



Stress-induced structural changes in plant chromatin

Aline V Probst¹ and Ortrun Mittelsten Scheid²



Stress defense in plants is elaborated at the level of protection and adaptation. Dynamic changes in sophisticated chromatin substructures and concomitant transcriptional changes play an important role in response to stress, as illustrated by the transient rearrangement of compact heterochromatin structures or the modulation of chromatin composition and modification upon stress exposure. To connect cytological, developmental, and molecular data around stress and chromatin is currently an interesting, multifaceted, and sometimes controversial field of research. This review highlights some of the most recent findings on nuclear reorganization, histone variants, histone chaperones, DNA- and histone modifications, and somatic and meiotic heritability in connection with stress.

Addresses

¹ CNRS UMR6293 – INSERM U1103 – Clermont University, GReD, Campus Universitaire des Cézeaux, 10 Avenue Blaise Pascal, TSA 60026, CS 60026, 63178 Aubiere Cedex, France

² Gregor Mendel Institute of Molecular Plant Biology, Austrian Academy of Sciences, Vienna Biocenter (VBC), Dr. Bohr-Gasse 3, 1030 Vienna, Austria

Corresponding author: Mittelsten Scheid, Ortrun
(ortrun.mittelsten_scheid@gmi.oewa.ac.at)

Current Opinion in Plant Biology 2015, 27:8–16

This review comes from a themed issue on **Cell signalling and gene regulation**

Edited by **Xiaofeng Cao and Blake C Meyers**

For a complete overview see the [Issue](#) and the [Editorial](#)

Available online 29th May 2015

<http://dx.doi.org/10.1016/j.pbi.2015.05.011>

1369-5266/© 2015 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

Introduction

Eukaryotes are distinguished from archaea and bacteria in part by the (a) presence of nuclei that spatially separate the genome from the cytoplasm by nuclear envelopes, and (b) by the organization of several linear chromosomes in multicomponent mega-complexes. These conglomerates of DNA, RNA, and proteins were discovered to be stainable, leading to the name ‘chromatin’. A distinction into heterochromatin and euchromatin (more or less stained) was made nearly a century ago [1], but the composition and functional relevance of chromatin organization was only studied much later. Now we know that the basal organization of chromatin into nucleosomes is conserved in all eukaryotes, and formed by DNA

wrapped around histone octamers of H3, H4, H2A, and H2B, sealed by linker histones. Chromatin-related research is proceeding with amazing speed and resolution, revealing sophisticated substructures and dynamics during all processes in living cells [2–4], including the ‘regular’ processes of transcription, repair, recombination, replication, mitosis, and meiosis. However, it is clear that adverse conditions interfering with normally programmed processes, commonly called stress, require plasticity also at the level of chromatin organization. Although there are numerous reports concerning chromatin changes connected with stress responses in many organisms, the number of reviews in this field appears disproportional to that of original reports.

Why then add another review, and why focus on plants? Plants are exposed to all kinds of biotic and abiotic stresses during their life, but cannot escape. Their stress defense is focused and elaborated at the level of protection and adaptation, including chromatin-based mechanisms and concomitant transcriptional changes. They also have plant-specific histone variants, DNA and histone-modifying enzymes, and some modifications have alternative roles in plants [5,6]. An additional important argument comes from the cytologically visible structural rearrangements of heterochromatin upon several types of stress within the nuclei of the model plant *Arabidopsis thaliana*. As similar alterations occur upon developmental transitions, it is likely that changes in nuclear organization have a functional connection with, or may even be a prerequisite for, stress responses.

Dynamic responses to stress at the nuclear structure level

Organization of plant nuclei

The size and shape of interphase nuclei are diverse and depend on DNA content, cell type, and physiological state, but little is known about the factors regulating nuclear morphology [7,8]. Plant nuclei differ from those in animal cells by components of the nuclear envelope [9–11] and exhibit a diverse and highly dynamic organization of their chromosome and chromatin content [recent reviews by 12–15]. Characteristic for several plant species is the tendency of heterochromatin to form clusters that appear condensed even in interphase. *Arabidopsis* nuclei have clearly visible chromocenters [16], consisting of centromeric and pericentromeric satellites and transcriptionally silent, highly repetitive, 45S and 5S rDNA arrays [17]. DNA FISH experiments and more recent Hi-C analysis have shown that euchromatic loops emanate from chromocenters [16,18,19], demonstrating their participation in the spatial organization of chromosomes.

Therefore, in *Arabidopsis*, chromocenter organization has been widely used as a read-out for chromatin changes during development or under stress conditions.

Changes in chromocenters during development and stress

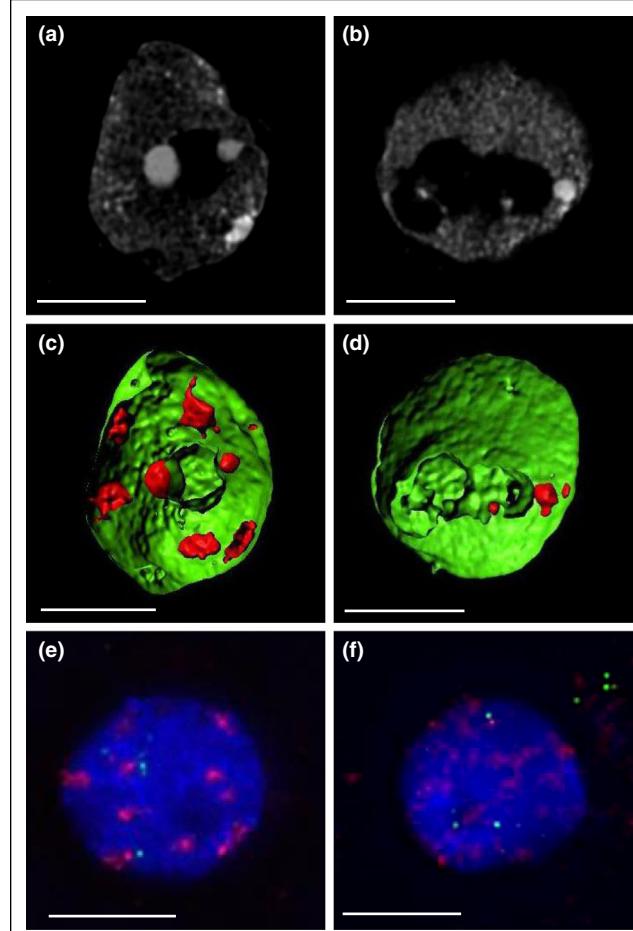
The number, organization, and position of chromocenters in *Arabidopsis* nuclei varies with ploidy [20], cell type [12,21], between accessions [22], and can be affected in plants lacking chromatin modifiers or remodelers [23,24]. Furthermore, specific developmental phase transitions, which require important changes in gene expression, are accompanied by transient alterations of chromocenter organization [17]. This is the case during the floral transition [25], when chromocenters temporarily decondense. Interestingly, this decondensation happens in terminally differentiated leaf tissue, and it remains to be investigated whether it also occurs in the meristem, the tissue which actually changes cell fate. Alterations in chromocenter organization also take place in cotyledon nuclei during seed maturation and germination [26], and post-germination development [27,28]. Further, chromatin organization is strongly affected by reprogramming differentiated cells during the preparation of protoplasts [29]. Protoplasts contain fewer and smaller chromocenters than the leaf cells from which they derive, and otherwise tightly clustered repetitive sequences are dispersed [29,30]. Other examples include structural alterations in nuclei during the initiation of embryo development from differentiated microspores [31,32], which might reflect a requirement to erase chromatin states of differentiated cells to establish new expression patterns during reprogramming. While these two examples are associated with developmental processes, they are also connected with external stress signals such as cell wall removal during protoplast preparation or temperature-stress induced dedifferentiation and reprogramming of microspores [reviewed in 33].

Direct effects of abiotic stresses on nuclear organization, independent of specific developmental processes, occur in rice and rye seedlings, in which 45S rDNA loci undergo decondensation upon heat stress [34,35]. Decondensation of centromeric repeats and 5S rDNA was also observed after prolonged heat-stress in *Arabidopsis* leaf tissue [36] (Figure 1). These structural changes could either reflect stress effects on the global arrangement of chromatin in nuclear space or the consequences of tethering particular genes to the nuclear periphery or transcriptional hotspots, in connection with modified gene expression.

Stress types modifying chromatin parameters

Although reports on extensive chromatin rearrangements are so far limited to the previously mentioned triggers, responses at the molecular level can be induced by many more types of stress. Drought, a drastic condition for plants and signaled through a pathway involving abscisic

Figure 1



Current Opinion in Plant Biology

Higher order chromatin changes upon heat stress. *Arabidopsis* leaf nuclei isolated from control plants (a, c, e) and plants submitted to prolonged heat stress at 37 °C for 30 h (b, d, f) illustrate decondensation of most chromocenters except those associated with the nucleolus and likely harboring the nucleolar organizing region, as well as enlargement of the nucleolus in response to heat stress. (a, b) Single planes of confocal image stacks of DAPI-stained nuclei. (c, d) 3D reconstructions of the confocal image stacks in A and B, respectively, obtained by intensity-based thresholding and image segmentation. The red clusters represent chromocenters embedded in euchromatin (green). (e, f) Nuclei after FISH with probes for centromeric repeats (red) and 5S rDNA (green) illustrate dispersion of repetitive sequences induced by heat stress, DNA is counterstained with DAPI (blue). Scale bars represent 5 μm.

Images: Courtesy Nina Daubel, Gregor Mendel Institute.

acid, is linked to chromatin changes [reviewed in 37–39]. Often connected with dehydration is osmotic stress or salinity, also elucidating responses at the chromatin level [reviewed in 40]. Extreme temperatures induce specific responses affecting chromatin configurations: cold stress [41–43] and heat stress for higher plants [36,44–46] and in algae [47,48]. Light deficiency induces chromatin

changes, signaled by light perception factors [22,49,50]. Exposure to energy-rich radiation or chemically induced damage of DNA exerts chromatin changes [51], and at least one chromatin remodeling factor supports the efficiency of DNA repair [52]. Toxic components might contribute to chromatin patterns, exemplified by the effect of cadmium in sea water algae [53]. In addition to abiotic factors, attacks by pathogens are signaled to the chromatin to induce defensive gene expression [54,55]. Finally, intrinsic responses to wounding [56] or senescence [57] are able to modify chromatin configurations.

General chromatin responses

Role of chaperones and remodelers

The organization of DNA into densely packed nucleosomal structures occludes access of transcription factors and passage of polymerases. To facilitate access to DNA, nucleosomes can be displaced or evicted, their composition altered by the incorporation of histone variants that affect nucleosome stability, or histones can be post-translationally modified to weaken histone-DNA contacts or to recruit interacting proteins. Chromatin remodeling complexes have been implicated in stress responses, such as ATCHR12, a SNF2/Brahma-type chromatin remodeling protein and its parologue ATCHR23 which mediate growth responses under stress conditions [58,59], or SPLAYED which is involved in biotic stress signaling and pathogen resistance [60]. How these chromatin remodelers integrate stress signals and whether they control a gene-specific or genome-wide response remains to be determined.

The reduction of nucleosomal density, independent of transcriptional reactivation, is an example of a genome-wide response, and provided the first evidence that histone chaperones might be involved, at least in post-stress periods, as mutants lacking CHROMATIN ASSEMBLY FACTOR 1 (CAF-1) subunits were impaired in nucleosome reassociation [36]. Histone chaperones control histone storage, assembly, and eviction [reviewed in 61,62]. Transcript levels of some histone chaperone genes in Arabidopsis and rice are differentially regulated upon abiotic stress [61,63], suggesting that they could be crucial players in the chromatin response to stress. Vice versa, genes encoding stress-responsive proteins are up-regulated in mutants lacking CAF-1 or ANTI-SILENCING FUNCTION 1 (ASF1) proteins, other H3/H4 chaperones [64^{••},65]. Plants expressing a truncated NUCLEOSOME ASSEMBLY PROTEIN 1 (NAP1), an H2A-H2B chaperone [66], or lacking ASF1 [64^{••}] show hypersensitivity to stress. ASF1 proteins bind directly to certain heat shock genes in a stress-dependent manner, where they may facilitate nucleosome dissociation and gene activation [64^{••}].

Role of histone variants

The replacement of canonical histones with variants confers specific features to the nucleosomes. Similar to

histone chaperones, genes encoding specific histone variants are differentially expressed upon stress in Arabidopsis and rice [61,67]. An example are certain genes encoding the histone variant H2A.Z that, in both species, are down-regulated upon salt or drought stress. This is particularly interesting in light of the role described for H2A.Z as a thermosensor [46], and suggests that H2A.Z may have a more general role in chromatin responses to stress [68]. Furthermore, plants express a specific class of stress-inducible H1 variants [61,69], which, upon over-expression, confers tolerance to several abiotic stresses [70]. Whether the plant-specific histone variant H2A.W, which is associated with heterochromatin [71[•]], is involved in stress-induced decondensation needs to be investigated.

Role of histone and DNA modifications

Besides varying histones themselves, the most obvious response of plant chromatin to stress signals is the modulation of post-translational modifications of histones and DNA itself [39 and references therein, 72]. Changes in histone marks can take place either globally or locally at specific stress-induced genes. Recent examples include the observation of a global histone hyperacetylation in response to various abiotic stresses in rice and maize [73–75], or the demonstration of a specific local gain of H3K9ac [76,77^{••},78] and H3K4me3 [77^{••},79] at genes activated in response to drought or salt stress in different species. How activating or suppressing histone marks are specifically modified at a particular set of genes remains to be elucidated, but it is likely coupled to the binding of specific transcription factors. One hint comes from the analysis of genes induced by endoplasmic reticulum stress caused by misfolded proteins in Arabidopsis. The sequence-specific transcription factors bZIP28 and bZIP60 involved in this stress response bind to promoters of downstream targets and increase H3K4me3 by recruiting the COMPASS-like complex through direct interaction with its components Ash2 and WDR5a [80[•]]. In addition to histone modifications, global and local changes in DNA methylation can occur in response to stress. DNA methylation levels are coordinated by balancing methylating and demethylating activities [reviewed in 72], and changing this equilibrium can affect the response to biotic stress in a negative [81] or positive manner [82]. An interesting observation in this respect is the occurrence of DNA methyltransferase CMT2 mutant alleles in natural Arabidopsis populations [83[•]]. These alleles might confer some evolutionary advantage as plants with this mutation have a higher tolerance to heat stress. Genetic variation in CMT2 is also associated with temperature-dependent levels of methylcytosine in the sequence context CHH, mainly at transposable elements, while more extensive gene body methylation at CG sites is temperature-independent but genetically determined by colder habitats [84^{••}].

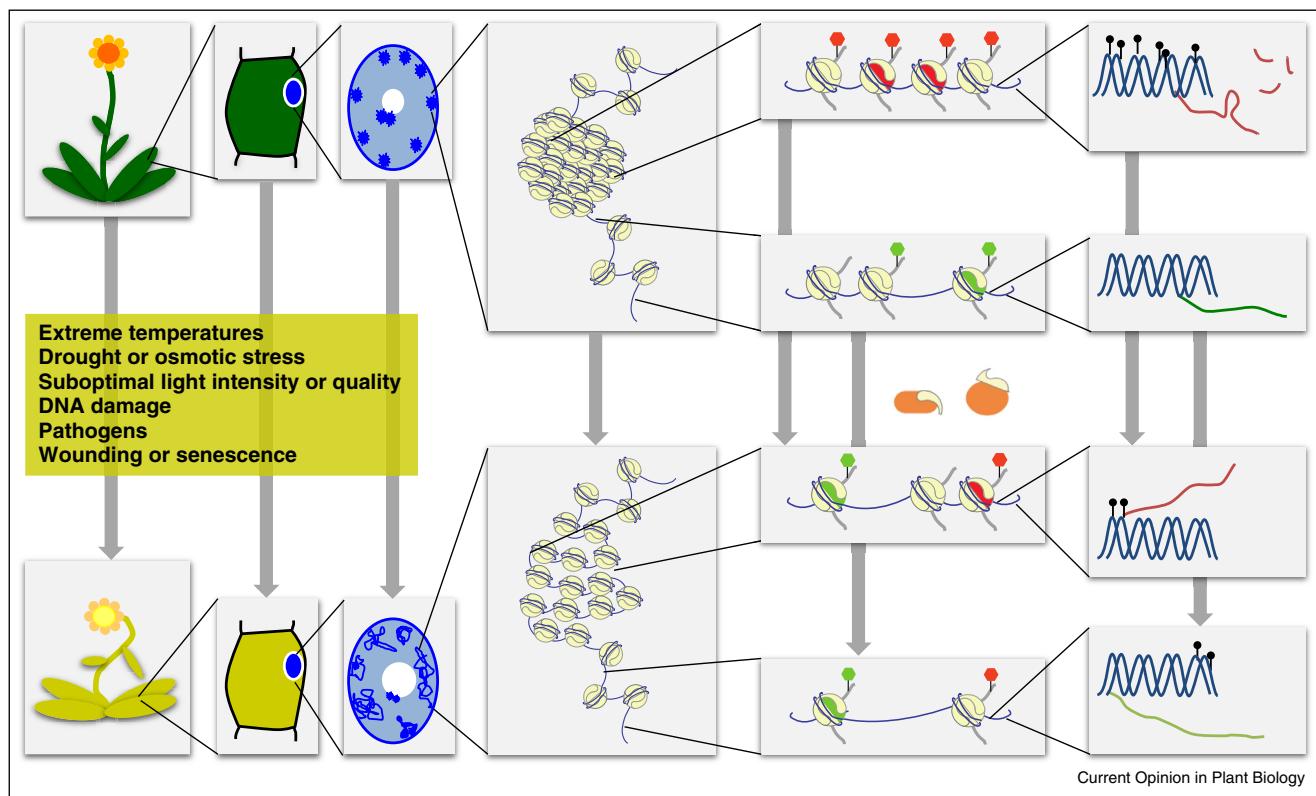
Taken together, changes in chromatin composition and modification are integral and complex elements of stress responses in plants (Figure 2). Future research needs to dissect further causal relationships between gene activation, local or global chromatin modification, and changes in higher-order organization. Histone chaperones are likely to play an important role by modulating nucleosomal density, distribution of histone variants, or the erasure of post-translation marks by histone eviction. Furthermore, histone chaperones might maintain a reservoir of evicted and soluble histones, facilitating the restoration of chromatin structures during recovery.

New non-histone nuclear proteins associated with stress responses

Histones represent the bulk of chromatin proteins. Although histone variants, their modifications, and their dynamic exchange already provide a construction kit with

immense combinatorial options, there are numerous non-histone but chromatin-associated proteins. Several of them were determined to be relevant upon stress reactions. Levels of Arabidopsis DEK3 define salinity tolerance, and the protein appears to work in collaboration with DNA topoisomerase 1 α . DEK3 is a member of the conserved DEK domain-containing protein family and interacts with H3 and H4, determines nucleosome occupancy, and associates with chromatin at specific loci [85**]. Rice plants under drought stress express a nuclear-localized protein that, based on sequence homology, is a member of the Alba (acetylation lowers binding affinity) family, but a chromatin connection in plants is not yet evident [86]. A screen for reduced heat stress tolerant Arabidopsis mutants lead to the identification of the plant-specific protein HEAT INTOLERANT 4 (HIT4). A HIT4 missense mutation interferes with the release of transcriptional gene silencing upon heat stress

Figure 2



Schematic representation of stress-associated chromatin changes. Under optimal growth conditions (upper part), heterochromatin in interphase nuclei is highly condensed, with repressive chromatin marks and a different histone composition than in the surrounding euchromatin. Abiotic and biotic stress conditions (lower part) affect plant fitness, physiology and higher-order chromatin organization. Different stress types can induce chromatin responses at the level of the chromatin fiber: displacement or eviction of nucleosomes, change in nucleosome composition by incorporation of histone variants or modification of histones by installing or removing repressive (red) and permissive (green) post-translational marks. These changes are likely to involve histone chaperones (orange). DNA methylation levels can also be affected, together reflecting and likely reinforcing an altered transcriptional program that may implicate reactivation of silent repetitive or transposable elements (red), altered expression of protein coding genes (dark green), or expression of specific stress-induced transcripts (light green). Some of these chromatin changes are reversible during recovery; others are long lasting, somatically heritable and may affect the plants response to further stresses. The scheme is based on observations in *Arabidopsis thaliana*, and the heterochromatin organization can be different in other species.

but does not reduce the induction of heat shock proteins. HIT4 associates with chromocenters and is involved in their decondensation during extended periods of heat stress [87^{••}]. Preceding the decondensation, HIT4 is delocalized to the nucleoli but this is not sufficient to achieve decondensation [88]. Association with nucleoli during stress responses was also described for RESTRICTED TO NUCLEOLUS 1 (REN1), a member of the heat shock transcription factor family and required for regular pollen development in *Arabidopsis* [89]. Mutations in genes for two DEAD box RNA helicases, STRESS RESPONSE SUPPRESSOR 1 and 2 (STRS 1 and 2) render *Arabidopsis* plants more resistant to several kinds of stress [90], while overexpressing lines are hypersensitive. The proteins are enriched at chromocenters and the nucleolus, dissociating transiently from the latter upon different stress treatments, with different kinetics. Some genes inactivated by the RNA-dependent DNA methylation (RdDM) pathway are upregulated in *strs* mutants, and several mutations in genes for epigenetic regulators affect the intranuclear localization of STRSs, suggesting their role in chromatin-based silencing of stress response genes [91]. A further interesting response to different stresses is post-translational protein modification by the attachment of SUMO [92[•]]. Examples for chromatin targets that show increased sumoylation upon stress are the histone-binding protein NRP1 (NAP related protein 1) [93] and MORC1 [94] involved in heterochromatin condensation.

Heritable changes at the chromatin level?

While chromatin is extensively investigated as a regulatory component of gene expression, it is also a focus of research in epigenetics, which asks if and how gene expression patterns can be stably maintained during somatic and sexual propagation after the original trigger has disappeared. Plants provide an interesting phenomenon to study somatic inheritance in connection with stress: ‘priming’ them with short or mild stress provides faster and stronger response to more dramatic or prolonged stress in the future [for review 95]. There is indeed good evidence that chromatin is part of this somatic memory. Mild salt stress of young *Arabidopsis* plants, which does not affect their growth, renders them more salt-tolerant than control plants upon a second exposure. This is associated with tissue and gene-specific changes of histone modifications that last a couple of days [96^{••}]. Higher resistance against bacterial pathogens, primed non-specifically by different abiotic stresses, was linked to the histone acetyltransferase HAC1 [97]. An analysis of histone modifications after priming by dehydration stress revealed some, but not uniform, changes of H3K4 trimethylation at specific ‘memory genes’ [79]. Surprisingly, persistence of H3K27 trimethylation did not interfere with strong transcriptional activation, although the lack of one Polycomb complex H3K27 methyltransferase modified the range of the

priming response [98]. Previous stress exposure can also dampen future response, as shown for drought-responsive genes [99[•]]. Involvement of the same histone modifications at different target genes in these converse reactions indicates a complexity that requires experimental refinement.

Although priming effects are often reset in the progeny of primed plants, recent reports indicate that the induced responses can become apparent in the progeny, and the data are extensively reviewed [100–106]. Although the concept of a meiotically heritable ‘epigenetic memory’ is attractive, also in the light of training or selecting trained plants with improved resistance, it is a challenge to unambiguously separate carryover of signals, parental effects via seed size or vigor, from stable adaptation that last more than 1–2 generations. The chance that chromatin changes will be inherited certainly depends on the genetic configuration of the chromatin regulators [e.g. 107,108]. As stress-induced chromatin changes are prone to activate transposable elements, new insertion sites can contribute to modified phenotypes in the progeny: the influence of many different TE insertions on transcriptional responses to stress in maize [109^{••}] clearly demonstrates the important role of this genetic component.

Conclusions

Current data leave no doubt that stress communicates with chromatin, and chromatin shapes stress responses and plant defense, but we are far from understanding the underlying molecular mechanisms. Some limits of experimental approaches are likely to remain: even under lab conditions, controlled application of well-defined stress treatments is difficult, and in nature, plants are almost always confronted with several stress factors simultaneously, resulting in overlapping, additive, or antagonistic responses. Direct events are rapidly followed by secondary effects, often leaving unanswered the classic question of cause and consequence. Current analytical tools require a minimum of material, blurring tissue and cell-specific responses, and quality and specificity of antibodies is often another limiting factor. However, new techniques in proteomics and chromatin analysis have lowered the thresholds substantially, and single cell analysis in the context of tissue becomes imaginable for some questions. Although nuclear substructures are much more complex and dynamic than text book illustrations suggest, new imaging techniques will also allow crossing borders towards high(er) resolution insights into living cells. Even without the potential to make agriculture more productive, a potential that is nowadays obligatory to emphasize in every grant proposal, the insight into processes in the highly dynamic headquarter of a cell in communication with the environment provide an exciting ground of future fundamental research.

Acknowledgments

We thank J. Matthew Watson for carefully editing the manuscript and Nina Daubel for Figure 1. The authors were supported by Agence Nationale de la Recherche grant 'Dynam'Het' ANR-11 JSV2 009 01 and ANR grant 'SINUDYN' ANR-12 ISV6 0001 to A.V.P. and Austrian Science Fund (FWF I1107, FWF W1238) and Vienna Science and Technology Fund (WWTF LS13-057) to O.M.S. We apologize to our colleagues whose work we were not able to discuss because of space constraints.

References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

- of special interest
 - of outstanding interest
1. Heitz E: **Das Heterochromatin der Moose.** *Jahrbücher für Wissenschaftliche Botanik* 1928, **69**:762-818.
 2. Misteli T: **The cell biology of genomes: bringing the double helix to life.** *Cell* 2013, **152**:1209-1212.
 3. Edelman LB, Fraser P: **Transcription factories: genetic programming in three dimensions.** *Curr Opin Genet Dev* 2012, **22**:110-114.
 4. Deng L, Blobel GA: **Manipulating nuclear architecture.** *Curr Opin Genet Dev* 2014, **25**:1-7.
 5. Talbert PB, Ahmad K, Almouzni G, Ausio J, Berger F, Bhalla PL, Bonner WM, Cande WZ, Chadwick BP, Chan SWL et al.: **A unified phylogeny-based nomenclature for histone variants.** *Epigenet Chromatin* 2012, **5**:7.
 6. Fuchs J, Demidov D, Houben A, Schubert I: **Chromosomal histone modification patterns – from conservation to diversity.** *Trends Plant Sci* 2006, **11**:199-208.
 7. Jevtic P, Edens LJ, Vukovic LD, Levy DL: **Sizing and shaping the nucleus: mechanisms and significance.** *Curr Opin Cell Biol* 2014, **28**:16-27.
 8. Walters AD, Bommakanti A, Cohen-Fix O: **Shaping the nucleus: factors and forces.** *J Cell Biochem* 2012, **113**:2813-2821.
 9. Guo T, Fang Y: **Functional organization and dynamics of the cell nucleus.** *Front Plant Sci* 2014, **5**:378.
 10. Petrovská B, Šebela M, Doležel J: **Inside a plant nucleus: discovering the proteins.** *J Exp Bot* 2015, **66**:1627-1640.
 11. Zhou X, Graumann K, Meier I: **The plant nuclear envelope as a multifunctional platform LINCed by SUN and KASH.** *J Exp Bot* 2015, **66**:1649-1659.
 12. Del Prete S, Arpon J, Sakai K, Andrey P, Gaudin V: **Nuclear architecture and chromatin dynamics in interphase nuclei of *Arabidopsis thaliana*.** *Cytogenetic Genome Res* 2014, **143**:28-50.
 13. Fransz P, de Jong H: **From nucleosome to chromosome: a dynamic organization of genetic information.** *Plant J* 2011, **66**:4-17.
 14. Matsunaga S, Katagiri Y, Nagashima Y, Sugiyama T, Hasegawa J, Hayashi K, Sakamoto T: **New insights into the dynamics of plant cell nuclei and chromosomes.** *Int Rev Cell Mol Biol* 2013, **305**:253-301.
 15. Tiang C-L, He Y, Pawlowski WP: **Chromosome organization and dynamics during interphase, mitosis, and meiosis in plants.** *Plant Physiol* 2012, **158**:26-34.
 16. Fransz P, de Jong JH, Lysak M, Castiglione MR, Schubert I: **Interphase chromosomes in *Arabidopsis* are organized as well defined chromocenters from which euchromatin loops emanate.** *Proc Natl Acad Sci U S A* 2002, **99**:14584-14589.
 17. Benoit M, Layat E, Tourmente S, Probst AV: **Heterochromatin dynamics during developmental transitions in *Arabidopsis* – a focus on ribosomal DNA loci.** *Gene* 2013, **526**:39-45.
 18. Feng S, Cokus SJ, Schubert V, Zhai J, Pellegrini M, Jacobsen SE: **Genome-wide Hi-C analyses in wild-type and mutants reveal high-resolution chromatin interactions in *Arabidopsis*.** *Mol Cell* 2014, **55**:694-707.
 19. Grob S, Schmid MW, Luedtke NW, Wicker T, Grossniklaus U: **Characterization of chromosomal architecture in *Arabidopsis* by chromosome conformation capture.** *Genome Biol* 2013, **14**:R129.
 20. Schubert V, Berr A, Meister A: **Interphase chromatin organisation in *Arabidopsis* nuclei: constraints versus randomness.** *Chromosoma* 2012, **121**:369-387.
 21. de Nooijer S, Wellink J, Mulder B, Bisseling T: **Non-specific interactions are sufficient to explain the position of heterochromatic chromocenters and nucleoli in interphase nuclei.** *Nucleic Acids Res* 2009, **37**:3558-3568.
 22. Tessadori F, van Zanten M, Pavlova P, Clifton R, Pontvianne F, Snoek LB, Millenaar FF, Schulkes RK, van Driel R, Voesenek L et al.: **PHYTOCHROME B and H ISTONE DEACETYLASE 6 control light-induced chromatin compaction in *Arabidopsis thaliana*.** *PLoS Genetics* 2009, **5**:e1000638.
 23. Mittelsten Scheid O, Probst AV, Afsar K, Paszkowski J: **Two regulatory levels of transcriptional gene silencing in *Arabidopsis*.** *Proc Natl Acad Sci U S A* 2002, **99**:13659-13662.
 24. Probst AV, Fransz PF, Paszkowski J, Mittelsten Scheid O: **Two means of transcriptional reactivation within heterochromatin.** *Plant J* 2003, **33**:743-749.
 25. Tessadori F, Schulkes RK, van Driel R, Fransz P: **Light-regulated large-scale reorganization of chromatin during the floral transition in *Arabidopsis*.** *Plant J* 2007, **50**:848-857.
 26. van Zanten M, Koini MA, Geyer R, Liu Y, Brambilla V, Bartels D, Koornneef M, Fransz P, Soppe WJJ: **Seed maturation in *Arabidopsis thaliana* is characterized by nuclear size reduction and increased chromatin condensation.** *Proc Natl Acad Sci U S A* 2011, **108**:20219-20224.
 27. Mathieu O, Jasencakova Z, Vaillant I, Gendrel AV, Colot V, Schubert I, Tourmente S: **Changes in 5S rDNA chromatin organization and transcription during heterochromatin establishment in *Arabidopsis*.** *Plant Cell* 2003, **15**:2929-2939.
 28. Douet J, Blanchard B, Cuvillier C, Tourmente S: **Interplay of RNA Pol IV and ROS1 during post-embryonic 5S rDNA chromatin remodeling.** *Plant Cell Physiol* 2008, **49**:1783-1791.
 29. Tessadori F, Chupeau MC, Chupeau Y, Knip M, Germann S, van Driel R, Fransz P, Gaudin V: **Large-scale dissociation and sequential reassembly of pericentric heterochromatin in dedifferentiated *Arabidopsis* cells.** *J Cell Sci* 2007, **120**:1200-1208.
 30. Florentin A, Damri M, Grafi G: **Stress induces plant somatic cells to acquire some features of stem cells accompanied by selective chromatin reorganization.** *Dev Dyn* 2013, **242**:1121-1133.
 31. Testillano PS, Gonzalez-Melendi P, Coronado MJ, Segui-Simarro JM, Moreno-Risueno MA, Risueno MC: **Differentiating plant cells switched to proliferation remodel the functional organization of nuclear domains.** *Cytogenetic Genome Res* 2005, **109**:166-174.
 32. Segui-Simarro JM, Corral-Martinez P, Corredor E, Raska I, Testillano PS, Risueno MC: **A change of developmental program induces the remodeling of the interchromatin domain during microspore embryogenesis in *Brassica napus* L.** *J Plant Physiol* 2011, **168**:746-757.
 33. Feher A: **Somatic embryogenesis – stress-induced remodeling of plant cell fate.** *Biochim Biophys Acta* 2015, **1849**:385-402.
 34. Santos AP, Ferreira L, Maroco J, Oliveira MM: **Abiotic stress and induced DNA hypomethylation cause interphase chromatin structural changes in rice rDNA loci.** *Cytogenetic Genome Res* 2011, **132**:297-303.
 35. Tomas D, Brazao J, Viegas W, Silva M: **Differential effects of high-temperature stress on nuclear topology and transcription of repetitive noncoding and coding rye sequences.** *Cytogenetic Genome Res* 2013, **139**:119-127.

36. Pecinka A, Dinh HQ, Baubec T, Rosa M, Lettner N, Mittelsten Scheid O: **Epigenetic regulation of repetitive elements is attenuated by prolonged heat stress in *Arabidopsis*.** *Plant Cell* 2010, **22**:3118-3129.
37. Han SK, Wagner D: **Role of chromatin in water stress responses in plants.** *J Exp Bot* 2014, **65**:2785-2799.
38. Mehrotra R, Bhalothia P, Bansal P, Basantani MK, Bharti V, Mehrotra S: **Abscisic acid and abiotic stress tolerance – different tiers of regulation.** *J Plant Physiol* 2014, **171**:486-496.
39. Kim J-M, Sasaki T, Ueda M, Sako K, Seki M: **Chromatin changes in response to drought, salinity, heat, and cold stresses in plants.** *Front Plant Sci* 2015, **6**:114.
40. Deinlein U, Stephan AB, Horie T, Luo W, Xu GH, Schroeder JI: **Plant salt-tolerance mechanisms.** *Trends Plant Sci* 2014, **19**:371-379.
41. Kim JM, To TK, Nishioka T, Seki M: **Chromatin regulation functions in plant abiotic stress responses.** *Plant Cell Environ* 2010, **33**:604-611.
42. Roy D, Paul A, Roy A, Ghosh R, Ganguly P, Chaudhuri S: **Differential acetylation of histone H3 at the regulatory region of OsDREB1b promoter facilitates chromatin remodelling and transcription activation during cold stress.** *Plos One* 2014, **9**:e100343.
43. Hu Y, Zhang L, He S, Huang M, Tan J, Zhao L, Yan S, Li H, Zhou K, Liang Y, Li L: **Cold stress selectively unsilences tandem repeats in heterochromatin associated with accumulation of H3K9ac.** *Plant Cell Environ* 2012, **35**:2130-2142.
44. Lang-Mladek C, Popova O, Kiok K, Berlinger M, Rakic B, Aufsatz W, Jonak C, Hauser MT, Luschnig C: **Transgenerational inheritance and resetting of stress-induced loss of epigenetic gene silencing in *Arabidopsis*.** *Mol Plant* 2010, **3**:594-602.
45. Tittel-Elmer M, Bucher E, Broger L, Mathieu O, Paszkowski J, Vaillant I: **Stress-induced activation of heterochromatic transcription.** *PLoS Genet* 2010, **6**:e1001175.
46. Kumar SV, Wigge PA: **H2A.Z-containing nucleosomes mediate the thermosensory response in *Arabidopsis*.** *Cell* 2010, **140**:136-147.
47. Lee TC, Hsu BD: **The reversible degeneration of heat-treated *Scenedesmus vacuolatus* under continuous light cultivation conditions.** *Protoplasma* 2014, **251**(5):1201-1211.
48. Schröder M, Hemme D, Mühlhaus T: **The Chlamydomonas heat stress response.** *Plant J* 2015. ahead of print.
49. van Zanten M, Tessadori F, Peeters AJ, Franz P: **Shedding light on large-scale chromatin reorganization in *Arabidopsis thaliana*.** *Mol Plant* 2012, **5**:583-590.
50. van Zanten M, Tessadori F, McLoughlin F, Smith R, Millenaar FF, van Driel R, Voesenek LACJ, Peeters AJM, Franz P: **Photoreceptors CRYPTOCHROME2 and phytochrome B control chromatin compaction in *Arabidopsis*.** *Plant Physiol* 2010, **154**:1686-1696.
51. Braszewska-Zalewska A, Tylikowska M, Kwasniewska J, Szymanowska-Pulka J: **Epigenetic chromatin modifications in barley after mutagenic treatment.** *J Appl Genet* 2014, **55**:449-456.
52. Rosa M, Von Harder M, Cigliano RA, Schloegelhofer P, Mittelsten Scheid O: **The *Arabidopsis* SWR1 chromatin-remodeling complex is important for DNA repair, somatic recombination, and meiosis.** *Plant Cell* 2013, **25**:1990-2001.
53. Greco M, Chiappetta A, Bruno L, Bitonti MB: **In *Posidonia oceanica cadmium* induces changes in DNA methylation and chromatin patterning.** *J Exp Bot* 2012, **63**:695-709.
54. Berr A, Menard R, Heitz T, Shen W-H: **Chromatin modification and remodelling: a regulatory landscape for the control of *Arabidopsis* defence responses upon pathogen attack.** *Cell Microbiol* 2012, **14**:829-839.
55. Schenke D, Cai DG, Scheel D: **Suppression of UV-B stress responses by flg22 is regulated at the chromatin level via histone modification.** *Plant Cell Environ* 2014, **37**:1716-1721.
56. Lewandowska-Gnatowska E, Polkowska-Kowalczyk L, Szczegielniak J, Barciszewska M, Barciszewski J, Muszynska G: **Is DNA methylation modulated by wounding-induced oxidative burst in maize?** *Plant Physiol Biochem* 2014, **82**:202-208.
57. Ay N, Janack B, Humbeck K: **Epigenetic control of plant senescence and linked processes.** *J Exp Bot* 2014, **65**:3875-3887.
58. Mlynarova L, Nap JP, Bisseling T: **The SWI/SNF chromatin-remodeling gene AtCHR12 mediates temporary growth arrest in *Arabidopsis thaliana* upon perceiving environmental stress.** *Plant J* 2007, **51**:874-885.
59. Folta A, Severing EI, Krauskopf J, van de Geest H, Verter J, Nap JP, Mlynarova L: **Over-expression of *Arabidopsis* AtCHR23 chromatin remodeling ATPase results in increased variability of growth and gene expression.** *BMC Plant Biol* 2014, **14**:76.
60. Walley JW, Rowe HC, Xiao Y, Chehab EW, Kliebenstein DJ, Wagner D, Dehesh K: **The chromatin remodeler SPLAYED regulates specific stress signaling pathways.** *PLoS Pathog* 2008, **4**:e1000237.
61. Zhu Y, Dong A, Shen W-H: **Histone variants and chromatin assembly in plant abiotic stress responses.** *Biochim Biophys Acta-Gene Regul Mech* 2012, **1819**:343-348.
62. Otero S, Desvoyes B, Gutierrez C: **Histone H3 dynamics in plant cell cycle and development.** *Cytogenetic Genome Res* 2014, **143**:114-124.
63. Tripathi AK, Singh K, Pareek A, Singla-Pareek SL: **Histone chaperones in *Arabidopsis* and rice: genome-wide identification, phylogeny, architecture and transcriptional regulation.** *BMC Plant Biol* 2015, **15**:414.
64. Weng M, Yang Y, Feng H, Pan Z, Shen W-H, Zhu Y, Dong A: **• Histone chaperone ASF1 is involved in gene transcription activation in response to heat stress in *Arabidopsis thaliana*.** *Plant Cell Environ* 2014, **37**:2128-2138.
- This study shows that the *Arabidopsis* small histone chaperone proteins ASF1a and b are involved in thermotolerance and heat-response, binding directly to certain heat shock factor genes where their presence is required to achieve maximal transcriptional response and nucleosome removal.
65. Schönrock N, Exner V, Probst A, Gruissem W, Hennig L: **Functional genomic analysis of CAF-1 mutants in *Arabidopsis thaliana*.** *J Biol Chem* 2006, **281**:9560-9568.
66. Liu Z-Q, Gao J, Dong A-W, Shen W-H: **A truncated *Arabidopsis NUCLEOSOME ASSEMBLY PROTEIN 1*, AtNAP1;3T, alters plant growth responses to abscisic acid and salt in the AtNap1;3-2 mutant.** *Mol Plant* 2009, **2**:688-699.
67. Hu Y, Lai Y: **Identification and expression analysis of rice histone genes.** *Plant Physiol Biochem* 2015, **86**:55-65.
68. Talbert PB, Henikoff S: **Environmental responses mediated by histone variants.** *Trends Cell Biol* 2014, **24**:642-650.
69. Jerzmanowski A: **SWI/SNF chromatin remodeling and linker histones in plants.** *Biochim Biophys Acta-Gene Struct Exp* 2007, **1769**:330-345.
70. Wang W, Wang Y, Du Y, Zhao Z, Zhu X, Jiang X, Shu Z, Yin Y, Li X: **Overexpression of *Camellia sinensis* H1 histone gene confers abiotic stress tolerance in transgenic tobacco.** *Plant Cell Rep* 2014, **33**:1829-1841.
71. Yelagandula R, Stroud H, Holek S, Zhou K, Feng S, Zhong X, Muthurajan UM, Nie X, Kawashima T, Groth M et al.: **The histone variant H2A.W defines heterochromatin and promotes chromatin condensation in *Arabidopsis*.** *Cell* 2014, **158**:98-109.
- This article describes a new plant-specific H2A.W. variant that is associated with heterochromatin and required for its condensation. Stress-related decondensation may therefore connect with H2A.W.
72. Meyer P: **Epigenetic variation and environmental change.** *J Exp Bot* 2015. ahead of print.
73. Wang P, Zhao L, Hou H, Zhang H, Huang Y, Wang Y, Li H, Gao F, Yan S, Li L: **Epigenetic changes are associated with**

- programmed cell death induced by heat stress in seedling leaves of Zea mays.** *Plant Cell Physiol* 2015; ahead of print.
74. Zhao L, Wang P, Hou HL, Zhang H, Wang YP, Yan SH, Huang Y, Li H, Tan JJ, Hu A et al.: **Transcriptional regulation of cell cycle genes in response to abiotic stresses correlates with dynamic changes in histone modifications in maize.** *PLoS One* 2014, 9:e106070.
75. Fang H, Liu X, Thorn G, Duan J, Tian L: **Expression analysis of histone acetyltransferases in rice under drought stress.** *Biochem Biophys Res Commun* 2014, 443:400-405.
76. Li H, Yan SH, Zhao L, Tan JJ, Zhang Q, Gao F, Wang P, Hou HL, Li LJ: **Histone acetylation associated up-regulation of the cell wall related genes is involved in salt stress induced maize root swelling.** *BMC Plant Biol* 2014, 14:105.
77. Widiez T, Symeonidi A, Luo CY, Lam E, Lawton M, Rensing SA: **•• The chromatin landscape of the moss *Physcomitrella patens* and its dynamics during development and drought stress.** *Plant J* 2014, 79:67-81.
- This is a study of genome-wide distribution of histone H3 modifications in a model moss species. The authors describe specific chromatin states and their changes during the transition from juvenile to adult stage and upon dehydration.
78. Kim J-M, To TK, Ishida J, Matsui A, Kimura H, Seki M: **Transition of chromatin status during the process of recovery from drought stress in *Arabidopsis thaliana*.** *Plant Cell Physiol* 2012, 53:847-856.
79. Ding Y, Fromm M, Avramova Z: **Multiple exposures to drought 'train' transcriptional responses in *Arabidopsis*.** *Nat Commun* 2012, 3:740.
80. Song Z-T, Sun L, Lu S-J, Tian Y, Ding Y, Liu J-X: **Transcription factor interaction with COMPASS-like complex regulates histone H3K4 trimethylation for specific gene expression in plants.** *Proc Natl Acad Sci U S A* 2015, 112:2900-2905.
- This study shows that specific stress-activated transcription factors can lead to accumulation of H3K4me3 at downstream target genes through specific interaction with subunits of the COMPASS-like complex.
81. Le T-N, Schumann U, Smith NA, Tiwari S, Au PCK, Zhu Q-H, Taylor JM, Kazan K, Llewellyn DJ, Zhang R et al.: **DNA demethylases target promoter transposable elements to positively regulate stress responsive genes in *Arabidopsis*.** *Genome Biol* 2014, 15:9.
82. Dowen RH, Pelizzola M, Schmitz RJ, Lister R, Dowen JM, Nery JR, Dixon JE, Ecker JR: **Widespread dynamic DNA methylation in response to biotic stress.** *Proc Natl Acad Sci U S A* 2012, 109:E2183-E2189.
83. Shen X, De Jonge J, Forsberg SKG, Pettersson ME, Sheng Z, Hennig L, Carlborg O: **Natural CMT2 variation is associated with genome-wide methylation changes and temperature seasonality.** *PLoS Genetics* 2014, 10:e1004842.
- This work provides evidence for the presence of mutant alleles of the DNA methyltransferase CMT2 in natural populations of *Arabidopsis thaliana*. Mutant alleles may provide evolutionary advantages by improving heat stress tolerance, linking changes in DNA methylation with adaptation to varying temperatures.
84. Dubin MJ, Zhang P, Meng D, Remigereau MS, Osborne EJ, Paolo Casale F, Drewe P, Kahles A, Jean G, Vilhjálmsson B, Jagoda J et al.: **DNA methylation in *Arabidopsis* has a genetic basis and shows evidence of local adaptation.** *ELife* 2015 <http://dx.doi.org/10.7554/eLife.05255>.
- This publication describes direct evidence for temperature-dependent levels of DNA methylation mainly at transposable elements and a genetically determined global increase in gene body methylation in plants from colder regions.
85. Waidmann S, Kusenda B, Mayerhofer J, Mechtler K, Jonak C: **A DEK domain-containing protein modulates chromatin structure and function in *Arabidopsis*.** *Plant Cell* 2014, 26:4328-4344.
- This study describes the chromatin-associated protein DEK3 that determines nucleosome occupancy and expression of target genes. DEK3 overexpression reduces salt tolerance.
86. Verma JK, Gayali S, Dass S, Kumar A, Parveen S, Chakraborty S, Chakraborty N: **OsAlba1, a dehydration-responsive nuclear protein of rice (*Oryza sativa* L. ssp *indica*), participates in stress adaptation.** *Phytochemistry* 2014, 100:16-25.
87. Wang L-C, Wu J-R, Chang W-L, Yeh C-H, Ke Y-T, Lu C-A, Wu S-J: **•• Arabidopsis HIT4 encodes a novel chromocentre-localized protein involved in the heat reactivation of transcriptionally silent loci and is essential for heat tolerance in plants.** *J Exp Bot* 2013, 64:1689-1701.
- This article describes the identification of a novel plant-specific protein required for heat tolerance. In its absence, heat-induced heterochromatin decondensation and release of transcriptional silencing is attenuated.
88. Wang L-C, Wu J-R, Hsu Y-J, Wu S-J: **Arabidopsis HIT4, a regulator involved in heat-triggered reorganization of chromatin and release of transcriptional gene silencing, relocates from chromocenters to the nucleolus in response to heat stress.** *New Phytol* 2015, 205:544-554.
89. Renak D, Gibalova A, Solcova K, Honys D: **A new link between stress response and nucleolar function during pollen development in *Arabidopsis* mediated by AtREN1 protein.** *Plant Cell Environ* 2014, 37:670-683.
90. Kant P, Kant S, Gordon M, Shaked R, Barak S: **STRESS RESPONSE SUPPRESSOR1 and STRESS RESPONSE SUPPRESSOR2, two DEAD-box RNA helicases that attenuate *Arabidopsis* responses to multiple abiotic stresses.** *Plant Physiol* 2007, 145:814-830.
91. Khan A, Garbelli A, Grossi S, Florentin A, Batelli G, Acuna T, Zolla G, Kaye Y, Paul LK, Zhu J-K et al.: **The *Arabidopsis* STRESS RESPONSE SUPPRESSOR DEAD-box RNA helicases are nucleolar- and chromocenter-localized proteins that undergo stress-mediated relocation and are involved in epigenetic gene silencing.** *Plant J* 2014, 79:28-43.
92. Miller MJ, Scalf M, Rytz TC, Hubler SL, Smith LM, Vierstra RD: **• Quantitative proteomics reveals factors regulating RNA biology as dynamic targets of stress-induced SUMOylation in *Arabidopsis*.** *Mol Cell Proteomics* 2013, 12:449-463.
- Analyzing the dynamics of SUMOylation in stressed *Arabidopsis*, the authors found quantitative differences to control plants mainly for proteins involved in RNA processing and DNA modification.
93. Zhu Y, Dong A, Meyer D, Pichon O, Renou J-P, Cao K, Shen W-H: ***Arabidopsis* NRP1 and NRP2 encode histone chaperones and are required for maintaining postembryonic root growth.** *Plant Cell* 2006, 18:2879-2892.
94. Moissiard G, Cokus SJ, Cary J, Feng S, Billi AC, Stroud H, Husmann D, Zhan Y, Lajoie BR, McCord RP et al.: **MORC family ATPases required for heterochromatin condensation and gene silencing.** *Science* 2012, 336:1448-1451.
95. Holeski LM, Jander G, Agrawal AA: **Transgenerational defense induction and epigenetic inheritance in plants.** *Trends Ecol Evol* 2012, 27:618-626.
96. Sani E, Herzyk P, Perrella G, Colot V, Amtmann A: **Hyperosmotic priming of *Arabidopsis* seedlings establishes a long-term somatic memory accompanied by specific changes of the epigenome.** *Genome Biol* 2013, 14:R59.
- The authors show that mild salt stress in *Arabidopsis* induces small but specific changes in the distribution of histone modifications, lasting for several days and influencing the transcriptional response upon later stress exposure.
97. Singh P, Yekondi S, Chen PW, Tsai CH, Yu CW, Wu KQ, Zimmerli L: **Environmental history modulates *Arabidopsis* pattern-triggered immunity in a HISTONE ACETYLTRANSFERASE1-dependent manner.** *Plant Cell* 2014, 26:2676-2688.
98. Liu N, Fromm M, Avramova Z: **H3K27me3 and H3K4me3 chromatin environment at super-induced dehydration stress memory genes of *Arabidopsis thaliana*.** *Mol Plant* 2014, 7:502-513.
99. Liu N, Ding Y, Fromm M, Avramova Z: **Different gene-specific mechanisms determine the 'revised-response' memory transcription patterns of a subset of *A-thaliana* dehydration stress responding genes.** *Nucleic Acids Res* 2014, 42:5556-5566.
- This paper describes a phenomenon that appears as reversed priming and link it to histone modification and a specific transcription factor.

100. Iwasaki M, Paszkowski J: **Epigenetic memory in plants.** *EMBO J* 2014, **33**:1987-1998.
101. Kinoshita T, Seki M: **Epigenetic memory for stress response and adaptation in plants.** *Plant Cell Physiol* 2014, **55**:1859-1863.
102. Eichten SR, Schmitz RJ, Springer NM: **Epigenetics: beyond chromatin modifications and complex genetic regulation.** *Plant Physiol* 2014, **165**:933-947.
103. Saze H: **Transgenerational inheritance of induced changes in the epigenetic state of chromatin in plants.** *Genes Genetic Syst* 2012, **87**:145-152.
104. Avramova Z: **Transcriptional ‘Memory’ of a stress; transient chromatin and memory (epigenetic) marks at stress response genes.** *Plant J* 2015. ahead of print.
105. Mueller-Xing R, Xing Q, Goodrich J: **Footprints of the sun: memory of UV and light stress in plants.** *Front Plant Sci* 2014, **5**:474.
106. Pecinka A, Mittelsten Scheid O: **Stress-induced chromatin changes: a critical view on their heritability.** *Plant Cell Physiol* 2012, **53**:801-808.
107. Iwasaki M, Paszkowski J: **Identification of genes preventing transgenerational transmission of stress-induced epigenetic states.** *Proc Natl Acad Sci U S A* 2014, **111**:8547-8552.
108. Baubec T, Finke A, Mittelsten Scheid O, Pecinka A: **Meristem-specific expression of epigenetic regulators safeguards transposon silencing in *Arabidopsis*.** *Embo Rep* 2014, **15**:446-452.
109. Makarevitch I, Waters AJ, West PT, Stitzer M, Hirsch CN, Ross-
• Ibarra J, Springer NM: **Transposable elements contribute to activation of maize genes in response to abiotic stress.** *PLoS Genetics* 2015, **11**:e1004915.
This article demonstrates the high variability of transposable element insertions near stress responsive genes in maize and the consequences for transcriptional regulation upon stress exposure.