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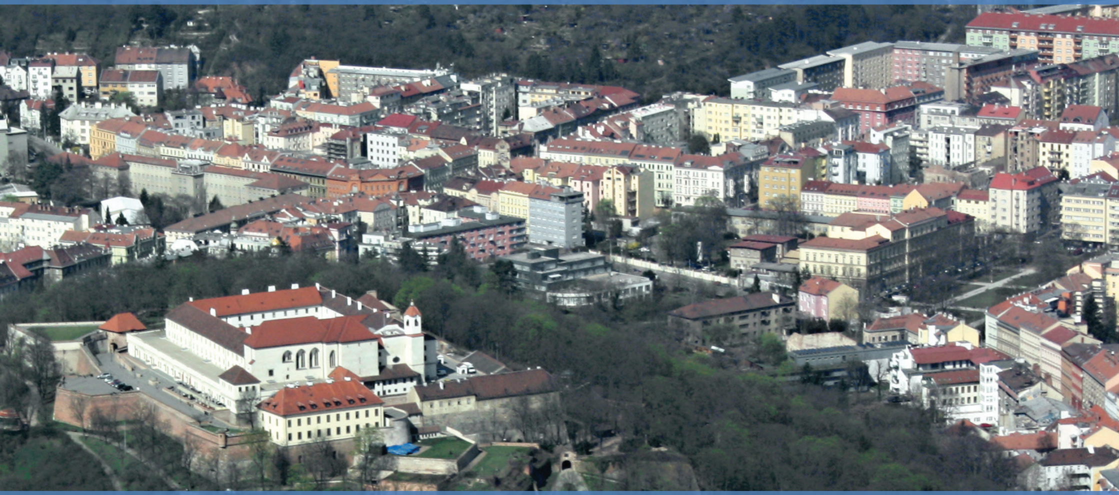

Modulation of plant UV-responses by environmental factors

Book of Abstracts

Otmar Urban & Marcel A.K. Jansen (eds.)

Global Change Research Institute, The Czech Academy of Sciences
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The workshop "Modulation of plant UV-responses by environmental factors" was organised by the Global Change Research Institute CAS, v.v.i. (Dr Otmar Urban) and University College Cork, Ireland (Dr Marcel Jansen) as an official action of the International Association for Plant UV Research, UV4Plants. Hosting of the meeting was supported by the Czech Ministry of Education under the grant numbers LO1415 and CZ.02.1.01/0.0/0.0/16_013/0001609, and by Science Foundation Ireland, grant number 11/RFP.1/EOB/3303.

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Contents

Preface

There is clear evidence that anthropogenic activities lead to an increase in CO_2 and other greenhouse gases in the lower atmosphere. Such changes in the chemistry of the atmosphere have the potential to perturb its thermodynamic equilibrium and to contribute to an increase in global temperature by up to 4.8 °C, as compared to the 1989–1999 epoch. In addition, increased frequency, intensity, and/or duration of extreme events including heat waves and drought periods are predicted by global coupled climate models. Indirectly, climate change can also alter parameters as diverse as nitrogen availability, pest and disease prevalence, and changes in intensity and spectral quality of incident solar radiation, including changes in the intensity of solar UV-B radiation and changes in the ratios of blue to UV-A to UV-B, reaching the Earth´s surface. Thus, many of the well-studied plant UV-B responses are superimposed on those induced by climate change.

Although substantial progress has been made in elucidating plant responses to a wide variety of different environmental drivers and/or stressors, the potential of terrestrial plants and ecosystems to tolerate, acclimate and/or adapt to complex conditions of global climate change remains uncertain. This is particularly so in the case of exposure to multiple stressors, abiotic and/or biotic, a scenario that is common in nature. In this workshop we explore the impacts of UV-radiation in the context of the wider environment. For example, in nature high levels of UV-B radiation are commonly accompanied by high levels of photosynthetic radiation (i.e. risk of photoinhibition), while heat and drought are also most likely to be relevant under such conditions. Co-occurrence of stressors may have been a driving factor in the evolution of complex stress responses, whereby exposure to one stressor induces tolerance to multiple stressors (Sinclair BJ et al. (2013) Integrative and Comparative Biology 53: 545-556). At the molecular level, different response pathways may share signalling components or induce common protective mechanisms, thus leading to the phenomena of “cross-talk” or “cross-tolerance”. It seems that an occurrence of these phenomenon depends on both severity and timing of exposure to interacting stressors; however, robust datasets are still lacking. Moreover, the terminology for communicating such multifactorial studies is not consistent and is leading to confusion and misunderstanding across the disciplines.

The objective of the workshop is to bring together plant-scientists with an interest in the cross-talk between UV-B and other environmental drivers such as CO_2, drought, temperature and/or various stressors and thus to generate collaborative interactions across disciplines, and to connect different research institutions and countries. It is expected that an important topic at the workshop will be UV-mediated cross-tolerance and/or cross-sensitivity at the biochemical, physiological and organismal levels.

The workshop addresses three topical questions; (1) is the UV-sensing capability of plants simply linked to UV-protection, or does it contribute to a more comprehensive priming of plant protective responses? (2) can UV-B be exploited to boost plant tolerance to other environmental parameters? (3) should published reports on UV-mediated stress be interpreted in the context of a wider range of environmental parameters?

The aim of round table discussions is to standardise terminology, to identify knowledge gaps, to improve experimental design, data analysis and reporting of multifactorial studies, and to encourage and develop "best practice" in multiple driver/stressor studies.

The workshop on "Modulation of plant UV-responses by environmental factors" is co-organized by Global Change Research Institute, Czech Academy of Sciences (CzechGlobe) and University College Cork, Ireland (UCC) as a part of the activities of The International Association for Plant UV Research, UV4Plants (http://uv4plants.org/).

We wish you a productive and enjoyable meeting!

Dr Otmar Urban (CzechGlobe), and

Dr Marcel Jansen (UCC)

About UV4Plants

The international workshop on “Modulation of plant UV-responses by environmental factors” (Brno, Czech Republic, June 27-28, 2017) is organized under the patronage of The International Association for Plant UV Research, UV4Plants. UV4Plants was established in 2014 and built on the achievements and network of collaborative interactions of UV4Growth, COST Action FA0906.

The overall aim of the Association is to promote excellence in Plant UV research, scholarship and outreach. The specific objectives of the Association are:

- to advance Plant UV Research by promoting sharing of knowledge and collaboration among researchers, both from academic and non-academic organizations,
- to promote and foster a culture of research-excellence and good practice in Plant UV Research through the organisation of innovative events in research, public engagement and education,
- to provide communication channels for members to inform the Plant UV Research community about relevant activities or events of common interest,
- to enhance the usefulness of Plant UV Research by facilitating the transfer of knowledge from academia to stakeholders and the general public,
- to initiate and foster stakeholder contacts as part of an agenda of product development,
- to liaise with scientific funding bodies to inform their research agenda,
- to liaise with other learned-scientific bodies for the benefit of the members, and
- to develop with its members the benefits of membership and the relevance of the Association.

These objectives are fulfilled through the publication of monographs and an open-access journal entitled "UV4Plants Bulletin", the organization of conferences and training events, and the maintaining of communication through public social media and a private mail list of members.

More information about the UV4Plants Association can be found at the official homepage http://uv4plants.org/.

Scientific programme

“Modulation of Plant UV-responses by environmental factors”

Brno, Czech Republic
June 27 – 28, 2017

June 27

8:30-8.45	*Welcome*
8:45-9:05	**Nybakken, L.**: Eight years of combined UV and temperature exposure studies of dioecious Salicaceae species – what have we learned?
9:05-9:25	**Urban, O.**: “Short- and long-term interactive effects of ultraviolet radiation and elevated CO_2 concentration on physiological traits of European beech saplings”
9:25-9:45	**Llorens, L.**: “Modulation of plant UV-responses by water availability in Mediterranean plant species”
9:45-10:05	**Mátai, A.**: “Combined effects of drought and UV in growth chamber experiments”
10:05-10:40	*Coffee/tea break*
10:40-11:20	**Roy, J.**: “The crucial aspect of the interactions between ecosystems environmental factors and the role of shared international infrastructures …” (**invited lecture**)
11:20-11:40	**Olsen, J.E.**: “Does UV-B affects sensitivity to gamma radiation in plants?”
11:40-12:00	**Aphalo, P.**: “UV-responses as drivers of pre-emptive cross acclimation”
12:00-13:00	Round-table discussion-1
13:00-14:00	*Lunch*
14:00-14:20	**Sharma, A.**: “Integrating UV-B signalling in to plant shade avoidance and thermomorphogenesis networks”
14:20-14:40	**Brelsford, C.C.**: “Does simulated understorey blue light and UV-A radiation provide acclimation to high-light stress in photoreceptor mutants of *Arabidopsis thaliana*?”
14:40-15:00	**Yan, Y.**: “Different responses to solar ultraviolet (UV) and blue radiation in two cultivars of *Vicia faba*”
15:00-15:20	**Nezval, J.**: “Spectral quality and total irradiance of visible light as important environmental factors enhancing production of UV-protective phenolic compounds”
15:20-16:00	*Coffee/tea break*
16:00-17:30	Round-table discussion-2
18:00	*Excursion to Mendel Museum / Social dinner*

June 28

08:30-09:00	**Schenke, D.**: "Influence of abiotic UV-B stress responses on biotic stress exerted by bacterial pathogens"
09:00-09:20	**Solhaug, K.A.**: "Effects of UV on secondary compounds and growth rate in lichens"
09:20-09:40	**Bilger, W.**: "Low temperature induced epidermal screening in Arabidopsis thaliana leaves protects against enhanced damage of photosystem II by UV-B radiation"
09:40-10:00	**Jansen, M.A.K.**: "The UVB photoreceptor UVR8 mediates accumulation of UV-absorbing pigments, but not changes in plant morphology, under outdoor conditions"
10:00-10:20	**Klem, K.**: "Interactive effects of ultraviolet radiation and nitrogen supply on photoprotection in plants"
10:20-10:45	*Coffee/tea break*
10:45-12:00	<u>Discussion-3</u> / Concluding remarks
12:00-13:30	*Lunch / Closure of the meeting*

Eight years of combined UV and temperature exposure studies of dioecious Salicaceae species – what have we learned?

Nybakken L.[1,*], Nissinen K.[2], Sivadasan U.[2], Strømme C.[1], Virjamo V.[2], Lavola A.[2], Randriamanana T.[2], Julkunen-Tiitto R.[2]

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Although both ultraviolet-B (UV-B) radiation and warming has been shown to affect growth and metabolism of plants, the combined effects of the two environmental factors has been little studied under field conditions. In Joensuu (Eastern Finland), a field for modulated enhancements of UV-B and temperature was set up in 2009. So far, it has hosted two separate 3-year studies of both sexes of the dioecious *S. myrsinifolia* and *Populus tremula*. In addition, we studied the same *P. tremula* clones in a set-up with UV-filters along a natural UV-and temperature gradient in south-central Norway. In the present synthesis, we will concentrate on the results on UV and temperature effects on phenology, growth and secondary metabolism.

Higher temperatures delayed autumnal bud formation and thus prolonged the growing season, while UV-B partly counteracted this effect. Warming also advanced bud break in spring, and this increased to some extent under UV-B in the first year. Male plants were often more responsive to both treatments. The extended growing season under enhanced temperature was important for the increases seen in most growth parameters, and the counteractive UV-B effect was also visible on total biomass measurements.

In general, most phenolic compounds decreased under elevated temperatures, but there were examples of increases in individual compounds in single years. In *S. myrsinifolia* UV-B increased some leaf flavonoids, typically quercetins, but in the third year also salicortin and condensed tannins increased. Interestingly this increase was facilitated by enhanced temperature under the combined treatment. In *P. tremula*, UV-B induced increases in total flavonoids in all years, and in phenolic acids in the first year.

Our results have proved previously unknown regulatory effects of UV-B on phenology, and show important interactions between UV-B and temperature for both growth and metabolism. The next step will be to initiate projects mining the underlying mechanisms of the observed effects.

Notes

Short- and long-term interactive effects of ultraviolet radiation and elevated CO_2 concentration on physiological traits of European beech saplings

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Global climate models predict a gradual increase in atmospheric CO_2 concentration and global temperature by as much as 700 µmol CO_2 mol^{-1} by 2100 (RCP6.0 scenario; IPCC, 2013). Generally, elevated CO_2 concentration (EC) leads, under sufficient light intensity, to enhanced photosynthetic CO_2 uptake in C3 plants. Such enhancement is caused by depressed photorespiration, and stimulated binding of substrate by Rubisco enzyme (ribulose-1,5-bisphosphate carboxylase/oxygenase). Substantial reductions in CO_2-enhanced photosynthesis (termed acclimation or down-regulation) may, however, occur over long time periods of EC treatment. Accordingly, we tested the hypothesis that short- and long-term interactive effects of ultraviolet radiation and elevated CO_2 concentration on plant physiological processes differ.

To test this hypothesis, European beech (*Fagus sylvatica*) saplings (4 to 5-year-old) were grown under ambient (AC, 400 µmol mol^{-1}) and elevated (EC; 700 µmol mol^{-1}) CO_2 concentrations using a field experimental facility – glass domes with adjustable windows. Plants in both CO_2 treatments were exposed to ambient UV radiation (UV0; UV-B_{BE} ranged between 11.6 and 20.5 kJ m^{-2} day^{-1}), enhanced UV (UV+ = 1.5 × UV0; modulated lamp system), and reduced UV (UV–; exclusion of UV-A and UV-B). Such treatments were applied for two vegetation seasons (May–October).

We have found that short-term (weeks) application of EC led to a typical stimulation of light-saturated rate of CO_2 assimilation. Such stimulation however diminished during the vegetation season (long-term effect; months) under the interaction of UV radiation. In contrary, EC-stimulated rates of CO_2 assimilation persisted under the conditions of excluded UV. These changes are consistent with changes in Rubisco carboxylation activity. Changes in the acclimation of photochemical reactions of photosystem II (primary phase of photosynthesis) were also found. EC treatment led to a substantial stimulation of light-saturated quantum yield of PS II photochemistry under UV– and UV0, but not under UV+ conditions.

Based on these results we conclude that UV radiation reduces positive effects of EC on photosynthetic carbon uptake and photochemistry, particularly under the long-term application (i.e. an antagonistic interaction).

Reference

IPCC. 2013. Cambridge, UK and New York, NY, USA: Cambridge University Press, 3–29.

Acknowledgement

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Notes

Modulation of plant UV-responses by water availability in Mediterranean plant species

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Climatic models predict an increase in the levels of UV radiation reaching Mediterranean ecosystems in the coming decades mainly due to a decrease in cloud cover, which will also reduce precipitation, especially in summer. It is well known that primary exposure to a single stress can alter responses to other stresses (cross-tolerance effects). In particular, drought-induced changes in plant functioning and development could modify plant tolerance to UV radiation and vice versa. In this context, the objective of this presentation is to summarise the results we have obtained after 10 years of research regarding the interactive effects of UV radiation and reduced water availability on the morphology, physiology, biochemistry and growth of different Mediterranean plant species. To achieve this goal, we present results from three experiments where UV radiation and water availability levels were modified, going from the greenhouse to the field and from seedlings growing in pots to naturally growing plants.

At leaf morphological level, most of the parameters studied (leaf area, density and thickness, LMA, parenchyma and epidermis thickness, etc.) did never respond to the interaction between UV and watering levels, although UV effects on cuticle thickness were modulated by water availability in *Daphne gnidium* (3-8 species studied). Regarding plant physiological traits, the most sensitive parameter to the combination of both factors was leaf g_s (it was affected in 2 of 4 species), while other parameters (such as leaf RWC, ETR, A, E, WUE and NPQ) responded in only 25% of the 4-8 species studied, or in only 1 species of 8 in the case of Fv/Fm. At biochemical level, we found significant interactive effects between UV and water availability on foliar chlorophyll content in 1 of 3 species, but not on total carotenoids, although, in *Laurus nobilis*, the UV-response of several carotenoids (β-carotene, α-carotene, lutein-5,6-epoxide, and lutein+lutein-5,6-epoxide) was modulated by water availability at predawn. Total emission rates of volatile terpenes did neither respond to the interaction between UV and watering levels; however, emission rates of specific terpenes were sensitive to this interaction in the 4 species studied. Similarly, UV effects on the total leaf content of phenols or UACs were never dependent on water availability (6-8 species studied), but watering modulated the UV response of specific flavonols in 2 of 3 species. UV effects on foliar antioxidant activity and glutathione levels were also modulated by watering in *A. unedo*, but not in *Q. suber*. In any of these two species, UV levels affected total root content of starch, sugar or phenols regardless of the watering regime.

Finally, regarding plant growth, root biomass was the parameter most sensitive to the combination of UV and water availability since it responded in 50% of the species, followed by above-ground biomass (which was affected in 2 of the 6 species studied). Other parameters, such as stem diameter, plant shoot/root ratio, height, or relative growth rates did not respond to the interaction between UV and watering (2-4 species studied). Overall, our results suggest that moderate reductions in water availability will not modify substantially short-term UV responses of most

Mediterranean woody species; however, species-specific effects on plant growth and functioning might eventually alter the competitive relationships among co-occurring species.

Abbreviations

LMA=leaf mass area, g_s=stomatal conductance, RWC=relative water content, ETR=electron transport rates, A=net photosynthetic rates, E=transpiration rates, WUE=water use efficiency, NPQ=non-photochemical quenching, Fv/Fm=maximum photochemical efficiency of PSII.

Notes

Combined effects of drought and UV in growth chamber experiments

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Solar UV-B radiation has already been demonstrated to ameliorate the effects drought in a field study (Robson et al. 2015). The present work is part of a series aimed at studying interactions between responses to drought and UV at the level of antioxidants. Exposure to mild non-lethal drought stress has already been shown to improve the UV-B sensitivity of tobacco plants (Hideg et al. 2003), and the ongoing series of experiments is aimed exploring a reverse order of factors. The other difference is in UV doses: while the earlier work employed damaging UV-B doses capable of decreasing photochemical yields of photosynthesis by 40-60%, the present study uses lower UV-B doses.

In this study *Nicotiana benthamiana* plants were grown in plant chambers (175 µmol m^{-2} s^{-1} PAR, 16 h/day, 25°C / 20°C day / night temperatures, 70% humidity). Water supply resulting in full soil hydration was regarded as 100%. Controls received PAR only and 100% water at 70% humidity. Other plants were exposed to supplemental UV and/or drought. 6.9 kJ m^{-2} d^{-1} biologically active UV-B from was applied either before or in parallel to 75% water supply at 55% humidity. Leaf photosynthesis was measured as dark adapted (Fv/Fm) or light acclimated (Y(II)) photochemical yield and non-photochemical energy dissipation parameters (Y(NO), Y(NPQ), NPQ) (Klughammer and Schreiber, 2008). Flavonoid and chlorophyll contents were estimated with Dualex. Non-enzymatic antioxidants were assessed using total capacities (TAC) and ROS neutralizing special enzymes (SOD, peroxidase (POD)) were also measured.

A 4-day exposure to supplemental UV increased leaf flavonoid content, but had no significant effect on photochemical yields. Increased flavonoid contents were maintained several days after the cessation of UV. Thus we assume that the positive effect of UV pre-treatment on drought tolerance is promoted by the availability of higher levels of antioxidant flavonoids already from the onset of drought. Plants exposed to drought only showed an increased flavonoid content, too, but this effect was not as strong as the influence of UV and developed slowly in response to drought. Cross reactions between UV and drought affected mainly the non-photochemical energy dissipation parameters. When applied together, UV and drought were more stressing than drought itself, and the synergic effect was shown by a decrease in TAC, indicating the exhaustion of the non-enzymatic antioxidants.

The long-term goal of the experiments is to explore the use of UV to improve drought tolerance, for example as pre-treatment to protect potted plants during transportation.

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Acknowledgement

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Notes

The crucial aspect of the interactions between ecosystems environmental factors and the role of shared international infrastructures to address this interaction challenge with, in particular, the case of light quality in growth chambers.

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The various drivers of plants and ecosystems functioning most of the time co-vary and their interactions are often significant. It challenges our experimental approach of the impact of these factors because the number of our experimental units and/or our task force or funding to conduct the experiments are limited. Results on the combined impact of drought and elevated CO_2 on ecosystem functioning from various experiments suggest that these interactions are complex and encompass mechanisms beyond leaf and plant physiology and they also vary with time. Investments in larger individual experimental infrastructures as well as their sharing and integration at the international level are needed. The examples of the Montpellier European Ecotron and its Ile-de-France counterpart will be given and the European infrastructure AnaEE (Analysis and Experimentation on Ecosystems) will be presented. Experiments in these infrastructures can be done either with natural light or in growth chambers with artificial light. In the latter case, it is a real challenge to provide the relevant light level and spectrum quality. Developments in the Ecotron to meet this light challenge will be mentioned and a forthcoming collaborative experiment testing the interaction between light spectrum quality and biotic and abiotic stresses will be presented.

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Notes

Does UV-B affects sensitivity to gamma radiation in plants?

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Although UV has been suggested to contribute to priming of protective responses towards various stressors in plants, and it has been speculated that UV radiation may affect the sensitivity towards ionizing radiation, knowledge about interactive UV-gamma effects is scarce. The conifer Scots pine is considered a radiosensitive species although few systematic studies of radiosensitivity in plants have been performed. Our recent detailed studies showed negative effects on growth and development in Scots pine at 10 times lower gamma dose rates than in *A. thaliana*. Using a ^{60}Co gamma source to provide different gamma dose rates (20, 40 and 100 mGy $h^{-1)}$ and UV-B fluorescent tubes providing UV-B irradiance within the natural range, we aimed to investigate interactive gamma-UV-B effects on seedlings of Scots pine grown under controlled environmental conditions. After 6 days of radiation increasingly reduced plant size was observed in response to increasing gamma dose rates with a slight trend only of an additional decrease in size in UV-gamma-exposed plants. At termination of the radiation (one hour after the light was turned on in the morning) increased ROS levels (H_2O_2) with increasing gamma dose rate were observed but there was no significant difference between the gamma only and UV-gamma treatments. However, increased DNA damage (strand breaks as measured with Comet assay), with increasing gamma dose rate was then observed with an additive effect of gamma and UV-B, most clearly so at the highest gamma dose rate. The significance of this is still unclear; at least there were no clear negative after-effects of this additive effect on subsequent plant growth and development. The negative, dose-rate-dependent effect of gamma radiation on plant growth and development persisted after termination of exposure but there were no clear differences between plants previously exposed to gamma-UV and gamma only (needle formation rate, shoot and needle elongation, recorded up to 23 days after the exposure). Thus, so far no UV-B boosting of tolerance to gamma radiation has been found in Scots pine seedlings, at least not under the gamma and UV-B conditions applied. To further evaluate if there is any UV modulation of the responses to gamma radiation in Scots pine seedlings, analyses of antioxidants, DNA repair genes and histology are also carried out. In addition to co-exposure experiments, sequential exposure to UV-B and gamma will be performed.

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Notes

UV-responses as drivers of pre-emptive cross-acclimation

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The objective of the experiments I will summarize has been to investigate "the other side of the coin" compared to the traditional view: what are the benefits plants gain from responses to UV, not in relation to tolerance of UV itself, but with respect to tolerance of other stressors for which UV-exposure could function as an "early warning" cue.

Gas-exchange and porometre-based measurements of stomatal conductance in species, accessions and cultivars adapted to environments differing in UV-exposure (latitude and elevation), aridness, and shadiness have been compared. Main treatments have been long-term exposure to filtered sunlight. In some cases, complemented with different light treatments during gas-exchange measurement. In some experiments water supply restriction was included as an additional factor, and applied after several weeks of exposure to the UV-radiation and light treatments.

The main results could be summarised as: the long-term response to UV tends to be a modulation of the shorter-term responsiveness of stomata to light, and this modulation is complex. In the shade-tolerant species that we studied, opening speed of stomata was much slower in plants which had grown in full sunlight compared to those which had grown protected from UV radiation by filters, irrespective of the PAR irradiance and possibly red:far-red ratio during growth.

When measured under the growing conditions, depletion of blue light, decreases stomatal conductance as expected. The blue-dependence of stomatal opening depends on the genotype, and seems to be strongly dependent on the aridness of the environment to which the genotypes are adapted.

The significance is that these results give support to the idea that we should interpret responses to UV radiation in the same way as we do with responses to R:FR photon ratio. The main role of R:FR-perception is as a source of information on neighbours and the risk of future competition for light. The R:FR ratio has intrinsically very little relevance for the metabolism of plants other than the information this cue carries about neighbours. I propose that also in the case of *solar* UV radiation the most important role is as a source of information, at least for plants not subjected to unnaturally sudden exposure to UV. That UV-exposure enhances drought tolerance has been earlier proposed. What is new in my argument is that as with most other photoreceptor-mediated responses the *main* role of UV perception by plants is related to acquisition of advance information about changes in the environment that are correlated to changes in UV exposure rather than UV exposure itself.

Acknowledgements

The data to be presented originates from experiments where Luis Morales, Neha Rai, Yan Yan, David Israel, Saara Hartikainen, Matthew Robson, Mikael Brosché, Fred Stoddard, Sari Siipola and Krõõt Aasamaa have played a central role. Exchanges of ideas and collaboration with Anders Lindfors, Victor O. Sadras, Titta Kotilainen, Tarja Lehto, Riitta Tegelbeg, Ariel Novoplansky, Alexey Shapiguzov, Marcel Jansen and others have contributed over several years to the development of these ideas.

Notes

Integrating UV-B signalling in to plant shade avoidance and thermomorphogenesis networks

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Plants are sensitive to light and temperature, and changes in these stimuli significantly affect growth and development. Plants have evolved different classes of photoreceptor to detect variations in the light environment and trigger adaptive responses to protect them from adverse conditions. In canopy shade, reduced red/far-red (R:FR) light ratio is perceived by phytochromes and plants re-allocate resources towards stem elongation to overtop competitors. UV-B is perceived by the UV RESISTANCE LOCUS8 (UVR8) photoreceptor and inhibits these shade avoidance responses. UVR8 activation increases DELLA protein stability and degradation of PHYTOCHROME INTERACTION FACTOR (PIF) transcription factors. Collectively, these processes inhibit auxin biosynthesis and stem elongation [1,2]. The transcription factors ELONGATED HYPOCOTYL 5 (HY5) and its close relative, HY5 HOMOLOG (HYH) act redundantly to control UV-B mediated gene expression. We have identified the *GA2ox* gibberellic acid catabolism genes as UV-B-mediated HY5 and HYH targets in shade avoidance inhibition (2). RNA sequencing analysis has been used to further understand role of HY5/HYH in this process. High temperature can also trigger stem elongation, in a process termed thermomorphogenesis. This involves increased auxin synthesis, but unlike shade avoidance, is largely mediated by a single transcription factor, PIF4. UV-B perceived by UVR8 strongly inhibits thermomorphogenesis via multiple mechanisms repressing PIF4 abundance and activity [3]. Importantly, the molecular mechanisms through which UV-B inhibits shade avoidance differ from those involved in thermomorphogenesis inhibition. Collectively, we have established direct cross talk between UV-B, shade avoidance and thermomorphogenesis signalling. We are currently investigating the detailed molecular mechanisms through which UV-B signals control PIF abundance and activity. Our study will elucidate how plants integrate UV-B with other environmental signals to regulate growth and development in sunlight.

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Notes

Does simulated understorey blue light and UV-A radiation provide acclimation to high-light stress in photoreceptor mutants of *Arabidopsis thaliana*?

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Plants utilise light cues perceived by a suite of photoreceptors to coordinate their strategy for growth, defence and photosynthetic performance to the changing light conditions in understorey environments. We aim to describe the role of photoreceptors in facilitating mechanisms that allow plants to capitalise on the dynamic shifts between understorey shade and high light in sunflecks. Here, we tested responses to simulated understorey blue light and UV-A radiation of several *Arabidopsis thaliana* mutants deficient in activity of blue-light-and-UV photoreceptors including: phototropin 1 (phot1); cryptochromes (cry1 and cry2), and UV RESISTANT LOCUS 8 (UVR8), in comparison to their wild-type (WT). This was achieved using LED lamps in chambers to create treatments with or without blue light, in a split-plot design with or without UV-A. To simulate the transition from shade to sunflecks, plants from each treatment were exposed to 30 minutes of high-light stress. We compared the leaf pigments under growth conditions and after high-light stress, and likewise the actual photochemical yield (*F*v`/*F*m` - as a proxy for photosynthetic performance) and dark-adapted maximum quantum yield (*F*v/*F*m - to assess damage to PSII). Under blue light, cry1 and cry2 were required for the induction of phenolic-acid derivatives and kaempferol derivatives; whereas both classes of photoreceptors, UVR8 and cry1 and cry2, induced their production in response to UV-A. Whilst phot1 was not required for the production of phenolic compounds in response to blue light or UV-A, it was implicated in their induction in the absence of blue light phot1. This suggests that phot1 may be important for the constitutive regulation of flavonoids and phenolic acid derivatives. Photoreceptors cry1 and cry2 maintained a higher *F*v`/*F*m` and *F*v/*F*m in plants growing under blue light, and a higher *F*v`/*F*m` under high-light stress; whereas other photoreceptors produced no significant differences from the WT. Our results indicate that cryptochromes are the main photoreceptors regulating the accumulation of phenolic compounds in response to blue and UV-A, and their function is required for the maintenance of PSII under high-light stress. Our findings also reveal a role for UVR8 in accumulating phenolic compounds in response to UV-A. In particular, this suggests a role for blue light and UV-A radiation in facilitating the transition from shaded to high-light conditions, considering that drastic changes in the ratio of solar UV-A:blue light occur in many environments.

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Notes

Different responses to solar ultraviolet (UV) and blue radiation in two cultivars of *Vicia faba*

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Plant depends on sunlight not only as primary energy source but also as signal from the environment. UV light, although constituting a small part of the solar spectrum, has big influence on plant growth. Our study aims at understanding the effect of solar UV and blue radiation on two cultivars of *Vicia faba*. The two cultivars: Aurora and ILB938 originate respectively from Sweden and Ecuador and differ in drought and UV tolerance [1]. An experiment was done outdoors with four optical filters that attenuate different wavelength from the sunlight.

On whole plant level, data showed that ILB938 was taller (p=0.002) and the deprivation of blue light increased plant height and leaf area in both cultivars. Gas exchange data showed Aurora had higher stomatal conductance (p=0.0022), and blue light affected the two cultivars differently: it increased stomatal conductance in Aurora but decreased stomatal conductance in ILB938. Aurora also had higher photosynthesis (p=0.0102) and chlorophyll fluorescence (p=0.0132). Dualex measurements indicate that the upper epidermis of leaves contained more flavonoids. Short UV and blue light strongly induced flavonoid in upper leaf epidermis.

Detailed leaf phenolic profile was analyzed using HPLC-DAD-ESI-MS^n method. There was higher concentration of quercetin than kaempferol in both cultivars. Total kaempferol didn't respond to light in either cultivar, but the concentration was higher in Aurora. This is because kaempferol derivatives in Aurora are mostly tri-glycoside, tetra-glycoside and acetylated-glycoside while there are mainly di-glycoside in ILB938. The molar concentration of kaempferol didn't differ in two cultivars. Total quercetin was induced strongly by short UV (p<0.0001) in both cultivars. The variation of total quercetin concentration was higher in ILB938 (p=0.0387), and this was due to high variation in the concentration of one quercetin derivative: quercetin-3-O-rhamnoglucoside (p=0.0021). We detected 10 quercetin derivatives in Aurora but fewer in ILB938. Different quercetin derivatives in the two cultivar responded differently to light. In Aurora, quercetin-3-O-rhamno-7-O-galactoside was induced upon short UV (p=0.0287), which is the most abundant quercetin in Aurora. In ILB938, Quercetin-3-O-rhamnoside-7-O-rhamnoside and Quercetin-3-O-rhamno-rahmno-galactoside was increased upon both short UV (p<0.0001) and blue light (p<0.0001). The most abundant quercetin derivative in ILB938 didn't respond to blue light or UV radiation.

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Notes

Spectral quality and total irradiance of visible light as important environmental factors enhancing production of UV-protective phenolic compounds

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Strong absorption in both UV-A and UV-B spectral region together with often-pronounced antioxidative properties predestines phenolic compounds (PheCs) to serve as very effective plant UV-protectants. Still, PheCs are involved in many others stress-related responses (temperature, drought, biotic stress, etc.) thus their production can be induced/modulated by ostensibly independent environmental stimuli which could subsequently lead to enhanced tolerance to excessive light (of UV-B or photosynthetically active radiation - PAR). On the other hand, appropriate UV-B and PAR pre-acclimation may enhance the plant tolerance to abovementioned environmental stresses. These multi-factor interactions are intensively studied nowadays. However, even cross-talks within the light signalling pathways themselves are not very well understood yet, although their knowledge is essential for understanding of many light involved cross-tolerance responses. In this work we focus on the interaction of high irradiance and spectral quality in the regulation of plant PheCs metabolism and the function of cryptochromes photoreceptors in this process. For this purpose, spring barley *Hordeum vulgare* L. was grown from seeds under low irradiance of PAR (LI; 100 µmol m^{-2} s^{-1}). Cultivation light contained different portion of blue spectral component (B) relatively to green (G) and red (R) light, achieved by adjustment of individual R, G, B LEDs in growth chambers. After seven days of cultivation in LI, half of plants was exposed to higher irradiance (HI; 400 µmol m^{-2} s^{-1}) of the same spectral composition for 7 days, the rest of plants were kept as LI control samples. During acclimation period dynamics of UV-A shielding was recorded using Dualex instrument (Force-A, France). Detailed spectral analysis of UV-shielding (measurement of chlorophyll excitation spectra in UV-B and UV-A region; ChlExS) as well as HPLC-DAD analysis of PheCs were performed just before the beginning and at the end of HI treatment. Similar (simplified) experiment was performed to elucidate the role of cryptochromes (CRY) in HI acclimation, using *Arabidopsis thaliana* Ler and its double mutant lacking CRY1 and CRY2 (CRY1CRY2). Plants were grown under LI for 7 weeks and then exposed to HI for 2 weeks. Our results indicated that during the acclimation of spring barley to HI of PAR the presence of B is essential for effective accumulation of PheCs in epidermis. Intriguingly, under low light (LI) conditions no biologically relevant differences in epidermal UV-A shielding were observed amongst various spectral treatments (even between B-LI x G-R-LI) and its values reached only the basal level of ca. 0.2. The parallel experiment with *Arabidopsis thaliana* (Ler) and its CRY1CRY2 mutant led to the conclusion that primarily B light activated CRYs are responsible for enhancing UV shielding during acclimation to HI (under no UV conditions). This metabolic response is probably initiated through B->CRY->COP1->HY5 signalling pathway. On the other hand, low irradiance of B in predominantly G-R or R light conditions did not caused enhancement of UV-A shielding suggesting existence of activation threshold in blue-light induced response. This threshold could be inherent to CRY signalling pathway itself (e.g. inactivation of CRY by G) or be the consequence of other signals originating e.g. in photosynthesis related processes such as lower production/availability of assimilates or impaired acclimation of photosystems to HI in the absence of B. Response of UV-A shielding (315–360 nm) to different

spectral quality of light during HI acclimation determined based on ChlExS is in good accordance with the results obtained using Dualex instrument. UV-B shielding (280-315 nm) exhibited similar response as UV-A shielding, but it was less pronounced in general. HPLC-DAD analysis confirmed positive effect of B on the production of leaf soluble PheCs during acclimation of plants to HI as well as the important role of CRYs in this response.

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Influence of abiotic UV-B stress responses on biotic stress exerted by bacterial pathogens

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Plants respond to abiotic UV-B stress with enhancing the expression of genes, especially the key-enzyme chalcone synthase (CHS), required to produce flavonoids, which are UV-B protective secondary metabolites. When challenged with concomitant biotic stress (simulated e.g. by the bacterial peptide flg22, which induces MAMP triggered immunity, MTI), the production of flavonoids is strongly suppressed in both cell cultures [1] and plants [2]. On the other hand, flg22 induces the production of defense related compounds, such as the phytoalexin scopoletin, as well as lignin, a structural barrier thought to restrict pathogen spread. Since all these metabolites require the precursor phenylalanine for their production, suppression of the flavonoid production appears to allow the plant to focus its secondary metabolism on the production of pathogen defense related compounds during MTI [1].

However, flavonoids are also reported to have inhibiting activity towards bacteria, fungi, nematodes and insects, which implies that UV-B could render a plant also more resistant towards biotic stress. This means that suppression of UV-B induced flavonoids could have both positive or negative effects on the pathogen defense response of plants, which shall now be investigated. We will 1) pretreat plants with UV-B to induce flavonoids in WT Arabidopsis and compare their resistance to the bacterial pathogen *Pseudomonas syringae pv. tomato* (Pst) DC3000 with a *chs/f3h* mutant unable to accumulate flavonoids and control plants (no UV-B pretreatment). 2) Furthermore, we will compare virulent Pst DC3000 with Pst mutants impaired in the production of effectors (suppressing e.g. MTI), so we can exclude bacterial manipulation of host plant defense responses.

We expect that this approach will allow us to shed light on the true outcome of natural responses involving both abiotic (UV-B) and biotic (bacterial infection) stresses. Also the role of flavonoids will be clarified and if plants with elevated flavonoids show a higher resistance to bacteria we have to overthink the role of flavonoid suppression during MTI. Finally, we present an up-dated working model to explain the antagonistic regulation of flavonoid genes in response to UV-B and flg22.

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Notes

Effects of UV on secondary compounds and growth rate in lichens

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UV-B induces synthesis of various secondary compounds as parietin, usnic acid and melanic compounds in lichens (Solhaug and Gauslaa 2012 and references therein). The fungal partner produces the lichen secondary compounds. The cortex of lichen thalli efficiently screen UV-B radiation from reaching the photobiont also without secondary compounds. We measured cortical transmittance close to 0% of wavelengths <325 nm in the lichen *Lobaria pulmonaria*, and maximum photosystem II efficiency (Fv/Fm) was not reduced in intact thalli even after 4 days exposure to a continuously high UV-B level of 1.5 Wm^{-2} (Gauslaa et al. 2017).

Melanic compounds screen solar radiation and reduce quantum yield (QY) of CO_2 uptake in low light without affecting maximum rates of photosynthesis. This have the cost of reduced photosynthetic efficiency under low light (Mafole et al. unpublished).

However, the effects of UV on growth in lichens has rarely been studied. A field experiment was done with *L. pulmonaria* and *Lobaria virens* with three screening treatments: 1) full solar radiation, 2) full solar radiation minus UV-B and 3) full solar radiation minus UV-A and UV-B. The thalli receiving solar radiation without UV had higher relative growth rate (RGR) than thalli exposed to solar radiation + UVA or full solar radiation (Kann et al 2017 unpublished). Reduced RGR under UV is probably caused by adverse effects of UV on the fungal partner because light level in this open site most of the time was above light saturation with similar photosynthesis in melanic and pale thalli.

Conclusions:

- Lichen compounds may be induced by UV-B. However, they are not necessary for protecting the photobiont against UV-B.
- Increased protection against high visible light causes reduced photosynthetic efficiency under low light.
- Because UV-B radiation affects RGR more than may be explained by reduced photosynthetic responses, the mycobiont is likely the more UV-B-susceptible partner.

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Notes

Low temperature induced epidermal screening in Arabidopsis thaliana leaves protects against enhanced damage of photosystem II by UV-B radiation

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In many plants epidermal UV screening is induced by low temperature even in the absence of UV irradiation. We investigated the function of this reaction in *Arabidopsis thaliana*. Exposure of plants grown at warm temperature (21°C) to UV-B radiation at 9°C resulted in significantly higher damage of photosystem II (PS II) as compared to exposure at 21°C. The higher damage at low temperature was connected to slower recovery from damage at this temperature. Epidermal UV transmittance was measured using a method based on chlorophyll fluorescence measurements. Acclimation to low temperature enhanced epidermal UV screening and improved the UV-B resistance considerably.

Differences in the apparent UV-B sensitivity of PS II between warm and cool grown plants almost disappeared when damage was related to the UV-B radiation reaching the mesophyll (UV-B_{int}) as calculated from incident UV-B irradiance and epidermal UV-B transmittance.

The data suggest that enhanced epidermal UV screening at low temperature functions as compensation of a deceleration of repair processes of UV-B damage at these temperatures. It is proposed that the UV-B irradiance reaching the mesophyll should be considered as an important parameter in experiments on UV-B resistance of plants.

Notes

The UVB photoreceptor UVR8 mediates accumulation of UV-absorbing pigments, but not changes in plant morphology, under outdoor conditions.

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UVB radiation is biologically active; in plants, it can induce a range of molecular, biochemical, morphological and developmental responses. Although much progress has been made in elucidating UVB perception and signalling pathways under controlled laboratory conditions, the understanding of the adaptive, ecological role of UVB responses is still very limited. Under natural growth conditions, the complexity of plant responses to the changeable nature of their surroundings can make identifying one particular response difficult. The objective of this study was to investigate the functional role of UVR8 under outdoor conditions, where plants are exposed to fluctuating environmental parameters such as light, and temperature. The used light filtration methodology was based on the use of cladding materials with different transmission profiles in the UV part of the spectrum. Furthermore, we used both a wild type Arabidopsis, as well as a mutant that lacks a functional UVR8 protein. Measurements included those of photosynthetic competence, accumulation of UV-absorbing pigments and rosette morphology. This study revealed clear seasonal UV effects. It was found that the influence of UVB on morphology is restricted to the summer, and is independent of UVR8. In contrast, UVB had an effect on the content of UV-absorbing pigments and the maximal efficiency of photosystem II (PSII) of photosynthesis in the *uvr8-1* mutant throughout the year. It is concluded that the UVR8 photoreceptor plays a role throughout the year, in the temperate climate zone, even when UVB levels are relatively low. Impaired PSII function and a reduction in UV-screening pigments in the *uvr8-1* mutant lead us to conclude that a functional UVR8 pathway is necessary for optimized plant growth year round under natural light conditions.

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Notes

Interactive effects of ultraviolet radiation and nitrogen supply on photoprotection in plants

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High doses of ultraviolet-B radiation (UV-B; 280–315 nm) can negatively affect carbon assimilation, growth, development, and crop yield. Plants acclimate to UV-B levels through several defence responses, including accumulation of UV-screening compounds. Among other studies, Klem et al. (2015) have shown that ecologically relevant doses of UV radiation are necessary for efficient accumulation of xanthophylls and epidermal flavonols. Such accumulation correlates with enhanced photoprotection.

In the present multifactorial study we tested the hypotheses that (1) biosynthesis of phenolic compounds (and particularly epidermal flavonols) is primarily induced by UV radiation, and (2) their biosynthesis is strongly related to carbon and nitrogen metabolism (C:N ratio). Accordingly, the accumulation of phenolic compounds is modulated by both irradiance and plant nitrogen status.

Four spring barley (*Hordeum vulgare*) varieties with differing in sensitivity to a photooxidative stress – Barke, Bonus, Prestige, Sebastian – were pot grown and fertilized with nitrogen [$Ca(NO_3)_2$] to achieve final doses of 0 and 10 g N m^{-2}. UV plastic filters and shading net were used to exclude UV-A and UV-B (UV0) and to reduce UV and PAR (photosynthetically active radiation) by approx. 50% (UV50, PAR50), respectively. Four light treatments (UV0PAR50, UV0PAR100, UV50PAR50, and UV100PAR100) were thus applied for 8 days.

Based on *in vivo* measurements of epidermal flavonols and chromatographic analyses (HPLC-MS) of individual phenolic compounds we conclude that UV radiation, particularly in combination with high PAR intensity, leads to an increase in flavonols of young leaves, but not in old ones. It also seems that low C:N ratio is associated with reduced accumulation of flavonols in epidermis; however, this response is genotype specific.

HPLC-MS data have shown that some phenolic compounds may decrease with higher UV radiation (e.g. vanillic acid), accumulation of some compounds is stimulated mainly by PAR but not by UV radiation (e.g. ferulic acid), and/or some are strongly genotype-related (e.g. kaempferol, homoorientin). Accumulation of main phenolic compounds like isovitexin is, however, induced particularly by UV radiation.

The contradictory effects of UV radiation and C:N balance may thus indicate that phenolic compounds (and particularly flavonols) play a multi-functional role in plant photoprotection depending also on their location within plant tissues.

Reference

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Notes

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