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EDITORIAL

UV-B radiation: "When does the stressor cause stress?"

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Exposure to UV-B radiation can cause stress in plants

Solar UV-B radiation (280 - 315 nm) has long been recognized as being potentially damaging to living organisms. Indeed, the literature on plant UV-B radiation effects has for decades been dominated by reports on UV-B mediated stress, including growth retardation, macroscopic injuries and oxidative damage (Caldwell et al., 1994; Searles et al., 2001). These negative effects comprise damaging effects on genetic material (formation pre-mutagenic cyclobutane pyrimidine dimers [CPD] and pyrimidine [6-4] pyrimidinone dimers), photosynthetic performance (in-tandem degradation of D1-D2 core proteins of photosystem II, inactivation RUBISCO, altered stomatal function) and a range of other cellular targets (see Jansen et al., 1998; Searles et al., 2001; Jordan 2002; Rozema et al., 2005; Jenkins, 2009). In this issue Lidon et al. (2012a) review our current understanding of the deleterious effects of UV-B on photosynthesis. UV-B damage is paralleled by the formation of lipid peroxidation products such as malondialdehyde (MDA) (Hideg et al., 2003; Lidon and Ramalho, 2011) and increased oxidation of antioxidants such as glutathione (Kalbin et al., 1997), both of which reflect the oxidative character of the UV-caused stress conditions. Consistently, UV-induced ROS have been measured using EPR spin trap reporters in both leaves (Hideg and Vass, 1996) and in isolated thylakoids (Lidon et al., 2012b) exposed to high doses of UV-B.

UV-B acclimation

Many studies have failed to find substantial, negative effects when plants are grown for prolonged periods under realistic levels of UV-B (Ballaré et al., 2011). Consistently, in this issue, Costa et al. (2012) conclude that there is no evidence that increases in UV-B influence wheat production. A major factor responsible for this lack of UV-B damage is the capability of plants to acclimate to ambient levels of UV-B. UV-B acclimation refers to the physiological adjustments that generate tolerance to transitory stress conditions. In the case of UV-B exposure, key components of the acclimation response are the increased capability of photorepair and the accumulation of UV-B absorbing flavonoids and other phenolics. These pigments have long been thought to accumulate mostly in the vacuoles of epidermal cells and to protect underlying tissues by absorbing UV-B photons. More recently, it has been argued that the main protective role of these phenolics is associated with their antioxidative capabilities (Agati and Tattini, 2010), and this fits the observation that flavonoids can be found in tissues not directly exposed to UV-B and also in sub-cellular domains as far apart as chloroplasts, vacuoles and nuclei, and roots and leaves. The UV-B induced increase in antioxidative defenses is further demonstrated by increases in both the reduction state and pool-size for antioxidants such as ascorbate, glutathione, xanthophylls, and tocopherol (Jansen et al., 2008). Moreover, numerous studies have reported upregulation of enzymatic antioxidant activities, including Cu or Zn superoxide dismutase (SOD), ascorbate peroxidase (APX), dehydroascorbate reductase (DHR), glutathione peroxidase (GPX), glutathione reductase (GR) and catalase activities (Hideg et al., 2006; Agrawal and Rathore, 2007; Xu et al., 2008). In this issue, Pessoa (2012) further highlights a range of UV-induced biochemical protection responses in algae and aquatic macrophytes. Interestingly, UV-protection appears to be largely dependent on physiological UV-acclimation. Few studies have reported evidence for UV-B driven genetic adaptation. In this issue Biswas and Jansen (2012) report that adaptation of local *Arabidopsis thaliana* accessions comprises the altered regulation of UV acclimation, thus again emphasize the relative importance of induced, physiological processes for UV-B protection.

Is the concept of "UV-B stress" still relevant?

Because of effective acclimation responses, UV-B mediated stress is in many circumstances a *potential* oxidative stress, and most studies report, at most minor, effects on plant growth (Ballaré et al., 2011). This triggers the question whether "UV-B stress" is still a relevant concept. To address this question COST-Action FA0906, UV4Growth, organised a conference to review the roles of antioxidants, pro-oxidants and stress in plant responses to UV-B (Copenhagen, February 2012). Discussions revealed three key areas where the concept of oxidative UV-B stress is particularly relevant.

1) Oxidative UV-B stress and cross-tolerance

All stresses, biotic or abiotic, may cause a degree of oxidative stress. Understanding UV-B mediated stress and stress-defence responses, including ROS formation, activation of molecular targets, and induced antioxidant defences, therefore, has a generic relevance. Indeed, upregulation of antioxidant defences may result in a degree of cross-tolerance towards other stressors. UV-B acclimation has been shown to increase tolerance to, for example, low temperatures (Chalker-Scott and Scott, 2004), and drought (Manetas et al., 1997; Poulson et al., 2006). The reverse is also true, in this issue, Majer and Hideg (2012) show that a high light treatment can protect tobacco against subsequent UV-B exposure, notwithstanding subtle differences in the properties of high light and UV-B induced antioxidative defences. Such cross-tolerances are of particular interests to horticulturists. It is, however, not just the UV-induced upregulation of the antioxidant defence system that plays a part in cross-tolerances, other UV-induced physiological and morphological adjustments are also likely to contribute to such tolerances. Indeed, Kravets et al. (2012) report that both pre-exposures to UV-B or heat can induce UV-tolerance in barley cultivars, and this is linked to the development of complex changes at an anatomical, cytological, physiological level. Despite the relevance and importance of concurrent exposure to enhanced UV-B radiation and other global change factors (water availability, increased temperature, CO2, available nitrogen and altered precipitation), Zlatev et al. (2012) conclude in this issue that such responses are not fully understood so far.

2) UV-B stress as a relevant environmental factor

In general, realistic UV-B studies tend to show no negative impacts of UV-B radiation on plant growth (Ballaré et al., 2011). However, a number of field-based studies have shown that UV-B can cause stress under realistic conditions, especially when plants are simultaneously challenged by other environmental conditions, such as extreme climatic conditions of the polar zones, nutrient deficiencies or drought (Albert et al., 2010; Lau et al., 2006; Belnap et al., 2008). In this issue, Doupis et al. (2012) analyse the responses of grapevines to combinations of drought and UV-B stress, while Reboredo et al. (2012) present data on interactions between CO_2 and UV-B and ABA and UV-B. It appears that simultaneous exposure to multiple stressors can at times overwhelm oxidative defence capacity. This concept of UV-B stress in plants already challenged by another environmental parameter will be particularly relevant for plants growing near the limit of their distribution and/or subjected to changes in climate. Thus, the study of oxidative UV-B stress has clear (but under explored) links to evolutionary plant ecology.

3) UV-B as an exploitable regulator in horticulture

UV-B can induce a range of specific plant responses, some of which are particularly desirable from a horticultural perspective. For example, the potential to increase the content of specific phenolic, terpenoid and alkaloid compounds metabolites with nutraceutical or pharmaceutical value, is recognized as a useful tool for commercial plant manipulation (Jansen et al., 2008; Zhang and Bjorn 2009; Schreiner et al., 2012). UV-B can also increase development of colour in, for example, salad leaves (Park et al., 2007) or fruits (Dong et al., 1995), and control plant disease-tolerance and morphology (Wargent et al., 2006). In this issue, Jug and Rusjan (2012) describe several positive effects of UV-B radiation on grapevine biochemistry and physiology, while Ribeiro et al. (2012) review the use of post-harvest UV-B applications. Some of the reported UV-B responses are known to be mediated by a dedicated UV-B photoreceptor, UVR8, which operates under low UV-B levels (Jenkins 2009; Heijde and Ulm, 2012). Here, Krasylenko et al. (2012) report on the possible involvement of cytoskeleton components in further downstream signaling. Exploitation of the specific, low UV-B effects requires precision manipulation (wavelength selective cladding materials, UV-reflective mulches and/or supplemental UV-B light systems in pre- or post-harvest settings) whereby general, oxidative stress must be avoided. Clearly, a solid understanding of physiological and environmental conditions that cause UV-B stress is required in order to establish a (stress-free) window-of-opportunity for horticultural exploitation.

In summary

During the last decade it has become clear that UV-B mediated stress in plants is a relatively rare event (Ballaré et al., 2011), and emphasis has increasingly shifted towards perception and signaling of low UV-B levels (Jenkins, 2009; Ulm and Heijde, 2012). Paradoxically, this shift has triggered new research questions for those researchers investigating UV-B stress, as there is now a clear need to accurately delineate the conditions that cause UV-B stress. Identifying the environmental conditions where UV-B causes oxidative stress will contribute both to our understanding of the ecological role of UV-B in a changing and/or hostile climate, as well as to the development of horticultural practices that exploit low UV-B effects. The manuscripts in this special issue reflect the various aspects of UV-B stress biology, and result from discussions between researchers at the COST-Action UV*4*Growth network meeting, held in February 2012 in Copenhagen, Denmark.

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