■ Report on the discussions at Bled

Importance and direction of current and future plant-UV research

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Background

During the 2nd Network Meeting of UV4Plants at Bled (14th–18th April, 2018) the delegates engaged in a group discussion of prescient questions concerning the future of in plant-UV

Table 7.1: Participants in group discussions at the UV4Plants 2nd Network Meeting in Bled on 17 April 2018 that form the basis of this document.

Molecular Biochemical Physiological: Gareth Jenkins, Filip Vandenbussche, Eleni Tavridou, Marie-Theres Hauser, Wolfgang Bilger, Andreas Albert, Pedro Aphalo, Aneta Bażant, Åke Strid, Katazyna Banas, Gyula Czegeny, Minjie Qian, Susanne Neugart, Yan Yan, Luis Morales, Kristof Csepregi, Marieke Trasser, Arnold Rácz, Andrew O'Hara, Aniko Matai, Neha Rai, Aranza Diaz Ramos, Éva Hideg, Piotr Zglobicki, Justyna Łabuz.
Ecological and Plant Production: Paul Barnes, Marcel Jansen, Marco Santin, Craig Brelsford, Knut Solhaug, Robert Logan, Daniela Festi, Twinkle Solanki, Thais Huarancca Reyes, Antonella Castagna, Maria Hock, Laura Llorens, Eva Rosenqvist, Claudia Rodriguez Hidalgo, Louise Ryan, Lars Olof Björn, Mara Pieriste, Alenka Gaberščik, Tjasa Jug, Mateja Germ, Alexandra Golob, Alistair Seddon, Titta Kotilainen, Javier Martinez-Abaigar, Lorenzo Guglielminetti, Jana Stelzner, Tadeja Trost Sedej, Frauke Pescheck.

research. The discussion group was tasked to identify the most valuable directions for plant UV research to take, and to create a coherent framework for how to move the field forward.

Here, the outcome of these discussions is summarised in sections that follow the composition of discussion groups as ideas taken from a molecular, biochemical and physiological perspective followed by those from an ecological and plant production perspective. In each case, first basic research questions are considered and then applications and methodological considerations are put forward. Finally, some common ground bringing the two perspectives together is discussed, with the aim of solving scaling problems and ways in which the UV4Plants network might be put to good use.

Research in Molecular Biology, Biochemistry and Physiology (discussion led by G. I. Jenkins and F. Vandenbussche)

What are the research priorities that will shape the focus of plant UV-research in a "post-UVR8-discovery research environment"?

1. Investigate signalling independent of UVR8: in three possible directions
    a) Unspecific non-photoreceptor mechanisms induced by UV-B radiation, e.g. via reactive oxygen species (ROS), damage, and class 3 peroxides, hormones such as jasmonic acid (JA) and abscisic acid (ABA) (Jenkins 2009; Vanhaelewyn et al. 2016).
    b) Via another unknown UV-B-specific photoreceptor: e.g. a response at very low fluence rate independent of UVR8; CRY3 (localised to the chloroplasts and mitochondria); retrograde signalling and UV-B response (Tilbrook et al. 2013; Yu et al. 2010).
    c) Distinguish between experiments in which UV-B exposure under controlled conditions is inducing responses and experiments in which uvr8 or other photoreceptor mutants are exposed to natural sunlight. The results of the UV4growth-consortium experiment growing uvr8 mutants across Europe and comparing their gene expression and biochemistry should give answers to this sort of question.

Figure 7.1: Discussions on plant UV research in molecular biology, biochemistry, and physiology led by G.I. Jenkins and F. Vandenbussche (Photo credit: T. M. Robson).

2. Roles/mechanism of UVR8? Spatially separated across on the plant (shoots and roots) and cells (cytosol, cell membranes and vacuoles).
   a) UVR8 could have a role in UV-A signalling because its absorption spectrum extends into the UV-A region and because solar spectrum has much higher irradiance of UV-A than UV-B, which potentially makes even a relatively small response in the UV-A region important. UV-A radiation also penetrates deeper into the leaf than UV-B radiation. How is this affected by hydroxycinnamic acids (HCA) and flavonoid (FLAV) contents? IS the mechanism of UVR* signalling the same in all tissues? What are the roles of cytosolic UVR8 (Bernula et al. 2017; Yin and Ulm 2017)?
   b) Regulation of gene expression by UVR8: What are the roles of those transcription factors recently reported to interact with UVR8? Are there more players in addition to HY5/HYH downstream of UVR8? Is there a complex associated with chromatin (Jenkins 2017; Yin and Ulm 2017)
3. Photoreceptor cross-talk

   We can draw an analogy between perception by plant photoreceptors and perception of light by the human eye: the sum is much more than the single parts. A more holistic approach is required, considering all photoreceptors acting together.
   a) How does HY5 integrate signals from multiple photoreceptors (Gangappa and Botto 2016)?
   b) What is the relative contribution of each different plant photoreceptor to COP1 binding/regulation when plants are exposed to the full spectrum of sunlight (Morales et al. 2012)

4. Upscaling to the natural environment to transfer knowledge beyond *Arabidopsis thaliana*

   This suggestion goes hand in hand with determining typical physiological combinations of UV-B radiation and other stresses (e.g. drought), which will differ on a species-specific basis (Hofmann et al. 2003; Robson et al. 2014). Ecologists and agronomists should give suggestions on which species to tackle with novel techniques such as CRISPR-Cas9 and fast sequencing methods. Options for broadening the species considered

   a) Using different Arabidopsis accessions; e.g. Cape Verde Islands (Cvi-0) accession from a UV-high environment (Botto 2003; Jansen and Biswas 2012).

   b) Finding alternative species to Arabidopsis: using new species (mutants/CRISPR; genome sequencing), note some species have more than one gene for UVR8; crop species potentially originating from the Mediterranean and cultivated over a large latitudinal gradient potentially offer high utility and intra-specific variability in UV response; the response of obligate shade species to UV-B may be very different to species from open-environments like Arabidopsis and will give a different perspective on shade responses (Ballaré and Pierik 2017).

   c) With respect to the CRISPR-Cas9 approach, it is imperative to follow up the state of legislation on CRISPR-generated plants. EU has not yet decided on the limitations; however the Swedish Board of Agriculture has given positive advice (for organisms that do not contain a transgene). It may be worthwhile for the UV4Plants network to look for partners in countries where a decision has already been made: e.g. in Argentina, CRISPR-generated plants are already allowed to be grown outdoors.

   In the end, all of this should lead to a greater number of specific model species/cultivars, well suited for UV-research. Such species preferably have not too many isoforms of enzymes/proteins of interest. For these developments to proceed, we need to define priorities.

   Collaboration between ecologists and molecular biologists is much needed and networks like UV4Plants should be exploited to ensure that this is no longer a problem. To illustrate the sort of approach that is envisaged, we need “molecular informed ecologists” and “ecologically informed molecular physiologists”.

5. For further consideration

   How do we avoid unnecessary overlap? How can we prevent work from being duplicated? How can we communicate effectively whilst prevent parasitizing among groups?

Where are the key areas we need to improve when applying this research to practical questions?

1. Can we better harmonise methodologies to make experiments comparable, and to scale between the lab and the field?

   Improving the uniformity of experimentation appears rather difficult considering the quantity of different experimental set-ups and interests. Field work and laboratory work does not always lend itself to the same techniques, e.g. (1) when harvested samples need to be frozen immediately, fresh-weight determination is not very practical; and (2) repeated recording of flavonoid accumulation in the same leaf by monitoring changes in optical properties, using for instance a Dualex, is difficult to compare with the results of biochemical analysis of a leaf harvested at a single point in time.

However, as the UV4Plants network, we could suggest some guidelines: e.g. on what units to state for specific analyses and measurements, and the best way of normalizing results (per weight/volume/surface area), and under which conditions to use each approach. Some progress has already been made (Aphalo et al. 2012; Neugart 2017), but up-to-date standardisation of molecular and genetic protocols in UV photobiology are absent. Standardizing procedures such as those to produce "dry mass" may be proposed. A protocol paper, like the Julkunen-Tiitto et al. (2014) review of biochemistry methodology that came out of UV4growth, or online guidelines on the UV4Plants website, could be helpful here.

2. Repair machinery and RNA

   It is well known that UV-B damages DNA, and that the thymidine dimers can be repaired by photolyases. But what is the status on RNA? UV radiation can indeed damage RNA (Wurtmann and Wolin 2009), although damage to RNA appears to be less than to DNA (Kundu et al. 2004). Some data on RNA viruses in *Nicotiana* sp. are available. Studies from 1950-1970's on the TMV-RNA virus suggest that its UV-damaged RNA can be repaired by photoreactivation (Bawden and Kleczkowski 1959; Murphy and Gordon 1971). However, until now, true evidence for the mechanism of photorepair of TMV-RNA is missing (Wright and Murphy 1975).

   UV-B induced crosslinking between ribosomal proteins and ribosomes has been shown in maize (Casati 2004), and RNA-crosslinking has been associated with UV-B radiation in peas (Brosché et al. 1999). In the light of new developments enhancing our knowledge of RNA editing (PPR proteins) and RNA breakdown, it may be prescient to revisit this area of research. UV-B radiation and heat stress do not seem to generate transcript profiles that hugely overlap in chaperones, suggesting that any UV-B damage to proteins may be very different from that during heat stress.

3. Within-plant light signalling

   At the moment we do not know how the UV-B signal is propagated within plant tissue. This signal could be mediated through a transportable molecule, or by physical cell to cell contact. Associated with this problem, we often do not know how far light penetrates into plant tissues and thus directly, locally influences signalling. Some recently published data on light piping (mainly red light) in Arabidopsis seedlings (Gelderen et al. 2017), and reviews on (UV) plant tissue optics (Barnes et al. 2015) suggest this is a timely subject (Bailey-Serres et al., 2018). With respect to analysis, experimental methods based on microfibers have been developed in the previous century (Ålenius et al. 1995; Day et al. 1993; Liakoura et al. 2003), but were rarely used thereafter. It is said (Å. Strid personal communication) that Lund University had a device to measure the penetration of radiation into the leaf, but once it was deconstructed it could no longer be rebuilt!

   In addition, a separate way to follow local light-regulated signals is by optogenetics (Kianianmomeni 2015). Here, a photoreceptor-based system is used to drive a visible/detectable output. There is also a suggestion that light sheet microscopy can be used (Lichtenberg et al. 2017).

Figure 7.2: Discussions on plant UV research in ecology and plant production science led by P.W. Barnes (Photo credit: T.M. Robson).

Ecological Research and Plant Production (discussion led by P. Barnes and M. A. K. Jansen)

What are the priorities that will shape the focus of basic plant UV-research in a "post-ozone-depletion world"?

1. How will solar UV-B radiation reaching the ground change in a post-ozone-depletion world?

   Solar UV irradiance will change compared to present in the "post-ozone-depletion world". However, there is considerable uncertainty concerning the direction of the change with both increases and decreases being forecast for different geographical areas depending on, amongst other things, patterns of local cloud cover, which cause spectrally differentiated change in irradiance, particularly with respect to UV-B and UV-A radiation and are strongly influenced by climate change. Thus, unlike "classical" stratospheric ozone-layer depletion of the 1980s, patterns of UV-change will be complex. Understanding of these patterns will be required to facilitate relevant plant UV-research (Bais et al. 2018; Bornman et al. 2015).

2. How will the UV-exposure of plants change and what are the implications?

   The UV exposure of plants in managed and unmanaged systems will also change as climate change shifts the geographical ranges of crops and wild plants. Climate-induced changes in plant phenology and modification of vegetation-land cover will determine UV penetration patterns through canopies. Depending on the situation and species, UV exposures could increase or decrease. Thus, future research needs to explore how both increases and decreases in UV radiation, at exposures and times of year relevant to projected future scenarios, influence plants and ecosystems (Bais et al. 2018). Information about how plants and ecosystems have responded to past changes in UV radiation at different points in Earth's history can also provide important insights here, but a better understanding how to reconstruct solar UV radiation based on proxy records, derived from UV-absorbing compounds in pollen, over geological time is first required ((Jardine et al. 2016) reviewed by (Bais et al. 2018)).

3. How do responses to UV radiation interact with responses to other environmental variables associated with climate change?

   Gaining an understanding of the interactions between UV-radiation and climate change variables (e.g., drought, temperature, carbon dioxide, and other abiotic factors) will be a major goal in the next decade. However, we need to be aware that climate change and UV-radiation both alter the environment in complex ways that are often specific to particular geographical regions (Bais et al. 2018; Bornman et al. 2015). Capturing these interactions and testing their consequences is a very broad and challenging aim, and distinctions need to be made across different organisational levels, including:

   a) Elucidating the interactions between climate change and UV-radiation, and how (1) these affect global meteorological phenomena, (2) co-exposure to these variables affects ecosystems, and (3) co-exposure can affect the physiology, biochemistry and/or molecular biology of individual plants.
   b) Assessing whether new experimental approaches are needed to explore how UV interacts with multiple environmental factors simultaneously.

4. Can we scale the knowledge of UV-responses gained under specific conditions across organisational and temporal scales, and make generalisations among organisms?

   Continuing from the previous point, the plant-UV research community has made major advances in linking molecular, genetic, physiological, biochemical, organismal, and ecosystem-approaches, yet, understanding across organisational and temporal scales is still in its infancy (Paul et al., 2012). Although there is evidence that some patterns are consistent across plant types, particular UV-responses can't yet confidently be attributed to specific functional traits, nor can particular taxonomic and geographic lineages be classified as susceptible or resistant to UV radiation.

   The increasing availability of non-GM mutants in key UV-response genes enables researchers to make advances in scaling across organisational scales (Li et al. 2018). In fact, it can be argued that the plant-UV research community is in a strong position to be a model community (i.e. an example for others) that can generate an integrated vision across multiple organisational levels.

   Our understanding of the relevant time-scales for UV-B responses is improving, but we still struggle to connect a UV-cue with the rate of response or acclimation. Recent research has shown that responses within the day are possible (Barnes et al. 2017) and yet responses over the course of a growing season can often also be interpreted with respect to the UV dose received – these two perspectives need to be reconciled. Much less is understood about the down-regulation of UV responses than about their stimulation and in particular what happens with respect to physiological UV protection at the end of the growing season is poorly understood. The presence of UV-absorbing compounds in senescent tissue and during the early stages of decomposition may continue to mediate the effect of sunlight on photodegradation and associated ecosystem processes. Further research encompassing a range of time periods is needed to reveal the temporal patterns in, and mechanisms that regulate, UV-absorbing compounds through the life and subsequent decomposition of plants, and to apply this knowledge to better model ecosystem processes.

5. Can we establish the role of UV-B photoreceptor-activated responses in an ecological context?

   While great progress has been made in understanding the mechanisms underlying the action of UV-B photoreceptor UVR8 and associated signalling pathways, many gaps remain in clarifying the importance of UVR8's role in ecological contexts and establishing how UV-B specific or more-generic plant UV-perception and response functions are. For instance, do these responses only imply UV-protection or is there a role associated with other seasonal changes such as drought, heat or high-light acclimation, or herbivores, pests and pathogens, coinciding with high UV-B radiation (Ballaré and Austin 2017; Paul et al. 2012)?

   We still need to establish the model of how plants respond to the full range of solar radiation that they receive, which contains different spectral compositions of light. These spectral regions are perceived by multiple photoreceptors which presumably interact allowing a coherent response to be produced. Describing this model will require a better understanding of cross-talk between different signalling pathways that operate following photoreceptor activation (Barnes et al. 2017). This information is needed to obtain a fuller understanding of the ecological function of the UV-B photoreceptor in plants of various growth forms and functional groups inhabiting different types of environments.

Practical Questions: Where can the application of UV research in plant production take us?

There remains understandable scepticism among growers concerning the horticultural applications of UV research. The plant UV-community has been preaching the usefulness of exposing plants in greenhouses and other indoor crops to UV-B for some time, but uptake among growers is very limited.

Research consistently finds that crop UV-exposure increases flavonoids and other desirable secondary metabolites that are considered by nutritionists to be beneficial for human consumers. Recently, the European Union has permitted the use of UV radiation to fortify Vitamin D in mushrooms (Taofiq et al. 2017). Likewise, post-harvest UV-exposure technology is promising in improving colouration and secondary metabolite content. Crop exposure to UV-B radiation can trigger plant defence compounds and responses, decreasing the need to use pesticides and reducing the impact of pests and diseases. These UV-B responses can be useful in crop production and include dwarfed architecture and increased branching, replacing the need for use of plant growth regulators for certain crops (Neugart and Schreiner 2018).

A number of practical and scientific steps need to be taken before we can know whether the use of UV in plant production can become a commercial reality. These include: detailed analysis of the regulatory aspects of crop UV-exposure, as well as health and safety considerations for workers. Greater interaction with legislators is also needed to ensure that rules for the safe use of UV radiation with crops and food are internationally-harmonised and fair. A comprehensive cost-benefit analysis is required.

As part of space-research, where plants need to be grown in either entirely artificial environments without the protection offered by the atmosphere or with respect to theoretical

Figure 7.3: Discussions on plant UV research in ecology and plant production science led by M.A.K. Jansen (Photo credit: T.M. Robson).

extra-terrestrial colonisation of other bodies, there is scope to consider plant responses to all UV-(and shorter)-wavelengths.

Practical Questions: How do we transition the knowledge we have from simple, short, controlled UV-experiments to understand highly-complex natural environments?

The key component of this question is the complexity of scaling between various organisational levels (from the molecule to ecosystem), which inherently requires scaling across spatial and temporal scales. Even though different approaches are available to combine –omics data, there is no reliable way to link this to the physiological change in UV-exposed plants. This point is made worse by the use of different UV-spectra, UV-doses, and exposure kinetics (Aphalo et al. 2012). It is widely acknowledged that we are still struggling to link organisational scales. For example, it is very difficult to extrapolate aspects of gene-regulation to ecologically-relevant scenarios, or to attribute changes in plants under natural conditions to a particular photoreceptor.

A specific gap in our understanding is how to develop the knowledge we have of plant UV-responses obtained using stable "low PAR" growth chambers, and make the transition to highly-dynamic, high-PAR outdoor environments (Coffey et al. 2017; Morales et al. 2012).

Challenges and possible solutions:

1. The UV4Plants network could play a role in facilitating large-scale experiments whereby UV-mutants are tested across multiple sites with different UV-regimes (latitudes and elevations). This sort of experiment could be a way to decrease void between organisational levels.

2. Imaginative meta-analysis could be a way to combine, contrast and connect disparate datasets referring to different organisational levels.

3. Techniques can be used or developed in remote sensing to assess plant and vegetation responses to UV radiation at the regional scale i.e., we can remotely-sense flavonoid levels in leaves in complex canopies (Gitelson and Solovchenko 2018). Recently, these techniques have been tested in Antarctica (Turner et al. 2018) and in the tropics (Asner and Martin 2016).

4. A greater quantitative understanding of how UV-driven processes, such as photodegradation, influence biogeochemistry and carbon storage/cycling at large spatial and temporal scales is desperately needed to understand important feedbacks in the climate system that involve UV radiation.

5. Significant gaps in knowledge still exist in understanding how UV mediates species interactions (e.g., plant-plant; plant-insect; plant-pathogen) and how these interactions will be influenced by climate change as plants encounter novel suites of interacting species as a result of species migrations, biodiversity loss and species invasions. Understanding how UV influences belowground processes and interactions with soil organisms is still minimal.

6. As the climate continues to change, does UV play any role in influencing species migrations (e.g., to higher elevations in mountains) and are invasive species more or less sensitive to UV than native species (Václavík et al. 2017).

Interdisciplinarity: What do we want from molecular biologists, physiologists and biochemists?

A key requirement is better knowledge of those regulatory processes that occur in a UV-exposed plant. There is a great demand for more non-GM mutants, disabled in key UV-responses, for testing under natural/outdoor conditions. Furthermore, there is a strong interest in having mutants in species other than Arabidopsis. While ecotypes of Arabidopsis exist, this species does not encompass the range of functions, adaptations, growth forms and physiology displayed by higher plants. Because of the strong site-specific evolutionary pressures that occur in nature, no single model plant species exists for ecological UV research. It would be best to focus on several plant species that represent the breadth of plant functional types (e.g., using Grime's CSR or other recent functional analyses of plants as selection criteria).

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