

Molecular responses of plant cells to UV-B radiation

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Abstract. UV-B radiation (UV-B: 280-320 nm) can cause a wide range of responses in plant cells. These responses depend on the perception of the UV-B radiation, signal transduction mechanisms and modification of gene expression. Studies over the last ten years have revealed a complex molecular response of plant cells to UV-B radiation. Specific changes in gene activity take place and a number of signal transduction pathways are established. In addition, other environmental parameters strongly influence the UV-B-induced response. Although molecular studies have advanced our knowledge, our understanding of UV-B-induced cellular changes remains limited compared to other areas of plant photobiology/molecular biology.

Introduction

Plants, due to their sessile nature are potentially very susceptible to ultraviolet-B radiation UV-B effects, however, vary among species and varieties of the same species. This variation is largely dependent upon the molecular response of plant cells to implement a UV-B protection mechanism. Light, including ultraviolet-B radiation, is also one of the most important environmental factors controlling plant growth and development. Light provides energy to support photosynthesis and different wavelengths provide environmental cues that modify developmental processes as diverse as de-etiolation, phototropism and flowering. To bring about these changes in development, light must first be perceived by the plant and in turn regulate gene expression through a signal transduction pathway. UV-B radiation is known to change gene expression in plants, both by up-regulation and down-regulation. Genes that encode for enzymes of the phenylpropanoid pathway have been shown to be up-regulated at the transcription level, leading to the biosynthesis of UV-B protecting pigments. Many other defence related genes are also 'switched on' by UV-B radiation. In contrast, many genes associated with photosynthetic proteins (32 kDa PSII protein, *Lhcb*, RuBisco, etc) are down-regulated. This down-regulation could be caused by direct UV-B induced damage to these genes. However, this is much more likely to be a specific response. It therefore appears that UV-B radiation causes a diverse and specific set of responses at the level of gene regulation (for a comprehensive review see Jordan, 1996).

Signal transduction and gene expression

Like other wavelengths, UV-B can act as a signal to induce changes in gene expression at a distance from its origin of perception (Jordan, 1996). This perception mechanism for UV-B must then stimulate a signal transduction system through a series of intermediates that control/regulate the activity of genes. No specific

photoreceptor molecule, however, has been identified that can perceive the UV-B signal. This is made more complex as the UV-B region of the spectrum is strongly absorbed by a wide range of biologically active molecules, such as nucleic acids, aromatic amino acids, lipids and phenolic compounds. Thus a crucial question is how is UV-B perceived and the response generated at the molecular level. In addition, the plant must also translate a number of other signals generated within the environment (different wavelengths of light, temperature, draught, pollutants, etc) or by biotic factors (pathogens, symbionts, etc). The signal transduction pathway(s) must therefore be able to recognise and differentiate between signals and interpret them prior to any response.

We have studied this signal transduction pathway (Mackerness and Jordan, 1999; Mackerness *et al.*, 1999). Reactive oxygen species (ROS) increase in response to UV-B and are an important component in the regulation of both up-regulated and down-regulated genes. The nature and origin of the ROS involved in the early part of UV-B-induced signalling pathways have been investigated in *Arabidopsis thaliana*. The increase in *PR-1* transcript and decrease in *Lhcb* transcript in response to UV-B exposure was shown to be mediated through pathways involving hydrogen peroxide (H_2O_2) derived from superoxide ($O_2^{\bullet-}$). In contrast, the up-regulation of *PDF1.2* transcript was mediated through a pathway involving $O_2^{\bullet-}$ directly. The origins of the ROS were also shown to be distinct and to involve NADPH oxidase and peroxidase(s). The up-regulation of *Chs* by UV-B was not affected by ROS scavengers, but was reduced by inhibitors of nitric oxide synthase (NOS) or NO scavengers. Together these results suggest that UV-B exposure leads to the generation of ROS, from multiple sources, and NO, through increased NOS activity, giving rise to parallel signalling pathways mediating responses of specific genes to UV-B radiation (Fig. 1).

In addition to the increase in ROS other known signal transduction intermediates increase their levels. These include salicylic acid (SA), jasmonic acid (JA) and ethylene. Using *Arabidopsis* mutants that are insensitive to SA, JA and ethylene (*NahG*, *jar 1* and *etr 1-1* respectively), we have demonstrated clear differences in gene activity response. For instance, an increase in expression of the two pathogen-related genes *PR-1* and *PDF1.2* are depended on SA and ethylene or JA and ethylene respectively. In contrast, down-regulation of RNA transcripts for photosynthetic proteins was independent of all three compounds. Furthermore, although ROS is involved in down-regulation of RNA for photosynthetic proteins, the chloroplast signal may not be involved (Jordan *et al.*, 1998). Overall, these results suggest that there are at least three separate signal

transduction pathways involved in UV-B gene regulation and substantial “cross-talk” must take place.

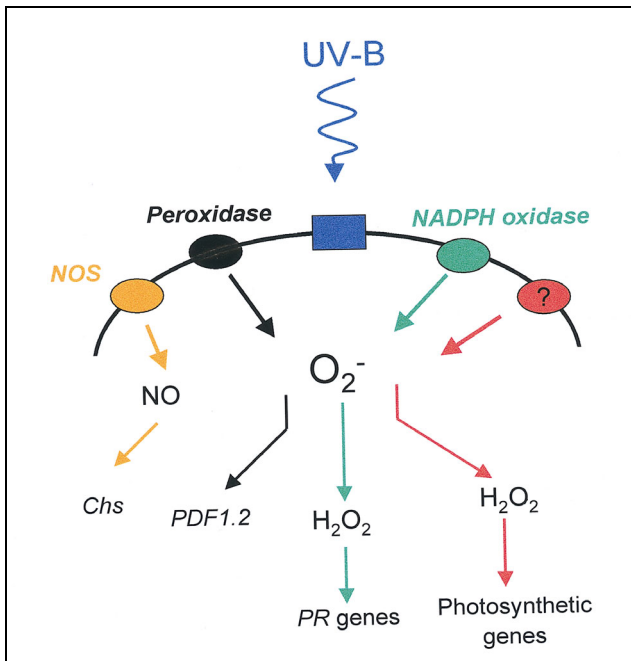


Figure 1: Schematic illustration of signal transduction pathways induced by UV-B radiation (from Mackerness *et al.*, 2001, Fig. 4)

A unique response of plants to UV-B radiation relates to the property of high photosynthetically active radiation (PAR) to ameliorate its damaging impact. The interaction of UV-B and PAR was initially discovered at the physiological level, but Jordan *et al.*, (1992) demonstrated that high PAR also reduced down-regulation of gene expression. This ‘protection’ against UV-B damage did not involve synthesis of protective pigments, but was related to the function of the photosynthetic apparatus itself (Mackerness *et al.*, 1996). The photosynthetic system can act as a photoreceptor (Chow *et al.*, 1990) and specific wavelengths can change chloroplast gene expression (Tullberg *et al.*, 2000). Research conducted by Jordan *et al.*, (1994) on etiolated tissue is also indicative of a strong link between the development of the photosynthetic apparatus and UV-B-induced gene expression. The connections between UV-B radiation and photosynthesis, and the signal transduction pathways that lead to modification of gene expression remain a “black hole” in our knowledge of UV-B-induced responses.

In addition to defence and photosynthesis-related genes, we have also examined the relationship between UV-B induced stress and changes in gene expression with senescence. Our results show, for the first time, that exposure to UV-B can lead to cellular decline through active and regulated processes involving genes associated with natural senescence (John *et al.*, 2000).

In mammalian systems, the UV-inductive response is characterised by activation of several transcription factors, including NF- κ B and AP-1, which lead to subsequent changes in expression of many genes. Over the last

decade, promoter elements and candidate transcription factors have also been identified in plants (Schulze-Lefert *et al.*, 1989; Jenkins *et al.*, 2001; Gittins *et al.*, 2002; Logemann and Halbrock, 2002). Initially two minimal responsive units were identified in parsley protoplasts for light-responsive *chs* transcription (see review in Jordan, 1996). These cis-acting elements are now called ACE (ACGT containing elements that recognise common plant regulatory factors) and MRE (Myb recognition elements). Although some differences exist, consistent structural similarities are found in *chs* promoters between species (Gittins *et al.*, 2002). A number of other UV-B inducible transcription factors have recently been identified (van der Krol *et al.*, 1999; Jin *et al.* 2000). In addition, a novel 11bp GC rich sequence has been identified in the pea *sadA* and *C* genes (Gittins *et al.*, 2002). The *sad* genes are particularly interesting as they are up-regulated rapidly by UV-B and at a relatively low irradiance level. The *sad* genes are also affected by other environmental stress and therefore elements in the promoter must be a point of convergence for multiple environmental signals. This concept is supported by an inversely regulated promoter unit that has recently been identified (Logemann and Halbrock, 2002). This promoter responds positively to UV and negatively to pathogen derived elicitor. This research suggested that this unit could function as a convergence for largely distinct signal pathways and may also operate through common plant regulatory factors. This is another important area that would provide opportunities to increase the understanding of molecular responses to UV-B.

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