Stress Under the Sun: Spotlight on Ultraviolet-B Responses

The UV-B spectral band (280–315 nm) contributes less than 2% of the short-wave photons received by terrestrial organisms in most natural environments. Concerns about potential impacts of stratospheric ozone depletion contributed to spark interest in studies of plant responses to enhanced UV-B levels during the last two decades (Caldwell et al., 2003). In connection with this research, two related questions have attracted increasing attention in recent years: (a) What are the impacts of ambient, present-day levels of UV-B on plant and ecosystem function? And (b), which are the mechanisms that mediate plant responses to solar UV-B?

Regarding impacts of ambient UV-B, two generalizations are beginning to emerge from field experiments carried out in natural and cultivated ecosystems (Fig. 1). First, ambient UV-B at mid latitudes appears to have a measurable (but generally modest) effect reducing plant growth, particularly in the case of herbaceous plants (e.g. Ballaré et al., 1996; Krizek et al., 1998; Mazza et al., 1999a). Second, modification of ambient UV-B levels may have large impacts on the interactions between plants and phytophagous insects (Ballaré et al., 2001; Paul and Gwynn-Jones, 2003). Although there is variation among ecosystems, the most common effect of solar UV-B is increased plant resistance to insects, measured in terms of leaf area consumed and/or insect growth in standard feeding bioassays (Ballaré et al., 1996; Rousseaux et al., 1998; Mazza et al., 1999b; Zavala et al., 2001).

Progress in the understanding of the mechanisms that mediate these effects of ambient UV-B has been slow for various reasons. First, no specific UV-B receptors have yet been identified in plants, and no UV-B-perception mutants are available for comparative studies. Second, most of the information on UV-B effects at the molecular level has been obtained in indoor-exposure experiments, with monochromatic or heavily-unbalanced UV-B sources [i.e. sources that produce unnaturally high UV-B to photosynthetically-active radiation (PAR) ratios]. Under monochromatic UV-B, other photoreceptors can be activated (e.g. the phytochromes) and therefore the results cannot be interpreted as specific UV-B responses. Under conditions of unbalanced light treatments (i.e. high UV-B:PAR ratio), the effects of UV-B on plant growth are often greatly exaggerated. Because no major effects of ambient UV-B on growth rate have been detected under field conditions in any system, the physiological significance of the molecular changes observed under conditions of unbalanced UV-B is unclear. Third, UV-B has the potential to damage key macromolecules and cellular structures, particularly when high doses are used in laboratory studies; therefore, specific UV-B responses are difficult to separate from secondary consequences of generalized damage under these conditions.

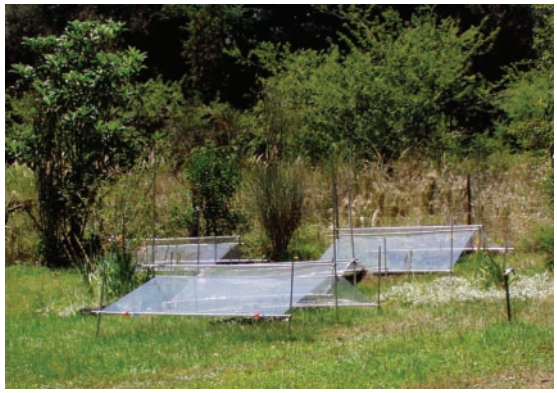

Figure 1. Detail of a field site showing spectral filters used to manipulate the UV environment of plants grown under natural conditions. The site is in the natural area of distribution of *N. longiflora,* near Huerta Grande (Córdoba, Central Argentina). UV-B absorbing and UV-B transparent filters are shown. Because the UV-B absorbing filters selectively attenuate solar UV-B with minimal effects on PAR, phytochrome-absorbable radiation or total energy balance, the setup is ideally suited to detect highly specific effects of solar UV-B radiation.

In this issue, three papers shed new light into the mechanisms that mediate plant responses to solar UV-B radiation.

TRANSCRIPTIONAL PROFILING OF PLANTS EXPOSED TO SOLAR UV-B IN THE FIELD

Casati and Walbot (2003) grew maize (*Zea mays*) plants in California under field conditions and examined the expression responses of c. 2500 genes to solar UV-B using microarray analysis. Plants were grown for various weeks under filters that either had very high transmittance over the whole UV spectrum or selectively attenuated the UV-B component (Fig. 1). The comparison between filtering treatments revealed a significant effect of solar UV-B on the expression of various groups of genes. This effect was particularly clear in an inbred line that, like modern maize varieties, has reduced flavonoid accumulation. Several functional groups of genes were up-regulated by solar UV-B. Among these groups were genes encoding proteins involved in protein translation, proteins of the ubiquitin- and proteasome-dependent pathway, cell cycle regulatory proteins, proteins putatively involved in signal transduction and the control of gene expression, antioxidant enzymes, and several proteins of unknown function. The increased expression of antioxidant genes, such as ascorbate peroxidase, is consis-

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tent with the results of field studies with other monocot species that revealed increases in activity of antioxidant enzymes in response to solar UV-B (Mazza et al., 1999a). Few genes were down-regulated by solar UV-B, a significant exception being genes encoding proteins involved in photosynthesis. This down-regulation is consistent with the results of previous laboratory studies (A.-H.-Mackerness et al., 1996; Sävenstrand et al., 2002) and field experiments with other species (Izaguirre et al., 2003). Taken together, the data of Casati and Walbot (2003) suggest that plant exposure to solar UV-B demands a genome-wide re-adjustment of transcription, which is likely to play a role in the maintenance of physiological homeostasis, minimizing the inhibitory impacts of UV-B on growth rate. Interestingly, the pattern of transcriptional response elicited by solar UV-B in the field had relatively little overlap with the effect of a high-dose UV-B supplementation treatment applied in the greenhouse. The results of this study represent the most comprehensive data set currently available on effects of solar UV-B on plant gene expression. Apart from unraveling UV-B-regulation in genes not previously associated with UV-B responses, these results provide a reference framework that will be most useful to evaluate the possible ecological significance of expression changes detected under conditions of artificial UV-B exposure.

Izaguirre et al. (2003) looked at the transcriptional impact of solar UV-B radiation using a boutique microarray enriched in insect-regulated *Nicotiana attenuata* genes (Halitschke et al., 2003). They tested the hypothesis that the negative impacts of solar UV-B on insect growth and performance are mediated by activation of defense-related mechanisms similar to those activated by insect attack. Plants of *Nicotiana longiflora* (a relative of *N. attenuata* of South American origin), exposed to solar UV-B in their area of natural distribution in central Argentina exhibited significant changes in the expression of insect-regulated genes, compared with plants grown under attenuated UV-B levels. Remarkably, the impacts of UV-B exposure and simulated herbivory on various functional categories of genes were similar in magnitude and direction. A clear convergence was seen for several photosynthesis-related genes, which were down-regulated by both treatments, and for genes involved in fatty-acid metabolism and oxylipin synthesis, which were up-regulated. The results suggest a convergence in UV-B- and insect-induced reorganization of transcription. This convergence is consistent with the similar effects of solar UV-B exposure and insect elicitation on plant resistance to herbivory, which is increased by both treatments.

CONVERGENCE IN UV- AND INSECT-INDUCED SIGNALING

Holley et al. (2003) used tomato (*Lycopersicon peruvianum*) cell suspension cultures to test the hypothesis that the signaling cascades engaged by UV radiation, oligosaccharide elicitors, and systemin (a small peptide hormone involved in wound signaling) share common components. All these stresses induce mitogen-activated protein kinase (MAPK) activity. Reciprocal desensitization assays on the MAPK response suggested that UV-B and these various molecules activate identical signaling components. The authors cloned and sequenced three MAPKs from tomato (LeMPK1–3) based on homology to the two major stress-responsive MAPKs from tobacco (SIPK and WIPK). Using member-specific antibodies and immunocomplex kinase assays, Holley et al. (2003) were able to show that the pathways triggered by UV-B pulses, systemin, and oligosaccharide elicitors overlap at the level of two highly-homologous MAPKs, LeMPK1 and LeMPK2. Interestingly, the kinetics of LeMPK1/2 activation by elicitors and UV-B were different, and UV-B activated an additional MAPK (LeMPK3) not activated by elicitors.

MECHANISMS AND IMPLICATIONS

While the observed convergence between UV- and insect- or systemin- elicitation at the levels of gene expression and MAPK activation in the solanaceous species investigated by Izaguirre et al. (2003) and Holley et al. (2003) may begin to suggest a functional explanation for the effects of solar UV on plant resistance to insects, it is still unclear where this convergence actually takes place. One possibility is that UV-B and the biotic elicitors activate completely different cellular targets (receptors), which engage separate signaling cascades that eventually converge at the level of MAPKs of the type identified by Holley et al. (2003). Another possibility is that the convergence takes place up-stream in the signaling cascade, perhaps at the level of the systemin receptor (SR160; Scheer and Ryan, 2002). This hypothesis has been suggested by Yalamanchili and Stratmann (2002), based on pharmacological experiments with suspension-cultured tomato cells. This is an exciting possibility, particularly in the light of recent evidence suggesting multiple roles of SR160 in the perception of diverse hormonal signals (Montoya et al., 2002). In the tomato system, hydrogen peroxide generated in response to systemin elicitation through a NADPH oxidase is believed to play an important role in the activation of defense-related genes (Orozco-Cárdenas et al., 2001). Activation of a NADPH oxidase by UV has been demonstrated in laboratory studies in Arabidopsis (Rao et al., 1996), and it is most interesting to note that the results of Casati and Walbot (2003) show clear up-regulation of a NADPH oxidase gene by solar UV-B in field-grown plants. Finally, as discussed by Izaguirre et al. (2003), it is also possible that UV-B- and insect-activated signaling cascades have additional points of convergence, at the level of reactive oxygen species generated by diverse mechanisms. UV-B may activate

a variety of molecular sensitizers and give rise to enhanced hydrogen peroxide levels, which may lead to convergence with the wound-induced cascade downstream of NADPH oxidase.

There is a long way ahead before we can piece together a model of how plants acclimate to solar UV-B and how the responses to UV-B interact with those elicited by other stress factors to generate a plant phenotype that maximizes fitness in a complex environment. Studies such as the ones reported in this issue are beginning to reveal the full magnitude of these interactions at the level of gene expression in plants grown under natural conditions. This information will be most valuable at the time of devising genetic tools and stress treatments for the next generation of field experiments, which will provide critical insights into the mechanisms whereby plants perceive and integrate multiple of stress signals.

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