Cellular and Molecular Life Sciences (2021) 78:4467–4486
https://doi.org/10.1007/s00018-021-03794-x

Cellular and Molecular Life Sciences

REVIEW

Histone acetylation dynamics regulating plant development and stress responses

Verandra Kumar[1] · Jitendra K. Thakur[1] · Manoj Prasad[1]

Received: 14 December 2020 / Revised: 21 January 2021 / Accepted: 18 February 2021 / Published online: 27 February 2021

Abstract

Crop productivity is directly dependent on the growth and development of plants and their adaptation during different environmental stresses. Histone acetylation is an epigenetic modification that regulates numerous genes essential for various biological processes, including development and stress responses. Here, we have mainly discussed the impact of histone acetylation dynamics on vegetative growth, flower development, fruit ripening, biotic and abiotic stress responses. Besides, we have also emphasized the information gaps which are obligatory to be examined for understanding the complete role of histone acetylation dynamics in plants. A comprehensive knowledge about the histone acetylation dynamics will ultimately help to improve stress resistance and reduce yield losses in different crops due to climate changes.

Keywords Histone acetylation · Histone acetyltransferases (HATs) · Histone deacetylases (HDACs) · Epigenetics · Plant development · Biotic and abiotic stress responses

Introduction

In a eukaryotic nucleus, DNA is organized into a DNA–protein structure known as chromatin. A nucleosome is the central unit of chromatin consisting of 147 bp of DNA wrapped in ~ 1.7 turns around the histone proteins octamer, which is composed of two copies of each core histones H2A, H2B, H3, and H4 [1]. The amino-termini of these histones protrude out from the nucleosomal core structure and function as the preferred targets for different histone modifiers for a series of post-translational modifications (PTMs), including acetylation, methylation, phosphorylation, ubiquitylation, ADP-ribosylation, sumoylation, carbonylation and biotinylation. In addition to amino-terminal tails, the internal globular parts of histones are also subjected to PTMs. Several PTMs of histones regulate gene expression by modulating chromatin structure [2–4]. Hence, combinations of such modifications have been proposed to serve as a 'histone code' specifying a chromatin state that may govern the transcriptional status of genes [5].

Histone acetylation dynamics is one of the most studied PTM mechanisms. Like most of the other PTMs, acetylation is also reversible, which is dynamically modulated by the action of histone acetyltransferases (HATs) and histone deacetylases (HDACs). Generally, HATs cause gene activation through the addition of acetyl groups (CH_3COO-) onto the lysine residues of *N*-terminal tails [6–8] as well as globular domains [9, 10] of histones. On the other hand, these acetyl groups are removed by HDACs to counter the result of HATs by restoring the histones to its basal state, which mostly cause gene repression [6] (Figs. 1, 2). In rare exceptional cases, HATs and HDACs may cause repression and activation of genes, respectively [11–13]. Both HATs and HDACs target the lysine residues present in the histones, including H3K9, H3K14, H3K36, H4K5, H4K8, H4K12, and H4K16 to maintain the histone acetylation dynamics [8]. The histone acetylation dynamics create hyper- and hypo-acetylation, which are usually associated with gene activation and repression, respectively [6]. Histones may also be subjected to several other modifications apart from acetylation and deacetylation. The different combinations of specific modifications at various amino acid residues of nucleosomal histones have different effects on the local structure of chromatin that may lead to either activation or repression of the specific genomic loci [5, 14]. For instance, the combinations of histone acetylase/deacetylase complex

---

✉ Manoj Prasad
manoj_prasad@nipgr.ac.in

[1] National Institute of Plant Genome Research, Aruna Asaf Ali Marg, New Delhi 110067, India

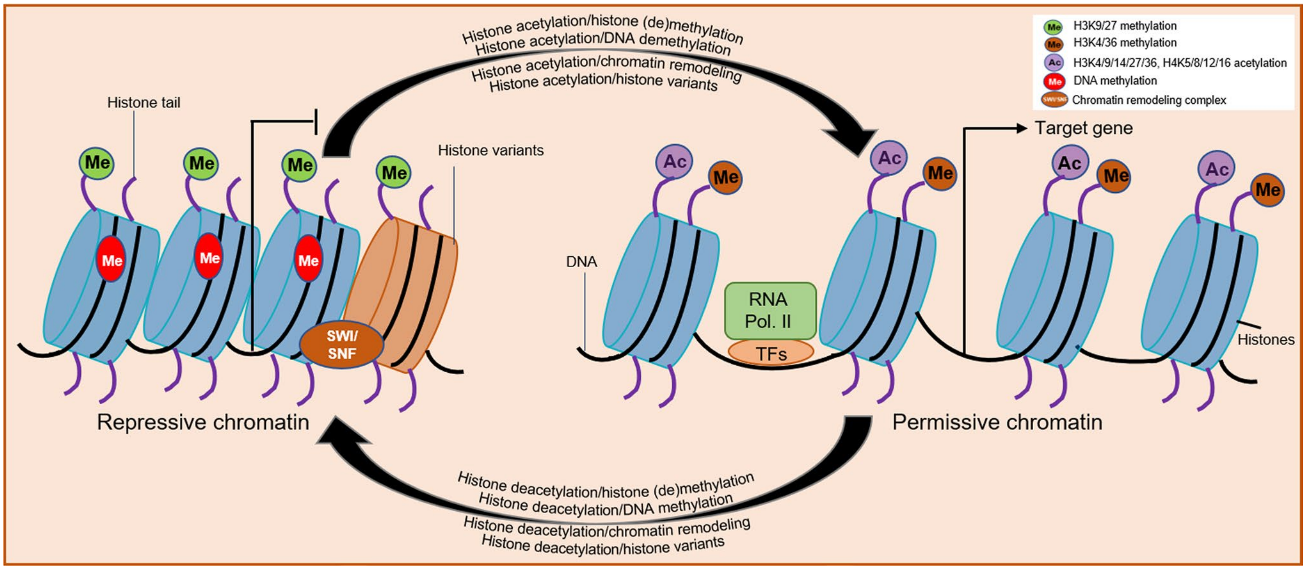

Fig. 1 Modulation of chromatin status by histone acetylation dynamics and other modifications. A combination of acetylation and methylation of different lysine residues in nucleosomal histones may cause expression (permissive chromatin) and repression (repressive chromatin) of genes. Besides, the combination of histone deacetylation and DNA methylation may also convert permissive chromatin to repressive chromatin which generally leads to gene repression. The regulation of gene expression is also affected by chromatin remodelling complex (such as SWI/SNF complex). Ac represents acetylation on lysine 4/9/14/27/36 of H3, and lysine 5/8/12/16 of H4 histone (H3K4/9/14/27/36 and H3K5/8/12/16), Me in the green coloured circles represent methylation on lysine 9/27 of H3 histone (H3K9/27), Me in the brown-coloured circles represent methylation on lysine 4 and 36 of histone H3 (H3K4/36), Me in the red coloured circles represent DNA methylation (cytosine methylation), SWI/SNF: SWITCH/SUCROSE NONFERMENTING chromatin remodelling complex. *TFs* transcription factors, *RNA Pol. II* RNA polymerase II. This is a simplified figure describing only combinatorial effect of histone acetylation and histone/DNA methylation and chromatin remodelling

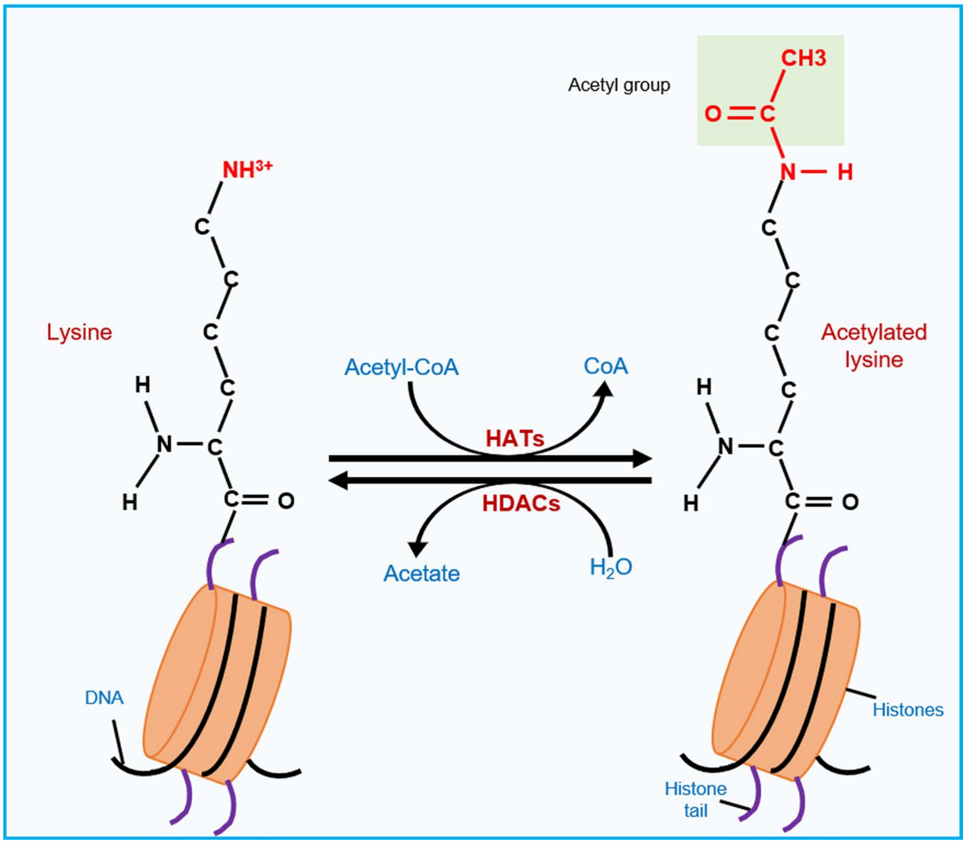

Fig. 2 Regulation of histone acetylation dynamics. HATs (histone acetyltransferases) transfer acetyl group from Acetyl Co-enzyme A (Acetyl-CoA) to the lysine residue of the histone proteins. In contrast, HDACs (histone deacetylases) remove acetyl groups from the acetylated lysine and form acetate as a by-product

with histone methylase/demethylase [15–17], chromatin remodelling complex [18, 19] and DNA methylase/demethylase complex [18, 20, 21] affect the transcriptional status of the genomic loci (Fig. 1).

Molecular mechanism of gene regulation by histone acetylation

Chromatin is dynamically organized into two-states, euchromatin and heterochromatin, which are interconvertible depending upon the stimuli. Euchromatin (loose structure) is an expressive state, while heterochromatin (compact structure) is a repressive state of gene expression. The compact structure of nucleosomes causes an obstacle for gene expression. Histone acetylation is a PTM that regulates chromatin structure and genome accessibility in collaboration with other histone modification(s) and DNA methylation. HATs act as coactivators, which are primed to the nucleosome by sequence-specific DNA-binding proteins. As shown in Fig. 1, HATs neutralize the positive charge of the core histones of the nucleosomes through the addition of acetyl groups (Fig. 2) and cause weakening of the DNA-histone interaction. This results in the switching from repressive (closed chromatin) to expressive state (open chromatin) of chromatin [22–24]. This conversion further allows the binding of RNA polymerase and transcription factors to the promoter region of the target genes for initiating their transcription. The promoter is the gene regulatory DNA stretch situated upstream of the transcription start site (TSS) [25]. The histone acetylation enrichment around TSS has been found to be positively correlated with the gene expression [26, 27]. On the other hand, the expressive state is converted to chromatin's repressive state by HDACs. HDACs act as the repressor proteins which are targeted on the active promoters through sequence-specific DNA-binding corepressor proteins. HDACs remove acetyl groups (Fig. 2) from the core histones of the nucleosomes and enhance the affinity between DNA and histones. The increased interaction between DNA and histones results in the compaction of chromatin structure, ultimately causing gene repression [28, 29] due to inaccessibility of the template DNA to the transcriptional machinery [30] (Fig. 1). Generally, histone acetylation is associated with gene activation and deacetylation is associated with the gene repression. However, these correlations are not always true. There are few reports that have shown association of HATs and HDACs with gene repression and activation, respectively [11–13]. This is because of the fact that the overall combination of histone modifications (acetylation, methylation, ubiquitination, phosphorylation, sumoylation, etc.) at different amino acid residues have different result on the chromatin structure and so on the process of transcription. Thus, the effect of HATs and HDACs is not always linear but combinatorial and it should be seen in the overall context of 'histone code'.

Histone acetyltransferases

Histone acetyltransferases act as the "writer" by adding an acetyl group in the lysine residues of histones and generally cause gene activation. Histone acetyltransferases gene family having the varying number of members in different plants. There are 12 HATs in Arabidopsis [6], 32 in tomato [31], 6 in litchi [32], 7 in grape [33] and 8 in rice [34]. Based on sequence similarity and domains organization, HATs are subdivided into four groups; GNAT (General Control Non-depressible 5 (GCN5)-related Acetyltransferase), MYST (MOZ-YBF2/SAS3-SAS2/TIP60), CBP (cAMP-Responsive Element Binding Protein (CREB)-Binding Protein) and $\text{TAF}_{\text{II}}250$ (TATA-binding protein Associated Factor 1) [6, 35] (Fig. 3). These families are symbolized by the acronyms HAG, HAM, HAC, and HAF, respectively [6]. These HAT proteins possess different conserved domains such as ELP3 (elongator complex protein 3), HAT1 (histone acetyltransferase 1), Chromodomain and Znf-C2H2 in HAG/HAM, KIX (Kinase-inducible domain interacting), PHD (Plant Homeodomain), Znf-ZZ and Znf-TAZ in HAC and Bromodomain, UBQ and Znf-C2HC in HAF for their activity [6, 33, 36]. These conserved domains of HATs make them efficient by performing different functions, including interaction with RNA Pol II during transcript elongation (ELP3), histone acetylation (HAT1), recognizing and binding with a specific acetylated histone residue (Chromo- and Bromo-domain), protein-DNA or protein–protein interactions (Znf-C_2H_2 and Znf-C_2HC, Znf-ZZ and Znf-TAZ domain), interaction with histones and other histone-recognition proteins (PHD), binding with the transactivation domain of transcription factors (KIX domain) and binding with acetylated histone lysine residues [6, 34]. Thus, HATs form multiprotein complexes through physical interaction with other co-factors, including transcription factors, activator proteins, and histone modifiers to control gene expression [23].

Histone deacetylases

Histone deacetylases work as the "eraser", which removes an acetyl group from the acetylated lysine residues of the core histones added by the HATs. Generally, deacetylation causes gene repression to regulate numerous biological processes. Just like HATs, the number of HDACs also varies in different plant species. For instance, there are 18 HDACs in Arabidopsis [6], 14 in tomato [31], 11 in litchi [32], 13 in grape [33], 28 in soybean [37], 30 in upland cotton [38] and 18 in rice [39]. Based on their sequence similarity, the HDAC family is comprised of three sub-families; RPD3/

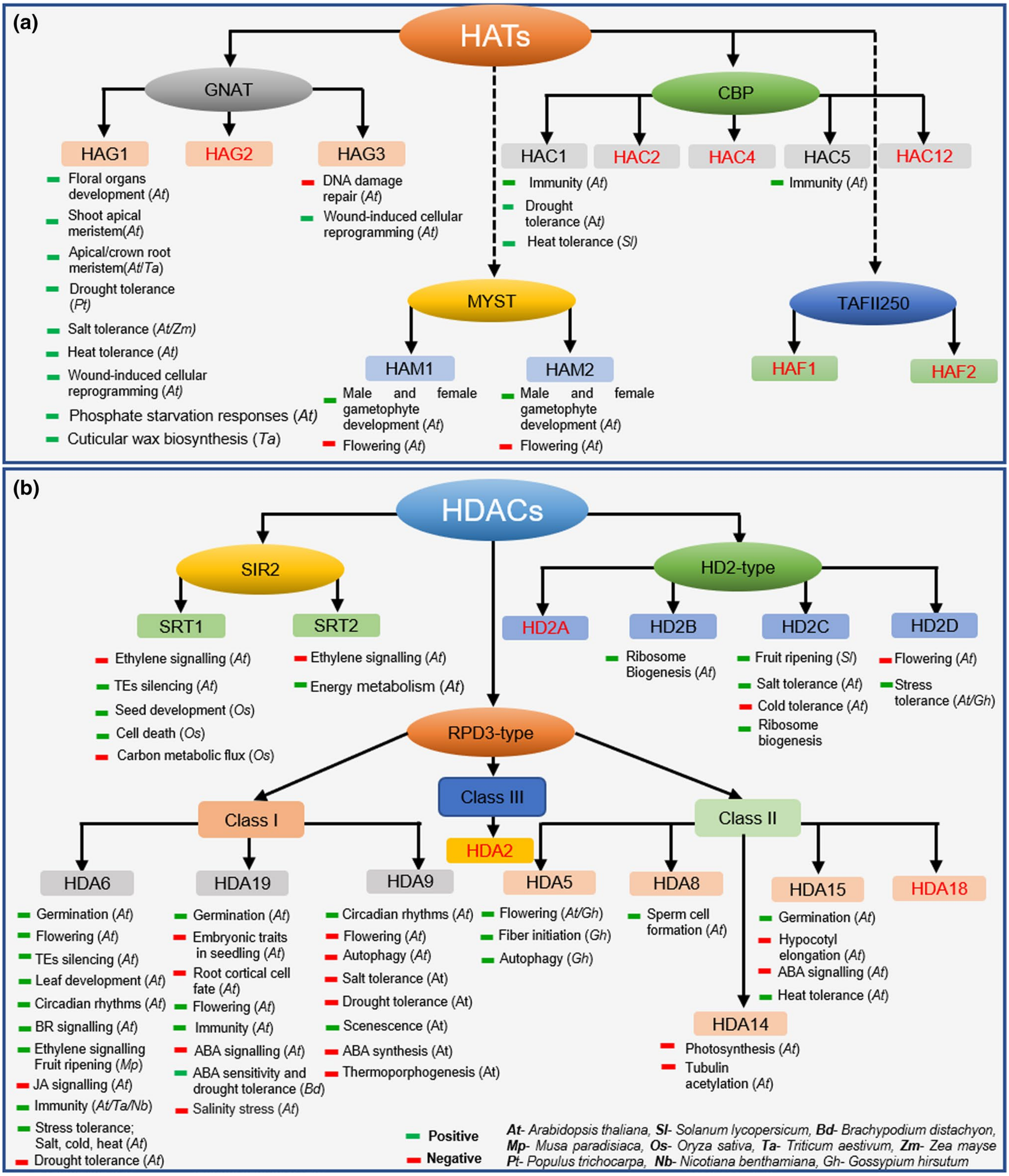

Fig. 3 A summary of the function of different HATs (**a**) and HDACs (**b**) in plants. Based on domain arrangements, HATs are categorised into GNAT, MYST, CBP and TAFII250 proteins. Similarly. HDACs are divided into groups of SIR2, RPD3-type and HD2-type proteins. This classification is mainly based on *Arabidopsis*. The green and red lines represent positive (activation) and negative (suppression) of the biological processes, respectively. Two-letters in bracket represent the name of plant species. *HATs* histone acetyltransferases, *GNAT* general control non-depressible 5 (GCN5)-related acetyltransferase, *MYST* MOZ-YBF2/SAS3-SAS2/TIP60, *CBP* cAMP-responsive element binding protein (CREB)-binding protein, *TAFII250* TATA-binding protein associated factor 1, *HDACs* histone deacetylases, *RPD3* reduced potassium dependency 3, *HDA* histone deacetylase, *SIR2* silent information regulator 2, *HD2* histone deacetylase 2. The red-coloured name of genes showed no recent reports on the respective gene

HDA1 (Reduced Potassium Dependency 3/histone deacetylase 1), SIR2 (Silent Information Regulator 2) and a plant-specific HD2 (histone deacetylase 2) (Fig. 3). The RPD3 (histone deacetylase; HDA2/5/6/8/9/14/15/18/19), SIR2 (SRT1/2) and HD2 (HD2A/B/C/D) members possess conserved histone deacetylase domain. Several members of HDACs also possess the Znf (zinc finger) motif which helps in protein–protein interactions [6, 32, 33, 38]. Most of the HDAC proteins lack the DNA binding domain and form the multiprotein repressor complex with other co-factors (transcription factors and or repressor proteins) to regulate different biological processes.

Functions of histone acetylation

Several reports have revealed the role of histone acetylation in the development and adaptation of plants during different stresses by regulating a specific set of genes for a specific purpose as shown in Fig. 3 and listed in Tables 1 and 2. Histone acetylation is also involved in the maintenance of genome stability through the regulation of

Table 1 Summary of known HAT and HDAC protein complexes crucial for the plant growth and development

HAT/HDAC complex	Target genes	Associated lysine moiety	Role	Plant	Reference
Seed germination and seedling development					
HDA15-PIF1	*Light-responsive genes*	H3ac	Seeds germination in the dark	*Arabidopsis*	[28]
HDA15-PIF3	*Photosynthesis-related genes*	H3 and H4ac	Seeds germination in the dark	*Arabidopsis*	[48]
HDA15-HY5	*XTH15*, *EXP2*, and *IAA19*	H4ac	Photomorphogenesis and hypocotyl cell elongation	*Arabidopsis*	[49]
HDA9-HY5	*ATG5 and ATG8e*	H3K9/K27ac	Seedling development	*Arabidopsis*	[29]
HDA19-SUVH5	*ABI3, RGA, DOG1*	H3ac and H3K9me2	Seed dormancy	*Arabidopsis*	[16]
HDA19-SCL15	*LEC1* and *ABI3*	H3K9/K14ac	Seedling development	*Arabidopsis*	[50]
HDA19-BES1-TPL	*ABI3*	H3ac	Early seedling development	*Arabidopsis*	[51]
HDA6-HDA19	*LEC1*, *FUS3*, and *ABI3*		After seed germination	*Arabidopsis*	[52]
Vegetative growth					
GCN5-ADA2-WOX11	*PIN9, EXPA23, CESA9, CSLF6, GLU5, BGLU5, ALDO*		Crown roots development	Rice	[55]
HDA9-PWR-HOS15	*ERF6* and *KINASE2*	H3K27/K36/K56ac	Plant development	*Arabidopsis*	[53]
HAG1-ADA2b			Regulation of leaf development and trichome morphogenesis	*Arabidopsis*	[57]
HDA6-AS1	*KNOX* gene (*KNAT1*, *KNAT2*, and *KNATM)*	H3ac	Leaf development	*Arabidopsis*	[58]
HDA19-SCR	*BR6OX2*	H3 and H4ac	Root cortical cell fate	*Arabidopsis*	[60]
HDA6-LDL1/2-TOC1	*CCA1/LHY*	H3ac	Circadian clock	*Arabidopsis*	[15]
HDA9-ELF3	*TOC1*	H3ac	Circadian clock	*Arabidopsis*	[64]
Flowering and reproductive organs development					
HAM1/2-MRG1/2	*FLC*	H4ac	Regulates flowering	*Arabidopsis*	[17, 66]
HD2C-MRG1/2	*FT*	H3K9/K23/K27ac	Flowering	*Arabidopsis*	[68]
HDA19-AP2-TOPLESS	*AG, AP3, PI, SEP3*	H3K9/H3K4/K16ac	Floral organ development	*Arabidopsis*	[69]
HDA9-LUX-HOS15	*GI*	H3ac	Photoperiodic flowering	*Arabidopsis*	[72]
HDA9-PWR	*AGL19*	H3ac	Regulates flowering	*Arabidopsis*	[73, 74]
HDA9-PRC2	*FLC*	H3K27me3	Regulates flowering	*Arabidopsis*	[75]
HDA5-HDA6-FVE-FLD	*MAF1-2*	H3K9/14ac	Regulates flowering	*Arabidopsis*	[80]
HAM1/2		H4K5ac	Male and female gametophyte development	*Arabidopsis*	[82]
HDA8-ARID1	*DUO POLLEN1* (*DUO1*)	H3K9ac	Controls sperm cell formation	*Arabidopsis*	[83]
Fruit ripening and aging					
HDA1-ERF11	*MaACO1, MaEXP2, MaEXP7 and MaEXP8*	H3 and H4ac	Fruit ripening	Banana	[87]
CpHDA3- CpERF9	*CpPME1, CpPG5*	H3 and H4ac	Fruit ripening	Papaya	[91]
HDA9-PWR-WRKY53	*WRKY57, APG9, and NPX1*	H3K9/K27ac	Regulation of aging	*Arabidopsis*	[94]

Table 2 Summary of known HAT and HDAC protein complexes have a vital role in different biotic and abiotic stress responses in plants

HATs/HDACs complex	Target genes	Associated histone marks	Functions	Plant	Reference
Biotic stress responses					
HDA19-WRKY38/62	*PR1*		Fine-tuning of basal defence-responses	*Arabidopsis*	[96]
HAC-NPR1-TGA	*PR*	H3ac	Immunity	*Arabidopsis*	[98]
HDA9-HOS15	*SNC1*	H3K9ac	Immunity	*Arabidopsis*	[99]
GCN5-ADA2-EPBM1	*ECR*	H3K4/K9/K14/K27ac and H4K5ac,	Cuticular wax biosynthesis	Wheat	[101]
TaHDA6-TaHOS15-TaHDT701	*TaPR1, TaPR2, TaPR5, and TaWRKY45*	H3K9/H4K16ac	Defence-responses against *Blumeria graminis*	Wheat	[102, 103]
Abiotic stress responses					
GCN5-ADA2b-AREB1	*NAC6/7/120,*	H3K9ac	Drought responses	Populus	[23]
ZmGCN5-ZmHATB	*ZmEXPB2 and ZmXET1*	H3K9ac	Salt stress responses	Maize	[107]
HDA15-MYB96	*ROP6/10/11*	H3 and H4ac	ABA signalling and early-stage stress responses	*Arabidopsis*	[126]
HDA19-MSI1	*PYL1, PYL4, PYL5, PYL6*	H3K9ac	ABA signalling	*Arabidopsis*	[127]
HDA9-ABI4-PWR	*CYP707A1/2*		ABA homeostasis	*Arabidopsis*	[132, 133]
HDA9-PWR	*PIF4, YUCCA8*	H3K9ac	Thermogenesis	*Arabidopsis*	[13]
HDA15-HFR1	*PIF4*, *HB2*, *XTR7*	H3K14ac	Heat stress	*Arabidopsis*	[118]
HDA6-HD2C	*ABI1/2*	H3K9/K14ac	ABA and salt responses	*Arabidopsis*	[114]
SRT1/2- ENAP1	*ETHYLENE RESPONSIVE GENES*	H3K9ac	Ethylene signalling	*Arabidopsis*	[121]
HD2C-HOS15	*CORs*	H3ac	Cold stress-responses		[122]
HD2C-BRAHMA	*HSP101* and *HSFA3*	H4K16ac	Heat stress-responsive	*Arabidopsis*	[19]
HDA1-IDS1-TPR1	*SOS1, LEA1*	H3ac	Salt stress-responses	Rice	[136]
MaHDA2-MaMYB4	*MaFAD3-1, MaFAD3-3, MaFAD3-4 and MaFAD3-7*	H3 and H4ac	Cold stress-responses	Banana	[142]

transposons. In the following sections, we have discussed different processes that are regulated by histone acetylation dynamics.

Maintenance of genome stability

Transposable elements (TEs) are itinerant DNA sequences that destabilize genome integrity through genome colonization. Acetylation of histones H3 and H4 and tri-methylation of lysine 4 of H3 (H3K4me3) are associated with the expression of TEs [40]. There are reports which showed that these TEs may be suppressed through different epigenetic modifications such as histone deacetylation and demethylation and DNA methylation in plants. For instance, in Arabidopsis, histone deacetylase 6 (HDA6) represses TEs through H3K9 deacetylation and methylation [41]. For this purpose, HDA6 interacts with SUVH4/5/6 (SUV(VAR)3–9 HOMOLOG 4/5/6). Similarly, a direct interaction of HDA6 with MET1 (methyltransferase 1) has been implicated in the silencing of TEs by controlling the status of histone acetylation and methylation and DNA methylation [40]. HDA6 and MET1 together regulate a large set of TEs and repeat sequences in Arabidopsis. Interaction of HDA6 with nuclear matrix protein TEK (TRANSPOSABLE ELEMENT SILENCING VIA AT-HOOK) and retinoblastoma-associated proteins FVE/MSI5 (MULTICOPY SUPPRESSOR OF IRA1 5) maintains genome integrity by suppressing the TEs and repeat-containing genes [42, 43]. Besides, HDA6 along with CHROMATIN REMODELING COMPLEX SUBUNIT B, SWI3B (SWITCH SUBUNIT 3) silences the transposable elements through H3K9 deacetylation [44]. HDA6 also causes gene repression through RNA-directed DNA methylation (RdDM) [45]. However, the IDM1 (INCREASED DNA METHYLATION 1)-mediated histone acetylation of H3K18 and H3K23 lysine residues enables the recruitment of DNA demethylase ROS1 (REPRESSOR OF SILENCING 1) to antagonize the RdDM at active DNA methylated sites [21]. In rice, deacetylation of lysine 9 of histone H3 (H3K9) by OsSRT1 (SIRTUIN 1) is implicated in transposon repression, DNA fragmentation, cell death and starch accumulation during seed development [46, 47] (Fig. 3). Thus, based on these recent studies, it can be concluded that both HDA6 and SRT1 deacetylate H3K9 residue and coordinate with histone and DNA methyltransferases to repress TEs and maintain genome stability in different plants [40–44, 46, 47]. There is a possibility that they might be physically interacting and functioning in the same complex. However, a molecular link between HDA6 and SRT1 is missing at present. Thus, the establishment of a relationship between them would help a better understanding of TEs repression and genome stability mechanism.

Regulation of plant development

Histone acetylation is an epigenetic modification that regulates different biological processes essential for the growth and development of plants. As summarized in Fig. 3, several recent studies have explored the role of HATs and HDACs in the growth and development are discussed below.

Vegetative growth and development

Vegetative growth is an essential phase of the plant's life cycle and has a considerable impact on productivity. Various studies have suggested the role of histone acetylation in the development of different vegetative organs (Fig. 3; Table 1).

Seed germination and seedling development

Seed germination and seedling development are the early phases of the plant's life cycle and light plays a very crucial role during these stages. HDA15 (histone deacetylase 15) is a light-regulated histone deacetylase, which interacts with PIF1 (PHYTOCHROME INTERACTING FACTOR 1) to suppress the light-responsive genes during seed germination in dark [28]. In the dark, HDA15 also restricts chlorophyll biosynthesis- and photosynthesis-related genes through its interaction with PIF3 [48]. Further, HDA15 with HY5 (ELONGATED HYPOCOTYL 5) also regulates photomorphogenesis by suppression of the hypocotyl cell elongation via H4 deacetylation of target genes involved in cell wall organization and auxin signalling in Arabidopsis [49]. HY5 also coordinates with histone deacetylase HDA9 (HISTONE DEACETYLASE 9) during photomorphogenesis. HDA9 and HY5 act synergistically to repress autophagy genes (*ATG5* and *ATG8e*) through deacetylation of H3K9 and H3K27. Expression of ATG genes is upregulated due to degradation of HDA9-HY5 complex during transition from light to dark and nitrogen starvation conditions [29]. Another histone deacetylase, HDA19 interacts with histone methyltransferase SUVH5 (SU(VAR)3–9 HOMOLOG 5) and regulates seed dormancy through ABA and GA signalling pathways by modulating overall histone H3 acetylation and H3K9me2 methylation on the promoter of the target genes *ABI3* (*ABA INSENSITIVE 3*), *RGA* (*REPRESSOR OF GA*) and *DOG1* (*DELAY OF GERMINATION 1*) [16]. HDA19 also interacts with SCL15 (SCARECROW-LIKE 15) to represses embryonic traits in the developing seedlings [50]. It forms a repressor complex with BES1 (BRI1-EMS-SUPPRESSOR 1) and TPL (TOPLESS) to regulate *ABI3* expression in the early seedling development governed by ABA signalling [51]. After seed germination, HDA19 (HISTONE DEACETYLASE 19) and HDA6 (HISTONE DEACETYLASE 6) together suppress embryo-specific transcription factors like *LEC1* (*LEAFY COTYLEDON 1*), *FUS3* (*FUSCA3*), and *ABI3* [52]. On the other hand, HDA9 interacts with PWR (POWERDRESS) and HOS15 (HIGH EXPRESSION OF OSMOTICALLY RESPONSIVE GENES 15) to suppress the expression of the target genes and ultimately governs developmental processes in Arabidopsis [53].

Meristems

In plants, meristems are the primary source of all the tissues and organ development. A histone acetyltransferase GCN5 of Arabidopsis has been found to control the shoot apical meristem through regulation of meristem-regulatory genes, including *WUS* (*WUSCHEL*), *LEAFY*, and *UFO* (*UNUSUAL FLORAL ORGANS*) [54]. The homolog of AtGCN5 in rice regulates crown root meristem by acetylating H3 on the crown root-specific genes. GCN5 forms a ternary protein complex with ADA2 (ALTERATION/DEFICIENCY IN ACTIVATION 2) and WOX11 (WUSCHEL-RELATED HOMEOBOX 11). The GCN5-ADA2-WOX11 module activates the target genes involved in auxin transport (*PIN-FORMED*; *OsPIN9*), cell wall biosynthesis (*EXPANSIN A23*; *OsEXPA23, CELLULOSE SYNTHASE A CATALYTIC SUBUNIT 9*; *OsCESA9, CELLULOSE SYNTHASE-LIKE F*; *OsCSLF6* and *ENDO-1,4-BETA GLUCANASE 2; OsGLU5*) and energy metabolism (*β-GLUCOSIDASE; Os1BGLU5* and *Os9BGLU33* and *ALDOLASE*; *OsALDO*) in the crown roots [55]. In azalea also, histone H4 deacetylation and DNA methylation has been reported to reorganize the chromatin to regulate Shoot Apical Meristem (SAM)-regulatory genes and control the vegetative growth and floral differentiation [56].

Leaf and root development

Leaf is an essential part that performs photosynthesis, and it generates food and energy for the whole plant. Thus, its development is very crucial for plant growth and cellular processes. The transcriptional adapter ADA2b (ALTERATION/DEFICIENCY IN ACTIVATION 2b) stimulates the transferase activity of GCN5 (HAG1) to regulate leaf development and trichome morphogenesis. HAG1 and ADA2b are also required for the coupling of endoreduplication and trichome branching in Arabidopsis [57]. Leaf development is also controlled by the synchronized action of HDA6 and AS1 (ASYMMETRIC LEAVES 1), which regulates the expression of *KNOX* (*KNOTTED1-LIKE HOMEOBOX*) genes *KNAT1*, *KNAT2* (*KNOTTED-LIKE FROM ARABIDOPSIS THALIANA 1/2*), and *KNATM* (*KNOTTED-LIKE FROM ARABIDOPSIS THALIANA MEINOX*) [58].

AtGCN5 increases the expression of the root-meristem gene loci, including *WOX5/14* (*WUSCHEL RELATED HOMEOBOX 5/14*), *SCR* (*SCARECROW*), and *PLT1/2* (*PLETHORA 1/2*) through histone acetylation during callus development [59]. The histone deacetylase, HDA19 forms a repressor complex with SCR to suppress the expression of BR (Brassinosteroid) biosynthesis gene *BR6OX2* (*BRASSINOSTEROID-6-OXIDASE 2*), which ultimately determines root cortical cell fate in Arabidopsis [60]. In Arabidopsis, a plant-specific HDAC, HDT1 controls stem vascular tissue development by regulating cell proliferation and differentiation [61], while RPD3-type HDAC, HDA19 controls the root cell elongation and modulates phosphate starvation responses [62].

Circadian cycle

Circadian rhythms occur in plants to synchronize with the light cycle of its surroundings. These rhythms are controlled by a set of genetic and epigenetic regulators including HATs and HDACs. HDA6 forms a repressor complex with histone demethylase LDL1/2 (LYSINE-SPECIFIC HISTONE DEMETHYLASE LIKE 1/2) and circadian clock protein TOC1 (TIMING OF CAB EXPRESSION 1). This complex represses expression of *CCA1* (*CIRCADIAN CLOCK ASSOCIATED 1*) and *LHY* (*LATE ELONGATED HYPOCOTYL*) genes and ultimately controls circadian rhythm [15]. Whereas, HDA6-LDL1/2 complex also physically interacts with CCA1/LHY to repress the TOC1 expression [63]. A recent study showed that the HDA9 and EARLY FLOWERING 3 (ELF3), an evening complex (EC) component, interacts with each other to regulate the declining phase of TOC1 after its peak expression [64]. These studies indicate that HDA6 and HDA9 might be working antagonistically to regulate the circadian rhythm during plant development. So, the insight into the establishment of the correlation between HDA6 and HDA9 will be helpful to a better understanding of the circadian rhythm.

Regulation of flowering

Flower is a fundamental structure of the reproductive stage of plants. Its differentiation is a transition from the vegetative to the reproductive phase [65]. Several genetic and epigenetic regulators govern this transition. FLC (FLOWERING LOCUS C) is a negative genetic regulator of flowering, which is highly expressed during the vegetative phase and is suppressed during the reproductive period [11, 17, 66]. Recent studies have elucidated that histone acetylation modulation by different HAT and HDAC epigenetic modifiers is responsible for the regulation of flowering in different plants. The acetylation of H3K9 on the *FLC* locus enhances its expression causes delayed flowering [67]. Also, the MYST histone acetyltransferase HAM1/2 enhances the expression of the *FLC* gene through H4K5 acetylation and results in delayed flowering [66]. In another study, it was shown that HAM1/2 interacted with histone methylat-ion reader proteins MRG1/2 (MORF RELATED GENE 1/2) to elevate the expression of flowering genes *FLC* and *FT* (*FLOWERING LOCUS T*) through bridge formation between two histone modifications, histone H4 acetylation and trimethylation of H3K36 [17]. On the other hand, a plant-specific histone deacetylase HD2C, along with MRG1/2, suppresses *FT* (*FLOWERING LOCUS T*) expression in the dark to control flowering [68]. These recent studies indicate that MRG1/2-dependent HAT and HDAC complexes mediate histone acetylation dynamics to modulate *FLC* and *FT* expression and so control the photoperiodic flowering pathway. Histone acetyltransferases usually cause gene activation. However, AtHAC1 regulates flowering time by suppressing the *FLC* expression in Arabidopsis [11]. There is a possibility that AtHAC1 might be inducing expression of any repressor factors acting upstream of the *FLC* gene.

The physical interaction of HDA19 with AP2 (APETALA 2) and TPL (TOPLESS) suppresses floral organ identity genes *AGAMOUS*, *APETALA3*, *PISTILLATA*, and *SEPALLATA3* to control the flower development [69]. Recent studies suggest that HDA19 controls flowering time in a photoperiod-dependent manner [70]. On the other hand, a plant-specific histone deacetylase HD2D is responsible for the delayed flowering in a photoperiod-independent manner in Arabidopsis [71]. These reports indicate that HDA19 and HD2D might be working differently to control the flowering time in a photoperiod-dependant and independent manner. Several studies implicate that HDA9 suppresses flowering. It forms a repressor complex with LUX and HOS15 to regulate photoperiod-dependent flowering via transcriptional repression of *GI* (*GIGANTEA*) [72]. HDA9 also interacts with PWR (POWERDRESS) and controls flowering time by repression of *AGL19* (*AGAMOUS-LIKE 19*) expression through histone H3 deacetylation [73, 74]. However, a recent study showed that HDA9 accelerated flowering by deacetylating H3K27 lysine residues, which is essential for PRC2 (POLYCOMB REPRESSIVE COMPLEX 2)-mediated trimethylation of H3K27 to suppress *FLC* expression in Arabidopsis [75]. Auxin signalling is important for flower development and subsequent silique development. It has been shown that the histone acetylation dynamics facilitate auxin signalling. HDA9 co-ordinates with HDA6 to regulate valve cell elongation by modulating the auxin signalling pathway during silique formation [76, 77]. In common bean, *HDA6* is upregulated in flowers and pods suggesting its role in the development [78]. AtHDA6 physically interacts with FLD and suppress the *FLC* and *MAF4* expression to control the flowering [79]. Another report showed that the AtHDA5 histone deacetylase forms a repressor complex with HDA6, FVE, and FLD (FLOWERING LOCUS D) and plays a decisive role in controlling flowering in Arabidopsis. This complex represses the expression of *FLC* and *MAF1-2* (*MADS-BOX AFFECTING FLOWERING GENES 1–2*) by the deacetylation of H3K9 and H3K14 lysine residues [80]. Also, the knockdown of *GhHDA5* was found to be responsible for delayed flowering in the cotton RNAi lines suggesting its pivotal role in the regulation of flowering time [38] (Fig. 3; Table 1). In azalea also, a combination of H4 acetylation and DNA methylation has been shown to reorganize the chromatin to regulate genes essential for floral differentiation [56]. Acetylation of K36 residue of H3 (H3K36ac) is conserved lysine acetylation across the plant kingdom and the actions of GCN5 and HDA19 have been found to antagonistically regulate its homeostasis [81]. It is profoundly enriched in the euchromatin regions, especially at the 5′ end (just downstream to the TSS) of the active genes overlapping with H3K36me3 histone methylation and H2A.Z histone variants.

Gamete development

Gametes are the essential structure for sexual reproduction. Unlike animals, where meiotic product directly forms the gametes, the germline in plants is established by two successive mitotic divisions after completion of meiosis. The HAM1/2 proteins are MYST histone acetyltransferases that regulate the mitotic cell cycle at the early stages of gametogenesis and so play an essential role in the development of male and female gametophyte in Arabidopsis [82]. On the other hand, histone deacetylase HDA8 interacts with ARID1 (AT-RICH INTERACTING DOMAIN 1) protein to control sperm cell formation by regulating the expression of *DUO POLLEN1* (*DUO1*) gene, an important regulator of male germline development [83]. Another HDAC, AtHDA7, has been found to control *ARABIDOPSIS HOMOLOG OF SEPARASE* (*AtAESP*) expression for female gametophyte and embryo development [84] (Fig. 3; Table 1).

Fruit ripening

Fruit development and its ripening involve different cellular, metabolic and molecular processes that determine fruit growth, fruit softening and accumulation of soluble sugars, aromatic volatile compounds and pigments in it. These processes are controlled by both genetic and epigenetic mechanisms. In pear fruits, sugar accumulation has been regulated by the histone acetyltransferase HLS1 (HOOKLESS1). HLS1 positively regulates the expression of *WRKY31* by histone acetylation on its promoter. Further, WRKY31 binds to the promoter and induces the transcription of a sugar transporter gene *SWEET15*, a positive regulator required for sugar accumulation in the fruits [85]. Ethylene is an essential phytohormone obligatory for the fruit ripening in climacteric (e.g., banana and tomato fruits) but not in non-climacteric (e.g., pear and orange fruits) fleshy fruits [86]. Several reports suggest that ethylene biosynthesis and signalling are regulated by histone acetylation dynamics. In banana, HDA1 physically interacts with ERF11 and delays fruit ripening by repressing ethylene biosynthesis gene *MaACO1* and the ripening-related *Expansin* genes *MaEXP2*, *MaEXP7*, and *MaEXP8* [87] (Table 1). Thus, HDA1 inhibits ethylene signalling. On the other hand, another HDAC MaHDA6 promotes ethylene signalling and fruit ripening by repressing *ERF11/15* genes [88]. Similarly, in tomato, different HDACs have different effects on fruit ripening. SlHDA3 functions as an inhibitor of fruit ripening by controlling ethylene biosynthesis [89] whereas SlHDT3 induces ethylene and carotenoid accumulation leading in fruit ripening [90]. In papaya, CpHDA3, which is an RPD3 type histone deacetylase, interacts with ERF9 to form a repressor complex that represses the expression of *PECTIN METHYLESTERASE* (*PME1*) and *POLYGALACTURONASE* (*PG5*) genes during fruit ripening and softening [91] (Table 1).

Aging

Leaf senescence is an age-dependent and environment stimulated catabolic process. It is a complex and programmed mechanism that leads to degradation of the macromolecules like nucleic acid, proteins and lipids into micronutrients. The micronutrients obtained by the degradation of macromolecules are used by the other developing organs, including young leaves, reproductive organs, and seeds. Several genetic and epigenetic regulators, including HATs and HDACs, have been reported to control the metabolic transition and nutrient recycling during senescence. The CREB-binding type histone acetyltransferase HAC1 has been found to regulate the process of senescence in Arabidopsis [92]. Around 43 genes, including ERF22, which is required for leaf senescence, have been found to be regulated by HAC1 during age-related senescence by the acetylation of H3K9 on their promoters [92]. On the other hand, mutant and RNAi plants of histone deacetylase HDA6 displayed increased leaf longevity [93]. Another HDAC, HDA9 forms a repressor complex with PWR and WRKY53 to suppress the expression of genes for inhibitors of senescence and thus monitors the process of aging in Arabidopsis [94] (Table 1).

Responses to different stresses

In their lifetime, plants cope up with different biotic and abiotic stresses. These stresses affect plant growth, development and productivity. Being sessile, plants cannot avoid these stresses. Instead, they sense the stress and respond by activating different signalling pathways leading to physiological and developmental adaptations. Several recent studies have shown that the HATs and HDACs are critical epigenetic regulators involved in the various biotic and abiotic stress responses assisting in plant adaptation during different stress conditions.

Regulation of biotic stress responses

Biotic stress can be caused by different pathogens leading to damage in the host plants, ultimately imposing a penalty on the yield. Numerous studies substantiate the role of different HATs and HDACs involved in biotic stress responses, increasing plant immunity against the causal organisms. Plant hormones like salicylic acid (SA), jasmonic acid (JA) and ethylene play a critical role in response to biotic and abiotic stresses. A recent study in Arabidopsis demonstrated that the GCN5 regulates SA-responsive genes by increasing the level of H3K14ac on their promoters in response pathogen challenge [27]. On the other hand, genes involved in JA and ethylene signalling in response to pathogen attack have been found to be regulated by HDA19 [95]. HDA19 also interacts with WRKY38 and WRKY62 to fine-tune the basal defense-responses by inhibiting the SA signalling [96]. A plant-specific histone deacetylase HD2B is phosphorylated by MPK3 (MITOGEN-ACTIVATED PROTEIN KINASE 3) upon pathogen (*Pseudomonas syringae* pv. tomato DC3000 (*Pst DC3000*)) infection to move from the nucleolus to the nucleoplasm [97]. Thus, the HD2B-MPK3 module maintains a basal level of several defense-related genes tomaintain the basal level of innate immunity. Accordingly, the *hd2b* mutant plants are more susceptible to the pathogen. The CBP/p300-type histone acetyltransferases AtHAC1/5 forms a coactivator complex with NPR1 (NON-EXPRESSER OF PR GENES 1) and TGA (TGACG- BINDING FACTOR) to activate transcription of *PATHOGENESIS RELATED* (*PR*) genes [98]. This acetylation-mediated epigenetic reprogramming eventually provides immunity to the host plants against *Pst DC3000*. On the other hand, a histone deacetylase HDA9 debilitates innate immunity by physically interacting with HOS15 [99]. The HDA9-HOS15 complex represses *NLR* (*NOD-LIKE RECEPTOR*) and *SNC1* (*SUPPRESSOR OF npr1-1, CONSTITUTIVE 1*) expression via H3K9 deacetylation during the infection of *Pst DC3000* pathogen. Cuticular wax is an essential constituent of the surface cuticle that plays a crucial role in protecting the plants from different environmental stresses. In Arabidopsis, GCN5 modulates wax biosynthesis-related gene *CER3* (*ECERIFERUM3*) expression by acetylation of H3K9/14 lysine residues [100]. In wheat, GCN5 forms a complex with ADA2 and EPBM1 (ECR PROMOTER-BINDING MYB TRANSCRIPTION FACTOR1) to activate the transcription of *ECR* (*ENOYL-COA REDUCTASE*) gene, which encodes for a key constituent of cuticular wax [101]. During wax biosynthesis, GCN5-ADA2-EPBM1 histone acetyltransferase complex activates *ECR* expression via acetylation of H3 and H4 histones. The fungus *Blumeria graminis* f.sp. tritici (*Bgt*) targets this cuticular wax for its conidia germination causing powdery mildew [101]. During *Bgt* infection, HDA6 and HOS15 associate to constitute a repressor complex that suppresses the defense-related genes *TaPR1*, *TaPR2*, *TaPR5 (Pathogenesis-Related1/2/5)*, and *TaWRKY45*. These genes play a crucial role in the plant defense against *Bgt* [102]. Other HDAC, TaHDT701 associates with HDA6-HOS15 complex to suppress *PR1/2/5* genes during *Bgt* infection [103]. Thus, these results reveal that histone deacetylases HDA6 and HDT701 are negative regulators of innate immunity in wheat. In rice also, HDT701 weakens the innate immunity through suppression of *PRR* (*PSEUDO-RESPONSE REGULATOR*) and defense-related genes by deacetylating histone H4 on their promoter [104]. DNA methylation is a gene silencing method that defends against viral infection. In tobacco, V2 protein of *Tomato yellow leaf curl virus* (*TYLCV*) interacts directly with NbHDA6 which is involved in gene silencing in cooperation with MET1 (METHYLTRANSFERASE 1) [20] (Fig. 3; Table 2). Surprisingly, only a few recent studies have reported the role of HATs in plant immunity. More research is required in this area to gain deeper insights into the role of HATs in regulating plant immunity.

Regulation of abiotic stress responses

Plants face different abiotic stresses (drought, salinity, heat, cold, etc.) responsible for the decline in growth and development, which ultimately causes loss of crop productivity. Numerous studies have shown that the histone acetylation dynamics plays a crucial role in controlling the stress responses facilitating plant adaptation in adverse conditions (Fig. 3; Table 2).

Salt and drought stress

Salt and drought stresses are known to inhibit plant growth and reduce the overall productivity. Numerous recent studies suggest that several HATs/HDACs have been involved in the salt and drought stress-responses in plants. The *gcn5* mutants were susceptible to salt stress due to disintegrated cell wall [105]. In Arabidopsis, AtGCN5 regulates expression of *MYB54*, *CTL1* (*CHITINASE-LIKE PROTEIN 1*), and *PGX3*

(*POLYGALACTURONASE INVOLVED IN EXPANSION3*) through H3K9/14ac providing salt stress tolerance. Moreover, GCN5-mediated histone acetylation also plays an essential role in the phosphate starvation responses (PSR) through At4–miR399–PHO2 pathway [106]. In *Populus trichocarpa*, GCN5 forms a protein complex with ADA2b and AREB1 (ABA-RESPONSIVE ELEMENT BINDING PROTEIN 1) and regulates the expression of drought-responsive genes such as *NAC006*, *NAC007*, and *NAC120* through enhancement of H3K9ac to confer the drought tolerance [23]. In maize, ZmGCN5 and ZmHATB increase the expression of cell wall-related genes *ZmEXPB2* (*EXPANSIN B2*) and *ZmXET1* (*XYLOGLUCAN ENDOTRANSGLUCOSYLASE 1*) through H3K9 hyperacetylation on the promoter region during salt stress [107]. Thus, GCN5 is a versatile epigenetic regulator that provides tolerance against different stresses in plants. Another histone acetyltransferase HAG3 has been reported to impede the UV-B-induced DNA damage repair and signalling in Arabidopsis [108]. On the other hand, GNAT-MYST activates wound-induced cellular reprogramming-related crucial genes, including *WIND1* (*WOUND INDUCED DEDIFFERENTIATION 1*), *ERF113/RAP2.6L* (*ETHYLENE RESPONSIVE FACTOR113/ RELATED TO AP2 6L*), and *LBD16* (*LATERAL ORGAN BOUNDARIES-DOMAIN 16*) through histone acetylation [109]. A positive effect of AtHAC1 on gene transcription was demonstrated by activating the endogenous promoter activity of *AREB1* (*ABA-RESPONSIVE ELEMENT BINDING PROTEIN 1*) through CRISPRa dCas9^{HAT} strategy. There was upregulation of *RD29A* (*RESPONSIVE TO DESICCATION 29A*) expression in the CRISPRa dCas9HAT harbouring transgenic plants resulting in increased drought tolerance in Arabidopsis [110]. The upregulation of four histone acetyltransferases *OsHAC703*, *OsHAG703*, *OsHAF701*, and *OsHAM701* and hyperacetylation at H3K9, H3K18, H3K27 and H4K5 lysine residues during drought stress suggest an involvement of HATs in the drought responses in rice [111] (Fig. 3; Table 2). HDA9 reduces the plant sensitivity to drought and salinity stresses by decreasing the H3K9ac level of the stress-responsive genes [112]. This function is an antagonist to WRKY53 function [113]. HDA6 interacts with HD2C to regulate the ABA- and salt stress-responsive genes through modulation of H3K9ac and H3K14ac lysine residues in Arabidopsis [114] and also controls the drought-responsive network through regulation of JA signalling [115].

Heat and cold stress

Worldwide, unexpected fluctuations in temperature are causing significant loss of crop productivity. There are several studies which suggest that HATs/HDACs are involved in responses to heat and cold stresses in plants. GCN5 provides thermotolerance by activating the expression of *HSFA3* (*HEAT SHOCK TRANSCRIPTION FACTOR A 3*) and *UVH6* (*ULTRAVIOLET HYPERSENSITIVE 6*) genes through H3K9/14 hyperacetylation on their promoter [116]. HAC1 has been found to maintain or restore the expression level of several viral and housekeeping genes through interaction with other activators like HsfB1 providing heat stress tolerance in tomato [117].

Several plants respond to the unfavourable high ambient temperature and try to facilitate cooling (thermomorphogenesis) through auxin signalling. In Arabidopsis, HDA9 forms complex with PWR and deacetylates H3K9 on the promoter of *PHYTOCHROME INTERACTING FACTOR4* (*PIF4*) and *YUCCA8* (*YUC8*) to control the thermomorphogenesis [13]. In addition, another study has revealed that HDA9 activates *YUCCA8* expression by net eviction of H2A.Z histone variants leading to PIF4 binding on its promoter. This enhances auxin production and thermomorphogenesis [12]. HDA15, another HDAC that interacts with HFR1 (LONG HYPOCOTYL IN FAR RED1) and represses the warm-temperature responsive genes at normal temperature [118]. The *hda6* plants show hypersensitivity to heat exposure [119]. HDA6 plays an essential role in freezing tolerance [120]. The two SIR-type HDACs SIRTUIN1/2 (SRT1 and SRT2) physically interact with the EIN2 NUCLEAR ASSOCIATED PROTEIN1 (ENAP1) to regulate the ethylene-responsive genes in Arabidopsis [121]. The HD2C interacts with a WD4-repeat protein HOS15 and CBFs (C-REPEAT BINDING FACTORS) during normal temperature to suppress the expression of *COR* (*COLD-RESPONSIVE*) genes *COR15A* and *COR47*. During cold, HOS15 facilitate ubiquitin-mediated degradation of HD2C, leading to the recruitment of CBFs on the promoter of *COR* genes for increasing their expression through hyperacetylation of histones [122]. HD2C also regulates heat stress-responsive genes. For this, HD2C coordinate with BRAHMA (BRM)-containing SWITCH/SUCROSE NONFERMENTING (SWI/SNF) chromatin remodelling complex [19]. Thus, HD2C is a suppressor of heat stress-responsive genes. However, another plant-specific histone deacetylase HD2D required for the regulation of the stress responses in Arabidopsis [123]. A cotton homolog of HD2D, GhHDT4D plays important role to regulate drought responses by deacetylation of H3K9 marks on the promoter, leading to the suppression of WRKY33, a suppressor of the drought responses in cotton [124, 125] (Fig. 3; Table 2).

ABA signalling

ABA is an essential hormone required for stress tolerance, and its signalling plays a dynamic role in adapting plants during different stresses. The ROP (RHO OF PLANTS) family of proteins such as ROP6, ROP10, and ROP11 regulate

ABA signalling at the early stages of stress [126]. The HDA15-MYB96 protein complex suppresses these genes through deacetylation of H3 and H4 histones at the cognate sites [126]. HDA19 with MSI1 (MULTICOPY SUPPRESSOR OF IRA1) regulates ABA signalling through H3K9 deacetylation-mediated suppression of ABA receptor encoding genes *PYL1*, *PYL4*, *PYL5*, and *PYL6* (*PYRABACTIN RESISTANCE 1 (PYR1)-LIKE 1/4/5/6*) in Arabidopsis [127]. The Arabidopsis *hda19* mutants showed higher ABA accumulation in young seedlings and acquired greater tolerance against different stresses [128–130]. For instance, the *hda19* mutant plants showed salt tolerance phenotype due to upregulation of LEA (LATE EMBRYOGENESIS ABUNDANT) and P5CS1 (D1-PYRROLINE-5-CARBOXYLATE SYNTHASE1) proteins which function in preventing protein aggregation and proline (an osmoprotectant) synthesis, respectively, during exposure of various environmental stresses. However, plants harbouring mutations in other histone deacetylases like *hda5*, *hda14*, *hda15* and *hda18* displayed sensitivity to salt stress [129]. HDA19 is a class I HADC, whereas HDA5, 14, 15 and 18 are class II HDACs belonging to RPD3 family. So, these results suggest that class I HDAC (HDA19) and class II HDACs (HDA5/14/15/18) work differently during salt stress in Arabidopsis. HDA19 and HDA6 may play a redundant role in modulating seed germination and salt stress response and ABA- and salt stress-induced gene expression in Arabidopsis [130]. In Brachypodium, a homolog of HDA19, BdHD1, is important in regulating ABA signalling and drought tolerance mechanism by suppressing the drought-responsive genes via deacetylation of H3K9ac lysine residues [131]. A complex of HDA9 with ABI4 (ABA INSENSITIVE 4) regulates ABA homeostasis through repression of (+)-ABA 8′-hydroxylase enzyme (involved in ABA catabolic pathways) encoding CYTOCHROME P450 genes *CYP707A1* and *CYP707A2* expression during drought stress [132]. Another recent study showed that HDA9 and PWR (POWERDRESS) interact with the ABI4 to regulate the ABA signalling and ABA-catabolism pathways in response to ABA and drought [133]. In normal conditions, CYP707A1/2 promotes inactivation of ABA by hydroxylation. During drought stress, the HDA9-PWR-ABI4 histone deacetylase complex suppresses *CYP707A1/2* genes and promotes ABA accumulation. [132, 133]. These reports indicate that there is a coordination between HDA9, HDA15 and HDA19 to control ABA signalling at several steps upon stress encounter (Fig. 3; Table 2).

In addition to the model plant Arabidopsis, histone deacetylases have been studied in other plants and trees as well. In common beans, HDA6 is upregulated during cold stress indicating its probable involvement in the abiotic stress tolerance [78]. In transgenic tobacco, overexpression of Populus histone deacetylase, 84KHDA903, increased drought stress responses by upregulating the expression of drought-responsive genes *DREB3*, *DREB4* (*DEHYDRATION-RESPONSIVE-ELEMENT-BINDING 3/4*), and *LEA5* (*LATE EMBRYOGENESIS ABUNDANT 5*) [134]. The over-expression of PtHDT902 (a plant-specific HD2 gene) activated the expression of GA (Gibberellic acid) biosynthesis-related genes, including *ENT-KAURENE OXIDASE* (*KO*), *ENT-KAURENOIC ACID HYDROXYLASE* (*KAO*), *GIBBERELLIN 20-OXIDASE* (*GA20ox*) [135]. As a result, there was an enhancement in primary root growth in transgenic Arabidopsis and inhibition of adventitious root formation in transgenic Populus. However, on the other hand, overexpression of PtHDT902 suppressed the expression of salt-responsive genes *HIGH-AFFINITY K*$^+$ *TRANSPORTER 1* (*HKT1*) and *GALACTINOL SYNTHASE 4* (*GOLS4*) in the transgenic lines. Thus, PtHDT902 is an interesting example of histone deacetylase that can regulate multiple signalling pathways in different manners. In rice, an RPD3-type histone deacetylase HDA1 interacts with IDS1 (INDETERMINATE SPIKELET1) and TPR1 (TOPLESS-RELATED PROTEIN 1) and suppresses the expression of salt stress-responsive genes such as *SOS1* (*SALT OVERLY SENSITIVE1*) and *LEA1* (*LATE EMBRYOGENESIS ABUNDANT PROTEIN1*) [136]. OsHDA705 is another RPD3-type histone deacetylase that regulates GA and ABA biosynthetic genes during rice seed germination. The overexpression of *OsHDA705* in rice decreases ABA level and salt stress resistance during seed germination. However, it enhances osmotic resistance during seedling stage [137]. In maize, heat stress affects growth and reduces crop yield. Heat stress induces ROS (Reactive oxygen species), which leads to programmed cell death (PCD) with modulation of chromatin structure by increasing the acetylation level of H3K9 and H4K5 and decreasing the methylation level of H3K9me2 in maize seedlings. The inhibition of HDACs by TSA causes hyperacetylation of histones and increases the superoxide level (O_2^-), leading to PCD [138]. Another study also revealed that short-term heat stress induces dynamic alterations in H3K9ac and H3K4me2 levels on the promoter region of upregulated heat stress factor (Hsf) and rRNA genes [139]. These genes accompanied by perturbations of cell membranes and increase in ROS levels in maize seedlings helped to counter the stress. These results indicate that HDACs positively regulate the expression of cold-induced gene *ZmDREB1* by histone modification and chromatin conformational changes [140]. In kenaf, there are six histone deacetylase genes *HcHDA2*, *HcHDA6*, *HcHDA8*, *HcHDA9*, *HcHDA19* and *HcSRT2* that are differentially expressed during different growth stages and drought and salt stresses suggesting their probable role in the plant development and also in the stress responses [141]. In banana, MaHDA2-MaMYB4 repressor complex is recruited on the promoter of $\omega - 3$ fatty acid desaturase genes *MaFAD3-1*, *MaFAD3-3*, *MaFAD3-4*, and *MaFAD3-7* to repress their transcription during cold stress [142] (Fig. 3; Table 2). Thus, modulations of histone acetylation by different HAT and HDAC have a significant effect on the signalling pathways that contribute to the stress responses.

Histone acetylation in crops

Crops fulfil the global demand for food, but different environmental stresses cause yield loss. The progressive climate change is also exerting pressure on the growth and development of plants. So, the development of climate resilience crop may be helpful to secure the food demand for the ever-increasing world population. As explained above in this review, different HATs and HDACs modulate histone acetylation to control growth and stress responses in different plants. In this section, the relevance of histone acetylation modulation in crop plants has been discussed (Fig. 3; Table 1, 2). For example, histone acetyltransferase GCN5 has been shown to promote crown root formation in rice plants to keep them erect [55]. A new-type GNAT-like protein OsglHAT1 has inherent H4 histone acetyltransferase activity and its gene is found in the grain weight quantitative trait loci (QTL) in rice [143]. It positively regulates the expression of *PGL2* (*6-PHOSPHOGLUCONOLACTONASE 2*), which is important for the grain length. The overexpression of OsglHAT1 increases several agronomical traits, including grain length, grain weight, yield, and total biomass. A SIR2-type HDAC in rice, OsSRT1 inhibits carbon metabolic flux (glycolysis pathway) in the developing seedling [144], and also promotes starch accumulation in the developing seeds [46, 47]. Other HDACs, OsHDA1 and OsHDA705 are associated with impeded response to salt stress [136, 137]. On the same note, the histone deacetylase OsHDT701 is also associated with weakened innate immunity in rice [104]. In wheat, histone deacetylases TaHDA6 and TaHDT701 have been found to control the innate immunity during *Bgt* infection [102, 103]. On the other hand, TaGCN5 induces cuticular wax biosynthesis and *Bgt* growth [101]. In maize, the histone deacetylase HDA108 controls plant height, leaf development, inflorescence patterning and fertility [145]. Besides, histone acetylation dynamics has been also shown to regulate heat stress tolerance [138, 139]. ZmGCN5 provides salt stress tolerance in maize [107], whereas, the HDACs activates the expression of cold-induced gene *ZmDREB1* to ensure cold tolerance [140]. There are few reports which have also explained the impact of histone acetylation modulation on fruit ripening. In banana, MaHDA1 impedes fruit ripening [87], whereas MaHDA6 promotes fruit ripening [88]. Similarly, in tomato, SlHDA3 delays fruit ripening [89], whereas, SlHDT3 promotes the fruit ripening [90]. In papaya, CpHDA3 promotes fruit ripening and softening [91]. Cotton is another important crop where few reports have shown the role of histone deacetylases in cotton fiber development and drought tolerance. Expression of *GhHDA5* is increased at the time of cotton fiber initiation and down-regulation of *GhHDA5* in RNAi lines reduces the cotton fiber initials due to H3K9 hyper-acetylation of *ATG8* (*AUTOPHAGY 8*) gene promoter leading to its higher expression [38]. This study suggests that HDA5 might control autophagy by the repression of *ATG8* gene expression via H3K9 deacetylation during cotton fiber initiation. Furthermore, this study also revealed that the activity of GhHDA5 could be inhibited by an HDAC inhibitor Trichostatin A (TSA). The application of the TSA in the in vitro cultured ovules reduces fiber differentiation suggesting that HDACs are essential for fiber development [38]. GhHDT4D histone deacetylase is required for the drought tolerance in cotton [124]. In rice, OsHDA710 has been found to be important for callus formation from the embryo. It represses the expression of *AUXIN RESPONSE FACTOR* genes *OsARF18* and *OsARF22* by deacetylating of H3. A mutation in *OsHDA710* (*hda710*) or inhibition of its activity by TSA affected callus formation [146]. Thus, all these examples from different crop plants suggest that the modulation of histone acetylation status can be used as a strategy to make the plants more stress-resilient and more productive. For this purpose, different HAT and HDAC genes could be targeted by molecular biology and molecular breeding approaches.

Acetylation of non-histone proteins

Non-histone proteins can also serve as substrates for lysine acetylation and subsequent deacetylation. Numerous studies have shown that lysine acetylation of non-histone proteins regulates diverse functions in plants [147–149]. Interestingly, some reports have revealed the role of HATs and HDACs in the lysine acetylation dynamics of non-histone proteins. For instance, HDA6 inhibits the kinase activity of BIN2 (BRASSINOSTEROID-INSENSITIVE 2) through deacetylation to enhance BR (Brassinosteroid) signalling in Arabidopsis [150]. A recent report shows that HDA9 and WRKY53 work in a mutually antagonistic manner to control stress responses. In this case, HDA9 interacts with WRKY53 and suppresses its transcriptional activity through lysine deacetylation. Conversely, WRKY53 also inhibits HDA9 activity [113]. HDA14 (HISTONE DEACETYLASE 14) is a chloroplast localized histone deacetylase which was found to control photosynthesis in Arabidopsis. HDA14 regulates lysine acetylation of RuBisCO activase to control the activation of RuBisCo (RIBULOSE-1,5-BISPHOSPHATE CARBOXYLASE/OXYGENASE) enzyme, which is essential for the photosynthesis [149]. It also deacetylates a non-histone protein α/β-tubulins, which is probably acetylated by a putative histone acetyltransferase ELP3 in the Arabidopsis [151]. Another histone deacetylase, HDA15 modulate COP1

(Constitutive Photomorphogenesis1) activity by lysine deacetylation to regulate the photomorphogenesis [152]. In rice, OsSRT1 represses glyceraldehyde-3-phosphate dehydrogenase (GAPDH) activity through deacetylation and inhibits carbon metabolic flux (glycolysis pathway) in the developing seedling [144]. SRT2 was also found to control energy metabolism and metabolite transport through deacetylation of inner membrane protein complexes in Arabidopsis [153]. Thus, all these reports suggest that the HAT and HDAC proteins control metabolic and biological functions by tuning the acetylation status of both histone and non-histone proteins. To understand the details of the functioning of HATs and HDACs in non-histone proteins modifications require comprehensive analyses. A comparative analysis of histone versus non-histone proteins as the substrates will be helpful to understand the broader aspects of the functionality of HATs and HDACs.

Undeciphered modules

1. Being a direct modulator of gene expression, usually, HATs and HDACs are at the end of the signaling cascades. How are the developmental and environmental signals transmitted to HATs and HDACs?
2. There are many uncharacterized HATs and HDACs in plants. What is their biological relevance in plant development and biotic and abiotic stress tolerance mechanisms? Few histone modulators (GCN5, HDA6, HDA9, and HDA19) are widely studied. To properly understand the dynamics of acetylation, the other family members should also be discussed in detail.
3. To fine-tune the critical process of gene transcription, there has to be equilibrium between the functions of HATs and HDACs. Which of the HATs and HDACs function synergistically or antagonistically?
4. What is the other HAT-/HDAC-associated genetic/epigenetic components of broad networks of histone acetylation?
5. What is the underlying mechanism of acetylation and deacetylation of non-histone proteins? Does acetylation of non-histone proteins sync with histone acetylation to control the plant's development and their adaptation in the adverse condition?

Conclusions and future prospects

Histone acetylation dynamics is a gene regulatory epigenetic mechanism that permits switching between permissive and repressive chromatin by HATs and HDACs upon sensing developmental and environmental cues. Once the respective receptors perceive the cues, the signalling cascades are evoked by hormones, secondary messengers and other signalling molecules. The signalling pathways lead to the expression of HATs and HDACs (Fig. 4) that activate and repress target genes, respectively, to regulate downstream pathways. These alterations in the biochemical pathways ultimately regulate development and stress tolerance in plants (Fig. 4). In the past decade, several studies substantiated that histone acetylation dynamics and other epigenetic modifications are integral parts of the transcription machinery for gene regulation during plant development and their adaptation in adverse conditions. This review summarized the recent findings establishing several HATs and HDACs as epigenetic regulators of physiological and biological processes in different plants (Fig. 3). Both epigenetic regulators control numerous developmental processes, including seedling, leaf, root and flower development, fruit ripening, and aging of plants as well as biotic and abiotic stress responses (Fig. 3). They control these processes by regulating biosynthesis and signalling pathways of different hormones, including Auxin, BRs, ethylene, JA, SA, and ABA. Although the field of epigenetics has been extensively explored, some aspects, especially in plants, are yet to be understood entirely. For instance, in many cases, the underlying mechanisms which cause, maintain and transduce these epigenetic modifications are still elusive. Recent studies have demonstrated that HATs/HDACs act in the multiprotein complexes to regulate different biological processes and stress responses (Table 1, 2). Most studies are focused on the identification of HATs/HDACs protein complexes and their targets. However, shreds of evidence are still lacking regarding the underlying mechanism that helps to sense the developmental and environmental cues that decide their co-factors such as TFs, activator and repressor proteins, and other histone modifiers for the action. The regulatory networks of histone acetylation and crosstalk with other histone modifications essential for the different biological processes are not well explored. Several studies have shown the involvement of different HATs and HDACs in the same biological processes; HDA6 and HDA9 in circadian rhythm and flowering [15, 64], HAM1/2 and HD2C with MRG1/2 in flowering [17, 68] and HDA19 and HD2D in photoperiod- dependent and independent flowering, respectively [70, 71]. However, the relationship and orchestration between them are still unestablished. Studies have shown that HDA9-PWR-HOS15 and HD2C-HOS15 associate in a core complex to repress different sets of genes responsible for development and stress responses [53, 72, 122], but the association of HOS15 with other HDACs is unknown. Although HATs and HDACs are histone acetylation modulating enzymes, recent studies have shown them to act on the non-histone targets as well [144, 149–151, 153]. However, the role of HATs/HDACs in the modification of non-histone proteins has not gained that much attention. A comparative analysis of histone targeted processes and non-histone targeted processes regulated by

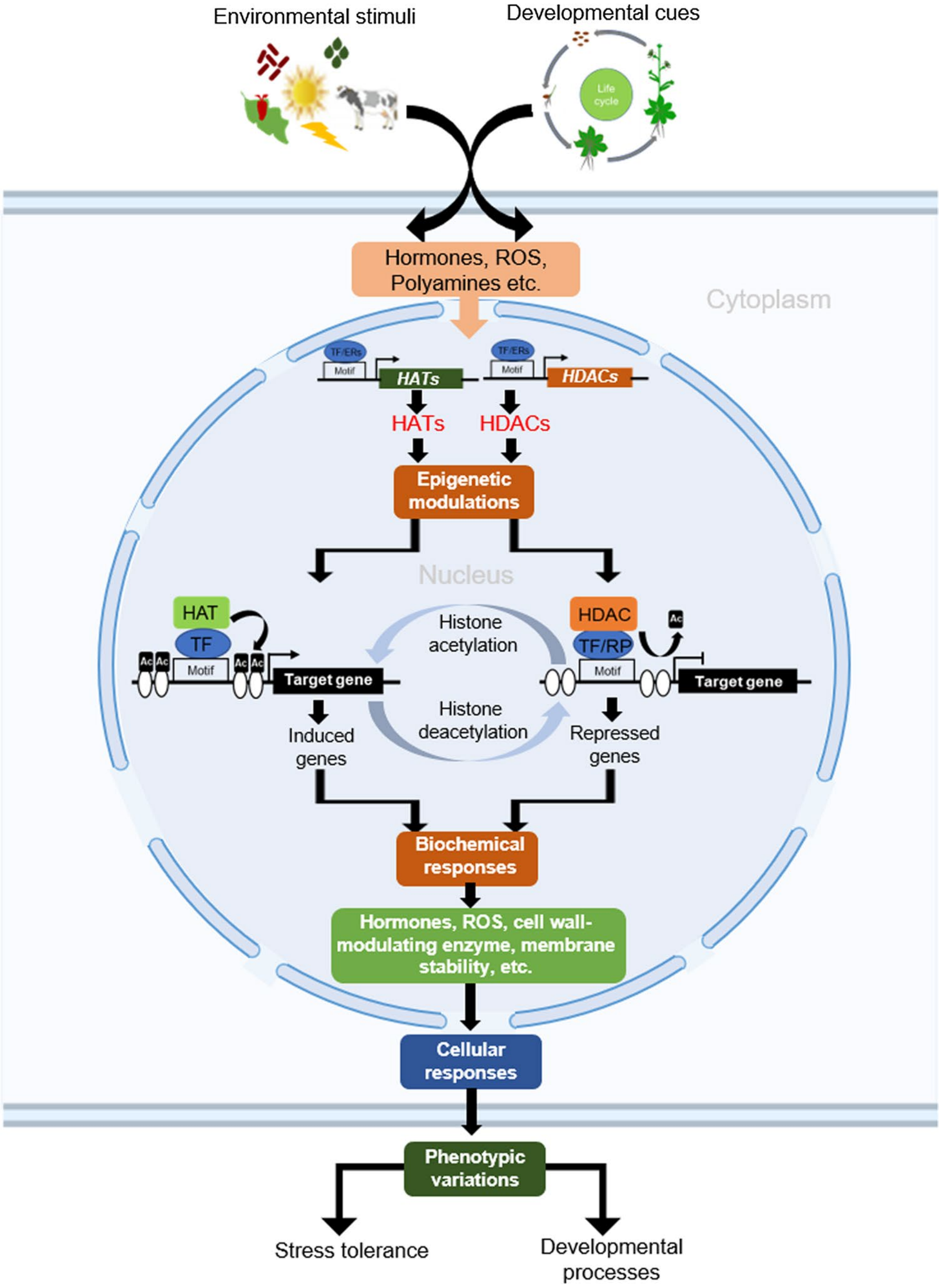

Fig. 4 An overview of histone acetylation-mediated epigenetic regulation of developmental processes and stress tolerance in plants. The developmental and environmental stimuli trigger signalling cascade that leads to the expression of HAT and HDAC genes. HATs and HDACs are recruited on the promoters of the target genes with the help of sequence-specific DNA-binding activator (co-activators) and repressor proteins (co-suppressor), respectively. HATs generally activate the target genes by adding an acetyl group on lysine residues of histones, while HDACs repress genes by removing acetyl groups added by the HATs. The products of these target genes constitute different biochemical pathways. Thus, HATs and HDACs affect the biochemical pathways and modulate hormones metabolism, ROS homeostasis, cell wall integrity, and membrane stability. They ultimately control developmental processes and adaptation of plants in different environmental conditions through regulation of stress tolerance mechanisms. *RGs* regulators, *TF* transcription factor, *RP* repressor protein, *Ac* acetyl group, *ROS* reactive oxygen species

these HATs/HDACs will be worthwhile to understand the functionality of these enzymes. As discussed above, histone modifications by HATs/HDACs have a prominent impact on crop productivity and yield. So, it is imperative to explore the possibility of targeting specific HATs/HDACs by chemical means or using molecular tools to enhance the yield. The CRISPRa dCas9 strategy may also be deployed to activate or repress target genes of HATs/HDACs that have a role in plant development and stress tolerance. These strategies will ultimately lead to improving the yield and stress resilience in crops.

Acknowledgements Authors' work in this area is supported by J.C. Bose National Fellowship Grant of Department of Science and Technology, Government of India (File No. JCB/2018/000001) and Core Grant of National Institute of Plant Genome Research, New Delhi, India. V. K. acknowledges the Science and Engineering Research Board, Government of India for National Post-Doctoral Fellowship Grant (File No. PDF/2017/000892). The authors are also thankful to DBT-eLibrary Consortium (DeLCON) for providing access to e-resources.

Author contributions MP conceived the idea and outlined the review. VK wrote the manuscript and prepare figures and tables, JKT provided extensive revisions to the technical content of the manuscript. All authors have read and approved the final version of the manuscript.

Funding This work is supported by the J.C. Bose National Fellowship Grant of Department of Science and Technology, Government of India (File No. JCB/2018/000001) and Core Grant of National Institute of Plant Genome Research, New Delhi, India and National Post-Doctoral Fellowship Grant (File No. PDF/2017/000892), Science and Engineering Research Board, New Delhi, Government of India.

Declaration

Conflict of interest The authors have no conflict of interest to declare.

References

1. Luger K, Mäder AW, Richmond RK et al (1997) Crystal structure of the nucleosome core particle at 2.8 Å resolution. Nature 389:251–260. https://doi.org/10.1038/38444
2. Strahl BD, Allis CD (2000) The language of covalent histone modifications. Nature 403:41–45. https://doi.org/10.1038/47412
3. Turner BM (2000) Histone acetylation and an epigenetic code. BioEssays 22:836–845. https://doi.org/10.1002/1521-1878(200009)22:9%3c836::AID-BIES9%3e3.0.CO;2-X
4. Jenuwein T, Allis CD (2001) Translating the histone code. Science 293:1074–1080. https://doi.org/10.1126/science.1063127
5. Dutnall RN (2003) Cracking the histone code: one, two, three methyls, you're out! Mol Cell 12:3–4. https://doi.org/10.1016/S1097-2765(03)00282-X
6. Pandey R, Mu A, Ller È et al (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. https://doi.org/10.1093/nar/gkf660
7. Kouzarides T (2007) Chromatin modifications and their function. Cell 128:693–705. https://doi.org/10.1016/j.cell.2007.02.005
8. Bjerling P, Silverstein RA, Thon G et al (2002) Functional divergence between histone deacetylases in fission yeast by distinct cellular localization and in vivo specificity. Mol Cell Biol 22:2170–2181. https://doi.org/10.1128/mcb.22.7.2170-2181.2002
9. Iwasaki W, Tachiwana H, Kawaguchi K et al (2011) Comprehensive structural analysis of mutant nucleosomes containing lysine to glutamine (KQ) substitutions in the H3 and H4 histone-fold domains. Biochemistry 50:7822–7832. https://doi.org/10.1021/bi201021h
10. Pradeepa MM, Grimes GR, Kumar Y et al (2016) Histone H3 globular domain acetylation identifies a new class of enhancers. Nat Genet 48:681–686. https://doi.org/10.1038/ng.3550
11. Deng W, Liu C, Pei Y et al (2007) Involvement of the histone acetyltransferase AtHAC1 in the regulation of flowering time via repression of FLOWERING LOCUS C in *Arabidopsis*. Plant Physiol 143:1660–1668. https://doi.org/10.1104/pp.106.095521
12. van der Woudea LC, Perrellab G, Snoekd BL et al (2019) HISTONE DEACETYLASE 9 stimulates auxin-dependent thermomorphogenesis in *Arabidopsis thaliana* by mediating H2A.Z depletion. Proc Natl Acad Sci U S A 116:25343–25354. https://doi.org/10.1073/pnas.1911694116
13. Tasset C, Singh Yadav A, Sureshkumar S et al (2018) POWERDRESS-mediated histone deacetylation is essential for thermomorphogenesis in *Arabidopsis thaliana*. PLoS Genet 14:1–21. https://doi.org/10.1371/journal.pgen.1007280
14. Bannister AJ, Kouzarides T (2011) Regulation of chromatin by histone modifications. Cell Res 21:381–395. https://doi.org/10.1038/cr.2011.22
15. Hung FY, Chen FF, Li C et al (2019) The LDL1/2-HDA6 histone modification complex interacts with TOC1 and regulates the core circadian clock components in *Arabidopsis*. Front Plant Sci 10:1–10. https://doi.org/10.3389/fpls.2019.00233
16. Zhou Y, Yang P, Zhang F et al (2020) Histone deacetylase HDA19 interacts with histone methyltransferase SUVH5 to regulate seed dormancy in *Arabidopsis*. Plant Biol (Stuttg) 22:1062–1071. https://doi.org/10.1111/PLB.13158
17. Xu Y, Gan ES, Zhou J et al (2014) Arabidopsis MRG domain proteins bridge two histone modifications to elevate expression of flowering genes. Nucleic Acids Res 42:10960–10974. https://doi.org/10.1093/nar/gku781
18. Nie WF, Lei M, Zhang M et al (2019) Histone acetylation recruits the SWR1 complex to regulate active DNA demethylation in *Arabidopsis*. Proc Natl Acad Sci U S A 116:16641–16650. https://doi.org/10.1073/pnas.1906023116
19. Buszewicz D, Archacki R, Palusiński A et al (2016) HD2C histone deacetylase and a SWI/SNF chromatin remodelling complex interact and both are involved in mediating the heat stress response in *Arabidopsis*. Plant Cell Environ 39:2108–2122. https://doi.org/10.1111/pce.12756
20. Wang B, Yang X, Wang Y et al (2018) Tomato yellow leaf curl virus V2 interacts with host histone deacetylase 6 to suppress methylation-mediated transcriptional gene silencing in plants. J Virol 92:138–145. https://doi.org/10.1016/B978-012374410-4.00717-2
21. Li J, Yang DL, Huang H et al (2020) Epigenetic memory marks determine epiallele stability at loci targeted by de novo DNA methylation. Nat Plants 6:661–674. https://doi.org/10.1038/s41477-020-0671-x
22. Eberharter A, Becker PB (2002) Histone acetylation: a switch between repressive and permissive chromatin. Second in review on chromatin dynamics. EMBO Rep 3:224–229. https://doi.org/10.1093/embo-reports/kvf053
23. Li S, Lin YCJ, Wang P et al (2019) The AREB1 transcription factor influences histone acetylation to regulate drought responses and tolerance in *Populus trichocarpa*. Plant Cell 31:663–686. https://doi.org/10.1105/tpc.18.00437
24. Clayton AL, Hazzalin CA, Mahadevan LC (2006) Enhanced histone acetylation and transcription: a dynamic perspective. Mol Cell 23:289–296. https://doi.org/10.1016/j.molcel.2006.06.017
25. Srivastava R, Rai KM, Srivastava M et al (2014) Distinct role of core promoter architecture in regulation of light-mediated responses in plant genes. Mol Plant 7:626–641. https://doi.org/10.1093/mp/sst146
26. Wang L, Zhang F, Rode S et al (2017) Ethylene induces combinatorial effects of histone H3 acetylation in gene expression in *Arabidopsis*. BMC Genom. https://doi.org/10.1186/s12864-017-3929-6
27. Kim S, Piquerez SJM, Ramirez-Prado JS et al (2020) GCN5 modulates salicylic acid homeostasis by regulating H3K14ac levels at the 5′ and 3′ ends of its target genes. Nucleic Acids Res 48:5953–5966. https://doi.org/10.1093/nar/gkaa369
28. Gu D, Chen CY, Zhao M et al (2017) Identification of HDA15-PIF1 as a key repression module directing the transcriptional network of seed germination in the dark. Nucleic Acids Res 45:7137–7150. https://doi.org/10.1093/nar/gkx283
29. Yang C, Shen W, Yang L et al (2020) HY5-HDA9 module transcriptionally regulates plant autophagy in response to light-to-dark conversion and nitrogen starvation. Mol Plant 13:515–531. https://doi.org/10.1016/j.molp.2020.02.011
30. Gallinari P, Di Marco S, Jones P et al (2007) HDACs, histone deacetylation and gene transcription: from molecular biology to cancer therapeutics. Cell Res 17:195–211. https://doi.org/10.1038/sj.cr.7310149

31. Aiese Cigliano R, Sanseverino W, Cremona G et al (2013) Genome-wide analysis of histone modifiers in tomato: gaining an insight into their developmental roles. BMC Genom 14:57. https://doi.org/10.1186/1471-2164-14-57
32. Peng M, Ying P, Liu X et al (2017) Genome-wide identification of histone modifiers and their expression patterns during fruit abscission in litchi. Front Plant Sci 8:1–16. https://doi.org/10.3389/fpls.2017.00639
33. Aquea F, Timmermann T, Arce-Johnson P (2010) Analysis of histone acetyltransferase and deacetylase families of *Vitis vinifera*. Plant Physiol Biochem 48:194–199. https://doi.org/10.1016/j.plaphy.2009.12.009
34. Liu X, Luo M, Zhang W et al (2012) Histone acetyltransferases in rice (*Oryza sativa* L.): phylogenetic analysis, subcellular localization and expression. BMC Plant Biol 12:145. https://doi.org/10.1186/1471-2229-12-145
35. Hu Y, Lu Y, Zhao Y, Zhou D-X (2019) Histone acetylation dynamics integrates metabolic activity to regulate plant response to stress. Front Plant Sci 10:1–9. https://doi.org/10.3389/fpls.2019.01236
36. Thakur JK, Agarwal P, Parida S et al (2013) Sequence and expression analyses of KIX domain proteins suggest their importance in seed development and determination of seed size in rice, and genome stability in *Arabidopsis*. Mol Genet Genom 288:329–346. https://doi.org/10.1007/s00438-013-0753-9
37. Yang C, Shen W, Chen H et al (2018) Characterization and subcellular localization of histone deacetylases and their roles in response to abiotic stresses in soybean. BMC Plant Biol 18:1–13. https://doi.org/10.1186/s12870-018-1454-7
38. Kumar V, Singh B, Singh SK et al (2018) Role of GhHDA5 in H3K9 deacetylation and fiber initiation in *Gossypium hirsutum*. Plant J 95:1069–1083. https://doi.org/10.1111/tpj.14011
39. Fu W, Wu K, Duan J (2007) Sequence and expression analysis of histone deacetylases in rice. Biochem Biophys Res Commun 356:843–850. https://doi.org/10.1016/j.bbrc.2007.03.010
40. Liu X, Yu CW, Duan J et al (2012) HDA6 Directly interacts with DNA methyltransferase MET1 and maintains transposable element silencing in *Arabidopsis*. Plant Physiol 158:119–129. https://doi.org/10.1104/pp.111.184275
41. Yu CW, Tai R, Wang SC et al (2017) Histone deacetylase6 acts in concert with histone methyltransferases SUVH4, SUVH5, and SUVH6 to regulate transposon silencing. Plant Cell 29:1970–1983. https://doi.org/10.1105/tpc.16.00570
42. Xu Y, Wang Y, Stroud H et al (2013) A matrix protein silences transposons and repeats through interaction with retinoblastoma-associated proteins. Curr Biol 23:345–350. https://doi.org/10.1016/j.cub.2013.01.030
43. Liu X, Yang S, Zhao M et al (2014) Transcriptional repression by histone deacetylases in plants. Mol Plant 7:764–772. https://doi.org/10.1093/mp/ssu033
44. Yang J, Yuan L, Yen M et al (2019) SWI3B and HDA6 interact and are required for transposon silencing in *Arabidopsis*. Plant J. https://doi.org/10.1111/tpj.14666
45. Earley KW, Pontvianne F, Wierzbicki AT et al (2010) Mechanisms of HDA6-mediated rRNA gene silencing: suppression of intergenic Pol II transcription and differential effects on maintenance versus siRNA-directed cytosine methylation. Genes Dev 24:1119–1132. https://doi.org/10.1101/gad.1914110
46. Huang L, Sun Q, Qin F et al (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. https://doi.org/10.1104/pp.107.099473
47. Zhang H, Lu Y, Zhao Y, Zhou DX (2016) OsSRT1 is involved in rice seed development through regulation of starch metabolism gene expression. Plant Sci 248:28–36
48. Liu X, Chen CY, Wang KC et al (2013) Phytochrome interacting factor3 associates with the histone deacetylase HDA15 in repression of chlorophyll biosynthesis and photosynthesis in etiolated Arabidopsis seedlings. Plant Cell 25:1258–1273. https://doi.org/10.1105/tpc.113.109710
49. Zhao L, Peng T, Chen CY et al (2019) HY5 interacts with the histone deacetylase HDA15 to repress hypocotyl cell elongation in photomorphogenesis. Plant Physiol 180:1450–1466. https://doi.org/10.1104/pp.19.00055
50. Gao MJ, Li X, Huang J et al (2015) Scarecrow-like15 interacts with histone deacetylase19 and is essential for repressing the seed maturation programme. Nat Commun 6:7243. https://doi.org/10.1038/ncomms8243
51. Ryu H, Cho H, Bae W, Hwang I (2014) Control of early seedling development by BES1/TPL/HDA19-mediated epigenetic regulation of ABI3. Nat Commun 5:4138. https://doi.org/10.1038/ncomms5138
52. Tanaka M, Kikuchi A, Kamada H (2008) The *Arabidopsis* histone deacetylases HDA6 and HDA19 contribute to the repression of embryonic properties after germination. Plant Physiol 146:149–161. https://doi.org/10.1104/pp.107.111674
53. Mayer KS, Chen X, Sanders D et al (2019) HDA9-PWR-HOS15 is a core histone deacetylase complex regulating transcription and development. Plant Physiol 180:342–355. https://doi.org/10.1104/pp.18.01156
54. Cohen R, Schocken J, Kaldis A et al (2009) The histone acetyltransferase GCN5 affects the inflorescence meristem and stamen development in *Arabidopsis*. Planta 230:1207–1221. https://doi.org/10.1007/s00425-009-1012-5
55. Zhou S, Jiang W, Long F et al (2017) Rice homeodomain protein WOX11 recruits a histone acetyltransferase complex to establish programs of cell proliferation of crown root meristem. Plant Cell 29:1088–1104. https://doi.org/10.1105/tpc.16.00908
56. Meijón M, Feito I, Valledor L et al (2010) Dynamics of DNA methylation and histone H4 acetylation during floral bud differentiation in *Azalea*. BMC Plant Biol 10:10. https://doi.org/10.1186/1471-2229-10-10
57. Kotak J, Saisana M, Gegas V et al (2018) The histone acetyltransferase GCN5 and the transcriptional coactivator ADA2b affect leaf development and trichome morphogenesis in *Arabidopsis*. Planta 248:613–628. https://doi.org/10.1007/s00425-018-2923-9
58. Luo M, Yu CW, Chen FF et al (2012) Histone deacetylase HDA6 is functionally associated with AS1 in repression of KNOX genes in *Arabidopsis*. PLoS Genet 8:4–13. https://doi.org/10.1371/journal.pgen.1003114
59. Kim J, Yang W, Forner J et al (2018) Epigenetic reprogramming by histone acetyltransferase HAG1/AtGCN5 is required for pluripotency acquisition in *Arabidopsis*. EMBO J 37:1–16. https://doi.org/10.15252/embj.201798726
60. Chen WQ, Drapek C, Li DX et al (2019) Histone deacetylase HDA19 affects root cortical cell fate by interacting with scarecrow. Plant Physiol 180:276–288. https://doi.org/10.1104/pp.19.00056
61. Zhang Y, Yin B, Zhang J et al (2019) Histone deacetylase HDT1 is involved in stem vascular development in *Arabidopsis*. Int J Mol Sci 20:3452. https://doi.org/10.3390/ijms20143452
62. Chen CY, Wu K, Schmidt W (2015) The histone deacetylase HDA19 controls root cell elongation and modulates a subset of phosphate starvation responses in *Arabidopsis*. Sci Rep 5:1–11. https://doi.org/10.1038/srep15708
63. Hung FY, Chen FF, Li C et al (2018) The *Arabidopsis* LDL1/2-HDA6 histone modification complex is functionally associated

with CCA1/LHY in regulation of circadian clock genes. Nucleic Acids Res 46:10669–10681. https://doi.org/10.1093/nar/gky749

64. Lee K, Mas P, Seo PJ (2019) The EC-HDA9 complex rhythmically regulates histone acetylation at the TOC1 promoter in *Arabidopsis*. Commun Biol 2:143. https://doi.org/10.1038/s42003-019-0377-7
65. Schultz EA, Haughn GW (1993) Genetic analysis of the floral initiation process (FLIP) in *Arabidopsis*. Development 119:745–765
66. Xiao J, Zhang H, Xing L et al (2013) Requirement of histone acetyltransferases HAM1 and HAM2 for epigenetic modification of FLC in regulating flowering in *Arabidopsis*. J Plant Physiol 170:444–451. https://doi.org/10.1016/j.jplph.2012.11.007
67. Xu D, Liu Q, Chen G et al (2019) Aldehyde dehydrogenase ALDH3F1 involvement in flowering time regulation through histone acetylation modulation on FLOWERING LOCUS C. J Integr Plant Biol 62:1080–1092. https://doi.org/10.1111/jipb.12893
68. Guo Z, Li Z, Liu Y et al (2020) MRG1/2 histone methylation readers and HD2C histone deacetylase associate in repression of the florigen gene FT to set a proper flowering time in response to day-length changes. New Phytol 227:1453–1466. https://doi.org/10.1111/nph.16616
69. Krogan NT, Hogan K, Long JA (2012) APETALA2 negatively regulates multiple floral organ identity genes in *Arabidopsis* by recruiting the co-repressor TOPLESS and the histone deacetylase HDA19. Development 139:4180–4190. https://doi.org/10.1242/dev.085407
70. Ning YQ, Chen Q, Lin RN et al (2019) The HDA19 histone deacetylase complex is involved in the regulation of flowering time in a photoperiod-dependent manner. Plant J 98:448–464. https://doi.org/10.1111/tpj.14229
71. Farhi J, Tian G, Fang H et al (2017) Histone deacetylase HD2D is involved in regulating plant development and flowering time in *Arabidopsis*. Plant Signal Behav 12:1–4. https://doi.org/10.1080/15592324.2017.1300742
72. Park HJ, Baek D, Cha JY et al (2019) HOS15 interacts with the histone deacetylase HDA9 and the evening complex to epigenetically regulate the floral activator *Gigantea*. Plant Cell 31:37–51. https://doi.org/10.1105/tpc.18.00721
73. 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. https://doi.org/10.1016/j.bbrc.2012.11.102
74. Kim YJ, Wang R, Gao L et al (2016) POWERDRESS and HDA9 interact and promote histone H3 deacetylation at specific genomic sites in *Arabidopsis*. Proc Natl Acad Sci 113:14858–14863. https://doi.org/10.1073/pnas.1618618114
75. Zeng X, Gao Z, Jiang C et al (2019) Histone deacetylase 9 functions with polycomb silencing to repress FLOWERING LOCUS C expression. Plant Physiol 182:555–565. https://doi.org/10.1104/pp.19.00793
76. Yuan L, Chen X, Chen H et al (2019) Histone deacetylases HDA6 and HDA9 coordinately regulate valve cell elongation through affecting auxin signaling in *Arabidopsis*. Biochem Biophys Res Commun 508:695–700. https://doi.org/10.1016/j.bbrc.2018.11.082
77. Nguyen CT, Tran GB, Nguyen NH (2020) Homeostasis of histone acetylation is critical for auxin signaling and root morphogenesis. Plant Mol Biol 103:1–7. https://doi.org/10.1007/s11103-020-00985-1
78. Hayford RKA, Ligaba-Osena A, Subramani M et al (2017) Characterization and expression analysis of common bean histone deacetylase 6 during development and cold stress response. Int J Genom 2017:2502691. https://doi.org/10.1155/2017/2502691
79. Yu CW, Liu X, Luo M et al (2011) Histone deacetylase6 interacts with FLOWERING LOCUS D and regulates flowering in *Arabidopsis*. Plant Physiol 156:173–184. https://doi.org/10.1104/pp.111.174417
80. Luo M, Tai R, Yu CW et al (2015) Regulation of flowering time by the histone deacetylase HDA5 in *Arabidopsis*. Plant J 82:925–936. https://doi.org/10.1111/tpj.12868
81. Mahrez W, Arellano MST, Moreno-Romero J et al (2016) H3K36ac is an evolutionary conserved plant histone modification that marks active genes. Plant Physiol 170:1566–1577. https://doi.org/10.1104/pp.15.01744
82. Latrasse D, Benhamed M, Henry Y et al (2008) The MYST histone acetyltransferases are essential for gametophyte development in *Arabidopsis*. BMC Plant Biol 8:1–16. https://doi.org/10.1186/1471-2229-8-121
83. Zheng B, He H, Zheng Y et al (2014) An ARID domain-containing protein within nuclear bodies is required for sperm cell formation in *Arabidopsis thaliana*. PLoS Genet 10:e1004421. https://doi.org/10.1371/journal.pgen.1004421
84. Cigliano RA, Cremona G, Paparo R et al (2013) Histone deacetylase AtHDA7 is required for female gametophyte and embryo development in *Arabidopsis*. Plant Physiol 163:431–440. https://doi.org/10.1104/pp.113.221713
85. Li X, Guo W, Li J et al (2020) Histone acetylation at the promoter for the transcription factor PUWRKY31 affects sucrose accumulation in pear fruit. Plant Physiol 182:2035–2046. https://doi.org/10.1104/PP.20.00002
86. Seymour GB, Ostergaard L, Chapman NH et al (2013) Fruit development and ripening. Annu Rev Plant Biol 64:219–241. https://doi.org/10.1146/annurev-arplant-050312-120057
87. Han YC, Kuang JF, Chen JY et al (2016) Banana transcription factor MaERF11 recruits histone deacetylase MaHDA1 and represses the expression of MaACO1 and expansions during fruit ripening. Plant Physiol 171:1070–1084. https://doi.org/10.1104/pp.16.00301
88. Fu CC, Han YC, Guo YF et al (2018) Differential expression of histone deacetylases during banana ripening and identification of MaHDA6 in regulating ripening-associated genes. Postharvest Biol Technol 141:24–32. https://doi.org/10.1016/j.postharvbio.2018.03.010
89. Guo JE, Hu Z, Yu X et al (2018) A histone deacetylase gene, SlHDA3, acts as a negative regulator of fruit ripening and carotenoid accumulation. Plant Cell Rep 37:125–135. https://doi.org/10.1007/s00299-017-2211-3
90. Guo JE, Hu Z, Li F et al (2017) Silencing of histone deacetylase SlHDT3 delays fruit ripening and suppresses carotenoid accumulation in tomato. Plant Sci 265:29–38. https://doi.org/10.1016/j.plantsci.2017.09.013
91. Fu C, Chen H, Gao H, Han Y (2019) Histone deacetylase CpHDA3 is functionally associated with CpERF9 in suppression of CpPME1/2 and CpPG5 genes during papaya fruit ripening. J Agric Food Chem 67:8919–8925. https://doi.org/10.1021/acs.jafc.9b03800
92. Hinckley WE, Keymanesh K, Cordova JA, Brusslan JA (2019) The HAC1 histone acetyltransferase promotes leaf senescence and regulates the expression of ERF022. Plant Direct 3:1–10. https://doi.org/10.1002/pld3.159
93. Wu K, Zhang L, Zhou C et al (2008) HDA6 is required for jasmonate response, senescence and flowering in *Arabidopsis*. J Exp Bot 59:225–234. https://doi.org/10.1093/jxb/erm300
94. Chen X, Lu L, Mayer KS et al (2016) POWERDRESS interacts with histone deacetylase 9 to promote aging in *Arabidopsis*. Elife 5:1–23. https://doi.org/10.7554/eLife.17214
95. Zhou C, Zhang L, Duan J et al (2005) Histone deacetylase19 is involved in jasmonic acid and ethylene signaling of pathogen

response in *Arabidopsis*. Plant Cell 17:1196–1204. https://doi.org/10.1105/tpc.104.028514

96. Kim KC, Lai Z, Fan B, Chen Z (2008) *Arabidopsis* WRKY38 and WRKY62 transcription factors interact with histone deacetylase 19 in basal defense. Plant Cell 20:2357–2371. https://doi.org/10.1105/tpc.107.055566
97. Latrasse D, Jégu T, Li H et al (2017) MAPK-triggered chromatin reprogramming by histone deacetylase in plant innate immunity. Genome Biol 18:1–19. https://doi.org/10.1186/s13059-017-1261-8
98. Jin H, Choi SM, Kang MJ et al (2018) Salicylic acid-induced transcriptional reprogramming by the HAC-NPR1-TGA histone acetyltransferase complex in *Arabidopsis*. Nucleic Acids Res 46:11712–11725. https://doi.org/10.1093/nar/gky847
99. Yang L, Chen X, Wang Z et al (2020) HOS15 and HDA9 negatively regulate immunity through histone deacetylation of intracellular immune receptor NLR genes in *Arabidopsis*. New Phytol 226:507–522. https://doi.org/10.1111/nph.16380
100. Wang T, Xing J, Liu X et al (2018) GCN5 contributes to stem cuticular wax biosynthesis by histone acetylation of CER3 in *Arabidopsis*. J Exp Bot 69:2911–2922. https://doi.org/10.1093/jxb/ery077
101. Kong L, Zhi P, Liu J et al (2020) Epigenetic activation of Enoyl-CoA reductase by an acetyltransferase complex triggers wheat wax biosynthesis. Plant Physiol 183:1250–1267. https://doi.org/10.1104/pp.20.00603
102. Liu J, Zhi P, Wang X et al (2019) Wheat WD40-repeat protein TaHOS15 functions in a histone deacetylase complex to fine-tune defense responses to *Blumeria graminis* f.sp. *tritici*. J Exp Bot 70:255–268. https://doi.org/10.1093/jxb/ery330
103. Zhi P, Kong L, Liu J et al (2020) Histone deacetylase TaHDT701 functions in TaHDA6-TaHOS15 complex to regulate wheat defense responses to *Blumeria graminis* f.sp. *tritici*. Int J Mol Sci 21:2640. https://doi.org/10.3390/ijms21072640
104. Ding B, del Bellizzi MR, Ning Y et al (2012) HDT701, a histone H4 deacetylase, negatively regulates plant innate immunity by modulating histone H4 acetylation of defense-related genes in rice. Plant Cell 24:3783–3794. https://doi.org/10.1105/tpc.112.101972
105. Zheng M, Liu X, Lin J et al (2019) Histone acetyltransferase GCN5 contributes to cell wall integrity and salt stress tolerance by altering the expression of cellulose synthesis genes. Plant J 97:587–602. https://doi.org/10.1111/tpj.14144
106. Wang T, Xing J, Liu Z et al (2019) Histone acetyltransferase GCN5-mediated regulation of long non-coding RNA At4 contributes to phosphate starvation response in *Arabidopsis*. J Exp Bot 70:6337–6348. https://doi.org/10.1093/jxb/erz359
107. Li H, Yan S, Zhao L et al (2014) Histone acetylation associated up-regulation of the cell wall related genes is involved in salt stress induced maize root swelling. BMC Plant Biol 14:1–14. https://doi.org/10.1186/1471-2229-14-105
108. Fina JP, Casati P (2015) HAG3, a histone acetyltransferase, affects UV-B responses by negatively regulating the expression of DNA repair enzymes and sunscreen content in *Arabidopsis thaliana*. Plant Cell Physiol 56:1388–1400. https://doi.org/10.1093/pcp/pcv054
109. Rymen B, Kawamura A, Lambolez A et al (2019) Histone acetylation orchestrates wound-induced transcriptional activation and cellular reprogramming in *Arabidopsis*. Commun Biol 2:1–15. https://doi.org/10.1038/s42003-019-0646-5
110. Paixão JFR, Gillet FX, Ribeiro TP et al (2019) Improved drought stress tolerance in *Arabidopsis* by CRISPR/dCas9 fusion with a histone acetyltransferase. Sci Rep 9:1–9. https://doi.org/10.1038/s41598-019-44571-y
111. Fang H, Liu X, Thorn G et al (2014) Expression analysis of histone acetyltransferases in rice under drought stress. Biochem Biophys Res Commun 443:400–405. https://doi.org/10.1016/j.bbrc.2013.11.102
112. Zheng Y, Ding Y, Sun X et al (2016) Histone deacetylase HDA9 negatively regulates salt and drought stress responsiveness in *Arabidopsis*. J Exp Bot 67:1703–1713. https://doi.org/10.1093/jxb/erv562
113. Zheng Y, Ge J, Bao C et al (2020) Histone deacetylase HDA9 and transcription factor WRKY53 are mutual antagonists in regulation of plant stress response. Mol Plant 13:598–611. https://doi.org/10.1016/j.molp.2019.12.011
114. Luo M, Wang Y, Liu X et al (2012) HD2C interacts with HDA6 and is involved in ABA and salt stress response in *Arabidopsis*. J Exp Bot 63:3297–3306. https://doi.org/10.1093/jxb/ers059
115. Kim JM, To TK, Matsui A et al (2017) Acetate-mediated novel survival strategy against drought in plants. Nat Plants 3:4–10. https://doi.org/10.1038/nplants.2017.97
116. Hu Z, Song N, Zheng M et al (2015) Histone acetyltransferase GCN5 is essential for heat stress-responsive gene activation and thermotolerance in *Arabidopsis*. Plant J 84:1178–1191. https://doi.org/10.1111/tpj.13076
117. Bharti S, Kumar P, Tintschl-ko A et al (2004) Tomato heat stress transcription factor HsfB1 represents a novel type of general transcription coactivator with a histone-like motif interacting with the plant CREB binding protein ortholog HAC1. Plant Cell 16:1521–1535. https://doi.org/10.1105/tpc.019927.1
118. Shen Y, Lei T, Cui X et al (2019) Arabidopsis histone deacetylase HDA15 directly represses plant response to elevated ambient temperature. Plant J 100:991–1006. https://doi.org/10.1111/tpj.14492
119. Popova OV, Dinh HQ, Aufsatz W, Jonak C (2013) The RdDM pathway is required for basal heat tolerance in *Arabidopsis*. Mol Plant 6:396–410. https://doi.org/10.1093/mp/sst023
120. To TK, Nakaminami K, Kim JM et al (2011) *Arabidopsis* HDA6 is required for freezing tolerance. Biochem Biophys Res Commun 406:414–419. https://doi.org/10.1016/j.bbrc.2011.02.058
121. Zhang F, Wang L, Ko EE et al (2018) Histone deacetylases SRT1 and SRT2 interact with ENAP1 to mediate ethylene-induced transcriptional repression. Plant Cell 30:153–166. https://doi.org/10.1105/tpc.17.00671
122. Park J, Lim CJ, Shen M et al (2018) Epigenetic switch from repressive to permissive chromatin in response to cold stress. Proc Natl Acad Sci U S A 115:E5400–E5409. https://doi.org/10.1073/pnas.1721241115
123. Han Z, Yu H, Zhao Z et al (2016) AtHD2D gene plays a role in plant growth, development, and response to abiotic stresses in *Arabidopsis thaliana*. Front Plant Sci 7:1–13. https://doi.org/10.3389/fpls.2016.00310
124. Zhang JB, He SP, Luo JW et al (2020) A histone deacetylase, GhHDT4D, is positively involved in cotton response to drought stress. Plant Mol Biol 1:1–13. https://doi.org/10.1007/s11103-020-01024-9
125. Wang NN, Xu SW, Sun YL et al (2019) The cotton WRKY transcription factor (GhWRKY33) reduces transgenic *Arabidopsis* resistance to drought stress. Sci Rep 9:1–13. https://doi.org/10.1038/s41598-018-37035-2
126. Lee HG, Seo PJ (2019) MYB96 recruits the HDA15 protein to suppress negative regulators of ABA signaling in *Arabidopsis*. Nat Commun 10:1–14. https://doi.org/10.1038/s41467-019-09417-1
127. Mehdi S, Derkacheva M, Ramström M et al (2016) The WD40 domain protein MSI1 functions in a histone deacetylase complex to fine-tune abscisic acid signaling. Plant Cell 28:42–54. https://doi.org/10.1105/tpc.15.00763
128. Ueda M, Matsui A, Nakamura T et al (2018) Versatility of HDA19-deficiency in increasing the tolerance of *Arabidopsis*

to different environmental stresses. Plant Signal Behav 13:e1475808. https://doi.org/10.1080/15592324.2018.1475808

129. Ueda M, Matsui A, Tanaka M et al (2017) The distinct roles of class I and II RPD3-like histone deacetylases in salinity stress response. Plant Physiol 175:1760–1773. https://doi.org/10.1104/pp.17.01332
130. Chen LT, Wu K (2010) Role of histone deacetylases HDA6 and HDA19 in ABA and abiotic stress response. Plant Signal Behav 5:1318–1320. https://doi.org/10.4161/psb.5.10.13168
131. Song J, Henry HAL, Tian L (2019) Brachypodium histone deacetylase BdHD1 positively regulates ABA and drought stress responses. Plant Sci 283:355–365. https://doi.org/10.1016/j.plantsci.2019.03.009
132. Baek D, Shin G, Kim MC et al (2020) Histone deacetylase HDA9 with ABI4 contributes to abscisic acid homeostasis in drought stress response. Front Plant Sci 11:143. https://doi.org/10.3389/fpls.2020.00143
133. Khan IU, Ali A, Khan HA et al (2020) PWR/HDA9/ABI4 complex epigenetically regulates ABA dependent drought stress tolerance in *Arabidopsis*. Front Plant Sci 11:1–13. https://doi.org/10.3389/fpls.2020.00623
134. Ma X, Zhang B, Liu C et al (2017) Expression of a populus histone deacetylase gene 84KHDA903 in tobacco enhances drought tolerance. Plant Sci 265:1–11. https://doi.org/10.1016/j.plantsci.2017.09.008
135. Ma X, Liang X, Lv S et al (2020) Histone deacetylase gene PtHDT902 modifies adventitious root formation and negatively regulates salt stress tolerance in poplar. Plant Sci 290:110301. https://doi.org/10.1016/j.plantsci.2019.110301
136. Cheng X, Zhang S, Tao W et al (2018) INDETERMINATE SPIKELET 1 recruits histone deacetylase and a transcriptional repression complex to regulate rice salt tolerance. Plant Physiol 178:824–837. https://doi.org/10.1104/pp.18.00324
137. Zhao J, Li M, Gu D et al (2016) Involvement of rice histone deacetylase HDA705 in seed germination and in response to ABA and abiotic stresses. Biochem Biophys Res Commun 470:439–444. https://doi.org/10.1016/j.bbrc.2016.01.016
138. Wang P, Zhao L, Hou H et al (2015) Epigenetic changes are associated with programmed cell death induced by heat stress in seedling leaves of *Zea mays*. Plant Cell Physiol 56:965–976. https://doi.org/10.1093/pcp/pcv023
139. Hou H, Zhao L, Zheng X et al (2019) Dynamic changes in histone modification are associated with upregulation of Hsf and rRNA genes during heat stress in maize seedlings. Protoplasma 256:1245–1256. https://doi.org/10.1007/s00709-019-01364-4
140. Hu Y, Zhang L, Zhao L et al (2011) Trichostatin a selectively suppresses the cold-induced transcription of the ZmDREB1 gene in maize. PLoS ONE 6:e22132. https://doi.org/10.1371/journal.pone.0022132
141. Wei F, Tang D, Li Z et al (2019) Molecular cloning and subcellular localization of six HDACs and their roles in response to salt and drought stress in kenaf (*Hibiscus cannabinus* L.). Biol Res 52:20. https://doi.org/10.1186/s40659-019-0227-6
142. Song C, Yang Y, Yang T et al (2019) MaMYB4 recruits histone deacetylase MaHDA2 and modulates the expression of $\omega - 3$ fatty acid desaturase genes during cold stress response in banana fruit. Plant Cell Physiol 60:2410–2422. https://doi.org/10.1093/pcp/pcz142
143. Song XJ, Kuroha T, Ayano M et al (2015) Rare allele of a previously unidentified histone H4 acetyltransferase enhances grain weight, yield, and plant biomass in rice. Proc Natl Acad Sci U S A 112:76–81. https://doi.org/10.1073/pnas.1421127112
144. Zhang H, Zhao Y, Zhou DX (2017) Rice NAD+-dependent histone deacetylase OsSRT1 represses glycolysis and regulates the moonlighting function of GAPDH as a transcriptional activator of glycolytic genes. Nucleic Acids Res 45:12241–12255. https://doi.org/10.1093/nar/gkx825
145. Forestan C, Farinati S, Rouster J et al (2018) Control of maize vegetative and reproductive development, fertility, and rRNAs silencing by histone deacetylase 108. Genetics 208:1443–1466. https://doi.org/10.1534/genetics.117.300625/-/DC1.1
146. Zhang H, Guo F, Qi P et al (2020) OsHDA710-mediated histone deacetylation regulates callus formation of rice mature embryo. Plant Cell Physiol 61:1646–1660. https://doi.org/10.1093/pcp/pcaa086
147. Nallamilli BRR, Edelmann MJ, Zhong X et al (2014) Global analysis of lysine acetylation suggests the involvement of protein acetylation in diverse biological processes in rice (*Oryza sativa*). PLoS ONE 9:1–12. https://doi.org/10.1371/journal.pone.0089283
148. Li X, Ye J, Ma H, Lu P (2018) Proteomic analysis of lysine acetylation provides strong evidence for involvement of acetylated proteins in plant meiosis and tapetum function. Plant J 93:142–154. https://doi.org/10.1111/tpj.13766
149. Hartl M, Füßl M, Boersema PJ et al (2017) Lysine acetylome profiling uncovers novel histone deacetylase substrate proteins in *Arabidopsis*. Mol Syst Biol 13:949. https://doi.org/10.15252/msb.20177819
150. Hao Y, Wang H, Qiao S et al (2016) Histone deacetylase HDA6 enhances brassinosteroid signaling by inhibiting the BIN2 kinase. Proc Natl Acad Sci U S A 113:2–7. https://doi.org/10.1073/pnas.1521363113
151. Tran HT, Nimick M, Uhrig RG et al (2012) Arabidopsis thaliana histone deacetylase 14 (HDA14) is an α-tubulin deacetylase that associates with PP2A and enriches in the microtubule fraction with the putative histone acetyltransferase ELP3. Plant J 71:263–272. https://doi.org/10.1111/j.1365-313X.2012.04984.x
152. Alinsug MV, Radziejwoski A, Deocaris CC (2020) AtHDA15 binds directly to COP1 positively regulating photomorphogenesis. Biochem Biophys Res Commun. https://doi.org/10.1016/j.bbrc.2020.09.089
153. König AC, Hartl M, Pham PA et al (2014) The *Arabidopsis* class II sirtuin is a lysine deacetylase and interacts with mitochondrial energy metabolism. Plant Physiol 164:1401–1414. https://doi.org/10.1104/pp.113.232496