

EDITORIAL

Chromatin and development: a special issue

It is now approximately 40 years since chromatin studies changed drastically with the first visualization of ‘nu bodies’, that we now know as nucleosomes. The ‘beads on a string’ that appeared in electron micrographs (Olins and Olins, 1974) showed the structural units of chromatin and provided the foundation for a field that has been expanding ever since then. One of the major advances in chromatin studies has been the identification of numerous connections between nucleosome organization, including the plethora of histone post-translational modifications, and gene function. Studies in an apparently different field, development of multicellular organisms, have also revealed that developmental transitions and organogenesis are strictly dependent on the establishment, maintenance and modification of highly regulated gene expression patterns. Therefore, efforts to learn about chromatin organization and function, gene expression and developmental transitions converge, contributing to provide a complete picture. In this Special Issue on ‘*Chromatin and epigenetics at the nexus between cell division, differentiation and development*’ we have gathered articles from leading scientists in their fields discussing a broad spectrum of topics relating chromatin structure and function with developmental transitions: the special organization and functional properties of centromeres and telomeres, genome maintenance and integrity, nucleosome remodeling and modification complexes, histone dynamics, epigenetic memory and chromatin during gametophyte development.

Centromeres, unique structural chromosomal entities important for genetic stability, have a complex biology both in somatic and reproductive stages (Lermontova *et al.*, 2015). One key aspect is identifying what elements contribute to define a centromere. Large arrays of satellite repeats are often found at centromeric regions of dicotyledonous species whereas retro-elements are found in many monocotyledonous species, in both cases with rapid evolutionary divergence even between close relatives. In contrast to the difficulties in defining centromeres at the sequence level, the presence of kinetochore complex, containing >100 proteins, is a general mark of a centromere. Linked to kinetochore assembly is the incorporation of the specific centromeric histone H3 (CENH3), which has gained wide attention in plant biology since the expression of certain artificial CENH3 fusion proteins can lead to genome haploidization. Plant telomeres and ribosomal genes are not only exceptional from their DNA composition and the repetitive sequence organization, but also from their chromatin status of both elements. This together with the surprising similarities between them is discussed in the corresponding review article (Dvořáčková *et al.*, 2015), including epigenetic modifications and the role of long non-coding RNAs.

Maintenance of genetic material and the necessary intermixing of the parental genotypes during propagation to the next generation are topics at the core of genome stability. Progression through the cell cycle depends on the occurrence of a series of events, several of which rely on drastic changes in chromatin organization. The intimate relationship between genome replication and chromatin landscapes is discussed by Sequeira-Mendes and Gutierrez (Sequeira-Mendes and Gutierrez, 2015). Although genome replication occurs during the S-phase, certain steps (access of replication initiation proteins to chromatin and specification of replication origins) take place soon after mitosis and during the G1 phase and are highly dependent on the chromatin status. Interestingly, they are multiple chromatin signatures associated with the origin location, some of which are remarkably similar to those identified in animal cells. Other aspects relevant for genome integrity and development such as prevention of duplicating genomic regions more than once per cell cycle (re-replication) and the transition from the cell cycle to the endocycle, which is a necessary step for many plants cells before they can fully differentiate, are also discussed. The exchange of genetic information between parental chromosomes, known as ‘cross-overs’ (COs), occur during meiotic recombination and are events required in plant breeding to unlink adverse from beneficial traits that are coded in close proximity on the same chromosome. This question of basic and applied relevance is discussed by Choi and Henderson (Choi and Henderson, 2015) by focusing on the study of CO hotspots. Interestingly chromatin structure plays a very important, but still not completely understood role in this process. Most often hotspots are found in association with genes and particularly within promoter regions of genes that have an open chromatin structure.

One of the major factors contributing to chromatin organization is nucleosome positioning and histone composition. The ATPase-containing chromatin remodeling complexes during plant development are discussed by D. Wagner and colleagues (Han *et al.*, 2015) with emphasis on SWI/SNF and CHD3. These factors function as enhancers with a role in pluripotency, differentiation and developmental phase transitions, and their defects lead to pleiotropic consequences. At the gene level, it is becoming clear that certain genes depend more on chromatin remodeling than others, in particular if they function as master

regulators in development. Thus, the plasticity of plant development may explain the occurrence of many more chromatin remodelers in plants than in animals. Besides chromatin remodelers histone chaperones are relevant for plant growth and development due to their influence on chromatin composition during nucleosome assembly and disassembly. The review by Wen-Hui Shen and colleagues (Zhou *et al.*, 2015) concentrates on the NAP1 and FACT families of H2A/H2B chaperones, which are influenced by multiple covalent modifications. The authors sum up our current state of knowledge of the NAP1 and FACT chaperones in relation to transcription, giving us insight into the complex interaction networks of these factors in DNA replication, DNA repair and finally in stress and development. In addition to the canonical histones, a number of variants exist for all histones except H4, that exhibit small changes in amino acid composition compared to the canonical forms, yet they confer highly specialized properties to the variant-containing nucleosomes. The case of the histone H2A.Z variant exemplifies the relevance of histone variants (Jarillo and Piñeiro, 2015); but see also (Zhou *et al.*, 2015) and (Sequeira-Mendes and Gutierrez, 2015) for other variants). H2A.Z exchange occurs through a sophisticated mechanism that relies on various ATP-dependent protein complexes. H2A.Z seems to be particularly relevant for nucleosome stability and, due to its role on gene expression, H2A.Z has a major relevance in the transition to reproductive development, a process for which the availability of plants carrying mutations in most of the genes encoding proteins of the H2A.Z chaperone are instrumental.

One paradigmatic form of gene repression, especially linked to developmental programs, depends on the function of Polycomb group (PcG) repressive complex, PRC1 and PRC2. PRC1 mediates histone H2A monoubiquitination at lysine 119 (H2AK119ub) in nucleosomes located at target genes. Genetic and molecular evidence support the notion that modification of nucleosomes by PRC2 leads to recruitment of PRC1 complex. Interestingly, recent findings apparently challenge this model (Merini and Calonje, 2015), since, at least in some cases, it is PRC1-mediated H2AK119ub that directs PRC2 binding, at least in some cases, to affect various stages in development. PRC2 complexes exist in different flavors that vary according to some of their subunits but all of them trimethylate histone H3 at lysine 27 (H3K27me3), a modification leading to long-lasting gene repression, although the detailed mechanism is not well understood yet (Mozgova *et al.*, 2015). The composition and function of different PRC2 complexes explain their activity at different plant developmental transitions, which are discussed in the light of recent molecular, genetic, and genomic evidence.

The perception of the appropriate environmental conditions for flowering and the epigenetic memory associated with this crucial phase in flowering plants is reviewed by Berry and Dean (Berry and Dean, 2015). The floral regulator FLC is transcriptionally repressed when the plant is exposed to prolonged cold temperatures and is epigenetically maintained in such state during growth in the warm through the concerted action of PRC2 complexes and long non-coding RNAs. The authors discuss also how the epigenetic status of FLC locus is reprogrammed in the seed to ensure correct response in the next generation. Plants are subjected to a plethora of environmental stresses including drought, salinity, nutrient restrictions, temperature variations and pathogen attacks. Zoya Avramova discusses the concept of 'stress memory', that is the plant response to a given stress after it has received the same stress earlier (Avramova, 2015), a mechanism that increases fitness through a better acclimation and adaptation to changing environmental conditions. Recent evidence points to a balance between H3K4me3 and H3K27me3 levels as the epigenetic basis for stress memory.

The final chapters focus on the initiation of meiosis and the establishment of the haploid gametophytic phase, a developmental phase transition where significant cellular reprogramming mediated by chromatin modifications occurs. The case of the female gametophyte together with the large-scale chromatin changes in the spore mother cell and the female gametes are reviewed by Baroux and Autran (Baroux and Autran, 2015). This includes heterochromatin reorganization, deposition and removal of histone modifications and nucleosome remodeling, and what is the participation of small RNAs in epigenetic modifications. Likewise, establishment and growth of the male gametophyte, reviewed by Borg and Berger (Borg and Berger, 2015) is also associated with drastic chromatin changes. The vegetative cell nucleus and the two sperm nuclei undergo specific changes in histone variants and modifications that play crucial roles in the male gametophyte biology. Quite interestingly, they are responsible for a sophisticated functional connection between the vegetative and the sperm nuclei to shut off expression of transposon elements in the sperm but also, most likely, to up- or down-modulate the expression of other genes before and after fertilization.

It is clear that chromatin organization and function is at the basis of all developmental transitions in plants and their response to the environment, which we have tried to cover in this Special Issue. There are of course topics that have not been included here due to space limitations but could probably be considered in the future. In any case, a deep understanding of the molecular basis of these chromatin modifications is of particular relevance, also because their potential impact not only in plants but also in other multicellular organisms that share many of these processes highly conserved in evolution. However, it must be emphasized that basic studies on chromatin complexes, their molecular nature and interactions, histone modifications throughout development, among others, also need to receive strong support in the future if we are to aim at applying this knowledge to biotechnological purposes. The changing environment is one of the major challenges to plant development and growth, which has direct influence on crop yield and tremendous consequences on the feeding

of mankind. *The Plant Journal* is willing to receive and publish articles describing major finding in this research area that should prove crucial in providing a rationale for manipulating chromatin-related responses to plant growth and development.

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