

Stress-induced structural changes in plant chromatin

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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.

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Introduction

Eukaryotes are distinguished from archaee 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

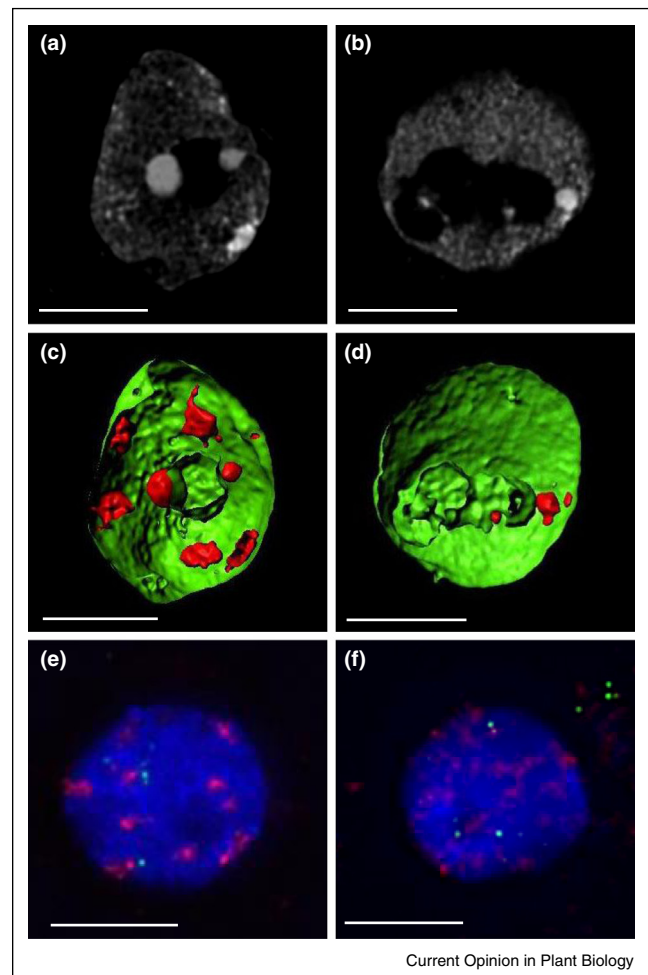
The number, organization, and position of chromocenters in *Arabidopsis* nuclei varies with ploidy [20], cell type [12,21], between accessions [22], and can be affected in plants lacking chromatin modifiers or remodelers [23,24]. Furthermore, specific developmental phase transitions, which require important 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



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 μ m. 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

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