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Editorial: Interactive effects of UV-B radiation in a complex environment☆

This editorial is inspired by discussions that took place during a workshop held in June 2017 at the Global Change Research Institute, in Brno in the Czech Republic. The workshop was organised by Dr Otmar Urban and Prof Marcel Jansen, under the auspices of UV4Plants, the International Association for Plant UV Research (https://www.uv4plants.org/), and focussed on interactive effects of UV-B radiation in a complex environment. Discussions at the workshop revealed both a divergent use of terminology, but also exciting new ideas about the functional role of UV-B sensing in plants. In this editorial, stress-terminology is reviewed with an emphasis on UV-B photobiology and the interactive effects of UV-B with other environmental variables. The scientific contribution of the papers published in this special issue of Plant Physiology and Biochemistry is then explored. The published papers reveal interactive effects of UV-B with a broad range of other environmental variables. This wide range of interactions triggers questions about the functional role of UV-B radiation, and indeed the UV-B photoreceptor UVR8 (UV RESISTANCE LOCUS 8). These questions are discussed in the final section where the function of UVR8 is discussed. This editorial is unlikely to be the "final word" on interactive effects of UV-B radiation in a complex environment, however, it is hoped that the text will stimulate development of "novel hypotheses" about the function of plant UV-sensing.

1. UV-B damage and acclimation

As a consequence of their photosynthetic life-style, plants are unavoidably exposed to solar ultraviolet (UV) radiation. Solar UV-A radiation (315–400 nm) can cause cellular damage, but it also drives acclimation reactions mediated by, amongst others, phototropins and cryptochromes (Verdaguer et al., 2017). Similarly, solar UV-B radiation (280–315 nm) drives a mix of damaging and acclimation responses (Jansen et al., 1998; Klem et al., 2015). Damaging reactions have long been known and include thymine-dimerization and/or inactivation of some reactions of the photosynthetic process (Britt, 1996; Vass, 2012; Jordan et al., 2016). Acclimation responses are, at least partially, mediated by the UV-B photoreceptor UVR8 which controls expression of hundreds of genes (Ulm and Nagy, 2005; Favory et al., 2009), and include changes in plant physiology, biochemical properties and plant architecture. The balance between damaging and acclimation responses depends to a large extent on experimental conditions, such as the UV-dose and the UV-spectrum. However, there is increasing evidence that a whole range of other environmental variables, such as photosynthetically active radiation or temperature, can modulate the balance between UV-damage and acclimation, and some examples will be highlighted in this editorial. Conversely, there is also emerging evidence that UV-exposure may modulate plant responses to these "other" environmental variables. This implies that plant UV-responses are highly relevant in the context of, for example, climate change mitigation and/or priming of crops to increase stress-resistance. The aim of this paper, and indeed this special issue of Plant Biochemistry and Physiology, is to explore these reciprocal interactions between UV-radiation and other environmental variables, and to improve the understanding of plant UV-effects, as well as the functional role of plant UV-sensing.

2. Terminology

Before exploring plant responses to combinations of UV-B and other environmental variables in more detail, it is important to consider the appropriate terminology. Stress biology is a popular field of plant research. But the term stress is often being used in a confusing and sometimes even contradictory way. It is especially important to be clear about the concepts underlying the terminology. While Selye (1973) used originally the term stress to describe the "state of an organism" after exposure to an unfavourable external variable, Levitt (1980) used an analogy with the physical sciences when he referred to the external variable as "stress" and called the resulting effect "strain". Building on early stress-concepts, Lichtenthaler (1996) and others (see Larcher, 1987) used three different parameters: (i) the external variable, termed stressor, (ii) a not-further-defined state of the plant, termed stress, and (iii) the stress response. The stress response can actually be measured whereas the state of stress can only be deduced from the stress response. Whatever terminology is used in stress biology, the basic situation is that a plant is exposed to a non-optimal environment which causes a reaction by the plant. Since plants are sessile, changing plant metabolism is a prime response of plants exposed to ever-changing environmental conditions. This is what Strasser et al. (1999) referred to "as the perpetual state changes in plants approaching harmony with their environment". The response of a plant to environmental conditions has often been presented as an optimum curve whereby the decline of the performance of the plant at the extreme values of the environmental variable is referred to as stress (or strain *sensu* Levitt, 1980). At near optimal environmental conditions, the response of the plant is fully reversible, reflecting the dependence of metabolism on the physicochemical conditions. Yet, when a certain limit is exceeded, the response to an environmental variable can become irreversible, at least for a

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given time period. The latter response was referred to as "plastic strain" by Levitt (1980), in contrast to the "elastic strain" which relates to instantaneously reversible responses. However, whether a given change in the environment causes a decline in the performance of the plant, be it elastic or plastic, is highly species dependent. For example, a liverwort taken out of its humid and shady habitat and transferred to an ordinary garden will suffer stress in an environment which for most plants is actually beneficial. On the other hand, alpine plants survive well in an extreme environment that is hostile for more than 99% of all plant species. Therefore, whether an environmental variable can be called a stressor is conditional, depending amongst others on the dose, the affected species, its developmental stage and the presence of other environmental variables. Therefore, referring to an environmental variable, as e.g. UV-B radiation, *per se* as a stressor, environmental constraint or stress factor is too simplistic and not necessarily correct.

The ability to survive exposure to a stressor is called resistance, which is species dependent. Levitt (1980) referred to resistance as the ability to survive unfavourable conditions, irrespective of the underlying mechanism. To distinguish different mechanisms that underlie resistance, Levitt (1980) used the terms "tolerance" and "avoidance". Resistance whereby an equilibrium is reached between plant cells and the environmental variable is referred to as "true" or "cellular" tolerance. In contrast, avoidance refers to the situation whereby the cell does not experience the stress variable. For example, in a poikilohydric moss or lichen exposed to dry air, cells will dry out almost completely, but the organism will "tolerate" the desiccation and resurrect after watering. On the other hand, cells of a higher plant such as a cactus will typically avoid reaching the same water potential as the dry air and therefore will survive through an "avoidance" mechanism. Avoidance can be achieved through different strategies, such as a water impermeable cuticle, development of a deep-root system, and/or leaf shedding. For sake of completeness, organisms can also "escape" exposure to a stressor through, for example, the phenological timing of growth. The distinction between avoidance and tolerance depends, however, which tissue of the plant is studied. The mesophyll cells in a leaf are mostly screened against UV-B radiation by epidermally located UV screening pigments and, therefore, are protected by an avoidance mechanism. However, if one considers epidermal cells, one should rather speak of tolerance. In contrast, DNA repair by photolyases is always considered a tolerance mechanism since the UV radiation has to reach the DNA for damage to occur. Thus, UV-protection is due to a mixture of tolerance and avoidance, and at the plant level should be referred to as UV-resistance. Nevertheless, many published papers refer to "UV tolerance" notwithstanding that avoidance based on UV-screening pigments is an important component of UV-protection.

If under particular environmental conditions avoidance is not sufficient, a state of stress (also simply referred to as "stress") is induced in a plant. This difficult-to-define-state is often quantified indirectly, through its impacts on physiology, e.g. down regulation of photosynthetic efficiency. If stress continues for a given time it may lead either to an acclimation response of the plant, enhancing its resistance, or to a further deterioration of the stress. While the first condition has been called "good stress" or "eustress", the other condition has been called "bad stress" or "distress" (Hideg et al., 2013). Acclimation responses taking place in a single plant should not be confused with adaptation which is an evolutionary response taking place over several generations. Accordingly, the frequently used term "adaptive response" is somewhat ambiguous and should be interpreted as an acclimation response being adaptive, i.e. improving plant fitness.

Acclimation may occur in response to a single environmental variable, or to multiple co-occurring variables. In the latter case, it is important to consider the terminology that describes the different types of outcomes that can be obtained. In fact, this terminology refers both to acclimation responses as well as stress responses caused by exposure to multiple environmental variables. Changing two environmental variables simultaneously can lead to an effect that is equal to the sum of the effects caused by the two environmental variables changed separately (termed an additive effect; Fig. 1). The effect on the plant of simultaneous exposure to two different environmental variables can be larger than the sum of the effects of separate changes of the same variables and this is referred to as a synergistic effect. A special case of a synergistic response is where both variables changed separately have no effect on the plant, but their combined change leads to a significant plant response. Finally, the effect obtained when changing two simultaneous environmental variables for the plant can be smaller than the sum of the effects after separate exposures to these environmental variables. In this last case, the effect is said to be antagonistic (Fig. 1). In this scenario the responses to two variables may even cancel each other out completely. Classifying plant responses to two or more environmental variables can create a conceptual framework for our understanding of these physiological adjustments. However, in practice there will be a continuum of plant responses, the classification of which will

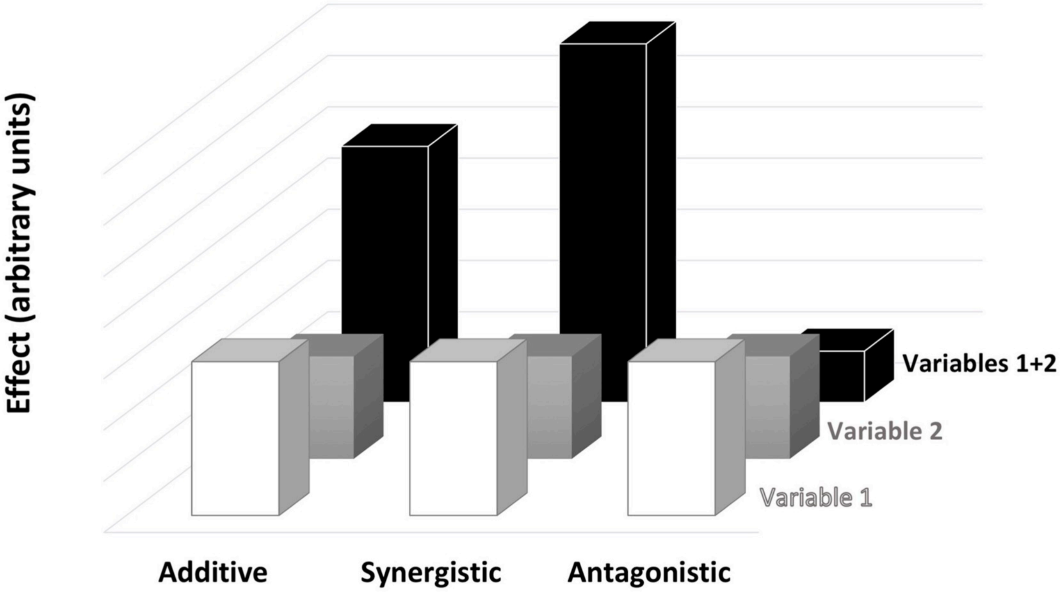

Fig. 1. *Interaction of two environmental variables.* Histogram showing the three general types of interaction between two types of environmental variables and their combined effect on the plant: additive, synergistic and antagonistic effects.

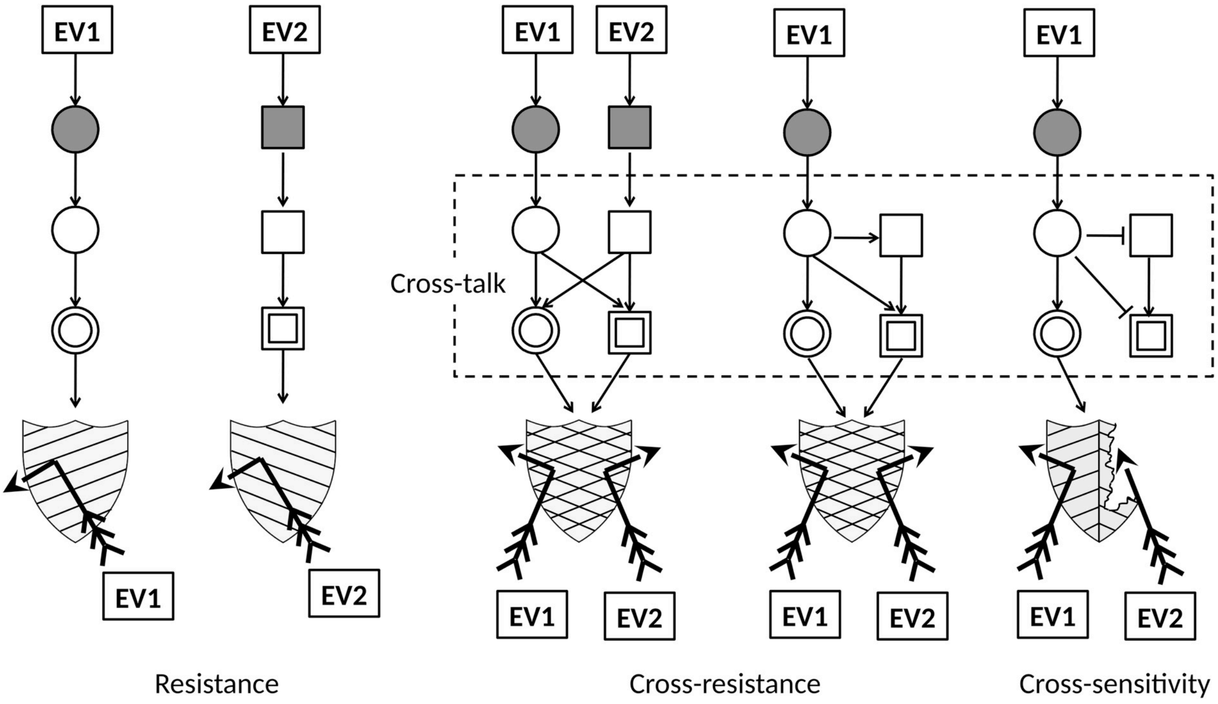

Fig. 2. *Possible responses to single or combined environmental variables*. Rectangles at the top of the diagram indicate different environmental variables (EVs). Circles and squares symbolize components of plant signalling pathways corresponding to the two different environmental variables (EV1 and EV2), with simple arrows indicating the flow and nature of information. Shields represent protective responses against the impact of environmental variables (EVs) indicated as feathered arrows.

be determined to some extent on both quantification procedures and data analysis.

Acclimation responses can sometimes induce either cross-resistance or cross-sensitivity as illustrated in Fig. 2. Cross-resistance refers to the situation whereby a cell or organism that has gained protection against one environmental variable has become also more tolerant towards another variable. The literature often refers to cross-tolerance, although in many cases cross-resistance is a more appropriate term (see above). *Sensu stricto*, cross-tolerance does only refer to cross-protection whereby the cell does still experience the second environmental variable. Induced cross-sensitivity refers to the situation whereby a cell that has been exposed to one environmental variable becomes more sensitive to a second variable. Induced cross-resistance may be achieved where one of the environmental variables primes the plant stress-defences to another variable. For example, in the case of the simultaneous exposure to two unfavourable environmental variables, the dose of each variable will determine the relative oxidative pressure that is exerted on the plant, and therefore it can be anticipated that small changes in the dose of each variable may have dramatic effects on the outcome for the plant (i.e. cross-sensitivity or cross-resistance). Accordingly, pre-acclimation to one environmental variable may already induce the cross-resistance to the second environmental variable, prior to the plant's exposure, a finding that has substantial potential for application in industry, especially in horticulture (Wargent et al., 2011). An example of cross-resistance is that leaf flavonoids induced in response to UV radiation, via the UVR8 photoreceptor mediated pathway, were shown to increase resistance against the caterpillar *Pieris brassicae* and the aphid *Myzus persicae* in broccoli (*Brassica oleracea*; Mewis et al., 2012). An example of induced cross-sensitivity is that the increased synthesis of the phytohormone ABA induced by drought or low temperature resulted in increased sensitivity to pathogens (Fujita et al., 2006). Another example of cross sensitivity is the low temperature-induced loss of the protective mechanism that shields photosystem I from high irradiance oxidative damage, resulting in deleterious effects caused by relatively low photosynthetically active radiation (PAR; Sonoike, 1996).

Analysing the mechanistic aspects underlying interactions between different environmental variables further emphasises the complexity of multifactorial studies. The concepts of cross-resistance and cross-sensitivity can in some cases be linked to the concept of cross-talk (Ramegowda et al., 2015). Cross-talk is a mechanistic concept that refers to interactions whereby two streams of information (signalling pathways) influence each other. Acclimation to an environmental variable is mediated by plant signalling pathways that transmit information from receptor systems to effectors, and involve a variety of chemical and/or electrical signals. Fig. 2 is a schematic representation of possible interactions between responses induced by multiple environmental variables. Activation of one response pathway may affect how the plant reacts to another variable via cross-talk between signalling pathways. Such interaction is rarely at the level of primary receptors and is more commonly realized using downstream components of the signalling pathways at the level of regulation of gene expression, proteins, or metabolites. In fact, the further down in the signalling cascade from genes to metabolites the more the responses to different environmental variables overlap, creating scope for cross-talk. For example, various biotic and abiotic variables lead to increased ROS (Reactive Oxygen Species) production and responses to these include mitogen-activated protein kinase (MAPK) pathways leading to activation of antioxidants (Scandalios, 2005).

Cross-talk between two signalling pathways (Fig. 2) may be realized when both environmental variables are present at the same time, for example as in the case of co-occurring UV and high irradiance PAR. Cross-talk may also take place, when one environmental variable is present alone and influences two signalling chains. Interactions can be stimulatory or inhibitory (Fig. 1), can involve shared components of different signalling pathways (i.e. COP1 is involved in both UVR8 and CRY signalling), as well as phosphorylation-events catalysed by MAP-kinases, and can even occur post-translationally. Cross-talk is important, common, and may ultimately result in outcomes such as cross-resistance or cross-sensitivity. Priming is a special case of induced cross-resistance. Priming refers to a process whereby an environmental variable enhances the speed of response to a later exposure to the same or a different environmental variable (Savvides et al., 2016).

The depictions (Figs. 1 and 2) on plant responses to the simultaneous exposure to multiple environmental variables are highly simplified. One complicating factor is that responses to a single environmental variable may be either positive or negative, depending on the duration and the intensity of the variable as well as on the physiological condition of the plant (Lichtenthaler, 1996). Thus, whilst UV-B may enhance plant antioxidant responses at low doses, high doses can have the opposite effect (Sztatelman et al., 2015). Distinct effects of low and high doses of UV-B may be related to different perception pathways (UVR8 vs damage-mediated signalling) and, thus, full dose-response curves are required for all environmental variables in order to understand interactions between UV-B and other environmental variables (Hideg et al., 2013). Previous studies have also shown that simultaneous exposure to two stressors can have a different effect on plants compared to sequential exposure to first one, and then another stressor (Hideg et al., 2003; Bandurska et al., 2012). Thus, interactions between multiple environmental variables are highly conditional, and exposure sequences need to be considered. The combination of multiple exposure regimes, together with outcomes ranging from additive, synergistic or antagonistic effects on cross-resistance or cross-sensitivity, underline that plant responses to environmental change can be highly complex. This complexity has not yet been appropriately studied in the case of plant UV-effects. Meta-analysis approaches can potentially elucidate patterns in the responses of plants to multiple environmental variables. However, it remains to be seen whether enough data is available in the literature to facilitate such an approach. Therefore, there is also a need for further multifactorial UV-B exposure studies whereby plants are simultaneously or sequentially exposed to UV-B and other environmental variables, and plant responses are measured at all organisation levels.

3. Co-occurrence of stressors

In their natural environment, plants are exposed to a multitude of abiotic and biotic environmental conditions (Mittler, 2006). Some of these environmental conditions may be in a range where they are unfavourable for growth, and can be defined as plant stressors. While in the laboratory any combination of biotic and abiotic stressors is possible, the co-occurrence of abiotic stressors in the natural environment is heavily influenced by diurnal, seasonal and climatic conditions. Thus, some combinations of stressors are more likely to occur than others. For example, in the natural environment, high irradiances of UV-B radiation are commonly accompanied by high irradiances of PAR (i.e. risk of photoinhibition), while heat and drought are also likely to be associated with such conditions in many areas, such as Mediterranean regions of the Northern hemisphere (Urban et al., 2012; Verdaguer et al., 2018), North Africa or Australia (Bornman et al., 2015). At lower latitudes, extended lack of rain is likely to be coupled to high UV-B irradiances, although the opposite is not necessarily true, i.e., high UV-B irradiance can also prevail in the presence of sufficient water supply (Krause et al., 2004). On a global scale, latitudinal gradients of temperature, global radiation and UV-radiation all show decreases with increasing latitude. Close, positive correlations have been found to occur between global radiation and UV radiation, across latitudinal gradients (e.g. Castagna et al., 2017). Indeed, since UV-B and PAR are both parts of the solar spectrum, the daily doses of these two wavelength-bands are strongly correlated to each other, with relative amounts being mainly determined by the solar angle and aerosol concentration. Nevertheless, the global ratio between PAR and UV-B irradiances is not constant. In particular, at low zenith angles UV-B radiation is more strongly decreased by the passage of the solar radiation through the atmosphere than PAR.

Positive associations between UV-B, PAR, temperature and drought exposure can also be seen in an evolutionary context. The earliest plants that emerged from an aquatic lifestyle and colonised the terrestrial environment in the Silurian would have faced simultaneously higher UV-B and PAR irradiance as well as a relative lack of water and temperature control once on land. Thus, it can be argued that simultaneous exposure to multiple unfavourable environmental variables has been important throughout plant evolution, and cross-resistance, and crosstalk would have been adaptive from early land plants and onwards.

4. In this special issue

As discussed in the preceding sections, there is a strong, existing framework of stress-terminology that can encapsulate the different outcomes of exposure to multiple changing environmental variables (i.e. see Figs. 1 and 2). Theoretically, UV-B can amplify, nullify or antagonise responses to other environmental variables, and *vice versa*, possibly involving crosstalk, and/or resulting in cross-resistance or cross-sensitivity. It is likely that small changes in environmental conditions can affect these outcomes. Indeed, long term, outdoor UV-exposure studies in Abisko have shown that UV-B induced stem elongation of *Vaccinium myrtillus* and *Vaccinium uliginosum* varies dramatically from one year to the next, presumably due to interactions of UV-B responses with those to other environmental variables (Phoenix et al., 2000). Unlike the realistic field studies in Abisko, many of the "stress-interaction" studies published in the last decade involve plants kept under near-optimal conditions of temperature, water supply, and fertilization in glasshouses or growth rooms, where they were exposed to supplemental UV radiation in combination with just one experimentally changed environmental variable. Such a simplification decreases the environmental relevance of studies, but facilitates analysis of plant responses, and will hopefully facilitate understanding of why similar, but not identical, exposures to two environmental variables can cause cross-tolerance in one study but cross-sensitivity in another.

Thus far, most studies on the interaction of UV-B and other environmental variables have focused on the interaction between UV-B and drought. For example, a recent study by Robson et al. (2015) showed that UV-B pre-exposure induced drought tolerance in silver birch (*Betula pendula*). However, research by Bandurska et al. (2012) on barley (*Hordeum vulgare*) seedlings showed that interactions between UV-B and drought are highly complex, depending amongst others on the specific response measured, as well as the tissue studied. In this issue, a paper by Rodríguez-Calzada et al. (2019 THIS SPECIAL ISSUE) reported an additive effect of UV-B and drought on stem elongation and a synergistic increase of the phenolic compound luteolin 6-C-pentoside-8-C-hexoside in Jalapeño pepper (*Capiscum annuum*). Also, in this issue, Mátai et al. (2019 THIS SPECIAL ISSUE) showed that exposure of *Nicotiana benthamiana* plants first to UV-B and subsequently to drought, resulted in an additive increase in the leaf flavonoid index, and in total antioxidant capacity. In contrast, when plants were simultaneously exposed to UV-B and drought, the flavonoid index was synergistically increased, while the increase in the total antioxidant activity was additive. Singlet oxygen scavenging capacity showed an additive increase as well. Responses depended on leaf age: the synergistic flavonoid increase in the two-factor parallel treatment was observed in both mature and younger leaves, additive antioxidant responses were observed in mature leaves only. These examples show that individual studies of drought – UV-B interactions can easily generate contradictory data and emphasize the need for a more global, conceptual framework to understand these interactive plant responses.

Interactive responses to UV-B and low temperatures have also been subject to a small number of studies. In this issue, Schultze and Bilger (2019 THIS SPECIAL ISSUE) showed low temperature-induced epidermal screening in *Arabidopsis thaliana*, and noted that this temperature-induced response can protect plants from UV-radiation under laboratory conditions, thus demonstrating cross-resistance. It will be interesting to determine whether UV-induced epidermal screening can also protect against low temperature induced stress, i.e. whether the observed cross-resistance is reciprocal. Reporting in this issue, Coffey and Jansen (2019 THIS SPECIAL ISSUE) and Pescheck and Bilger (2019 THIS SPECIAL ISSUE) both analysed how seasonal variables, such as air-temperature affect accumulation of UV-screening pigments in *Arabidopsis thaliana* plants grown outdoors. A strong effect of season was detected on both plant morphology and leaf UV-screening pigments, and the effect on the latter was predominantly associated with lower temperatures. Thus, raising the temperature from sub-optimal to optimal results in lower accumulation of UV-screening pigments in Arabidopsis (Schultze and Bilger, 2019 THIS SPECIAL ISSUE; Coffey and Jansen, 2019 THIS SPECIAL ISSUE), potentially causing cross-resistance to photoinhibitory UV. In comparison, no substantial effect of UV on the accumulation of UV-screening pigments was recorded (Coffey and Jansen, 2019 THIS SPECIAL ISSUE; Pescheck and Bilger, 2019 THIS SPECIAL ISSUE). Thus, effects of distinct environmental variables on a plant are not necessarily additive, but can also nullify each other. Remarkably, although the induced accumulation of flavonoids is one of the "classic" plant UV-B responses, interactions with "other" environmental variables can moderate, or completely mask, UV-induced flavonoid accumulation. A particularly challenging (but environmentally relevant) approach to analyzing interactive effects of low temperature is reported on by Solanki et al. (2019 THIS SPECIAL ISSUE), in this issue. The authors analysed variations in light irradiance, temperature and photosynthetic yield in *Vaccinium vitis-idaea* that were either covered by snow, or protruding just above the snow. Higher levels of UV-screening pigments in exposed leaves appeared to partially mitigate photoinhibitory stress caused by the combination of bright light and low temperatures, suggesting a degree of cross-resistance as also reported by Schultze and Bilger (THIS SPECIAL ISSUE), Coffey and Jansen (2019 THIS SPECIAL ISSUE) and Pescheck and Bilger (2019 THIS SPECIAL ISSUE).

Interactions between plant responses to UV-B and elevated temperature have been studied at the level of phenology. Strømme et al. (2019 THIS SPECIAL ISSUE) showed that elevated temperature delayed bud set in *Populus tremula,* while UV-B yielded an earlier bud set. Thus, the UV-B-induced earlier autumnal bud set appears to antagonise the positive effect of global warming and associated longer growing seasons. However, interactions between these two antagonistic variables are complex, as plants were found to become less responsive to the treatments with increasing age. A similar time-dependent change in the interactive response between environmental variables was observed by Urban et al. (2019 THIS SPECIAL ISSUE). These authors report that under realistic field conditions enhanced UV radiation stimulated the positive effect of elevated CO_2 on photosynthesis at the beginning of the vegetation season. However more long term exposure resulted in an antagonistic effect of UV-B whereby UV-B reduced the stimulatory effect of elevated CO_2 on photosynthetic carbon uptake and photochemistry of the European beech (*Fagus sylvatica*) grown in lamellar domes. A stimulatory effect of elevated CO_2 on biomass was also observed by Uchytilová et al. (2019 THIS SPECIAL ISSUE), and reported in this issue. These authors found that both low (below ambient) and high (above ambient) UV-doses reduced the stimulation of biomass production by elevated CO_2. This is an important observation, which goes back to the basics of stress biology, emphasizing the importance of dose-response curves, as there is no reason to assume that responses to particular environmental variable are linearly related to the concentration of that variable. Indeed, in this issue, a paper by Soriano et al. (2019 THIS SPECIAL ISSUE) compared UV-responses of two thalloid liverworts, two leafy liverworts and two mosses, and showed both linear as well as hyperbolic increases in soluble and insoluble UV-absorbing pigments with increasing UV dose, depending on the species. Furthermore, detailed transcriptional profiling shows a complex mixture of damage and stress at one given irradiance level in the moss *Pohlia nutans* (Li et al., 2019 THIS SPECIAL ISSUE). Species specificity was also an important theme in the paper by Holub et al. (2019 THIS SPECIAL ISSUE) who showed that two *Hordeum vulgare* (barley) cultivars displayed different acclimation strategies when exposed to combinations of high PAR and UV-B irradiance, with xanthophylls compensating for lower amounts of phenolic compounds in some genotypes.

Although most studies in this special issue refer to interactions between abiotic environmental variables and UV-B, there is evidence that similar relationships apply to biotic variables and UV-B. For example, Schenke et al. (2019 THIS SPECIAL ISSUE) showed that UV-B and biotic stressors have opposing effects on chalcone synthase (CHS) expression in *Arabidopsis thaliana*. While UV-B enhances CHS activity, the bacterial elicitor flg22 redirects the flow of metabolites towards biological defense compounds such as phytoalexins and lignin. This antagonism at the level of CHS expression is remarkable given the importance of flavonoids in protection against both biotic and abiotic stressors, but may well be part of a reciprocal crosstalk whereby UV-B can attenuate the expression of the flg22 receptor FLS2 (Schenke et al., 2019 THIS SPECIAL ISSUE). Another example of an interface between UV-B and a biotic variable is presented by Váczi et al. (2019 THIS SPECIAL ISSUE), who showed that the photobiont in foliose lichens (*Nephroma arcticum* and *Umbilicaria spodochroa*) is protected against UV-B by a screen of UV absorbing pigments provided by the mycobiont in the upper lichen cortex. Thus, the symbiotic interaction between the two species that make up a lichen extends to UV-B protection.

The studies mentioned above highlight that UV-B can act as a modulator of many distinct plant environment responses. However, outcomes for the plants are variable, and from a human perspective unpredictable. The papers presented in this special issue emphasise the importance of a number of factors that may modulate the responses of plants exposed to two or more changing environmental variables.

- The dose of each of the environmental variables
- The specific plant species used
- The exposure routine, including sequential (pre-) or parallel exposure
- The ontogeny of measured organ or organism
- The plant parameter measured, with antagonistic, additive and synergistic responses seemingly occurring in parallel in the same organism

Much work is needed to further understand interactive stress-responses. The study of interactive effects also requires careful experimental design and planning, sufficient replication and advanced data analysis. Furthermore, rather than correlations between exposure conditions and a particular acclimation response, improved mechanistic understanding of the contribution of interactive UV-B effects at molecular, cellular and physiological levels, to plant resistance is required. Furthermore, there is a need for increased emphasis on detailed multifactorial studies whereby plants are challenged by different irradiances of UV-B and another environmental variable. Such multifactorial experiments can allow modeling of interactions to create a predictive framework for analyzing UV-B effects in a complex environment.

The papers presented in this special issue demonstrate the extensive range of plant environment responses that can be modulated by UV-radiation, as well as conversely, the range of environmental conditions that may alter plant UV-responses. These observations trigger the question of why plants have a UV-sensing capability, when so many other environmental variables are already inducing cross-resistance against UV-radiation. Based on the data presented in this special issue, it could be hypothesized that UV-B sensing has an additional role as the ubiquitous modulator of all plant-environment responses. While this sweeping generalization remains unproven, it triggers important and novel questions about the evolutionary origins, and ecological function of plant UV-B sensing, and suggests that the functional role of UV-B sensing extends well beyond UV-protection.

5. Evolution and the functional role of UVR8

From an evolutionary perspective, UV-B radiation can be regarded as one of the earliest stressors. Oxygenic photosynthesis evolved in the absence of any stratospheric ozone layer and early cyanobacteria, living in water as they did, primarily would have had to balance exposure to PAR with avoidance of the strong UV-B component of the ozone-less atmosphere, possibly by localizing themselves at water depths that precluded UV-B exposure, or by movement between different water depths as the strength of the solar UV component varied.

Although there is at present no proof of any UV-B receptor similar to UVR8 in cyanobacteria (cyanobacteria also lack the COP1 component of the UVR8 signalling pathway, as well as the transcription factor HY5), UV-B-induced synthesis of photoprotectants was observed in *Nostoc commune* (Ehling-Schulz et al., 1997). Also, some species do possess genes for synthesis of flavonoidal protective pigments (such as *CHS* encoding chalcone synthase, the enzyme at the branching point into the flavonoid biosynthesis pathway). Indeed, *Nostoc* has been found to produce isoflavones and its glycosides (Klejdus et al., 2010) and *Arthrospira platensis* contained 4′,5,7-trihydroxyflavone (Goiris et al., 2014). In addition, cyanobacteria and a number of eukaryotic algae contain mycosporine-like amino acids that are considered to protect against UV-B (Llewellyn and Airs, 2010; Gao and Garcia-Pichel, 2011). A number of cyanobacterial species, including *Lyngbya* and *Nostoc*, also contain the UV-induced tryptophan-derived very efficient sunscreen scytonemin (Matsui et al., 2012). Thus, it can be concluded that in these cyanobacterial species UV-B acclimation responses had already evolved, but that this had occurred in the absence of UVR8-mediated UV-B sensing and signalling.

The *Chlorophyceae* (green algae) are the earliest phylogenetic division of the present day *Viridiplantae* kingdom in which UVR8 has been found. Among green algae, UVR8 homologs are found in unicellular species such as *Chlorella variabilis* and *Chlamydomonas reinhardtii,* and in a multicellular *Volvox* species (Fernández et al., 2016). UVR8 homologs have also been found in *Physcomitrella patens* (bryophyte) and in the lycophyte *Selaginella moellendorffii*. No UVR8 homolog has so far been found in the gymnosperms. This might, however, largely be explained by the absence of whole genome sequences (with the exception for *Picea abies*; Nystedt et al., 2013) for gymnosperm species. Also, in *Rhodophyta*, where whole genomes have been sequenced, no UVR8 genes were found. In addition, the absence of any UVR8 homolog in *Glaucophyta*, clearly points to the origin of UVR8 in the aquatic green algae of the *Viridiplantae* kingdom (Fernández et al., 2016) before or during transition of aquatic photosynthetic organisms to become land plants. Cyanobacteria had already developed UV-protective responses in the absence of UVR8, but at the stage of transition from aquatic to terrestrial life high PAR irradiance, heat and drought would have been novel stressors with the capability to negatively impact on plant growth and development (see below). Thus, it is possible that UVR8 from this early point in evolution did develop as a comprehensive regulator of UV protection and perhaps also of photosynthesis.

In plants, UVR8 plays a central role in the UV-B-mediated control of expression of hundreds of genes (Favory et al., 2009). Many of these UVR8-controlled genes are involved in defence responses. UVR8 is active as a photoreceptor in its dimeric form and is monomerized upon absorption of UV quanta. The UVR8 monomer interacts with the COP1 (CONSTITUTIVELY PHOTOMORPHOGENIC 1) E3 ubiquitin ligase to inhibit the ability of the latter to mark the HY5 (ELONGATED HYPOCOTYL 5) transcription factor for degradation. HY5 activates transcription of many of the UV-B-upregulated genes (Jenkins, 2017). *In vitro*, the UVR8 dimer monomerizes within 200 ms after absorption of UV-B (Miyamori et al., 2015) and completely re-dimerizes in its pure form on a timescale of days (Christie et al., 2012; Wu et al., 2012). *In planta*, and thereby in the presence of the RUP1 or RUP2 (REPRESSOR OF UV-B PHOTOMORPHOGENESIS) negative UVR8 signalling regulators, the re-dimerization process is enhanced and occurs in about 30 minutes to 2 hours (Heijde and Ulm, 2012). Thus, there is a large difference in timescale of monomerization and re-dimerization triggering the question how the oligomeric state of UVR8 is actually reflected in the physiology and/or morphology of plants, properties that change on a much slower timescale, ranging from many hours to weeks. In fact, in Arabidopsis plants, Findlay and Jenkins (2016) showed that there appears to be a photo-equilibrium (with some fluctuations) of UVR8 monomer vs. dimer under both controlled conditions and natural daylight, approaching 65% dimerized UVR8 in the latter case. Thus, UVR8 appears not to be particularly good in capturing information on the instantaneous UV-exposure conditions. Also, in mature leaves UV-B screening is possibly sufficient to reduce UVR8 monomerization considerably. Furthermore, the absorption wavelengths of UVR8 itself and the action spectrum of gene expression differs between *in vitro* studies and studies in whole plants. The monomerization of the isolated UVR8 protein and UVR8 in plant extracts peaks at 280 nm (Díaz-Ramos et al., 2018). In intact plants, 290 nm was most effective for monomerization, probably reflecting strong absorption by other biomolecules at shorter wavelengths. However, in the same plants, strictly UVR8-dependent HY5 expression peaked at 300 nm (Díaz-Ramos et al., 2018) rather than at 280 or 290 nm. This indicates additional UV-dependent control of UVR8-induced mechanisms in plants by unknown mechanism(s) and with unknown function.

Therefore, it is not clear what information the balance of the UVR8 oligomeric state actually confers to the plant transcriptional machinery under outdoor conditions. One intriguing possibility is that UVR8 functions as part of the regulatory framework of the cell that operates through the circadian clock. In addition to light absorbed through photoreceptors such as phytochromes and cryptochromes, UV-B in a UVR8-dependent fashion is involved in setting and maintaining the circadian clock (Fehér et al., 2011). This so-called entrainment of the clock is UV-specific. Arabidopsis *uvr8* mutants had an approximate 25 h circadian rhythm, compared with the 24 h rhythm in the wild type plants. Also, the entrainment was COP1-dependent but independent of HY5 (or its HYH homolog). Reciprocally, the circadian clock and its components have the ability to inhibit UV-B-induced expression of a number of genes (Takeuchi et al., 2014). The point of inhibition is downstream of COP1. The role in clock entrainment does suggest that UVR8 mediated signalling has a wide regulatory role in plant cells, most likely extending well beyond regulating plant UV-protection.

Consistently with a role for UVR8-mediated signalling extending beyond “simple” UV-protection, a further intriguing fact about the UVR8 protein is that it is also present in roots (Rizzini et al., 2011) together with the UV sensing proteins ROOT UV-B SENSITIVE (RUS; Tong et al., 2008; Yokawa and Baluska, 2015) for which there are six different genes in Arabidopsis (Leasure et al., 2009). One possible functional role for UV-sensing in roots may be regulation of light escape of roots through an auxin-regulated mechanism (Ge et al., 2010).

6. In conclusion

After establishment of the stratospheric ozone layer, it is doubtful that UV-B has ever posed any real threat to acclimated plants in their natural environment. Whilst UV-B radiation is potentially damaging, a range of protective plant responses effectively nullifies the threat to the plant. The risk of UV-stress seems even less probable when considering that a multitude of other environmental variables is inducing UV-B screening pigments with antioxidant properties in the absence of UV-B radiation. Nevertheless, the UVR8 gene has clung on to the plant genome through evolution. Why is this? It seems that the persistence of UVR8 is inconsistent with a functional role that is limited to UV-protection. This triggers the question what is the contemporary physiological function of both UV-B perception and UVR8? This is of course a question that has not yet been answered but that is of real importance to properly understand plant UV photobiology. One tempting hypothesis is that UV-B, actually, and through UVR8, functions as a proxy signal for other potential stress variables that a plant may encounter in its surroundings. For instance, in arid and semi-arid environments, the first rays of sunlight in the morning, containing low irradiances of UV-B, may be an early signal of heat or drought later in the day. In sub-arctic environments, it may be possible that UV-B can signal an upcoming threat caused by insects that are plentiful at such latitudes in spring and summer, or a potential night frost under a cloudless sky the coming night. The UV-B proxy hypothesis has bearing on the main topic of this editorial; predisposition, tolerance, cross-talk and other definitions of physiological events that plant scientists are happy to use with too low distinction or resolution. This editorial not only emphasises the almost ubiquitous impact of UV radiation on plant responses to other environmental variables, it also sets a novel hypothesis on the functional role of UV-B sensing that is relevant in the context of some of the biggest challenges facing mankind: anthropogenic climate change and the quest for a more sustainable crop-production.

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