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Review

# Histone variants in plant transcriptional regulation☆

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ABSTRACT

Chromatin based organization of eukaryotic genome plays a profound role in regulating gene transcription. Nucleosomes form the basic subunits of chromatin by packaging DNA with histone proteins, impeding the access of DNA to transcription factors and RNA polymerases. Exchange of histone variants in nucleosomes alters the properties of nucleosomes and thus modulates DNA exposure during transcriptional regulation. Growing evidence indicates the important function of histone variants in programming transcription during developmental transitions and stress response. Here we review how histone variants and their deposition machineries regulate the nucleosome stability and dynamics, and discuss the link between histone variants and transcriptional regulation in plants. This article is part of a Special Issue entitled: Plant Gene Regulatory Mechanisms and Networks, edited by Dr. Erich Grotewold and Dr. Nathan Springer.



## 1. Introduction

Eukaryotic DNA is packaged into an array of nucleosomes that consist of histone proteins H2A, H2B, H3 and H4 [1,2]. Nucleosomes connect with each other by a linear linker DNA that is associated with linker histone H1 proteins, which contribute to higher order chromatin structures [3]. During transcription, transcription factors and RNA polymerases must overcome the barriers formed by nucleosomes to get access to DNA for transcription initiation and elongation. Therefore, the positioning and assembly/disassembly of nucleosomes need to be dynamically regulated in the process of transcription [4,5]. This dynamics of nucleosome property is mediated by several distinct but linked mechanisms, including post-translational modification of histones, ATP-dependent sliding or eviction of nucleosomes across the DNA, and exchange of histone variants. Histone variants are related protein isoforms encoded by paralogous genes in each histone class and are distinguished from each other by specific amino acid sequences. In addition to the sequence divergence that may modify nucleosome properties, histone variants often differ by their timing of incorporation into chromatin. For instance, canonical histones are mainly expressed during the S phase of the cell cycle and incorporated into the newly replicated genome. In contrast, other variants are expressed throughout the cell cycle and could be exchanged against canonical histones when nucleosomes are disrupted (e.g. during transcription). These features enable histone variants to shape the chromatin landscapes and decorate regions with divergent transcriptional activities across the genome [6,7].

In vitro, strong electrostatic interactions between positively charged histones and the negatively charged DNA cause spontaneous, non-specific aggregates. Histone chaperones facilitate incorporation of histones on DNA by neutralizing their positive charges, and thus play key roles in regulating nucleosome assembly [8]. Nucleosomes are assembled via a stepwise process. First, the H3–H4 tetramer is deposited on DNA, followed by the addition of two flanking H2A–H2B dimers [9]. This process is reversible to allow disassembly of nucleosomes. Histone chaperones comprise a group of complexes containing much diversified proteins that interact either with H2A–H2B or H3–H4 specifically. Moreover, some chaperones exhibit selective binding to certain histone variants. However, the interaction between histone variants and chaperones are not always exclusive [10]. Histone chaperones modulate the dynamics of histone variants deposition into the genome in the right place and at the right time, contributing to the functions of histone variants in chromatin regulation.

Here we review recent advances of histone variants in plants, focusing on their function in transcriptional regulation. We describe the properties of histone variants and their chaperones, and highlight their impact in modulating the nucleosome dynamics and chromatin structure. In addition, we discuss recent functional analysis and genome-wide mapping of plant histone variants, their correlation with transcription activity as well as the mechanisms of histone variants in regulating transcription.

## 2. Core histone variants and chaperones in plants

In general, core histone families H2A, and H3 comprise variants, while members of H4 family share exact same amino acid sequence and to date only a few variants have been described from the H2B family in mammals [11,12] and in plants [13].

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Although they evolved independently in animals and plants, plants H2A and H3 variants acquired very similar specialized features as their counterparts in animals, suggesting evolutionary convergence. The *Arabidopsis* genome encodes four major types of H2A variants. Among them, canonical H2A, H2A.X and H2A.Z are variants found both in animals and plants. In contrast, H2A.W is a class of variants restricted to the plant kingdom. H2A variants have many amino acids differences across the length of the protein and particularly differ from each other by feature sequences at three regions, the L1 loop, the docking domain and the C-terminal tail (Fig. 1A) [14]. Amino acids in these three regions mediate H2A interaction with other histones within both the same nucleosome and the neighboring nucleosomes, and thus influence the stability and compaction of nucleosomes [14].

The H3 family consists of three major types of variants, H3.1, H3.3 and CenH3 (Fig. 1B). CenH3 is highly divergent from other H3 variants especially at its N-terminal tail [15,16]. It is deposited specifically at centromeres and is essential for the assembly of kinetochore and correct chromosome segregation during nuclear division [17,18]. *Arabidopsis* H3.1 and H3.3 variants exhibit only four different amino acids at the positions 31, 41, 87 and 90. Studies of H3.3 deposition at rDNA loci suggested that amino acids 87 and 90 in the core domain of H3.3 guide assembly of H3.3 into the nucleosome, whereas amino acids 31

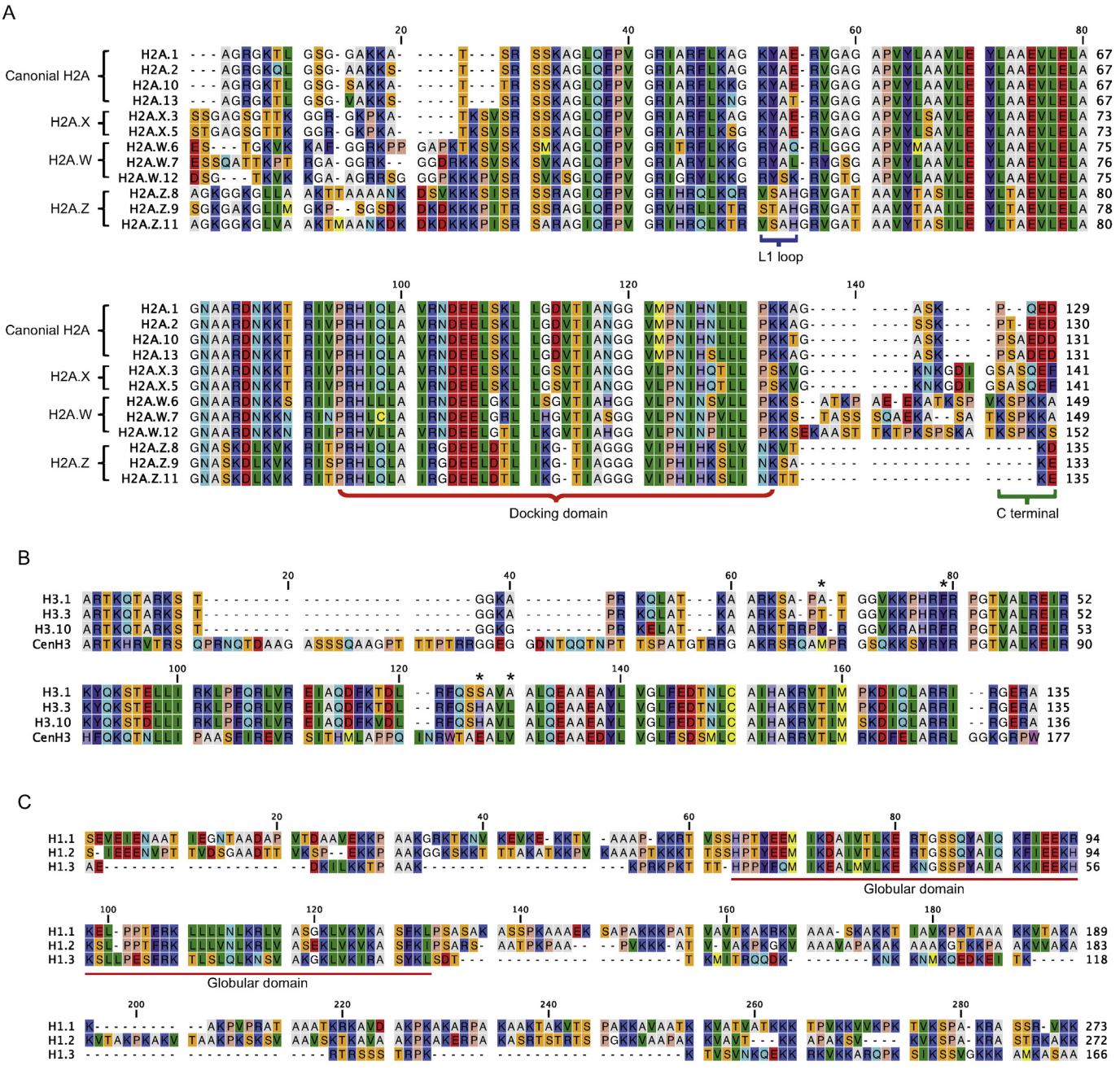


**Fig. 1.** Sequence characteristics of main H2A, H3 and H1 variants in *Arabidopsis*. (A) Sequence alignment of H2A variants. Amino acids in the L1 loop, docking domain and C-terminal regions are indicated by brackets. Canonical H2A and H2A.X variants share common sequences at the L1 loop and docking domain but are distinguished from each other at C-terminal tails, such that canonical H2A ends with a cluster of acidic amino acids; while H2A.X C-terminal harbors conserved SQEF motif that is crucial for H2A.X function in modulating DNA repair, as the serine is phosphorylated at the sites of DNA breaks when DNA damage occurs. Both H2A.Z and H2A.W variants contain unique sequences at the L1 loop, the docking domain and the C-terminal tail. The distinct sequences in the docking domain of H2A.Z are critical for its specific deposition into and exchange from the nucleosome. The C-terminal KSPKK motif of H2A.W may facilitate the formation of higher-order chromatin structures. (B) Sequence alignment of H3.1, H3.3, H3.10 and CenH3. Different Amino acids between H3.1 and H3.3 variants are marked by asterisks. (C) Sequence alignment of linker histone H1 variants. Conserved globular domain is underlined.

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