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Review

Plant responses to abiotic stress: The chromatin context of transcriptional regulation

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ABSTRACT

The ability of plants to cope with abiotic environmental stresses such as drought, salinity, heat, cold or flooding relies on flexible mechanisms for re-programming gene expression. Over recent years it has become apparent that transcriptional regulation needs to be understood within its structural context. Chromatin, the assembly of DNA with histone proteins, generates a local higher-order structure that impacts on the accessibility and effectiveness of the transcriptional machinery, as well as providing a hub for multiple protein interactions. Several studies have shown that chromatin features such as histone variants and post-translational histone modifications are altered by environmental stress, and they could therefore be primary stress targets that initiate transcriptional stress responses. Alternatively, they could act downstream of stress-induced transcription factors as an integral part of transcriptional activity. A few experimental studies have addressed this 'chicken-and-egg' problem in plants and other systems, but to date the causal relationship between dynamic chromatin changes and transcriptional responses under stress is still unclear. In this review we have collated the existing information on concurrent epigenetic and transcriptional responses of plants to abiotic stress, and we have assessed the evidence using a simple theoretical framework of causality scenarios.

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1. Introduction

Plants experience an ever changing environment, ranging from fast fluctuations of light and humidity caused by clouds, wind or rain, to larger diurnal and seasonal changes in temperature, light, rainfall and nutrient availability. In some environments plants have to deal with extreme conditions of permanent or frequent nature, whereas in other environments serious stress only occurs sporadically and therefore does not provide evolutionary pressure for permanent adaptations. Nevertheless plants need to have a safety net in place to deal with occasional stress events. Flexibility is an essential requirement for surviving stress at a sedentary life style. Plants maintain this flexibility by operating a signal-response network that allows them to rapidly re-programme their development, physiology and metabolism in response to environmental stress [1,2]. The ability of plants to perceive and integrate an enormous amount of environmental information and to respond to any given situation in an *ad hoc* manner has often led to comparisons with intelligent behaviour of animals, although in the absence of a central brain, the regulatory circuits that generate adaptive responses in plants differ considerably from those in animals [3]. What is common to adaptive responses in all life forms is that they depend to a large extent on dynamic changes in gene expression.

Transcriptional responses of plants to environmental stress factors have been investigated extensively over the last decades, from genome-wide transcript profiling under multiple stress combinations to the unravelling of specific signalling pathways and the identification of individual regulatory proteins and their targets. The research has generated a large body of detailed information on how plants respond to abiotic stresses such as cold, heat, drought, salinity or flooding [4–9]. The knowledge gained has already been used to improve crop resilience, e.g. through stress-inducible up-regulation of transgenes encoding enzymes that produce stress protectants or their regulators [10]. Over recent years scientists have become increasingly aware of the fact that transcriptional regulation cannot be fully understood unless we consider the structural context in which it occurs. DNA is assembled with histone proteins to form chromatin, which enables a higher order structure. Chromatin provides a means to stabilise and condense DNA but it is much more than a packaging device; it is dynamic and can be altered by developmental or environmental stimuli [11–16]. It is often assumed that environmentally induced changes in chromatin status control, or at least modify, transcriptional responses

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but this notion is still built on relatively spare evidence. In this review we have tried to collate and to assess the existing information that links epigenetic processes with transcriptional responses of plants to abiotic stress.

1.1. Chromatin structure – setting the scene

DNA is wrapped around protein units called nucleosomes. Each nucleosome is an octamer composed of two copies of histones H2A, H2B, H3, and H4, which associates with approximately 146 bp of DNA [17]. H1 is associated with the linker DNA between nucleosomes (30–100 bp), and causes further compaction [18,19]. While this overall arrangement is ubiquitous its exact composition and structure can change, both locally and temporally [20]. The chromatin status determines the accessibility and effectiveness of the transcriptional machinery (polymerases and regulatory proteins), and therefore chromatin remodelling is a potential means to control gene expression. The basic molecular processes underpinning chromatin dynamics are (1) the exchange of histone variants, (2) DNA-methylation and (3) histone modifications. The fact that these processes impact on gene expression, and hence on the phenotype of a plant, without altering the genetic code, has led to their general association with the term 'epigenetics', although some scientists argue that this term should be reserved to heritable phenomena.

1.1.1. Histone variants

Each histone type is represented by a number of variants with small differences in amino acid sequence and structure. Histone variants differ in their affinity for DNA and for histone binding proteins, and therefore replacement of one histone variant by another could alter compaction status and recruitment of regulatory protein complexes. The H3 variants H3.1 and H3.3 of *Arabidopsis* differ only in four amino acids [21], yet they are associated with different parts of the genome [22]. While H3.1 correlates with silenced genomic regions, H3.3 preferentially occurs in regions of active gene transcription and rapid nucleosome turnover [23–25]. Replacement of H3.1 by H3.3 accompanies important processes such as developmental re-reprogramming [26]. Similarly, the H2A variant H2AZ replaces H2AX in genome regions with active transcription [27]. Another H2A variant, H2AW, functions in the silencing of heterochromatic sequences [28,29]. The *Arabidopsis* genome also contains three genes encoding variants of the linker histone H1 [30]. H1.1 and H1.2 are most likely products of gene duplication and exist in a stable pool occupying preferentially heterochromatic regions. By contrast, H1.3 is more divergent and has a faster turnover; it shows specific expression in guard cells, and can be induced in other tissues by abiotic stress [31–35]. Stress-dependent deposition of histone variants provides a potential means to link environmental signals to downstream transcriptional responses. Current evidence supporting this paradigm will be reviewed below.

1.1.2. DNA-methylation

DNA-methylation (5-methylcytosine in various sequence contexts) is particularly prominent in the centromeric and pericentromeric regions of the chromosomes that are rich in transposable elements (TEs). Accumulation of DNA-methylation in all cytosine contexts results in highly condensed chromatin (heterochromatin), which prevents transcription thereby silencing TEs [36,37]. The mechanism of silencing through DNA-methylation, involving small RNAs and histone modifications such as H3K9me2 has been investigated in great detail and is reviewed elsewhere [38–42]. Removal of linker histones seems to be required to allow access for the DNA-methylation machinery [30,43].

In the laboratory, certain stress treatments, e.g. prolonged or repeated high temperature, can release silencing of transgenes or TEs, and in some case of neighbouring genes [44]. Vice versa, transcriptional regulation in response to low-phosphate stress of rice has been reported to cause transient hypermethylation of TEs in the vicinity of the stress-induced genes [45]. Furthermore, some DNA-demethylases target TE sequences within the promoters of stress-regulated genes [46]. The question whether stress-induced changes in DNA-methylation status could be heritable and generate a trans-generational memory of stress experience has been a matter of intense research, but remains controversial. In order to progress into the next generation stress-induced changes of DNA-methylation status would need to 'slip' through a very effective resetting process in the germ line [47–49]. Inheritance of re-activated TEs or transgenes into the next generation is therefore a very rare event, although it can be observed in mutants with defects in the processes underpinning resetting, for example the generation of siRNAs [50–52]. Importantly, however, if changes in DNA-methylation patterns are artificially introduced, e.g. through mutations in genes that maintain DNA-methylation, these can be inherited over many generations, even if the original mutant allele is outcrossed. This has allowed the generation of stable epi-RILs and new phenotypic variation [53,54].

The vast majority of transcriptional responses to environmental stress will occur outside the heterochromatic regions in the transcriptionally competent euchromatin, which harbours most genes (Fig. 1). Euchromatin has generally a low level of DNA methylation, although CG DNA methylation occurs within gene bodies of 13.5% *Arabidopsis* genes, and might be an important feature of highly expressed, constitutively active genes [55,56].

1.1.3. Histone modifications

Euchromatin is less compact than heterochromatin and accessible to the transcriptional machinery including polymerases and transcription factors. It is therefore primarily at this level of chromatin organisation that short-term regulation of gene expression occurs. Signalling pathways involving plant hormones such as abscisic acid (ABA), ethylene, jasmonate or brassinosteroids, connect environmental stress perception with activation of transcription factors, which in turn bind to the promoter regions of their target genes and either induce or repress them. This process occurs within the local chromatin context, which potentially provides an additional level of control.

The important dynamic features of euchromatin are post-translational modifications of the histones. The so-called 'histone code' is complex [57,58]; it includes a range of chemical modifications (methylation, acetylation, phosphorylation, ubiquitination) of different residues (mostly lysines and arginines in the N-terminal histone tails) at various levels (e.g. mono-, di- and tri-methylation) and in multiple combinations (e.g. the same residue can be both methylated and phosphorylated) [59–64]. In this review we will employ the usual terminology to label histone modifications, e.g. H3K4me3 standing for histone H3 tri-methylated in lysine 4. Considerable effort has been made to monitor histone modifications in individual genes and genome-wide, and to correlate them with each other and with downstream processes such as transcription, DNA repair and chromatin condensation. Therefore, the majority of studies investigating chromatin processes in relation to transcriptional stress responses have focussed on histone modifications. Before describing these studies in more detail, we will discuss possible causal relationships between signals, chromatin, transcription and responses in order to establish a conceptual framework for assessing and interpreting the empirical evidence.

1.2. Chromatin modifications and transcription - causal scenarios

Considering the importance of chromatin structure for transcriptional competence and transcriptional regulation it is clear that changes in this structure will have effects on processes that require transcriptional re-programming. It is therefore not surprising that mutants that are impaired in crucial processes underpinning chromatin structure will be affected in developmental transitions, such as germination and flowering, or in responses to environmental stresses. However, the