediated proteasome pathway and/or GENERAL CONTROLNON-DEREPRESSIBLE5 (GCN5). Under cold stress conditions, HOS15 recruits the CULLIN4-based E3 ubiquitin ligase complex (CRL complex) to induce the dissociation and degradation of HD2C, resulting in the hyperacetylation of histone H3 on *COR* gene chromatin. In addition, GCN5 modulates the histone acetylation of *COR* genes.

OTHER HISTONE MODIFICATIONS

Other histone modifications, including phosphorylation, ubiquitination, and glycosylation, also regulate chromatin-associated processes, such as transcriptionally active/inactive states (Lu & Hyun 2021). Protein ubiquitination, such as monoubiquitination and polyubiquitination, is a common regulatory mechanism used to control protein quality and can be utilised to degrade misfolded or redundant proteins (Balchin *et al.* 2016). In plant chromatin, monoubiquitination found both in histone H2A and H2B is the most abundant ubiquitin conjugate, and is linked to active gene transcription (Woloszynska *et al.* 2019). Histone H2B monoubiquitination (H2Bub1) occurs on K143 or K145 by the heterodimeric HISTONE MONOUBIQUITINATION1/2 (HUB1/2) E3 ubiquitin ligase in *Arabidopsis*

(Bergmuller *et al.* 2007). H2Bub1 regulates the transcription of *FLC* and circadian clock genes such as CIRCADIAN CLOCK ASSOCIATED 1 and TIMING OF CAB EXPRESSION 1 by stimulating H3K4me3 modification (Cao *et al.* 2008; Himanen *et al.* 2012; Malapeira *et al.* 2012). In addition, growing evidence indicates that HUB1/2 is required for the response to abiotic and biotic stresses (Dhawan *et al.* 2009; Hu *et al.* 2014; Zou *et al.* 2014; Chen *et al.* 2019). HUB1/2-mediated H2Bub1 is required for controlling the transcription of the auxin biosynthesis genes TRYPTOPHAN BIOSYNTHESIS 2/TRYPTOPHAN SYNTHASE BETA-SUBUNIT 1, ANTHRANILATE SYNTHASE BETA 1/WEAK ETHYLENE INSENSITIVE7, YUCCA7, and AMIDASE 1 (Zhang *et al.* 2021). In switchgrass, the overexpression of miR393 downregulates the expression of those genes involved in the auxin signaling pathway, resulting in the enhancement of cold tolerance by increasing the expression of cold tolerance-related genes (Liu *et al.* 2017). Although the regulation of histone ubiquitination in cold responses is poorly understood, these findings indicate the possible link between histone ubiquitination and cold responses through the auxin signaling pathway. Therefore, it will be interesting to determine the cold stress response using the gain-of-function and the loss-of-function mutants in HUB1/2.

In yeast, mammalian cells, and plants, the phosphorylation of histone H3 can occur on serine 10 (H3S10ph), serine 28 (H3S28ph), threonine 3 (H3T3ph), and threonine 11 (H3T11ph), and is involved in transcriptional activation, chromosome condensation/segregation, and DNA damage repair (Rossetto *et al.* 2012; Zhang *et al.* 2014). MUT9P-LIKE-KINASES (MLKs) target diverse proteins involved in light signaling, circadian rhythms, phytohormones, and plant defense (Kang *et al.* 2020). In *Arabidopsis*, MUT9P-LIKE-KINASE (MLK) 1 and 2 function as kinases to induce H3T3ph, and MLK4 phosphorylates H2A at serine 95, a plant-specific site (Wang *et al.* 2015; Su *et al.* 2017). When tobacco BY-2 and *Arabidopsis* T87 cells were exposed to salt and cold stresses, dynamic changes in histone H3 phosphorylation were observed (Sokol *et al.* 2007), suggesting that histone phosphorylation is involved in cold-induced transcriptional reprogramming, although the specific mechanisms underlying the relationship between histone phosphorylation and stress responses have not been identified.

CONCLUSIONS

Over the last two decades, several exciting studies have provided models to illuminate the role of histone modification in response to cold stress. Although cold-histone modification appears to be essential for the transcriptional reprogramming which regulates plant physiological and developmental processes, including vernalisation, epigenetic memory, and cold tolerance, the studies conducted to date have yielded relatively little knowledge on the distribution pattern of histone marks in response to cold stress, the distribution patterns required for cold-induced transcriptional reprogramming, and the interactions among different histone modifications. The answers to these questions are essential not only to increase our knowledge but also to facilitate agricultural applications. In addition, comparative genome-wide analysis of the distribution of histone marks under different stress conditions will provide a solid foundation for further evaluation of the potential of histone modification in stress tolerance. Explorations of the physiological functions of histone modification are an interesting and important endeavour which will serve to shed light on the hidden wonders of plant life under cold conditions.

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REFERENCES

Aquea F, Timmermann T & Arce-Johnson P. 2010. Analysis of histone acetyltransferase and deacetylase families of *Vitis vinifera*. *Plant Physiology and Biochemistry* **48**: 194–199.

Balchin D, Hayer-Hartl M & Hartl FU. 2016. In vivo aspects of protein folding and quality control. *Science* **353**: aac4354.

Bergmuller E, Gehrig PM & Gruissem W. 2007. Characterization of posttranslational modifications of histone H2B-variants isolated from *Arabidopsis thaliana*. *Journal of Proteome Research* **6**: 3655–3668.

Black JC, van Rechem C & Whetstine JR. 2012. Histone lysine methylation dynamics: establishment, regulation, and biological impact. *Molecular Cell* **48**: 491–507.

Borg M, Jacob Y, Susaki D, Leblanc C, Buendía D, Axelsson E, Kawashima T, Voigt P, Boavida L, Becker J, Higashiyama T, Martienssen R & Berger F. 2020. Targeted reprogramming of H3K27me3 resets epigenetic memory in plant paternal chromatin. *Nature Cell Biology* **22**: 621–629.

Cao Y, Dai Y, Cui S & Ma L. 2008. Histone H2B monoubiquitination in the chromatin of FLOWERING LOCUS C regulates flowering time in *Arabidopsis*. *Plant Cell* **20**: 2586–2602.

Chen H, Feng H, Zhang X, Zhang C, Wang T & Dong J. 2019. An *Arabidopsis* E3 ligase HUB2 increases histone H2B monoubiquitination and enhances drought tolerance in transgenic cotton. *Plant Biotechnology Journal* **17**: 556–568.

Chinnusamy V, Zhu J & Zhu JK. 2007. Cold stress regulation of gene expression in plants. *Trends in Plant Science* **12**: 444–451.

Crevillén P, Yang H, Cui X, Greeff C, Trick M, Qiu Q, Cao X & Dean C. 2014. Epigenetic reprogramming that prevents transgenerational inheritance of the vernalized state. *Nature* **515**: 587–590.

Dhawan R, Luo H, Foerster AM, Abuqamar S, Du HN, Briggs SD, Mittelsten Scheid O & Mengiste T. 2009. HISTONE MONOUBIQUITINATION1 interacts with a subunit of the mediator complex and regulates defense against necrotrophic fungal pathogens in *Arabidopsis*. *Plant Cell* **21**: 1000–1019.

Eom SH & Hyun TK. 2021. Comprehensive analysis of the histone deacetylase gene family in Chinese cabbage (*Brassica rapa*): from evolution and expression pattern to functional analysis of BraHDA3. *Agriculture* **11**: 244.

Gan L, Wei Z, Yang Z, Li F & Wang Z. 2021. Updated mechanisms of GCN5-the monkey king of the plant kingdom in plant development and resistance to abiotic stresses. *Cells* **10**: 979.

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

Himanen K, Woloszynska M, Boccardi TM, de Groeve S, Nelissen H, Bruno L, Vuylsteke M & van Lijsebettens M. 2012. Histone H2B monoubiquitination is required to reach maximal transcript levels of circadian clock genes in *Arabidopsis*. *Plant Journal* **72**: 249–260.

Hu M, Pei BL, Zhang LF & Li YZ. 2014. Histone H2B monoubiquitination is involved in regulating the dynamics of microtubules during the defense response to *Verticillium dahliae* toxins in *Arabidopsis*. *Plant Physiology* **164**: 1857–1865.

Hu Y, Lu Y, Zhao Y & Zhou DX. 2019. Histone acetylation dynamics integrates metabolic activity to regulate plant response to stress. *Frontiers in Plant Science* **10**: 1236.

Hu Y, Zhang L, He S, Huang M, Tan J, Zhao L, Yan S, Li H, Zhou K, Liang Y & Li L. 2012. Cold stress selectively unsilences tandem repeats in heterochromatin associated with accumulation of H3K9ac. *Plant, Cell & Environment* **35**: 2130–2142.

Hu Y, Zhang L, Zhao L, Li J, He S, Zhou K, Yang F, Huang M, Jiang L & Li L. 2011. Trichostatin A selectively suppresses the cold-induced transcription of the ZmDREB1 gene in maize. *PLoS One* **6**: e22132.

Hussain HA, Hussain S, Khaliq A, Ashraf U, Anjum SA, Men S & Wang L. 2018. Chilling and drought stresses in crop plants: implications, cross talk, and potential management opportunities. *Frontiers in Plant Science* **9**: 393.

Jenuwein T & Allis CD. 2001. Translating the histone code. *Science* **293**: 1074–1080.

Kang J & Wang Z. 2020. Mut9p-LIKE KINASE family members: new roles of the plant-specific casein kinase I in plant growth and development. *International Journal of Molecular Sciences* **21**: 1562.

Kwon CS, Lee D, Choi G & Chung WI. 2009. Histone occupancy-dependent and -independent removal of H3K27 trimethylation at cold-responsive genes in Arabidopsis. *Plant Journal* **60**: 112–121.

Liang Z, Riaz A, Chachar S, Ding Y, Du H & Gu X. 2020. Epigenetic Modifications of mRNA and DNA in Plants. *Molecular Plant* **13**: 14–30.

Liu Y, Dang P, Liu L & He C. 2019. Cold acclimation by the CBF-COR pathway in a changing climate: Lessons from *Arabidopsis thaliana*. *Plant Cell Reports* **38**: 511–519.

Liu Y, Wang K, Li D, Yan J & Zhang W. 2017. Enhanced cold tolerance and tillering in switchgrass (*Panicum virgatum* L.) by heterologous expression of Osa-miR393a. *Plant & Cell Physiology* **58**: 2226–2240.

Lu X & Hyun TK. 2021. The role of epigenetic modifications in plant responses to stress. *Botanica Serbica* **45**(1): 3–12.

Luo X & He Y. 2020. Experiencing winter for spring flowering: A molecular epigenetic perspective on vernalization. *Journal of Integrative Plant Biology* **62**: 104–117.

Malapeira J, Khaitova LC & Mas P. 2012. Ordered changes in histone modifications at the core of the Arabidopsis circadian clock. *Proceedings of the National Academy of Sciences USA* **109**: 21540–21545.

Miura K, Renhu N & Suzaki T. 2020. The PHD finger of *Arabidopsis* SIZ1 recognizes trimethylated histone H3K4 mediating SIZ1 function and abiotic stress response. *Communications Biology* **3**: 23.

Ouellet F. 2002. Out of the cold: Unveiling the elements required for low temperature induction of gene expression in plants. *In Vitro Cellular & Developmental Biology-Plant* **38**: 396–403.

Pandey R, Müller A, Napoli CA, Selinger DA, Pikaard CS, Richards EJ, Bender J, Mount DW & Jorgensen RA. 2002. Analysis of histone acetyltransferase and histone deacetylase families of *Arabidopsis thaliana* suggests functional diversification of chromatin modification among multicellular eukaryotes. *Nucleic Acids Research* **30**: 5036–5055.

Park J, Lim CJ, Shen M, Park HJ, Cha JY, Iniesto E, Rubio V, Mengiste T, Zhu JK, Bressan RA, Lee SY, Lee BH, Jin JB, Pardo JM, Kim WY & Yun DJ. 2018. Epigenetic switch from repressive to permissive chromatin in response to cold stress. *Proceedings of the National Academy of Sciences USA* **115**: E5400–E5409.

Pavangadkar K, Thomashow MF & Triezenberg SJ. 2010. Histone dynamics and roles of histone acetyltransferases during cold-induced gene regulation in *Arabidopsis*. *Plant Molecular Biology* **74**: 183–200.

Pikaard CS & Mittelsten Scheid O. 2014. Epigenetic regulation in plants. *Cold Spring Harbor Perspectives in Biology* **6**: a019315.

Rossetto D, Avvakumov N & Côté J. 2012. Histone phosphorylation: a chromatin modification involved in diverse nuclear events. *Epigenetics* **7**: 1098–1108.

Roy D, Paul A, Roy A, Ghosh R, Ganguly P & Chaudhuri S. 2014. Differential acetylation of histone H3 at the regulatory region of OsDREB1b promoter facilitates chromatin remodelling and transcription activation during cold stress. *PloS One* **9**: e100343.

Sokol A, Kwiatkowska A, Jerzmanowski A & Prymakowska-Bosak M. 2007. Up-regulation of stress-inducible genes in tobacco and *Arabidopsis* cells in response to abiotic stresses and ABA treatment correlates with dynamic changes in histone H3 and H4 modifications. *Planta* **227**: 245–254.

Su Y, Wang S, Zhang F, Zheng H, Liu Y, Huang T & Ding Y. 2017. Phosphorylation of histone H2A at serine 95: a plant-specific mark involved in flowering time regulation and H2A.Z deposition. *Plant Cell* **29**: 2197–2213.

Tang D, Gallusci P & Lang Z. 2020. Fruit development and epigenetic modifications. *New Phytologist* **228**: 839–844.

Tao Z, Shen L, Gu X, Wang Y, Yu H & He Y. 2017. Embryonic epigenetic reprogramming by a pioneer transcription factor in plants. *Nature* **551**: 124–128.

Tian Y, Zheng H, Zhang F, Wang S, Ji X, Xu C, He Y & Ding Y. 2019. PRC2 recruitment and H3K27me3 deposition at FLC require FCA binding of COOLAIR. *Science Advances* **5**: eaau7246.

To TK, Nakaminami K, Kim JM, Morosawa T, Ishida J, Tanaka M, Yokoyama S, Shinozaki K & Seki M. 2011. *Arabidopsis* HDA6 is required for freezing tolerance. *Biochemical and Biophysical Research Communications* **406**: 414–419.

Vlachonasios KE, Thomashow MF & Triezenberg SJ. 2003. Disruption mutations of ADA2b and GCN5 transcriptional adaptor genes dramatically affect Arabidopsis growth, development, and gene expression. *Plant Cell* **15**: 626-638.

Vyse K, Pagter M, Zuther E & Hincha DK. 2019. Deacclimation after cold acclimation-a crucial, but widely neglected part of plant winter survival. *Journal of Experimental Botany* **70**: 4595-4604.

Wang Z, Casas-Mollano JA, Xu J, Riethoven J-JM, Zhang C & Cerutti H. 2015. Osmotic stress induces phosphorylation of histone H3 at threonine 3 in pericentromeric regions of *Arabidopsis thaliana*. *Proceedings of the National Academy of Sciences USA* **112**: 8487-8492.

Woloszynska M, Le Gall S, Neyt P, Boccardi TM, Grasser M, Längst G, Aesaert S, Coussens G, Dhondt S, van de Slijke E, Bruno L, Fung-Uceda J, Mas P, van Montagu M, Inzé D, Himanen K, de Jaeger G, Grasser KD & van Lijsebettens M. 2019. Histone 2B monoubiquitination complex integrates transcript elongation with RNA processing at circadian clock and flowering regulators. *Proceedings of the National Academy of Sciences USA* **116**: 8060-8069.

Yamazaki T, Kawamura Y & Uemura M. 2009. Extracellular freezing-induced mechanical stress and surface area regulation on the plasma membrane in cold-acclimated plant cells. *Plant Signaling & Behavior* **4**: 231-233.

Yang HC, Howard M & Dean C. 2014 Antagonistic roles for H3K36me3 and H3K27me3 in the cold-induced epigenetic switch at *Arabidopsis* FLC. *Current Biology* **24**: 1793-1797.

Zeng Z, Zhang W, Marand AP, Zhu B, Buell CR & Jiang J. 2019. Cold stress induces enhanced chromatin accessibility and bivalent histone modifications H3K4me3 and H3K27me3 of active genes in potato. *Genome Biology* **20**: 123.

Zhang B, Dong Q, Su H, Birchler JA & Han F. 2014. Histone phosphorylation: its role during cell cycle and centromere identity in plants. *Cytogenetic and Genome Research* **143**: 144-149.

Zhang L, Luo P, Bai J, Wu L, Di DW, Liu HQ, Li JJ, Liu YL, Khaskheli AJ, Zhao CM & Guo GQ. 2021. Function of histone H2B monoubiquitination in transcriptional regulation of auxin biosynthesis in *Arabidopsis*. *Communications Biology* **4**: 206.

Zhang X, Bernatavichute YV, Cokus S, Pellegrini M & Jacobsen SE. 2009. Genome-wide analysis of mono-, di- and trimethylation of histone H3 lysine 4 in *Arabidopsis thaliana*. *Genome Biology* **10**: R62.

Zhao T, Zhan Z & Jiang D. 2019. Histone modifications and their regulatory roles in plant development and environmental memory. *Journal of Genetics and Genomics* **46**: 467-476.

Zhu J, Jeong JC, Zhu Y, Sokolchik I, Miyazaki S, Zhu JK, Hasegawa PM, Bohnert HJ, Shi H, Yun DJ & Bressan RA. 2008. Involvement of *Arabidopsis* HOS15 in histone deacetylation and cold tolerance. *Proceedings of the National Academy of Sciences of the United States of America* **105**: 4945-4950.

Zou B, Yang DL, Shi Z, Dong H & Hua J. 2014. Monoubiquitination of histone 2B at the disease resistance gene locus regulates its expression and impacts immune responses in *Arabidopsis*. *Plant Physiology* **165**: 309-318.

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Modifikacije biljnih histona kao odgovor na hladni stres

Tae Kyung Hyun

Hladni stres je glavni faktor životne sredine koji ograničava ekspanziju poljoprivrede i prinose useva, a biljke su razvile različite molekularne mehanizme koji im omogućavaju da se nose sa izlaganjem hladnom stresu tokom čitavog života. Modifikacije histona igraju osnovnu ulogu u regulisanju dinamike hromatina i aktivacije transkripcije, bilo direktno ili preko proteinskih adaptera koji se nazivaju efektori. Sve je više dokaza da su remodeliranje hromatina uzrokovano modifikacijama histona, uključujući acetilaciju, metilaciju, fosforilaciju i ubikvitinaciju potrebni za transkripciju koja reaguje na stres, adaptaciju na stres i memoriju stresa kod biljaka. U ovom preglednom radu sažeta su trenutna saznanja u vezi modifikacija histona povezanim sa odgovorima biljaka na stres od hladnoće i diskutovano o ulozi ovih modifikacija u poboljšanju tolerancije biljaka na hladnoću.

Ključne reči: aklimatizacija na hladnoću, epigenetska regulacija, vernalizacija, reprogramiranje transkripcije