

Supplementary Table S2. List of articles referring to the role of plant linker histones.

<b>Development</b>			
General	Arabidopsis	Downregulation of all three Arabidopsis H1 variants (RNAi) leads to pleiotropic developmental defects at the vegetative and reproductive stages and impaired DNA methylation profiles	(Wierzbicki and Jerzmanowski 2005)
Meiosis	Tobacco	A 4-fold reduction of H1A and H1B levels impairs male meiosis and pollen development.	(Prymakowska-Bosak, Przewloka et al. 1999)
Endosperm development	Maize	H1/DNA ratio levels decrease during endoreduplication in maize endosperm in parallel to massive expression of storage genes	(Zhao and Grafi 2000)
Cell fate	Arabidopsis	H1.1 and H1.2 somatic variants are evicted in male and female meiotic precursors cells, transiently restored at meiosis and undetectable again in the functional megaspore.	(She, Grimanelli et al. 2013) (She and Baroux 2015)
Differentiation	Maize	H1 variants' ratios are dynamically regulated along the division and differentiation zones of maize root. Notably, the H1 <sup>0</sup> variant increases in differentiation while H1A/H1B decrease	(Alatzas, Srebrevna et al. 2008)
Seed biology	Maize	GWAS association with seed composition traits identified H1 loci with starch, protein and oil content	(Cook, McMullen et al. 2012)
	Maize	Onset of grain filling is associated with a change in properties of linker histone variants in maize kernels	(Kalamajka, Finnie et al. 2010)
	Rapeseed	Osmopriming (exogenous control of seed imbibition) and seed germination correlate with decreased levels of H1 mRNAs in <i>Brassica oleracea</i>	(Soeda, Konings et al. 2005)
Fruit ripening	Banana	Fruit ripening and ethylene treatment increases the MaHIS1 H1 variant (homologous to the Arabidopsis H1.1 variant) in <i>Musa acuminata</i>	(Wang, Kuang et al. 2012)
<b>Biotic/abiotic stress</b>			
Drought	Tomato	H1-S variant is up-regulated under water deficit conditions. Antisense-mediated downregulation suggests a role of H1-S in plant water status regulation and stomatal functions.	(Scippa, Griffiths et al. 2000) (Scippa, Di Michele et al. 2004)
Drought	Arabidopsis	The stress-inducible H1.3 variant is distinct from H1.1 and H1.2 by its short C-terminal tail, few amino acid substitution in the binding domain and very high mobility. H1.3 is induced by combined light and water deficit and functions in stress responses and stomatal functions.	(Ascenzi and Gantt 1997) (Ascenzi and Gantt 1999) (Rutowicz, Puzio et al. 2015)
Drought	Cotton	Identification by mass spectrometry of a stress-inducible H1 variant in a drought tolerant cultivar (Vagad). This variant is absent from the drought sensitive cultivar RAHS-14.	(Trivedi, Ranjan et al. 2012)
Various biotic and abiotic stresses	Banana	Chilling or exogenous application of methyljasmonate, H <sub>2</sub> O <sub>2</sub> or ABA induced MaHIS1 (homologous to <i>AtH1.1</i> ) mRNA levels transiently. Exposure to the fungal pathogen <i>Colletotrichum musae</i> induced a prolonged increase in MaHIS1 mRNA levels.	(Wang, Kuang et al. 2012)
<b>Epigenetic regulation</b>			
DNA methylation	Arabidopsis	RNAi downregulation of the three H1 variants led to local fluctuations in DNA methylation patterns in both CG and non-CG contexts .	(Wierzbicki and Jerzmanowski 2005)
DNA methylation	Arabidopsis	Loss-of-function of the three main H1 variants causes hypermethylation at heterochromatic transposons and partially rescues the hypomethylation phenotype of <i>DECREASED IN DNA METHYLATION1 (ddm1)</i> mutants	(Zemach, Kim et al. 2013)
Imprinting	Arabidopsis	H1 variants interacts with the DNA glycosylase DEMETER (yeast two hybrid and GST pulldown assays). H1 depletion reduces maternal expression of DME target genes ( <i>MEA</i> , <i>FWA</i> , <i>FIS2</i> ) in correlation with increased DNA methylation levels.	(Rea, Zheng et al. 2012)
Histone deacetylation	Arabidopsis	H1 directly interacts with the Histone Deacetylase Complex 1 HDC1.	(Perrella, Carr et al. 2016)
<b>Transcriptional regulation</b>			
Lignin biosynthesis	Eucalyptus	H1.3 interacts with the transcription factor MYB1 and contributes to transcriptional repression of genes involved in lignin biosynthesis.	(Soler, Plasencia et al. 2016)

Enhances TF binding	Rice/wheat	H1 facilitates binding of the transcription factor EmBP-1 to the ABA-responsive gene <i>Em</i> .	(Schultz, Spiker et al. 1996)
Regulates stress-responsive genes	Arabidopsis	H1.3 contributes to induce stress-response associated factors under combined light and drought stress	(Rutowicz, Puzio et al. 2015)
<b>Structural function</b>			
Chromatin condensation	Pea	Lower chromatin condensation in callus cells compared to root cells correlate with varying levels of histone H1 variants	(Bers, Singh et al. 1992)
	Tobacco	Overexpression of an Arabidopsis H1 variants in tobacco induces strong heterochromatinization	(ŚLUSARCZYK, PRYMAKOWSKA-BOSAK et al. 1999)
	Pea, Maize, Bean	The proportion of extracted H1 correlates with the level of genomic repeats and the degree of chromatin condensation (transmission electron microscopy)	Oleszweska, 1988
<b>Other cellular functions</b>			
Microtubule organization	Tobacco	In tobacco BY-2 cells, H1B functions as a microtubule-organizing factor on the nuclear surface showing DNA independent functions. Probably interacting with tubulin.	(Hotta, Haraguchi et al. 2007) (Nakayama, Ishii et al. 2008) (Kaczanowski and Jerzmanowski 2001)

## References

- Alatzas, A., L. Srebrevna, et al. (2008). "Distribution of linker histone variants during plant cell differentiation in the developmental zones of the maize root, dedifferentiation in callus culture after auxin treatment." *Biol Res* **41**(2): 205-215.
- Ascenzi, R. and J. S. Gantt (1997). "A drought-stress-inducible histone gene in Arabidopsis thaliana is a member of a distinct class of plant linker histone variants." *Plant Mol Biol* **34**(4): 629-641.
- Ascenzi, R. and J. S. Gantt (1999). "Molecular genetic analysis of the drought-inducible linker histone variant in Arabidopsis thaliana." *Plant Mol Biol* **41**(2): 159-169.
- Ascenzi, R. and J. S. Gantt (1999). "Subnuclear distribution of the entire complement of linker histone variants in Arabidopsis thaliana." *Chromosoma* **108**(6): 345-355.
- Bers, E. P., N. P. Singh, et al. (1992). "Nucleosomal structure and histone H1 subfractional composition of pea (*Pisum sativum*) root nodules, radicles and callus chromatin." *Plant Mol Biol* **20**(6): 1089-1096.
- Cook, J. P., M. D. McMullen, et al. (2012). "Genetic architecture of maize kernel composition in the nested association mapping and inbred association panels." *Plant Physiol* **158**(2): 824-834.
- Hotta, T., T. Haraguchi, et al. (2007). "A novel function of plant histone H1: microtubule nucleation and continuous plus end association." *Cell Struct Funct* **32**(2): 79-87.
- Kaczanowski, S. and A. Jerzmanowski (2001). "Evolutionary correlation between linker histones and microtubular structures." *J Mol Evol* **53**(1): 19-30.
- Kalamajka, R., C. Finnie, et al. (2010). "Onset of grain filling is associated with a change in properties of linker histone variants in maize kernels." *Planta* **231**(5): 1127-1135.
- Nakayama, T., T. Ishii, et al. (2008). "Radial microtubule organization by histone H1 on nuclei of cultured tobacco BY-2 cells." *J Biol Chem* **283**(24): 16632-16640.
- Perrella, G., C. Carr, et al. (2016). "The Histone Deacetylase Complex 1 Protein of Arabidopsis Has the Capacity to Interact with Multiple Proteins Including Histone 3-Binding Proteins and Histone 1 Variants." *Plant Physiol* **171**(1): 62-70.
- Prymakowska-Bosak, M., M. R. Przewloka, et al. (1999). "Linker histones play a role in male meiosis and the development of pollen grains in tobacco." *Plant Cell* **11**(12): 2317-2329.
- Rea, M., W. Zheng, et al. (2012). "Histone H1 affects gene imprinting and DNA methylation in Arabidopsis." *Plant J* **71**(5): 776-786.
- Rutowicz, K., M. Puzio, et al. (2015). "A Specialized Histone H1 Variant Is Required for Adaptive Responses to Complex Abiotic Stress and Related DNA Methylation in Arabidopsis." *Plant Physiol* **169**(3): 2080-2101.
- Schultz, T. F., S. Spiker, et al. (1996). "Histone H1 enhances the DNA binding activity of the transcription factor EmBP-1." *J Biol Chem* **271**(42): 25742-25745.

- Scippa, G. S., M. Di Michele, et al. (2004). "The histone-like protein H1-S and the response of tomato leaves to water deficit." *J Exp Bot* **55**(394): 99-109.
- Scippa, G. S., A. Griffiths, et al. (2000). "The H1 histone variant of tomato, H1-S, is targeted to the nucleus and accumulates in chromatin in response to water-deficit stress." *Planta* **211**(2): 173-181.
- She, W. and C. Baroux (2015). "Chromatin dynamics in pollen mother cells underpin a common scenario at the somatic-to-reproductive fate transition of both the male and female lineages in Arabidopsis." *Front Plant Sci* **6**: 294.
- She, W., D. Grimanelli, et al. (2013). "Chromatin reprogramming during the somatic-to-reproductive cell fate transition in plants." *Development* **140**(19): 4008-4019.
- ŚLUSARCZYK, J., M. PRYMAKOWSKA-BOSAK, et al. (1999). "Ultrastructural Organization of Leaves of Transgenic Tobacco Overexpressing Histone H1 from Arabidopsis thaliana." *Annals of Botany* **84**(3): 329-335.
- Soeda, Y., M. C. Konings, et al. (2005). "Gene expression programs during Brassica oleracea seed maturation, osmopriming, and germination are indicators of progression of the germination process and the stress tolerance level." *Plant Physiol* **137**(1): 354-368.
- Soler, M., A. Plasencia, et al. (2016). "The Eucalyptus linker histone variant EgH1.3 cooperates with the transcription factor EgMYB1 to control lignin biosynthesis during wood formation." *New Phytol.*
- Trivedi, I., A. Ranjan, et al. (2012). "The histone H1 variant accumulates in response to water stress in the drought tolerant genotype of Gossypium herbaceum L." *Protein J* **31**(6): 477-486.
- Wang, J. N., J. F. Kuang, et al. (2012). "Expression profiles of a banana fruit linker histone H1 gene MaHIS1 and its interaction with a WRKY transcription factor." *Plant Cell Rep* **31**(8): 1485-1494.
- Wierzbicki, A. T. and A. Jerzmanowski (2005). "Suppression of histone H1 genes in Arabidopsis results in heritable developmental defects and stochastic changes in DNA methylation." *Genetics* **169**(2): 997-1008.
- Zemach, A., M. Y. Kim, et al. (2013). "The Arabidopsis nucleosome remodeler DDM1 allows DNA methyltransferases to access H1-containing heterochromatin." *Cell* **153**(1): 193-205.
- Zhao, J. and G. Grafi (2000). "The high mobility group I/Y protein is hypophosphorylated in endoreduplicating maize endosperm cells and is involved in alleviating histone H1-mediated transcriptional repression." *J Biol Chem* **275**(35): 27494-27499.