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Review

More than the sum of its parts – How to achieve a specific transcriptional response to abiotic stress

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ABSTRACT

A rapid and appropriate response to stress is key to survival. A major part of plant adaptation to abiotic stresses is regulated at the level of gene expression. The regulatory steps involved in accurate expression of stress related genes need to be tailored to the specific stress for optimal plant performance. Accumulating evidence suggests that there are several processes contributing to signalling specificity: post-translational activation and selective nuclear import of transcription factors, regulation of DNA accessibility by chromatin modifying and remodelling enzymes, and cooperation between two or more response elements in a stress-responsive promoter. These mechanisms should not be viewed as independent events, instead the nuclear DNA is in a complex landscape where many proteins interact, compete, and regulate each other. Hence future studies should consider an integrated view of gene regulation composed of numerous chromatin associated proteins in addition to transcription factors. Although most studies have focused on a single regulatory mechanism, it is more likely the combined actions of several mechanisms that provide a stress specific output. In this review recent progress in abiotic stress signalling is discussed with emphasis on possible mechanisms for generating specific responses.

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1. Introduction

Due to their sessile lifestyle plants are constantly confronted with unfavourable growth conditions. Extreme temperatures, drought, salinity, air pollutants, or changes in light intensity or quality – commonly referred to as "abiotic stress" – impose constraints on the plant. One of the hallmarks of plant defences against these stresses is a large reprogramming of gene expression through regulation of transcription. The development of microarray technology in the early 2000s led to identification of several hundred to thousands of genes in plants with altered expression in response to abiotic stress [1]. Genes with altered expression during stress are often important for adaptation to stress, and transgenic plants that overexpress such a gene can have increased stress tolerance [2–4].

Both specific and non-specific effects contribute to the mechanisms of damage for each abiotic stress. Examples of specific effects include salt stress, where the toxic Na^+ need to be transported out of the cytoplasm [5]. Another example is ultraviolet-B radiation (UV-B, 280–320 nm) which causes formation of cyclobutane pyrimidine dimers in DNA, a damage which can be repaired by DNA photolyases [6]. In addition to specific effects many stresses share a common mode of action (general effects): salt, drought and cold stress all lead to osmotic stress [3], and most (if not all) stresses lead to transient increase in reactive oxygen species (ROS) and cytosolic Ca^{2+}, and activation of kinase cascades [7–9]. Abiotic stresses also lead to increased concentrations of the stress related hormones salicylic acid (SA), jasmonic acid (JA), abscisic acid (ABA) and ethylene [10–14].

To translate a stress exposure into appropriate changes in gene expression suitable signalling pathways needs to be activated, ultimately ending up with a transcription factor (TF) at the promoter of the gene to be transcribed. Given that a stress is composed of specific and general effects on the plant it could be predicted that a comparison of several different stresses would reveal both specific and universal stress induced transcriptome changes. Indeed, such complex transcriptome changes were first described in yeast [15,16], subsequently meta-analysis of several hundred array experiments found a similar response in *Arabidopsis thaliana* [17–20]. What is the role of a universal stress response? In yeast it is involved in cross-protection, i.e. exposure to one stress increases the resistance to a second, unrelated stress [16]. In plants cross-protection (or cross-tolerance) has long been observed, although the mechanisms involved are still mostly unknown [21,22].

Changes in gene expression can be detected within 15–30 min of an applied stress [19] and can last for several days reflecting a remarkable capacity of the plant to regulate and adjust gene expression. We are still oblivious to many of the regulatory mechanisms integrating and controlling the specific and universal changes in gene expression that every stress induces. Gene specific TFs have long been studied as the executers of transcriptome changes [3]. Some of the mechanisms which can be used to generate a stress specific gene expression response include TF activation and nuclear transport, chromatin remodelling to allow appropriate DNA binding, and response element (RE) specificity. Undoubtedly post transcriptional events including mRNA splicing and stability, small RNA regulation and translation initiation are important as well to generate a specific response, for these mechanisms the reader is referred to a recent review [23]. This review focus mainly on *Arabidopsis*, but examples from other species will be used to illustrate key concepts.

2. Transcription factor activation and transport

TFs can be broadly classified into general TFs (transcription initiation complex) and gene specific TFs. The general TF complex is required to activate RNA polymerase II and transcription of genes. However, this complex has received relatively little attention in plants. Instead most focus has been directed towards studies on gene specific TFs which regulate several processes in plants including development and stress responses. To achieve specificity in abiotic stress responses, a specific TF should bind only to genes whose transcription is required for adaptation to that particular stress. The first step in gene regulation is to activate the TF through post-translational modification and/or import of the TF to the nucleus. Post-translational modifications of TFs include redox modification, proteolytic activation, protection from degradation, and phosphorylation (Table 1).

2.1. General and gene specific transcription factors

Transcription is initiated by the activation of RNA polymerase II at the transcription start site. General TF complexes bind to core promoter elements to form preinitiation complexes, exemplified by the TFIID complex containing a TATA binding protein (TBP) and several TBP-associated factors [24,25]. Our knowledge of these complexes is almost completely derived from non-plant species. However, components of the TFIID complex appear conserved across species, including *Arabidopsis*. Furthermore, protein interaction studies indicate a similar structure and function of the complex in plants [25]. Most studies in plants have instead focused on gene specific TFs, which bind to more upstream promoter elements and regulate genes in a specific context, for example development and stress. A TF typically contains at least two different domains – a DNA binding domain and a transcriptional activation or repressor domain. Slightly different classification criteria have been used by different authors in the definition of TFs, thus it was recently estimated that the *Arabidopsis* genome encodes about 2000 TFs, corresponding to 7% of the genes in this species [26]. This high number could contribute to strict control of transcription through regulated TF activation and location. Since protein synthesis takes place in the cytosol, in principle all TFs could be regulated by restricting access to the nucleus [27]. However, direct regulation of TF subcellular localization has only been demonstrated for relatively few TFs in response to abiotic stress. A frequent observation in genome-wide expression analysis is that many genes with rapid changes in gene expression after abiotic stress treatments encode TFs [19,20]. Therefore, gene specific TFs can be divided into two classes, early acting TFs have a role in the immediate response and are regulated through post-translational mechanisms. The early TFs increase the expression of a second class of TFs with a role in later and prolonged stress responses. A variety of post-translational modifications are used to activate TFs; these modifications should be rapid and target specific amino acids or amino acid motifs to provide specificity.

2.2. Regulation of transcription factors through redox modification

Cysteine residues in proteins provide a rich target for modification by a variety of oxidant molecules including ROS and nitric oxide, and reduction through enzymatic mechanisms [28]. The NPR1 (NONEXPRESSOR OF PATHOGENESIS-RELATED (PR) GENES1) protein provides protection against many biotic stresses; it is an essential regulator of many SA inducible genes and of systemic acquired resistance. In addition NPR1 is also a signalling component of abiotic stress responses, for example signalling induced by the air pollutant ozone [29]. Direct targets of NPR1 include several TGA class bZIP TFs that regulate responses to both biotic and abiotic stresses [30]. Localization, activation and interaction of NPR1 with TGA TFs are regulated through redox changes and protein–protein interactions. In non-stressed plant cells NPR1 is maintained in the