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Research Article

Histone deacetylase family in balloon flower (*Platycodon grandiflorus*): Genome-wide identification and expression analysis under waterlogging stress

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Abstract Histone deacetylases (HDACs) play a pivotal role in epigenetic regulation, affecting the structure of chromatin and gene expression across different stages of plant development and in response to environmental stresses. Although the role of HDACs in *Arabidopsis* and rice has been focused on in extensive research, the role of the *HDAC* gene family in various medicinal plants remains unclear. In the genome of the balloon flower (*Platycodon grandiflorus*), we identified 10 putative *P. grandiflorus* HDAC (PlgHDAC) proteins, which were classified into the three families (RPD3/HDA1, SIR2, and HD2 HDAC families) based on their domain compositions. These HDACs were predicted to be localized in various cellular compartments, indicating that they have diverse functions. In addition, the tissue-specific expression profiles of *PlgHDACs* differed across different plant tissues, indicating that they are involved in various developmental processes. Furthermore, the expression levels of all *PlgHDACs* were upregulated in leaves after waterlogging treatment, implying their potential role in coping with waterlogging-induced stress. Overall, our findings provide a comprehensive foundation for further research into the epigenetic regulation of PlgHDACs, and particularly, on their functions in response to environmental stresses such as waterlogging. Understanding the roles of these HDACs in the development and stress responses of balloon flower could have significant implications for improving crop yield and the quality of this important medicinal plant.

Keywords Histone deacetylase, histone acetylation, *Platycodon grandiflorus*, waterlogging stress

Introduction

Dynamic chromatin structures, as influenced by histone modifications, DNA methylation, and chromatin remodeling (Allis and Jenuwein 2016), play a key role in modulating gene activities in higher eukaryotes (Luger et al. 2012). Among histone modifications, histone acetylation is a dynamic and versatile epigenetic marker that occurs on the lysine (K) residues of histone tails. This process causes the charge of histones to shift from positive to neutral, typically facilitating a transcriptionally permissive, decondensed chromatin environment (de Rooij et al. 2020). Histone acetyltransferases (HATs) are responsible for adding acetyl groups, whereas histone deacetylases (HDACs) maintain the homeotic balance of histone acetylation by removing acetyl groups from hyperacetylated histones (Lu and Hyun 2021). These interactions emphasize the significant role of HATs and HDACs in the epigenetic regulation of gene transcription, which, in turn, governs various physiological and developmental processes (Jiang et al. 2020).

In eukaryotes, HDACs are typically categorized into two main groups based on their domain composition: the reduced potassium dependence 3/histone deacetylase 1 (RPD3/HDA1) family and the silent information regulator 2 (SIR2) family. Additionally, plants and certain streptophyte green algae contain an additional plant-specific HDAC family known as histone deacetylase 2 (HD2) (Pandey et al. 2002). Since HDACs were identified from various plants, genetic and physiological studies have revealed that HDA6, HDA9, HDA15, HDA19, HD2C, and SRT1 are integral to several plant biological processes including development, flowering, germination, and stress tolerance (Liu et al. 2014). For example, HDA19 is an important factor for proper vegetative development as *hda19* mutants displayed various developmental abnormalities (Long et al. 2006). HDA9

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controls flowering time by suppressing the AGAMOUS-LIKE19 which promotes flowering independently of the FLOWERING LOCUS C pathway (Kim et al. 2013). Under abiotic stress conditions including salt and drought stress, HDA19-deficiency leads to enhanced tolerance to high salinity, drought, and heat stress in *Arabidopsis* (Ueda et al. 2018; Zheng et al. 2016). In contrast, *AtHD2D* overexpression in *Arabidopsis* resulted in enhanced tolerance against salt and drought stresses (Han et al. 2016). In rice, OsHDA704, which is a RPD3/HDA1-type HDAC, enhanced drought and salt tolerance by regulating the stomatal aperture and density by inhibiting the expression of the drought and salt tolerance (*DST*) and abscisic acid-insensitive like 2 (*ABIL2*) genes (Zhao et al. 2021). Similarly, overexpression of *OsHDT701* (rice HD2 family) in transgenic rice leads to increased tolerance to NaCl and PEG stresses in two-week-old rice seedlings (Zhao et al. 2015). The physiological functions of HDACs have primarily been characterized in model plants such as *Arabidopsis* and rice. These findings indicate that HDACs play an important regulatory role in plant development and in the response to various abiotic stresses. Nevertheless, to gain a more comprehensive understanding of histone acetylation changes across different plant species, HDACs within different plant genomes must be identified and analyzed systematically.

In this study, we performed a comprehensive genome-wide analysis of balloon flower (*Platycodon grandiflorus*), a highly significant medicinal crop, using publicly available databases and bioinformatic tools. Phylogenetic classification and domain analyses were performed to predict the specific functions of *P. grandiflorus* HDACs (PlgHDACs) in comparison with the HDACs of other organisms. We conducted additional analyses of tissue-specific and waterlogging-stress-responsive expression profiles. Our genomic and bioinformatic analyses will serve as the basis for subsequent functional investigations of histone modifications in the balloon flower.

Materials and Methods

Identification and characterization of the HADC family in *P. grandiflorus*

To identify members of the PlgHDAC family, the genome sequences of *P. grandiflorus* were queried against the *Arabidopsis* and rice HDAC sequences using the Basic Local Alignment Search Tool (BLAST) algorithms BLASTp and tBLASTn. The conserved domains, molecular weight, phylogeny, and isoelectric point (pI) were analyzed, and subcellular localization (WoLF PSORT; https://wolfpsort.hgc.jp/) of putative PlgHDACs was conducted as described by Eom and Hyun (2021).

The propensity for the formation of alpha-helical coiled-coils within class I PlgHDAC proteins was analyzed using the PRABI-Lyon-Gerland program (https://npsa-pbil.ibcp.fr/cgi-bin/npsa_automat.pl?page=/NPSA/npsa_lupas.html).

Analysis of tissue-specific expression profiles

To analyze the tissue-specific expression of *PlgHDACs*, RNA-Seq data from eight different tissues were downloaded from NCBI GenBank (SRR8712510-SRR8712517). The expression levels of each gene were estimated in fragments per kilobase of transcript per million mapped read values, as described by Kim et al. (2020).

Plant growth and treatment

One-year-old balloon flower roots were transplanted into the soil and cultivated in a growth chamber in a controlled environment (temperature: 24°C; relative humidity: 50%). After four weeks of transplantation, we placed the healthy potted plants in a plastic water-filled container, ensuring that the water level was consistently maintained at 3 cm above the soil surface, as described by Ji and Hyun (2023). At the designated time points (0, 3, 5, 9, 13, and 18 days), leaves (fully expanded) and roots were harvested, frozen in liquid nitrogen, and stored at -80°C until further analyses.

Quantitative real-time PCR (qRT-PCR) analysis

To investigate the expression of *PlgHDAC* genes, qRT-PCR analysis was performed. The total RNA from the balloon flower leaves and roots was extracted according to the manufacturer's instructions (Favorgen, Ping Tung, Taiwan) and reverse-transcribed into cDNA. qRT-PCR was performed using the Toyobo SYBR-Green Master Mix (Toyobo, Co., Ltd., Osaka, Japan), with the balloon flower actin gene serving as the internal reference. The expression levels of each gene were normalized to the constitutive expression level of actin and were calculated relative to its values at 0 day. The expression level was represented as a log2 ratio. The primer sequences are listed in Table 1.

Results and Discussion

Identification of HDAC proteins in balloon flower

Using the sequences of HDAc proteins of *Arabidopsis* and

Table 1 Primer sequences for qRT-PCR analysis

Primer name	Sequence (5'-3')
PlgHDA1	F-GCAATCGCGACTAGCTTTCT R-CGAGGGTCCTTCCAGAACAT
PlgHDA2	F-CGTGCCGCTACTCTTATTGG R-AGCTGCCGGGAGTTCTTATT
PlgHDA3	F-GCCGGAGCTTCTTCTACATC R-GGCACATCGAAGTAGAGCTTG
PlgHDA4	F-CGGAAATGGAACTGCTGAGG R-GCACACTTGTAGCCCTTGTC
PlgHDA5	F-GGTTCTGGACCAACTTACGC R-CCAATGGGAGGGTTCTGACT
PlgHDA6	F-TGGAGAAGATTGCCCTGTCT R-AACCCAGATGCCTCACACTT
PlgHDA7	F-CTGTGATGTGACACCTGCTG R-GCAAGGACTTTCACCAAGCA
PlgHDT1	F-GAAAGAAAGGTGGAGGCCAT R-GCCTGGTTGTGGGATGAAAG
PlgSRT1	F-CGCTTAAATCACGGCCACTT R-TGCCCACAGCATTGATCTTG
PlgSRT2	F-GCTTTCCGACTTGTCAGAGC R-ACGCTGAGAGATCCAATGCT
PlgActin	F-CCATACAGTCCCCATTTATGAAG R-GCTAACTTCTCCTTCATGTCTCTCA

rice, candidate HDAC proteins were identified from the balloon flower genome data. The redundant sequences were removed, resulting in a total of 10 putative *HDAC* genes from balloon flower (Fig. 1 and Table 2). The identification of conserved domains, including the Hist_deacetyl domain (PF00850), SIR2 domain (PF02146), and ZnF_C2H2 domain (SM000355), allowed for the characterization of plant RPD3/HDA1, HD2, and SIR2 families (Peng et al. 2017; Zhang et al. 2020). As shown in Fig. 1, PlgHDACs were classified into three major families: RPD3/HDA1, HD2, and SIR2. The balloon flower genome encodes seven

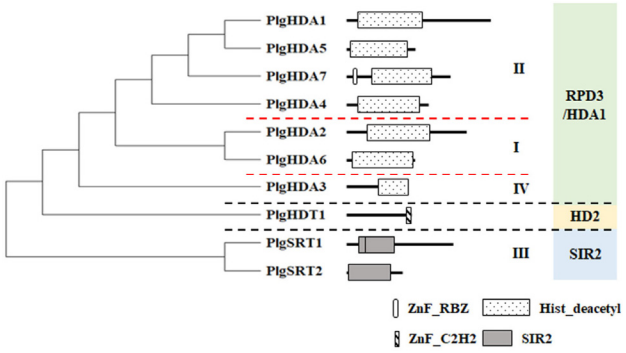

Fig. 1 The phylogenetic tree for the *P. grandiflorus* HDAC family was constructed using the neighbor-joining method in MEGA7. In addition, SMART program was employed to analyze the conserved domains

proteins that belong to the RPD3/HDA1 family; these proteins require Zn^{2+} as a cofactor for their deacetylase activity and contain the conserved Hist_deacetyl domain (Yruela et al. 2021). In addition, we identified two HDACs in the SIR2 family, which is characterized by their highly conserved SIR2 domain and by the use of NAD^{+} as a cofactor for the enzymatic reaction (Yruela et al. 2021). Furthermore, PlgHDT1 contains the ZnF_RTZ domain (SM000547), which has a high binding affinity to DNA or modulate protein-protein interactions (Yang et al. 2018). The presence of domains similar to those found in other plant HDACs suggested that all putative PlgHDACs were a part of the histone deacetylase family. The C-terminal of the human and mouse HDA2 proteins (class I HDAC) contains a coiled-coil region, which is involved in additional protein-protein associations and may account for some amount of functional differentiation (Gregoretti et al. 2004). Similarly, PlgHDA2 exhibits a C-terminal coiled-coil region, whereas PlgHDA6 does not possess this structural feature (Fig. 2). In yeast, the coiled-coil regions form the HDA2-

Table 2 Histone deacetylase gene family in *P. grandiflorus*

Name	Accession number	CDS (bp)	Amino acids	pI	MW (kDa)	Subcellular localization
PlgHDA1	PGJG203730	2007	668	5.29	74.5	nucleus: 5, cytosol: 4
PlgHDA2	PGJG219540	1674	557	5.13	62.4	chloroplast: 6, nucleus: 4
PlgHDA3	PGJG240380	891	296	5.79	33.3	cytosol: 7, chloroplast: 3, nucleus: 3
PlgHDA4	PGJG278370	1167	388	5.57	42.0	cytosol: 8, nucleus: 4
PlgHDA5	PGJG279580	972	323	5.61	34.9	endoplasmic reticulum: 3, cytosol: 2
PlgHDA6	PGJG302990	978	325	5.96	36.7	cytosol: 11
PlgHDA7	PGJG371110	1503	500	6.68	54.8	nucleus: 4, cytosol: 3.5
PlgHDT1	PGJG290750	924	307	4.66	33.7	nucleus: 14
PlgSRT1	PGJG183370	1476	491	9.27	55.0	cytosol: 5, nucleus: 4
PlgSRT2	PGJG193290	780	259	6.96	28.6	chloroplast: 9, nucleus: 4

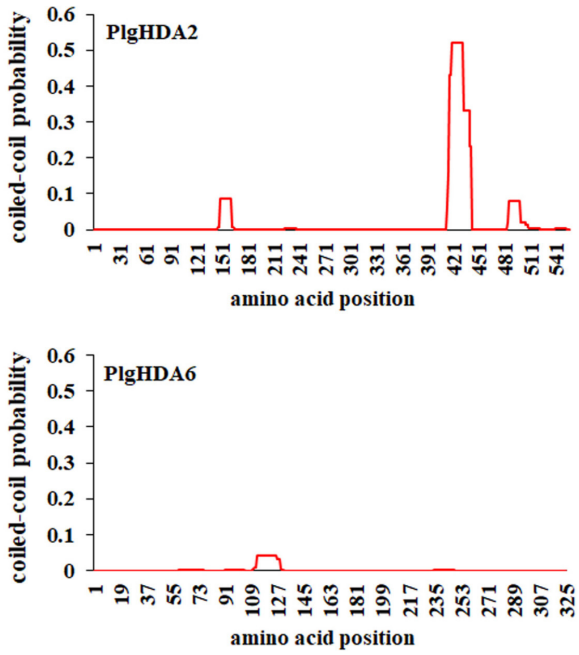

Fig. 2 Propensity for the formation of alpha-helical coiled-coils in Class I PlgHDACs as estimated using the PRABI-Lyon-Gerland program

HDA3 heterodimeric subcomplex, which serves as an unspecific DNA-binding module (Park and Kim 2020). Although whether PlgHDA2 (class I HDAC) forms dimers or oligomers remains unclear, the presence of the coiled-coil region in various HDACs suggests that self-association may be an ancestral feature that is common among class I HDACs. Therefore, the further characterization of PlgHDA2 will be essential to understand whether dimerization (homo or hetero) is required for its activity.

Among PlgHDACs, PlgHDA1 was the largest protein, with 668 amino acids (AAs), whereas PlgSRT2 was identified as the smallest protein with 259 AAs. The molecular weight of PlgHDACs varied according to protein size, ranging from 28.6 KDa to 74.5 KDa, and their pI values varied from 4.66 (PlgHDT1) to 9.27 (PlgSRT1). WoLF PSORT was used to predict the subcellular localization of the proteins. PlgHDACs were potentially localized in the cytosol, nucleus, and chloroplast (Table 2). Similar to the *Arabidopsis*, soybean, and *Brassica rapa* HD2 proteins (Eom and Hyun 2021; Yang et al. 2018; Zhou et al. 2004), the PlgHDT1 family were predicted to be nuclear proteins (Table 2). The nuclear localization of PlagHDACs may be associated with their primary histone deacetylation function because histone deacetylation primarily occurs in the nucleus. Meanwhile, certain PlagHDACs, such as PlgHDA5 and PlgHDA6, found in various organelles may also contribute to the acetylation of non-histone proteins. For example, the chloroplast-localized AtHDA14 regulates the lysine acetylation of rubisco activators to modulate the activation of the enzyme rubisco, which is an essential component in the process of photosynthesis (Hartl et al. 2017). AtSRT2, which is a mitochondrial lysine deacetylase, controls energy metabolism and metabolite transport through the deacetylation of endometrial protein complexes involved in energy metabolism and metabolite transport (König et al. 2014). Taken together, the various localization patterns of PlgHDACs indicate that they may have distinct roles.

Tissue-specific expression profiles of *HDAC* genes in balloon flower

Analysis of the tissue-specific expression patterns is helpful for determining whether the gene of interest plays a role in defining the function of the given tissues. The expression patterns of *PlgHDAC* genes were examined in different tissues including the leaf, root, stem, seed, petal, pistal, sepal, and stamen. As shown in Fig. 3, expression patterns of *PlgHDAC* genes could be divided into six groups. Genes in group I, II, and VI exhibited a higher expression level in the stem, leaf, and root, respectively, compared to their expression in other tissues. *PlgHDT1* exhibited higher expression levels in most of the tested tissues compared to other *PlgHDACs*, whereas *PlgSRT1* displayed low or no expression in the tested tissues. The distinct

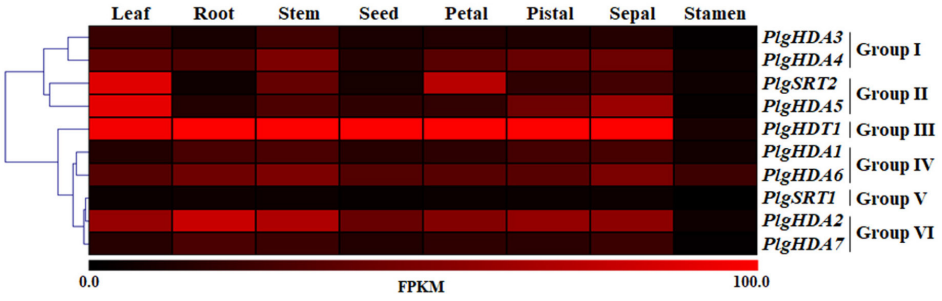

Fig. 3 Tissue-specific expression pattern of *PlgHDACs*. Data represent the FPKM values of RNA-Seq data generated from eight different tissues of *P. grandiflorus*

expression patterns of *PlgHDACs* suggest that they play varying functional roles in the development processes of the plant. In *Arabidopsis*, the loss-of-function *AtHDA19* mutant exhibited a variety of flower-development aberrations, including reduced female fertility, smaller siliques, and abnormal flowers (Tian and Chen 2001; Tian et al. 2005). Additionally, dysfunction of the *Arabidopsis* histone acetyltransferase AtGCN5 caused short stamens and petals (Vlachonasios et al. 2003). While the transcription levels of most *PlgHDACs* were lower in the stamen compared to that in other tissues, these observations suggest that histone deacetylation plays a key role in orchestrating gene expression during reproductive development.

Expression of *PlgHDACs* in response to waterlogging stress

Waterlogging affects crop production and yield quality by inhibiting aerobic respiration in the roots (Pan et al. 2021). The balloon flower possesses a taproot system, and the incidence of root rot disease was high in soil conditions with elevated moisture levels (Jeon et al. 2013), indicating that waterlogging directly and indirectly affects the quality and yield of balloon flower. To investigate the involvement of PlgHDACs in balloon flower during responses to waterlogging stress, the expression pattern of each gene was analyzed by qRT-PCR. As shown in Fig. 4, all expression levels of all *PlgHDACs* were upregulated in leaves after waterlogging treatment. In class I, the accumulation of *PlgHDA5* or *7* transcripts was transient, peaking at either 3 days or 9 days after waterlogging treatment, whereas the highest expression of *PlgHDA1* and *4* was observed at 18 days after waterlogging treatment. In rice, the acetylation of histone H3K18 and H3K27 was significantly elevated compared to that in the control group after drought treatment for 24 h, whereas increased acetylation level of histone H3K9 was observed when the rice plants were treated with drought for 33 h (Fang et al. 2014). This finding suggested that the variation in the acetylation patterns of histone 3 may be attributable to the distinct transcription patterns of histone-modifying enzymes under drought conditions, suggesting that the varying responses among *PlgHDACs* are likely necessary to account for the differences in the acetylation patterns of histone 3. In *Arabidopsis*, AtSRT2 positively regulates salt tolerance during seed germination by downregulating vesicle-associated membrane protein 714 (Tang et al. 2022). Similarly, *OsSRT1* overexpression enhanced the tolerance to oxidative stress (Huang et al. 2007). These findings indicate that the increasing level of *PlgSRT1* and *2* in leaves and roots (Fig. 4) might be required for tolerances against waterlogging stress. To support this hypothesis, further analysis with genetic mutants of *PlgSRT1* and *2* will be required.

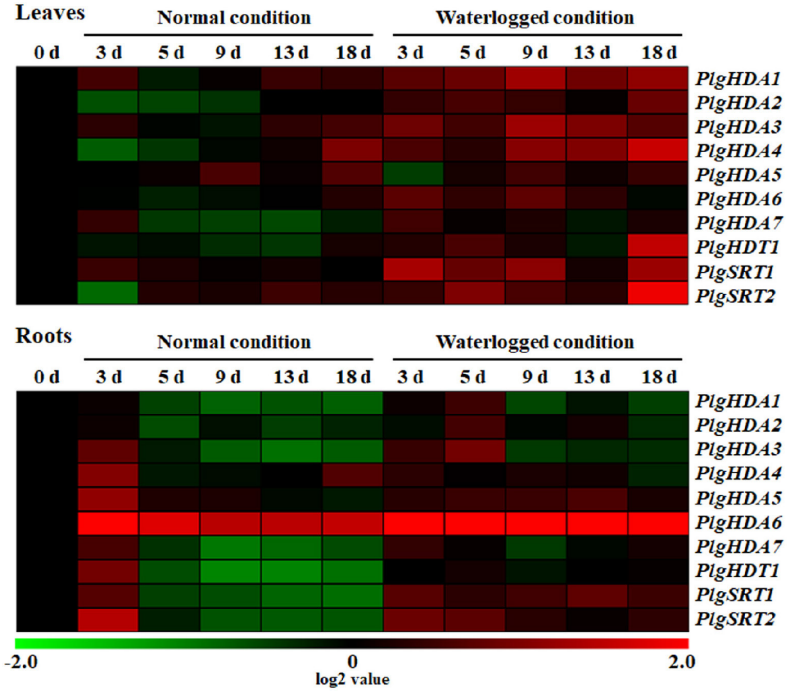

Fig. 4 The expression pattern of *PlgHDACs* of balloon flower in response to waterlogging stress. The expression level is represented as the log2 ratio, and the heatmap represents the expression levels of genes determined using qRT-PCR

Conclusion

We performed comprehensive analyses of the HDAC gene family in balloon flower and identified 10 putative HDAC genes that can be divided into three families: RPD3/HDA1, SIR2, and HD2. The expression profiles indicated that *PlgHDAC* genes are differentially expressed in all the tissues examined, and all of them were waterlogging-stress-responsive. Although additional research is required to fully characterize the functions of PlgHDACs, our results offer a sound starting point for future efforts aimed at understanding the epigenetic regulation of PlgHDACs in response to environmental stresses.

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References

Allis CD, Jenuwein T (2016) The molecular hallmarks of epigenetic control. Nat Rev Genet 17:487-500

de Rooij PGH, Perrella G, Kaiserli E, van Zanten M (2020) The diverse and unanticipated roles of histone deacetylase 9 in coordinating plant development and environmental acclimation. J Exp Bot 71:6211-6225

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

Fang H, Liu X, Thorn G, Duan J, Tian L (2014) Expression analysis of histone acetyltransferases in rice under drought stress. Biochem Biophys Res Commun 443:400-405

Gregoretti IV, Lee YM, Goodson HV (2004) Molecular evolution of the histone deacetylase family: functional implications of phylogenetic analysis. J Mol Biol 338:17-31

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*. Front Plant Sci 7:310

Hartl M, Füßl M, Boersema PJ, Jost JO, Kramer K, Bakirbas A, Sindlinger J, Plöchinger M, Leister D, Uhrig G, Moorhead GB, Cox J, Salvucci ME, Schwarzer D, Mann M, Finkemeier I (2017) Lysine acetylome profiling uncovers novel histone deacetylase substrate proteins in Arabidopsis. Mol Syst Biol 13:949

Huang L, Sun Q, Qin F, Li C, Zhao Y, Zhou DX (2007) Down-regulation of a SILENT INFORMATION REGULATOR2-related histone deacetylase gene, OsSRT1, induces DNA fragmentation and cell death in rice. Plant Physiol 144: 1508-1519

Jeon CS, Kim GH, Son KI, Hur JS, Jeon KS, Yoon JH, Koh YJ (2013) Root rot of balloon flower (*Platycodon grandiflorum*) caused by *Fusarium solani* and *Fusarium oxysporum*. Plant Pathol J 29:440-445

Ji HS, Hyun TK (2023) Physiological and sucrose metabolic responses to waterlogging stress in balloon flower (*Platycodon grandiflorus* (Jacq.) A. DC). Physiol Mol Biol Plants 29: 591-600

Jiang J, Ding AB, Liu F, Zhong X (2020) Linking signaling pathways to histone acetylation dynamics in plants. J Exp Bot 71:5179-5190

Kim J, Kang SH, Park SG, Lee Y, Kim OT, Chung O, Lee J, Choi JP, Kwon SJ, Lee K, Ahn BO, Lee DJ, Yoo Si, Shin IG, Um Y, Lee DY, Kim GS, Hong CP, Bhak J, Kim CK (2020) Whole-genome, transcriptome, and methylome analyses provide insights into the evolution of platycoside biosynthesis in *Platycodon grandiflorus*, a medicinal plant. Hortic Res 7: 1-12

Kim W, Latrasse D, Servet C, Zhou DX (2013) Arabidopsis histone deacetylase HDA9 regulates flowering time through repression of AGL19. Biochem Biophys Res Commun 432: 394-398

König AC, Hartl M, Pham PA, Laxa M, Boersema PJ, Orwat A, Kalitventseva I, Plöchinger M, Braun HP, Leister D, Mann M, Wachter A, Fernie AR, Finkemeier I (2014) The Arabidopsis class II sirtuin is a lysine deacetylase and interacts with mitochondrial energy metabolism. Plant Physiol 164:1401-1414

Liu X, Yang S, Zhao M, Luo M, Yu CW, Chen CY, Tai R, Wu K (2014) Transcriptional repression by histone deacetylases in plants. Mol Plant 7:764-772

Long JA, Ohno C, Smith ZR, Meyerowitz EM (2006) TOPLESS regulates apical embryonic fate in Arabidopsis. Science 312: 1520-1523

Lu X, Hyun TK (2021) The role of epigenetic modifications in plant responses to stress. Bot Serbica 45:3-12

Luger K, Dechassa ML, Tremethick DJ (2012) New insights into nucleosome and chromatin structure: an ordered state or a disordered affair? Nat Rev Molr Cell Biol 13:436-447

Pan J, Sharif R, Xu X, Chen X (2021) Mechanisms of waterlogging tolerance in plants: research progress and prospects. Front Plant Sci 11:627331

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 Res 30:5036-5055

Park SY, Kim JS (2020) A short guide to histone deacetylases including recent progress on class II enzymes. Exp Mol Med 52:204-212

Peng M, Ying P, Liu X, Li C, Xia R, Li J, Zhao M (2017) Genome-wide identification of histone modifiers and their expression patterns during fruit abscission in litchi. Front

Plant Sci 8:639

Tang WS, Zhong L, Ding QQ, Dou YN, Li WW, Xu ZS, Zhou YB, Chen J, Chen M, Ma YZ (2022) Histone deacetylase AtSRT2 regulates salt tolerance during seed germination via repression of vesicle-associated membrane protein 714 (VAMP714) in Arabidopsis. New Phytol 234:1278-1293

Tian L, Chen ZJ (2001) Blocking histone deacetylation in Arabidopsis induces pleiotropic effects on plant gene regulation and development. Proc Natl Acad Sci USA 98:200-205

Tian L, Fong MP, Wang JJ, Wei NE, Jiang H, Doerge RW, Chen ZJ (2005) Reversible histone acetylation and deacetylation mediate genome-wide, promoter-dependent and locus-specific changes in gene expression during plant development. Genetics 169:337-345

Ueda M, Matsui A, Nakamura T, Abe T, Sunaoshi Y, Shimada H, Seki M (2018) Versatility of HDA19-deficiency in increasing the tolerance of Arabidopsis to different environmental stresses. Plant Signal Behav 13:e1475808

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

Yang C, Shen W, Chen H, Chu L, Xu Y, Zhou X, Liu C, Chen C, Zeng J, Liu J, Li Q, Gao C, Charron JB, Luo M (2018) Characterization and subcellular localization of histone deacetylases and their roles in response to abiotic stresses in soybean. BMC Plant Biol 18:226

Yruela I, Moreno-Yruela C, Olsen CA (2021) Zn^{2+}-dependent histone deacetylases in plants: structure and evolution. Trends Plant Sci 26:741-757

Zhang K, Yu L, Pang X, Cao H, Si H, Zang J, Xing J, Dong J (2020) In silico analysis of maize HDACs with an emphasis on their response to biotic and abiotic stresses. PeerJ 8:e8539

Zhao J, Zhang J, Zhang W, Wu K, Zheng F, Tian L, Liu X, Duan J (2015) Expression and functional analysis of the plant-specific histone deacetylase HDT701 in rice. Front Plant Sci 5:764

Zhao J, Zhang W, da Silva JAT, Liu X, Duan J (2021) Rice histone deacetylase HDA704 positively regulates drought and salt tolerance by controlling stomatal aperture and density. Planta 254:79

Zheng Y, Ding Y, Sun X, Xie S, Wang D, Liu X, Su L, Wei W, Pan L, Zhou DX (2016) Histone deacetylase HDA9 negatively regulates salt and drought stress responsiveness in Arabidopsis. J Exp Bot 67:1703-1713

Zhou C, Labbe H, Sridha S, Wang L, Tian L, Latoszek-Green M, Yang Z, Brown D, Miki B, Wu K (2004) Expression and function of HD2-type histone deacetylases in Arabidopsis development. Plant J 38:715-724