



Review

The roles of histone acetylation in seed performance and plant development

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ABSTRACT

Histone acetylation regulates gene transcription by chromatin modifications and plays a crucial role in the plant development and response to environment cues. The homeostasis of histone acetylation is controlled by histone acetyltransferases (HATs) and histone deacetylases (HDACs) in different plant tissues and development stages. The vigorous knowledge of the function and co-factors about HATs (e.g. GCN5) and HDACs (e.g. HDA19, HDA6) has been obtained from model plant *Arabidopsis*. However, understanding individual role of other HATs and HDACs require more work, especially in the major food crops such as rice, maize and wheat. Many co-regulators have been recently identified to function as a component of HAT or HDAC complex in some specific developmental processes. The described findings show a distinctive and interesting epigenetic regulation network composed of HATs, HDACs and co-regulators playing crucial roles in the seed performance, flowering time, plant morphogenesis, plant response to stresses etc. In this review, we summarized the recent progresses and suggested the perspective of histone acetylation research, which might provide us a new window to understand the epigenetic code of plant development and to improve the crop production and quality.

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1. Introduction

In eukaryotes, histone acetylation is a reversible biological process in chromatin and considered as one of the major factors that facilitate the chromatin relaxation and gene transcription regulation (Waterborg, 2011). The acetylation at lysine residues of histones through the action of histone acetyltransferases (HATs) and histone deacetylases (HDACs) is in rapid response to the developmental and environmental clues (Waterborg, 2002). Up to now, many HATs or HDACs have been identified as transcriptional activators or repressors to be involved in a variety of biological processes in plants.

The active HATs have been isolated and partially or fully characterized since the early 1970's. Two types of taxonomy have been adopted. First, by the substrate specificity and intracellular localization, HATs have been grouped into two classes: A-type enzymes (HAT-A), which are localized into nucleus and acetylate the nucleosome core histones; B-type enzymes (HAT-B), which are localized in the cytoplasm with specificity to free histones (Eberharter et al., 1996). Second, on the basis of the sequence

characterization and preliminary experimental data *in silico*, all the plant HATs are divided into four categories: (1) HAG for HATs of the GNAT (GCN5-related N-terminal acetyltransferases) superfamily, (2) HAM for HATs of the MYST superfamily, (3) HAC for HATs of the CREB-binding protein (CBP) family, (4) HAF for HATs of the TATA-binding protein-associated factor (TAF_{II}250) family. In *Arabidopsis*, four (HAG1–HAG3, MMC1), two (HAM1 and HAM2), five (HAC1, HAC2, HAC4, HAC5 and HAC12), and two (HAF1 and HAF2) HAT genes have been identified (Pandey et al., 2002; Perrella et al., 2010).

HDACs can be classified into three families. The first family is homologous to the yeast Reduced Potassium Deficiency 3 (RPD3), which is present throughout eukaryotes and is most widely studied (Hollender and Liu, 2008). The second family, HD-tuins (HDT), is originally determined in maize (Lusser et al., 1997) and appears to be present only in plants (Dangl et al., 2001; Wu et al., 2000). The structurally-distinct third family, sirtuins, is homologous to the yeast Silent Information Regulator 2 (Sir2), which is a nicotinamide adenine dinucleotide (NAD)-dependent enzyme (Frye, 2000). Both HDACs and HATs can function in protein complexes as transcriptional co-repressors and co-activators or associated with chromatin remodelers as modulators of the accessibility of DNA to different machineries.

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Table 1
The genes encoding HATs and HDACs in Arabidopsis, rice, maize and tomato.

HAT or HDAC families	Gene name	Locus	Species	Co-factors	Functional analysis	References
GNAT	HAG1(GCN5)	At3g54610	<i>Arabidopsis thaliana</i>	–	Root and shoot development miRNA production Flower development	Long et al. (2006), Kornet and Scheres (2009) Kim et al. (2009)
	HAG2	At5g56740	<i>A. thaliana</i>	–	Light signaling Low temperature response	Vlachonasios et al. (2003), Long et al. (2006), Kornet and Scheres (2009) Benhamed et al. (2006, 2008) Vlachonasios et al. (2003)
	HAG3	At5g50320	<i>A. thaliana</i>	–	Cell proliferation	Nelissen et al. (2005)
	MCC1	At3g02980	<i>A. thaliana</i>	–	Leaf and flower development, male and female gametes development	Perrella et al. (2010)
	OsHAG702	Os10g0415900	<i>Oryza sativa</i> L.	–	High temperature response and ABA pathway	Liu et al. (2012)
	OsHAG703	Os04g0484900	<i>O. sativa</i> L.	–	High temperature response, High salt stress response and ABA pathway Drought stress response	Liu et al. (2012)
	OsHAG704	Os09g0347800	<i>O. sativa</i> L.	–	Temperature response and ABA pathway	Fang et al. (2014) Liu et al. (2012)
	SIHAG1	–	<i>Solanum lycopersicon</i>	–		
	SIHAG2	–	<i>S. lycopersicon</i>	–		
	SIHAG3	–	<i>S. lycopersicon</i>	–		
	SIHAG4	–	<i>S. lycopersicon</i>	–		
	SIHAG5	–	<i>S. lycopersicon</i>	–		
	SIHAG6	–	<i>S. lycopersicon</i>	–	Reproductive development	Aiese-Cigliano et al. (2013b)
	SIHAG7	–	<i>S. lycopersicon</i>	–		
	SIHAG8	–	<i>S. lycopersicon</i>	–	Vegetative development	Aiese-Cigliano et al. (2013b)
	SIHAG9	–	<i>S. lycopersicon</i>	–		
	SIHAG10	–	<i>S. lycopersicon</i>	–		
	SIHAG11	–	<i>S. lycopersicon</i>	–		
	SIHAG12	–	<i>S. lycopersicon</i>	–		
	SIHAG13	–	<i>S. lycopersicon</i>	–		
	SIHAG14	–	<i>S. lycopersicon</i>	–		
	SIHAG15	–	<i>S. lycopersicon</i>	–		
	SIHAG16	–	<i>S. lycopersicon</i>	–		
	SIHAG17	–	<i>S. lycopersicon</i>	–		
	SIHAG18	–	<i>S. lycopersicon</i>	–	Reproductive development	Aiese-Cigliano et al. (2013b)
	SIHAG19	–	<i>S. lycopersicon</i>	–		
SIHAG20	–	<i>S. lycopersicon</i>	–			
SIHAG21	–	<i>S. lycopersicon</i>	–			
SIHAG22	–	<i>S. lycopersicon</i>	–	Vegetative development	Aiese-Cigliano et al. (2013b)	
SIHAG23	–	<i>S. lycopersicon</i>	–			
SIHAG24	–	<i>S. lycopersicon</i>	–			
SIHAG25	–	<i>S. lycopersicon</i>	–			
SIHAG26	–	<i>S. lycopersicon</i>	–			
MYST	HAM1	AT5G64610	<i>A. thaliana</i>	–	Flowering time regulation and gamete formation	Latrasse et al. (2008), Xiao et al. (2013)
	HAM2	AT5G09740	<i>A. thaliana</i>	–	Flowering time regulation and gamete formation	Latrasse et al. (2008), Xiao et al. (2013)
	OsHAM701	Os07g0626600	<i>O. sativa</i> L.	–	High salt stress response and ABA pathway Drought stress response	Liu et al. (2012) Fang et al. (2014)
CBP	SIHAM1	–	<i>S. lycopersicon</i>	–	Seed and/or fruit development, gametogenesis	Aiese-Cigliano et al. (2013b)
	HAC1	At1g79000	<i>A. thaliana</i>	–	Sugar response Flowering time regulation	Deng et al. (2007), Heisel et al. (2013) Heisel et al. (2013)
	HAC2	At1g67220	<i>A. thaliana</i>	–		
	HAC4	AT1G55970	<i>A. thaliana</i>	–		
	HAC5	At3g12980	<i>A. thaliana</i>	–		
	HAC12	At1g16710	<i>A. thaliana</i>	–		
	OsHAC701	Os01g0246100	<i>O. sativa</i> L.	–	ABA pathway, temperature response, High salt stress	Liu et al. (2012)
	OsHAC703	Os02g0137500	<i>O. sativa</i> L.	–	ABA pathway, low temperature response, High salt stress response and SA pathway Drought stress response	Liu et al. (2012)
	OsHAC704	Os06g0704800	<i>O. sativa</i> L.	–	Temperature response and high salt stress response	Fang et al. (2014) Liu et al. (2012)
	SIHAC1	–	<i>S. lycopersicon</i>	–		Aiese-Cigliano et al. (2013b)
SIHAC2	–	<i>S. lycopersicon</i>	–		Aiese-Cigliano et al. (2013b)	
SIHAC3	–	<i>S. lycopersicon</i>	–		Aiese-Cigliano et al. (2013b)	
SIHAC4	–	<i>S. lycopersicon</i>	–	Fruit development	Aiese-Cigliano et al. (2013b)	
TAF _{II} 250	HAF1	At1g32750	<i>A. thaliana</i>	–		
	HAF2	At3g19040	<i>A. thaliana</i>	HY5	Light signaling	Bertrand et al. (2005)
	OsHAF701	Os06g0645700	<i>O. sativa</i> L.	–	Drought stress response Low temperature response	Fang et al. (2014) Liu et al. (2012)
HAT-A	SIHAF1	–	<i>S. lycopersicon</i>	–	Fruit maturation	Aiese-Cigliano et al. (2013b)
	HAT-A1	–	<i>Zea mays</i>	–	Embryo germination	Georgieva et al. (1991)
	HAT-A2	–	<i>Z. mays</i>	–	Embryo germination	Georgieva et al. (1991)

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