EFFECTS OF UV RADIATION AND DROUGHT ON THE ACCUMULATION OF UV-SCREENING COMPOUNDS AND PHOTOSYNTHETIC PARAMETERS IN SELECTED HERBS AND GRASSES OF THE MOUNTAIN GRASSLAND ECOSYSTEM

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ABSTRACT

The main objective of the experiment conducted on a mountain grassland ecosystem was to investigate the interactive effects of UV treatment and drought on the changes in accumulation of UV-screening compounds and photosynthetic parameters in selected herb (Hypericum maculatum) and grass (Agrostis tenuis). The experimental plots were manipulated using roof constructions enabling exclusion/transmission of incident precipitation and UV radiation, respectively. Generally, UV and drought treatments had a similar effect on the accumulation of flavonols. UV exclusion resulted in a slight reduction of UV-screening compounds, particularly under the conditions of ambient precipitation. Likewise, drought treatment caused an increase in the accumulation of flavonols per area unit. Under UV exclusion, drought slightly reduced light-saturated CO_2 assimilation rate (A_{max}) in the both species studied. The presence of UV radiation, however, led to less of a difference in A_{max} between [wet] and [dry] treatments. In addition to the increased induction of flavonols, UV radiation increased water use efficiency and alleviated thus the negative impact of drought on photosynthesis.

Key words: grassland, UV radiation, drought, flavonols, photosynthesis, water use efficiency

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INTRODUCTION

The functioning of many ecosystems and their associated resilience could become severely compromised by climate change over the 21st century (Heyder et al. 2011). The results of a macro-scale water balance model show that the frequency of extreme drought events is projected to increase in future (Tao et al. 2003), causing decrease in ecosystem productivity and ecosystem functions.

The effects of extreme weather events on vegetation and ecosystem functioning are likely to be much stronger than the effects of changes in mean values of temperature and precipitation (Easterling et al. 2000). In addition, among the abiotic stressors, drought and increased levels of ultraviolet-B (UV-B) radiation have received much more attention, because of their potential to impair many plant species (Agrawal et al. 2009).

Under natural conditions, plants usually experience more than one stress simultaneously. The stresses cause a variety of interactive responses which can be adaptive or cumulative. It can be due to a formation of similar protective mechanisms of plants against an oxidative stress caused by both drought and UV-B (Cechin et al. 2008). A highly efficient antioxidant defence system in plants for detoxification of reactive oxygen species includes either non-enzymatic (as flavonoids, carotenoids, tocopherols) or enzymatic constituents (Basu et al. 2010).

Several studies suggest antioxidative functions for UV-screening compounds and phenylpropanoid derivatives such as phenolic acids and flavonoids (e.g. Meijkamp et al. 1999). Some findings attribute the primary role for flavonoid induction to UV-B (Balakumar et al. 1993), whereas other results suggest an interaction with water stress (Nogués et al. 1998). Also accumulation of the osmoregulator proline has been observed in response to a number of environmental factors, including drought and UV-B (Shetty et al. 2002). UV radiation has been shown to increase proline accumulation and drought tolerance in pea, wheat (Alexieva et al. 2001) and clover (Hofmann et al. 2003). Moreover, exposure of a UV-sensitive *Arabidopsis* mutant to UV-B radiation increased production of dehydrin proteins, which may have contributed to increased drought tolerance (Schmidt et al. 2000).

Because these protective mechanisms play an adaptive role in both water stress regulation (Gitz and Liu-Gitz 2003) and attenuation of UV-B radiation (Ibañez et al. 2008), the interactive effects between UV-B exposure and drought stress in plants are assumed. However, present data concerning the interaction between UV-B and drought on plant biochemical processes are equivocal.

For example, a combination of drought and increased UV-B radiation resulted in alleviation of negative effect of drought on photosynthesis and transpiration in sunflower plants (Cechin et al. 2008). Alexieva et al. (2001) concluded that both stresses acted synergistically to induce protective mechanisms (antioxidant compounds). Since drought and UV-B radiation induce similar protective mechanisms (e.g. Hofmann et al. 2003; Cechin et al. 2008), we tested the hypothesis that the UV-B radiation moderates the negative effects of drought on photosynthesis. The hypothesis was tested under natural conditions of a mountain grassland ecosystem.

MATERIAL AND METHODS

The manipulation experiment, focused on the evaluation of combined effects of UV radiation and drought, was conducted in 2012 within the grassland ecosystem (association *Molinio-Arrhenatheretea*, class *Polygono-Trisetion*) at the experimental site Bílý Kříž, Moravian-Silesian Beskydy Mts. (altitude 890 m, latitude 49°30´ N, 18°32´ E). The mean long-term annual temperature and precipitation are 6.8 °C and 1312 mm, respectively. Spodo-dystric cambisol on

Flysch Godulian sandstone occurred in this site. The grassland is regularly cut once in growing season.

The effects of UV exclusion and drought on the changes in accumulation of UV-screening compounds (flavonols) and photosynthetic parameters were studied in selected herb (*Hypericum maculatum* Crantz) and grass (*Agrostis tenuis* Sibth.) species.

The experimental plot was manipulated by six roof constructions covered by plastic filter strips/lamellas enabling the natural incident precipitation to pass ([wet]; ambient treatment) or be excluded ([dry]; drought treatment). The lamellas were made from two types of acrylic (thickness of 3mm). The first one (UVT Solar, Quinn Plastics, UK) transmitted more than 90% of incident UV-A and UV-B radiation (UV+ treatment), whereas the second one (Quinn XT, Quinn Plastics, UK) filtered UV-B radiation and the large part of UV-A (UV– treatment). Thus 4 treatments were maintained: UV–[dry], UV+[wet], UV–[wet], and UV+[dry]. Exposure to the individual treatments started at the beginning of May and lasted for three months. Volumetric soil water content (ThetaProbe ML2x, Delta, UK) at depth 15 cm was reduced at the end of experiment to approximately 20% in [dry], whereas it was above 50% in [wet].

In situ measurements of UV-screening compounds and physiological parameters were done after 3 months of acclimation (end of July). The CO_2 assimilation rate (A_{max}) and stomatal conductance (Gs_{max}) at saturation irradiance were determined by the gas-exchange analyser Li-6400 (LiCor, USA). UV screening compounds (flavonols) were determined by the method of epidermal screening of chlorophyll fluorescence (Dualex 4 Flav, Force A, F).

RESULT AND DISCUSSION

Generally, UV and drought treatments had a similar effect on the accumulation of flavonols (Fig. 1). UV exclusion resulted in a slight reduction of UV-shielding compounds, in all species studied. This reduction was more pronounced under the conditions of ambient precipitation [wet]. Drought treatment [dry] caused an increase in the accumulation of flavonols compare to the [wet] treatment in all species studied and irrespective of UV treatment. Thus, the drought treatment reduced the differences in flavonol contents between the UV+ and UV– treatments, particularly in species with generally higher content of flavonols such as *H. maculatum*. These data support the hypothesis that flavonoids may serve antioxidant functions in response to excess light (particularly UV-B) and drought stress (Tattini et al. 2004).

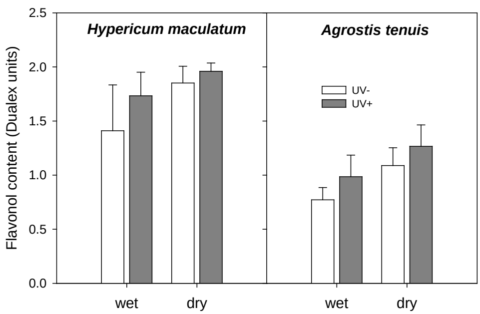

Fig. 1 Flavonol content measured in vivo using the instrument Dualex 4 Flav at the end of experiment. Data are presented for herb Hypericum maculatum and grass Agrostis tenuis. Means (columns) and standard deviations (error bars) are presented (n≥10).

Under the UV– treatment, drought markedly decreased light saturated assimilation rate A_{max} (Fig. 2). However, the presence of UV radiation led to lower differences in CO_2 assimilation rate between [wet] and [dry] treatments. We assume that this is due to protective mechanisms induced by UV radiation (accumulation of flavonols), which contribute to the mitigation of negative impacts of drought on photosynthesis. Similar results, demonstrating the moderating effect of UV radiation on the impact of drought have so far been found only in highly controlled studies on crop species. For example, Nogues et al. (1998) found that UV-B radiation both delayed and reduced the severity of drought stress through reductions in plant water-loss rates, stomatal conductance, and leaf area. Alexieva et al. (2001) have shown in pea as well as in wheat plants that under conditions with combined UV-B and drought stress, each of the stress factors seems to bring out some adaptive effects to reduce the damage experienced by plants caused by the other one.

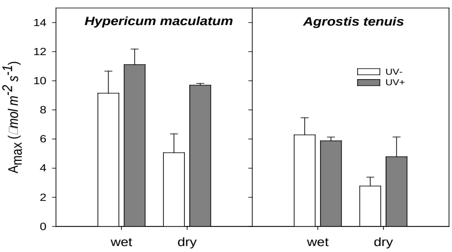

Fig. 2 The changes in light-saturated CO_2 assimilation rate A_{max} in response to drought and UV treatments at the end of experiment. Data are presented for herb Hypericum maculatum and grass Agrostis tenuis. Means (columns) and standard deviations (error bars) are presented (n≥5).

In addition to the increased induction of antioxidant accumulation (flavonols) by UV+ treatment, the negative effect of drought was also alleviated by increased water use efficiency, determined as a ratio A_{max}/Gs_{max} (Fig. 3). Both, UV radiation and drought increased A_{max}/Gs_{max} ratio in similar way. Likewise, Gitz et al. (2005) showed that some *Glycine max* cultivars respond to increased levels of UV-B by increasing water use efficiency and that this response could be manifested through changes in stomatal development and functioning.

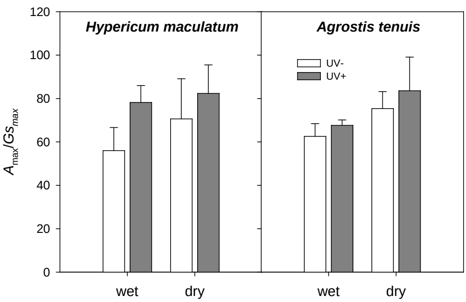

Fig. 3 The changes in apparent water use efficiency A_{max}/Gs_{max} in response to drought and UV treatments at the end of experiment. Data are presented for herb Hypericum maculatum and grass Agrostis tenuis. Means (columns) and standard deviations (error bars) are presented (n≥5).

CONCLUSIONS

UV-B radiation moderates the negative effects of drought on photosynthesis due to increased content of flavonols and improved water use efficiency. The initial hypothesis was confirmed in both mono- and dicotyledon species. Our study confirms the important role of UV radiation in the regulation of water use efficiency by UV reduction in natural ecosystem and is meaningful with respect to the ecosystem level responses to the abiotic factors and to the ecosystem functioning under potential future climate change.

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