



**Solar Ultraviolet-B radiation at Zackenberg: The impact on higher plants and soil microbial communities**

**In: High-arctic ecosystem dynamics in a changing climate (eds H. Meltofte, T.R. Christensen, B. Elberling, M. Forchhammer, M. Rasch)**

Albert, Kristian; Rinnan, Riikka; Ro-Poulsen, Helge; Mikkelsen, Teis; Håkansson, Kirsten; F. Arndal, Marie; Michelsen, Anders

*Publication date:*  
2008

*Document version*  
Publisher's PDF, also known as Version of record

*Citation for published version (APA):*

Albert, K., Rinnan, R., Ro-Poulsen, H., Mikkelsen, T., Håkansson, K., F. Arndal, M., & Michelsen, A. (2008). *Solar Ultraviolet-B radiation at Zackenberg: The impact on higher plants and soil microbial communities*. In: *High-arctic ecosystem dynamics in a changing climate* (eds H. Meltofte, T.R. Christensen, B. Elberling, M. Forchhammer, M. Rasch). New York: Elsevier. *Advances in Ecological Research*, Vol.. 40

# Solar Ultraviolet-B Radiation at Zackenberg: The Impact on Higher Plants and Soil Microbial Communities

KRISTIAN R. ALBERT, RIIKKA RINNAN, HELGE RO-POULSEN,  
TEIS N. MIKKELSEN, KIRSTEN B. HÅKANSSON, MARIE  
F. ARNDAL AND ANDERS MICHELSEN

Summary . . . . .	421
I. Introduction . . . . .	422
II. Vegetation and Plant Eco-Physiological Responses at Zackenberg . . . . .	424
III. Comparisons of Plant Responses Throughout the Polar Region . . . . .	430
IV. Below-Ground Responses . . . . .	432
V. Methodological Considerations of the Experimental Approaches . . . . .	434
VI. Conclusions and Future Directions . . . . .	436
Acknowledgments . . . . .	437
References . . . . .	437

## SUMMARY

Depletion of the ozone layer and the consequent increase in solar ultraviolet-B (UV-B) radiation may impact living conditions for arctic plants significantly. In order to evaluate how the prevailing UV-B fluxes affect the heath ecosystem at Zackenberg (74°30'N, 20°30'W) and other high-arctic regions, manipulation experiments with various set-ups have been performed.

Activation of plant defence mechanisms by production of UV-B-absorbing compounds was significant in ambient UV-B in comparison to a filter treatment reducing the UV-B radiation. Despite the UV-B screening response, ambient UV-B was demonstrated to decrease photosynthesis and shift carbon allocation from shoots to roots. Moreover, ambient UV-B increased plant stress with detrimental effects on electron processing in the photosynthetic apparatus. Plant responses did not lead to clear changes in the amount of fungal root symbionts (mycorrhiza) or in the biomass of microbes in the soil of the root zone. However, the composition of the soil microbial

community was different in the soils under ambient and reduced UV-radiation after three treatment years.

These results provide new insight into the negative impact of current UV-B fluxes on high-arctic vegetation. They supplement previous investigations from the Arctic focussing on other variables like growth and so on, which have reported no or minor plant responses to UV-B, and the presented synthesis clearly indicates that UV-B radiation is an important factor affecting plant life at high-arctic Zackenberg. However, long-time experiments are needed in order to see whether the observed changes are transient or whether they accumulate over years. Such experiments are especially important for valid determination of below-ground responses, which potentially lead to feedbacks on the ecosystem functioning.

## I. INTRODUCTION

The ecosystem responses to ultraviolet-B (UV-B) radiation (280–315 nm; CIE, 1999) in the Arctic are a research area of growing interest (Callaghan *et al.*, 2004a, 2005), motivating investigations focused to identify the targets and the relative importance of UV-B alone and in interaction with other global change factors. The increase in UV-B radiation is the result of stratospheric ozone depletion (Webb, 1997; Madronich *et al.*, 1998). The ozone-destroying chemical reactions are caused by chlorine and bromide released from emitted chlorofluorocarbons and halons (Farman *et al.*, 1985) and the very cold stratospheric temperatures (below  $-78^{\circ}\text{C}$ ). The process is highly temperature dependent, it is most pronounced during spring with cold stratospheric conditions and it also varies from year to year (Weatherhead *et al.*, 2005). Currently, the UV-B irradiance level in the arctic region is considered to be near its maximum, and the ozone column is estimated to recover towards the middle of the century, but the rate of ozone recovery is uncertain in the northern hemisphere (WMO, 2003). Increased cloudiness decreases the amount of UV-B radiation reaching the ground (Madronich *et al.*, 1998), but the predictions of future cloud cover and cloud types are uncertain (Weatherhead *et al.*, 2005). The UV-B fluxes at Zackenberg ( $74^{\circ}30'\text{N}$ ,  $20^{\circ}30'\text{W}$ ), where this study was performed, peak in late May and early June, and high doses still prevail during July and August (see Figure 1 in Rinnan *et al.*, 2005). This means that changes in snow-cover and length of the growing season may affect the UV-B exposure dose of the vegetation. Moreover, vegetation located in the snow-free patches will receive greatly increased UV-B dose because of irradiance reflected from the surrounding snow (Jokela *et al.*, 1993; Gröebner *et al.*, 2000).

High-arctic plants are “living on the edge” because they are growing on the limit of their distribution in an extreme environment with a short growing season, low temperatures and often nutrient limitation. Therefore, acclimation

is of special importance especially when the plants face environmental changes, such as increased UV-B radiation (Caldwell *et al.*, 1980; Robberecht *et al.*, 1980), which can cause additional stress under ambient conditions (Bredahl *et al.*, 2004; Albert *et al.*, 2005a, 2007a). In addition, because the vegetation in the Arctic is evolutionary adapted to low UV-B levels (Robberecht *et al.*, 1980; Caldwell and Flint, 1994), the potential impact on the vegetation is expected to be pronounced (Björn *et al.*, 1999; Paul, 2001). This leads to the hypothesis that arctic plants are negatively influenced by the current UV-B levels. Thus, if the present UV-radiation affects the vegetation significantly, then reduction of the irradiance load would improve the photosynthetic performance of the plants. Therefore, an experimental approach where ambient UV-irradiance is screened off by means of filters was chosen in this study.

The previous knowledge of polar ecosystem responses to UV-irradiance is the result of field experiments with various experimental approaches: UV-radiation has been elevated by various lamp setups (e.g., Johanson *et al.*, 1995a,b; Björn *et al.*, 1999; Gwynn-Jones *et al.*, 1997; Phoenix *et al.*, 2001 and others), transplants have been set up along latitudinal gradients (Lehrner *et al.*, 2001), or UV-radiation has been reduced by means of filters (Xiong and Day, 2001; Phoenix *et al.*, 2002; Robson *et al.*, 2003; Albert *et al.*, 2005a). In principle, the studies supplementing UV-B relate closely to scenarios with future increased UV-B levels, whereas experimental UV-reduction relates to the impacts of the current level of solar UV-radiation.

UV-exclusion experiments by means of filters are attractive in several ways. They are simple and do not require electrical power or any special technical maintenance, which is an advantage in remote areas. Further, differences in spectral ratios, which are a problem in the UV supplementation experiments (Caldwell and Flint, 1994), can be avoided. However, reduction of the UV-B irradiance by 60% or more implies a higher relative change in the UV-B load than is predicted to take place in nature. Anyhow, the clear advantage to emphasise here is that the interpretation of results from UV-exclusion experiments directly relates to the impact of current level of UV-radiation, and that the exposure includes the variability during the growing season and from year to year.

The prevalent view is that—although UV-radiation induces increased production of phenolics and berries and alters the below-ground processes (Gwynn-Jones *et al.*, 1997; Searles *et al.*, 2001a; Johnson *et al.*, 2002)—arctic plants are more or less tolerant to enhanced UV-B in the long term (Phoenix *et al.*, 2001; Callaghan *et al.*, 2004b; Rozema *et al.*, 2006). Moreover, as discussed by Phoenix *et al.* (2001) and Phoenix and Lee (2004), other climatic changes, such as increased CO<sub>2</sub>, temperature or changes in precipitation, may further negate the detrimental effects of enhanced UV-B in the sub-arctic.

## II. VEGETATION AND PLANT ECO-PHYSIOLOGICAL RESPONSES AT ZACKENBERG

The experiments at Zackenberg approached the effects of ozone depletion on ecosystems by comparing the responses to prevailing UV-B fluxes to responses to reduced UV-levels obtained by different filter arrangements, which covered plots of the ecosystem (see [Box 1](#) for an outline of the conducted

### Box 1

#### Overview of UV-B experiments at Zackenberg

UV-exclusion experiments were initiated in 2001, and until 2003 intensive monitoring of the microclimate in the experimental plots was done. The vegetation composition was mapped, and the hypothesised response parameters, such as photosynthesis, plant stress, leaf content of UV-B-absorbing compounds, carbon, nitrogen and soil characteristics, were investigated. The project is unique in the High Arctic and will be continued in cooperation with the ZERO programme.

**2001** Establishment of two permanent sites differing in inclination (“level” and “sloping” sites) with four treatments in four groups: Filter treatments with UV-AB-reducing Lexan, UV-B-reducing Mylar, UV-transparent Teflon and a treatment without filter being an open control ([Box Figure 1](#)). Two independent climatic stations continuously logged microclimate: Air and soil temperatures, and in one group soil humidity, under and outside the filters as well as air humidity, air temperature and irradiance of photosynthetically active radiation (PAR) and UV-B at each site. Weekly measures of chlorophyll *a* fluorescence induction curves were conducted on bog blueberry *Vaccinium uliginosum* and arctic willow *Salix arctica* and end season harvest of leaves enabled analysis of UV-B-absorbing compounds. Gas exchange was measured on *S. arctica*. Results were published by [Bredahl et al. \(2004\)](#).

**2002** Investigations on the permanent experimental plots were continued as the previous year. Moreover, two new experiments with UV-B-reducing Mylar and UV-transparent Teflon lasting one growth season were conducted: (1) Maximum irradiance experiment, where the irradiation doses were homogenised by controlling leaf angle on *S. arctica*, and intensive measures of chlorophyll fluorescence were conducted; (2) Robust measurements of photosynthesis were achieved by chamber measurements of gas exchange on whole canopies of *V. uliginosum* supplemented by chlorophyll fluorescence measurements. Results were published by [Albert et al. \(2005a, in press\)](#).

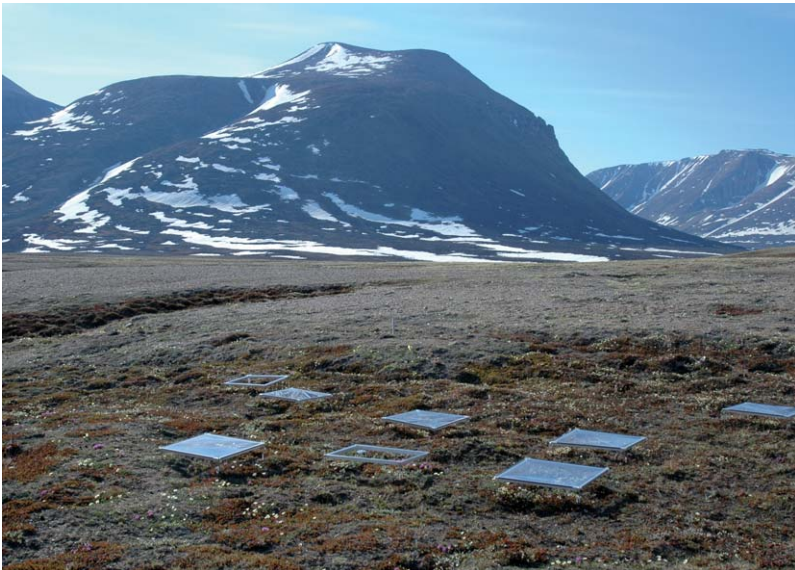
**2003** Investigations on the permanent experimental plots were continued as in previous years, and in addition soil samples for root

biomass and microbial community analyses were taken. Continued experimentation with homogenised irradiation doses on *S. arctica* were performed on new plants shoots designed to achieve two different irradiance levels. Here, intensive measurements of both gas exchange and of chlorophyll fluorescence were conducted. Results were published by [Albert \*et al.\* \(2005b\)](#), [Rinnan \*et al.\* \(2005\)](#) and [Håkansson \(2006\)](#).

**2004** No manipulations and no observations.

**2005** Re-establishment of the permanent experimental plots and continuation of the measurements on *S. arctica* and *V. uliginosum* as done in previous years. Moreover, dwarf birch *Betula nana* was included on a new site with the same setup and measurement campaign. The experimentation with effects of homogenised irradiation doses on *S. arctica* was continued and measures of simultaneous chlorophyll *a* fluorescence and gas exchange were performed. Reflectance measures in the range 325–1250 nm were performed on all species, and leaves were sampled for analysis of secondary compounds, chlorophyll, C and N. Results presented in 11th Annual ZERO Report, 2005.

**2006** Continuation of the measurement campaign on *V. uliginosum*, *S. arctica* and *B. nana*. Results presented in 12th Annual ZERO Report, 2006.



**Box Figure 1** The experimental setup on a part of one of the permanent experimental sites (Site 2) comprising open control, filter control, UV-B-excluding Mylar filter and UV-AB-excluding Lexan.

Vegetation below filters is dominated by *Vaccinium uliginosum* and *Salix arctica*. In the background, the Zackenberg Mountain is seen. Photo: [K. Albert, 2002](#).

experiments and their responses). The four main treatments comprised open control plots without any filters, UV-transparent filter controls, filters reducing UV-B (280–315 nm) and filters reducing both UV-B and UV-A (315–400 nm). These treatments exposed the vegetation to *c.* 100%, 91%, 39% and 17% of ambient UV-B radiation and 100%, 97%, 90% and 91% of the photosynthetically active radiation (PAR), respectively (Bredahl *et al.*, 2004). Filters also slightly changed the microclimate when compared to the open control. Three succeeding years of measurements during the growing season revealed that the filters increased the mean soil temperature up to 0.6°C, but this did not affect soil humidity. No significant mean air temperature difference was observed within the filter treatments or between the filter treatments and the open control. Between the filter treatments no microclimatic differences were found (K. Albert, unpublished).

From the range of UV-exclusion experiments conducted at Zackenberg, the emerging pattern is that there are significant plant-ecophysiological responses (Table 1). The chosen parameters, that is, photosynthesis and probing of plant stress, are generally expected to respond faster than many other important ecological processes, such as growth, phenology and species composition, which may respond to disturbances on a longer timescale (Callaghan *et al.*, 2004c). However, inter-species differences in plant performance characteristics are important since the traits are likely to influence competition and the resulting plant cover.

Measurements of chlorophyll *a* fluorescence induction curves led to calculation of the much reported parameter, maximal quantum yield ( $F_V/F_M$ ), which closely relates to photosystem II (PSII) function and is often interpreted as a proxy for plant stress related to photosynthetic performance (Strasser *et al.*, 2004; see Box 2 for more information on photosynthesis and plant performance). Also the so-called performance index, PI (Strasser *et al.*, 2004) was derived from the fluorescence measurements. The PI integrates into one parameter the proportional responses of energy fluxes related to trapping and dissipation within the PSII and also to the energy transport behind PSII. Hereby, the PI expresses the overall effective energy processing through PSII and is believed to sum up the accumulative stress effects on PSII.

The UV-exclusion experiments were initiated in 2001 (see Box 1), and it was found that a reduction in the ambient UV-B level resulted in decreased content of UV-B-absorbing compounds and lower stress level indicated by increased  $F_V/F_M$  (Bredahl *et al.*, 2004) and PI in arctic willow *Salix arctica* and Bog blueberry *Vaccinium uliginosum ssp. microphyllum*. Moreover, the analysis of leaf level gas exchange revealed a decreased stomatal conductance and internal CO<sub>2</sub> concentration in *S. arctica* when ambient UV-B was reduced (Bredahl *et al.*, 2004). These findings were initially concluded to indicate the important impact of UV-B in the short term. However, the greatly varying leaf angle results in differences in UV-B doses for the

**Table 1** Ecosystem responses to UV-B exclusion at Zackenberg

Response type	Parameters	Short-term effects			Long-term effects	
		<i>Salix</i>	<i>Vaccinium</i>	<i>Betula</i>	<i>Salix</i>	<i>Vaccinium</i>
Plant stress	Maximal photochemical efficiency ( $F_V/F_M$ )	↓ (~)	↓	↓	↓	↓
	Performance index (PI)	↓	↓	↓	↓	↓
Photosynthetic	Photosynthesis ( $P_n$ )	~	↓	#	#	#
	Respiration ( $R_d$ )	#	~	#	#	#
	Transpiration (Tr)	Δ	~	#	#	#
	Intercellular CO <sub>2</sub> concentration ( $C_i$ )	↓	#	#	#	#
	Stomatal conductance ( $g_s$ )	↑	#	#	#	#
Growth	Leaf biomass	~	~	#	~	~
	Stem biomass	~	~	#	~	~
	Root biomass	#	#	#	#	↓
	Leaf area	~	~	#	~	~
Leaf chemistry	Specific leaf area	~	~	#	~	~
	UV-B-absorbing compounds	↑	↑	↑	↑	↑
	Carbon	~	~	~	~	~
	Nitrogen	~	~	~	~	~
Plant species composition	Chlorophyll	#	#	↓	#	#
	Cover	~	~	~	~	~
Mycorrhiza	Mycorrhizal colonisation	#	#	#	#	↑↓
	Root ergosterol concentration	#	#	#	#	~
Microbial biomass	Microbial biomass carbon	#	#	#	~	~
	Microbial biomass nitrogen	#	#	#	~	~
	Microbial biomass phosphorous	#	#	#	~	~
	Soil ergosterol concentration	#	#	#	~	~
	Phospholipid fatty acid (PLFA) biomarkers	#	#	#	Δ	Δ

*Note:* Ambient UV-B responses are compared to reduced UV-B after 1 and 3 years labelled short- and long term. Only significant changes are labelled with arrows. Signatures: No effect (~); Negative impact (↓); Positive impact (↑); Changed (Δ); Not investigated (#).



## Box 2

### Photosynthesis and plant performance

The photosynthetic processes can be separated into energy-producing (sources) and energy-consuming processes (sinks). Source processes are involved in the capture of light and the processing through the photosynthetic apparatus, resulting in available energy equivalents. Sink processes are the energy-demanding processes, primarily CO<sub>2</sub> assimilation in the Calvin cycle. The molecules of CO<sub>2</sub> diffuse into the leaf through stomatal openings into the stomatal cavities and from here further through the internal leaf cells until finally reaching the chloroplast, where the Calvin cycle takes place. Here, the CO<sub>2</sub> molecules assimilated are stored in energy-rich metabolites, that is, sugar, which is allocated to different plant parts for growth and maintenance. Under field conditions, the often used methods to probe both the characteristics and activity of the source and sink sides are to do measurements of chlorophyll *a* fluorescence and CO<sub>2</sub> and H<sub>2</sub>O gas exchange. The sink processes are evaluated by parameters as, for example, net photosynthesis ( $P_n$ ), stomatal conductance ( $g_s$ ) and transpiration (Tr), while the source processes are evaluated by maximal quantum yield ( $F_v/F_M$ ), performance indexes (PI), and a range of other parameters related both to the handling of light in the photosynthetic apparatus and partitioning of energy fluxes. The much reported parameter, maximal quantum yield ( $F_v/F_M$ ), closely relates to photosystem II (PSII) function and is often interpreted as a proxy for plant stress. The PI integrates into one parameter the proportional responses of energy fluxes related to trapping and dissipation within the PSII and also to the energy transport behind PSII. Hereby, the PI expresses the overall effective energy processing through PSII and is believed to sum up the accumulative effects on PSII. Based on such measurements, the targets of environmental stressors can be both identified and quantified and the overall performance of the photosynthetic processes is assessed.

individual leaves, which probably confounded the effects. This hypothesis led to an experimental attempt to homogenise the UV-B dose received by the leaves by manipulative fixation of the plant leaves perpendicular to the Sun.

The second season (2002) included such a setup with fixation of leaves, and this led to clear-cut positive impacts on almost all measured and derived fluorescence parameters on *S. arctica*. The results on  $F_v/F_M$  and PI confirmed that ambient UV-B radiation is a significant plant stressor

(Albert *et al.*, 2005a). Also the proportions of energy fluxes per leaf cross section were quantified, and the dissipation of untrapped energy was highest under ambient UV-B, resulting in significantly lower flux of energy beyond the electron intersystem carriers (Albert *et al.*, 2005a). These responses are argued to be specifically due to the UV-B radiation (Albert *et al.*, 2005a), and they demonstrate a less effective energy processing in the photosynthetic machinery. For logistical reasons, no leaf level photosynthetic measurements were done on *S. arctica* that year, but measurements of photosynthesis and respiration were conducted on whole canopies of *V. uliginosum*. The *V. uliginosum* plants showed a decreased photosynthesis in parallel with decreased values of  $F_V/F_M$  and PI in ambient UV-B compared to the reduced UV-B treatment (Albert *et al.*, in press). This response was seen through most of the growth season, but in the senescence period in late August the treatment differences disappeared. These results clearly linked the decrease in net photosynthesis to the stress effects on the light-energy harvesting and processing machinery. Also the *V. uliginosum* plants had a higher level of UV-B-absorbing compounds in the leaves under ambient UV-B (Albert *et al.*, in press), but the possible protective screening by these compounds was obviously not sufficient to avoid negative effects on the photosynthetic machinery.

It has been argued by Searles *et al.*, (2001a) and others that changes in UV-B-absorbing compounds as such are not a good indicator of the degree of UV-B impact in plants, although the increase in UV-B-absorbing compounds in response to UV-B is the most consistent and frequent plant response (Searles *et al.*, 2001a). The pool here referred to as UV-B-absorbing compounds includes a range of secondary compounds, and moreover no distinction between wall bound and cellular compounds is generally made. These compounds have also other functions related to antioxidation (Bornman *et al.*, 1998; Rozema *et al.*, 2002) and plant defence against herbivores (Harborne and Grayer, 1993). Hence, the UV-induced alterations in the amount and quality of the UV-B-absorbing compounds may have implications for both herbivory (Ballaré *et al.*, 1996; Rousseaux *et al.*, 2004a) and litter decomposition (Björn *et al.*, 1999), affecting nutrient cycling, although this has not yet been investigated at Zackenberg.

For *S. arctica* plants, physiological responses between male and female plants may differ (Jones *et al.*, 1999; Håkansson, 2006). In a short-term study in 2003 on *S. arctica* at Zackenberg, the sex actually interacted with treatment responses, and surprisingly no significant treatment differences were found on  $F_V/F_M$ , photosynthesis or content of UV-B-absorbing compounds. The response was in general ascribed to the particularly high content of UV-B-absorbing compounds, being more than 50% higher than previous years, leading to effective screening against UV-B radiation. If this explanation is correct, then it suggests that plants under some conditions actually are able to cope with

the negative impact of UV-B. Håkansson (2006) also investigated the effect of sudden filter removal in filter treatments during peak season. Although no treatment-specific responses *per se* were detected hereafter, the plants actually became more stressed when re-exposed to ambient UV-B. This was indicated by decreased  $F_v/F_M$ , whereas the cohort of plants still being treated with filters showed the opposite and decreased their stress level.

Throughout the 3-year period (2001–2003), it was consistently found that *S. arctica* and *V. uliginosum* leaves exposed to current UV-B fluxes had higher content of UV-B-absorbing compounds and were experiencing a higher stress level than when UV-B was reduced (K. Albert, unpublished).

An investigation on dwarf birch *Betula nana* during 2005 clearly demonstrated a similar plant stress release by UV-reduction as earlier observed in *S. arctica* and *V. uliginosum*.  $F_v/F_M$  and PI were significantly increased throughout the experimental period in July and the beginning of August in the treatments where large proportions of UV-B and UV-AB were excluded as compared to both filtered and open control (Albert *et al.*, 2006). The stress response was previously hypothesized to be restricted to periods with high irradiance (of both PAR and UV) (Albert *et al.*, 2005a), and this was tested by measurements throughout a day under clear sky conditions. As expected, a midday depression in both  $F_v/F_M$  and PI was seen in *B. nana* across treatments in parallel with irradiance doses, which were maximal when the Sun was in Zenith. Surprisingly, the level of the PIs in the UV-reduction treatments stayed higher during all times of the day. This demonstrates that the control plants, which were exposed to the ambient level of UV-radiation, appear to be permanently stressed and do not recover after exposure to the midday high irradiation event by finalising repair processes. This new finding points to the importance of negative impacts of ambient UV-radiation on the photosynthetic apparatus in *B. nana*, which may be rendered as a UV-sensitive plant species, at least in the short term.

### III. COMPARISONS OF PLANT RESPONSES THROUGHOUT THE POLAR REGION

Although caution is needed when making generalisations of polar plant responses because of differences between Antarctic and arctic ecosystems (e.g., higher species diversity, more trophic interactions and lower UV-B fluxes in the Arctic) (Rozema *et al.*, 2005), our observations are in agreement with the UV-exclusion studies conducted in the Antarctic ecosystems showing that ambient UV-B can have significant impacts.

Responses from the UV-exclusion studies carried out on the Antarctic Peninsula and in sub-Antarctic Tierra del Fuego point to negative UV-B effects

on plant growth (Day *et al.*, 1999; Rousseaux *et al.*, 1999; Ruhland and Day, 2000; Ballaré *et al.*, 2001 and others) and increased phenolic production in most species (Day *et al.*, 2001; Searles *et al.*, 2001a,b). Further, DNA damage (Rousseaux *et al.*, 1999) has been observed particularly during the high spring-time UV-B fluxes (Xiong and Day, 2001; Ruhland *et al.*, 2005) and also in the longer term (Robson *et al.*, 2003). The negative impact on plant biomass production, as reported by Xiong and Day (2001), was not associated with reduced photosynthesis per leaf area, but rather with reduced photosynthesis per chlorophyll amount or leaf dry mass. Xiong and Day (2001) interpret this response as that under UV-B, the plants were denser and probably had thicker leaves with a higher amount of photosynthetic and UV-B-absorbing pigments per leaf area. On the other hand, the analysis of chlorophyll *a* fluorescence and photosynthetic light response curves demonstrated that photosynthesis was impaired in the upper cell layers, but this did not translate into changes in photosynthetic rates at the whole leaf level.

There are differences between the responses observed at high-arctic Zackenberg compared to high-arctic Svalbard and the sub-arctic Abisko in northern Sweden, where most UV-B supplementation studies have been conducted.

No effects of 7 years of UV-B supplementation were detected on plant cover, density, leaf weight, leaf area, reproductive parameters, leaf UV-B absorbance and content of total phenolics in plants on arctic Svalbard (Rozema *et al.*, 2006). The absence of responses to enhanced UV-B in Svalbard was discussed to indicate several aspects. First, the differences in UV-B levels posed in supplemental studies are less than in UV-B exclusion studies, where responses were argued to be more difficult to detect. Secondly, the tundra biome in Svalbard originates from latitudes with higher natural solar UV-B fluxes implying a possible higher tolerance to UV-B (Rozema *et al.*, 2006).

Based on long-term studies conducted in the area of Abisko, it has been concluded that the dwarf shrubs there seem tolerant to ambient UV-B (Phoenix *et al.*, 2001, 2002; Callaghan *et al.*, 2004b; Rozema *et al.*, 2006). In some instances, enhanced UV-B radiation reduced plant growth, modified plant—herbivore interactions (Gwynn-Jones *et al.*, 1997), slowed the rate of litter decomposition, altered microbial soil biomass (Johnson *et al.*, 2002) and reduced cyanobacterial nitrogen fixation (Solheim *et al.*, 2002), but did not change plant cover or DNA damage (Rozema *et al.*, 2005, and references herein).

The investigations in sub-arctic Abisko and high-arctic Svalbard have put more weight on traditional parameters such as various measures of growth, phenology and so on, while the Zackenberg research has had a more non-invasive approach by weighting photosynthetic and stress variables, which respond immediately to changes in radiation. To take advantage of both

approaches, work focused on linking variables across scales, that is, the photosynthetic response to other measures of growth, should be done. However, because of the difference in variables measured and also a different experimental approach (supplementing UV-B vs UV-B exclusion), direct comparisons are not always possible. In the [section V](#) below, these important issues are discussed further.

#### IV. BELOW-GROUND RESPONSES

While above-ground plant responses have received much attention over the years, possible effects of UV-B radiation on below-ground components of arctic ecosystems are less well understood. Although the presence of creeping tundra plants leads to higher UV penetration to the soil compared to the presence of more shading cushion plants, grasses and mosses ([Hughes \*et al.\*, 2006](#)), UV-radiation mainly affects the soil communities indirectly via effects on plants.

Ambient UV-B radiation at Zackenberg reduced root biomass of *V. uliginosum* as determined by soil core sampling after 3 years of UV-B exclusion ([Rinnan \*et al.\*, 2005](#)). The lower root biomass is well in agreement with the responses in the above-ground plant parts, as ambient UV-B also reduced photosynthesis and induced stress to the photosynthetic machinery ([Bredahl \*et al.\*, 2004](#); [Albert \*et al.\*, in press](#)) as discussed above. Reductions in below-ground plant components due to ambient UV-B levels have also been reported for southern high latitudes. For instance, root length production of *Carex* spp. at a fen in southern Argentina was significantly lower under near-ambient than under reduced UV-B radiation ([Zaller \*et al.\*, 2002](#)). At Palmer Station, at the Antarctic Peninsula, near-ambient UV-B radiation reduced root biomass of the Antarctic hair grass *Deschampsia antarctica* by 34% compared to the plants under reduced UV-B radiation ([Ruhland \*et al.\*, 2005](#)). However, in this case the above-ground biomass was reduced even more, which led to a higher root-to-shoot ratio under near-ambient UV-B ([Ruhland \*et al.\*, 2005](#)).

Changes in plant photosynthesis and carbon allocation are likely to have an impact on mycorrhizal symbionts living in association with plant roots. At Zackenberg, the response of mycorrhizal fungi to UV-B manipulations was unclear at the level site (see [Box 1](#) for the details of experimental setup). The light microscopical analyses indicated that the roots of *V. uliginosum* were more colonised by ericoid-type mycorrhiza under reduced UV-B radiation, but at the sloping site, the response was nearly opposite ([Rinnan \*et al.\*, 2005](#)). The only other report on effects of UV-B radiation on ericoid mycorrhiza that we are aware of states that 5 years of UV-B enhancement by fluorescent

lamp arrays simulating 15% ozone depletion at Abisko had no effects on mycorrhizal colonisation (Johnson, 2003).

Net primary production (Callaghan *et al.*, 2004c) often correlates with the soil microbial biomass (Wardle, 2002). At our sites at Zackenberg, microbial biomass determined by the fumigation–extraction technique was, indeed, significantly associated with the total root biomass per soil volume ( $R^2 = 0.23$ ,  $p < 0.01$ ). However, the UV-B manipulations had no statistically significant effects on the soil microbial biomass or concentrations of nitrogen and phosphorus in the biomass (Rinnan *et al.*, 2005). This is in contrast with the results from a sub-arctic heath at Abisko, where UV-B supplementation for 5 years resulted in lower soil microbial biomass carbon and higher microbial biomass nitrogen concentration (Johnson *et al.*, 2002). However, a similar UV-B supplementation as at Abisko had no effects on the soil microbial biomass in a mesotrophic sub-arctic mire in northern Finland (R. Rinnan, unpublished data).

Potential UV-B-induced changes in the chemical quality and quantity of the labile carbon substances exuded from plant roots (i.e., root exudates) could affect soil microbial community composition. In order to compare the composition of the microbial communities between the UV-B treatments in our experiments at Zackenberg, we extracted phospholipid fatty acids (PLFAs) from the soil, which are biomarkers specific to different bacteria and fungi (Zelles, 1999). The PLFA profiles were indeed different under ambient and reduced UV-B fluxes (Rinnan *et al.*, 2005), which indicates that ambient UV-B radiation in Greenland has indirect effects on the soil microbial communities. This finding is supported by results both from the sub-arctic (Johnson *et al.*, 2002; R. Rinnan, unpublished data) and from Antarctica (Avery *et al.*, 2003), which reported effects of UV-B radiation on the utilisation of different carbon sources by culturable soil bacterial community. As the fungal biomass in the soil from Zackenberg was not affected by UV-B radiation based on the quantity of fungal PLFA biomarkers and ergosterol concentration (Rinnan *et al.*, 2005), the community composition alterations appeared to occur within the bacterial community.

Relating microbial community composition to microbial-driven ecosystem processes such as decomposition and nutrient transformations in the soil is not straightforward. Therefore, it is not possible to extrapolate how UV-B radiation would affect ecosystem functioning based on the observed responses in microbial community composition. Further analyses of microbial community by molecular methods and targeted measurements of ecosystem processes, such as nitrogen transformations, could reveal whether a certain group of bacteria was especially affected. As the indirectly induced below-ground responses can first take place after a strong enough response has occurred in plants, a 3-year-long experiment may not be long enough to show the eventual responses.

## V. METHODOLOGICAL CONSIDERATIONS OF THE EXPERIMENTAL APPROACHES

In many cases, the drivers of ecosystem responses can best be identified by an experimental approach. Ideally, this implies well-documented long-term multi-factorial manipulations and comprehensive effects investigations. This approach takes advantage of testing the actual impact of the hypothesised driver and their interactions on ecosystem processes. If the environmental perturbations are realistic and well conducted they not only identify key ecosystem responses but also reveal their strength and relative importance in time and space. The syntheses of such results are the starting point for generation of novel hypotheses, which may be tackled via new experiments and relevant ecosystem modelling.

Concerning the responses to UV-B radiation: Is it possible to extrapolate results from UV-B exclusion experiments to future scenarios of ozone depletion and UV-B radiation climate? This exercise demands a range of premises to be discussed of which the most important are outlined below.

The supplemental studies which are closely simulating future scenarios may be argued to be far more realistic. UV-B exclusions substantially change the total UV-B irradiation to a much higher degree (up to 60%) than supplemental UV-B studies simulating 15–30% enhancement of UV-B do. Hence, UV-exclusion may *per se* be expected to induce greater responses in a dose-dependent context. Also the qualitative spectral differences existing between methodologies may be of importance. This is clearly indicated from studies applying treatments that reduce UV-B (UV-B-absorbing filter), ambient (UV-transmitting filter) and supplemental UV-B (UV-transmitting filter + lamps) in parallel (Gabeřšćik *et al.*, 2002; Rousseaux *et al.*, 2004b). Here, a stepwise dose-dependent UV-B response is to be expected on affected parameters, if responses are linear. Further, since the initiation of biological responses also are closely related to the spectral composition of light this adds to complexity.

To approximate the biological effective differences, which may be mediated by such differences in spectral composition, biological spectral weighting functions (BSWS) has been used by Rousseaux *et al.* (2004b). Here, biologically effective UV-B doses were calculated according to widely accepted and much used BSWS in an experiment with reduced UV, ambient UV-B and supplemental UV-B (30%) in parallel. Depending on BSWS, the doses differed by 1.4 to 6.4 times by comparing ambient UV-B to supplemental UV-B, whereas UV-doses differed by 1.5–77 times when comparing reduced UV-B to ambient UV-B. From this, it was concluded that considerable care is needed when comparing studies using the two different methodologies (Rousseaux *et al.*, 2004b).

If plants do not have linear responses to realistic doses of UV-B, are responses then subject to any thresholds? Does this relate to whether responses



are equally detectable by either approach? This is an area of dispute, but the directions of responses of parameters, such as UV-B-absorbing compounds, stomatal density, chlorophyll, transpiration and photosynthesis (although depending on species), are the same as with increases in UV-B within those few studies comprising reduced, ambient and enhanced UV-B radiation in parallel (Gabeřšcik *et al.*, 2002; Rousseaux *et al.*, 2004b). In addition, most of these responses display stepwise or dose-dependent changes (Gabeřšcik *et al.*, 2002; Rousseaux *et al.*, 2004b), although they probably are not universal. Concerning the phenolics, which also function as UV-B-absorbing compounds, UV-B exposure response curves have shown that the production of several phenolics quantitatively are UV-B dose dependent (de la Rosa *et al.*, 2001), but complex contrasting responses have also been seen. An increase in UV-B-absorbing compounds were found in supplemental UV-B (Phoenix *et al.*, 2000; Semerdjieva *et al.*, 2003a, 2003b), but no changes occurred when UV-B was excluded (Phoenix *et al.*, 2002) on sub-arctic *V. uliginosum*. Moreover, along a wide range of UV-B doses no evidence of a possible threshold UV-B dose for UV-B responses has been found (González *et al.*, 1998; de la Rosa *et al.*, 2001). Together these findings provide support that our approach is scientifically acceptable.

The fact that filter treatment may induce important microclimatic differences has to be taken into account. Filters may potentially change temperatures and humidity in air and soil and of course exclude rainwater. At Zackenberg, the filters were shown to only change soil temperature significantly, but this increase did not change the soil humidity. This was probably due to the very low precipitation during 2001–2003 growth seasons (Sigsgaard *et al.*, 2006) and that the filter plots were placed in an angle allowing vegetation to benefit from events of precipitation due to surface runoff from above the filters. Since filter treatments elevated mean soil temperature by 0.6°C, the UV effects may be viewed as a combined effect (warming plus UV-B reduction) compared to warming (filter control) and open control (no filter and no warming).

A special issue concerning the photosynthetic response is that the filter differences in PAR transmission may lead to differences in canopy photosynthesis (Flint *et al.*, 2003). The degree of photosynthesis impact depends on leaf area index (LAI) being increased by increased LAI. According to Flint *et al.* (2003), with an LAI of 1, 5–10% differences in PAR results in 2–4% difference in photosynthesis. Compared to the open control, the transmitted PAR is 97% and 90% in the filtered control and UV-B-reducing treatment, respectively. Thus, between filter treatments, the resulting difference is *c.* 7% less PAR-irradiance in the UV-B-reducing treatments, respectively. Since we observed a stepwise higher photosynthesis in parallel with less PAR-irradiance, the effect may be of little importance here.

In summary, taking the premises above into consideration, we believe that the UV-B exclusion approach is very well suited to identify the impact on



ecophysiological processes of current UV-B fluxes, whereas a UV-B supplemental approach may be better suited when evaluating their consequences. Hence, we argue that it is possible to indicate the direction of future ecosystem responses, but it remains speculative to actually quantify the responses within a particular UV-B radiation scenario, primarily because we do not know the UV-B exposure response curves and response to differences in the spectral composition of light.

## VI. CONCLUSIONS AND FUTURE DIRECTIONS

The range of significant responses seen in the UV-B exclusion experiments at Zackenberg clearly indicates that ambient UV-B is a plant stress factor in this area. This seems in contrast to the reported robustness towards supplemental UV-B for plants in sub-arctic Abisko and high-arctic Svalbard. However, the results from UV-B exclusion studies in the Antarctic region have demonstrated effects on plants, similar to the results from Zackenberg. There are differences in the chosen response variables, and the contrasting responses may be interpreted to be due to the climatic differences between the areas. Further, the extreme living conditions in the high-arctic Zackenberg and Antarctic region may to a larger degree amplify effects of the stress factors, leading to significant UV-B impacts here. Although the responses from Zackenberg provides new insight and supplements earlier work, more work dedicated to link variables across scales is needed to take full advantage of the earlier findings. Thus, only by making parallel UV-B supplementation and UV-B exclusion field experiments it is possible to exclude the methodological differences and validate the ecosystem responses. Furthermore, the experiments should be conducted over longer time periods and include more traditional parameters (e.g., shoot growth rate and biomass effects) in order to ease comparisons and to elucidate whether the observed changes are transient or whether they accumulate over years. Long-term experiments are especially important for valid determination of below-ground responses, which have the potential to pose great feedbacks on the ecosystem functioning.

If projections from climatic scenarios to future biological responses shall be made, the biological responses and their feedback must be detected in multi-factorial experiments closely resembling the climatic projections. If sufficient reliable biological response functions to climatic parameters can be established then ecosystem modelling shall be possible. Presently, we do not have sufficient knowledge of all responses of importance and their interactions. Concerning ozone layer depletion, a specific UV-B radiation scenario for Zackenberg is needed. What we can state is that ambient UV-B as a single factor affects plant life negatively at high-arctic Zackenberg, and that the methodology developed is very well suited for long-term monitoring.

## ACKNOWLEDGMENTS

The work was financially supported by DANCEA (Danish Co-operation for Environment in the Arctic) grant 123/000–0212, the Danish Environmental Protection Board, Climate and Environment Support MST grant 127/01–0205 and the Danish Natural Sciences Research Council grant 272–06–0230 and travel grants from the Svend G. Fiedler Foundation to Kristian Albert in 2005 and 2006. The Danish Polar Center provided excellent logistics and the dedicated staff personnel at the Zackenberg Research Station contributed by making stays in Zackenberg excellent conditions for research. Professor Sven Jonasson is acknowledged for enthusiastic support throughout all phases of the UV project. Finally, the authors thank Esben Vedel Nielsen, Gosha Sylvester, Niels Bruun, Karna Heinsen and Karin Larsen for help on soil and leaf chemical analyses and Svend Danbæk for solving all sorts of IT challenges.

## REFERENCES

- Albert, K.R., Mikkelsen, T.N. and Ro-Poulsen, H. (2005a) *Physiol. Plantarum* **124**, 208–226.
- Albert, K.R., Ro-Poulsen, H., Mikkelsen, T.N., Bredahl, L. and Haakansson, K.B. (2005b) *Phyton* **45**, 41–49.
- Albert, K.R., Arndal, M.F., Michelsen, A., Tamstorf, M.F., Ro-Poulsen, H. and Mikkelsen, T.N. (2006) In: *Zackenberg Ecological Research Operations, 11th Annual Report, 2005* (Ed. by M. Rasch and K. Caning), pp. 90–91. Danish Polar Center, Ministry of Science, Technology and Innovation, Copenhagen.
- Albert, K.R., Mikkelsen, T.N. and Ro-Poulsen, H. (in press) *Physiol. Plantarum* in press.
- Avery, L.M., Smith, R.I.L. and West, H.M. (2003) *Polar Biol.* **26**, 525–529.
- Ballaré, C.L., Scopel, A.L., Stapelton, A.E. and Yanovsky, M.J. (1996) *Plant Physiol.* **112**, 161–170.
- Ballaré, C.L., Rousseaux, M.C., Searles, P.S., Zaller, J.G., Giordano, C.V., Robson, T.M., Caldwell, M.M., Sala, O.E. and Scopel, A.L. (2001) *J. Photoch. Photobio. B* **62**, 67–77.
- Björn, L.O., Callaghan, T.V., Gehrke, C., Gwynn-Jones, D., Lee, J.A., Johanson, U., Sonesson, M. and Buck, N.D. (1999) *Polar Res.* **18**, 331–337.
- Bornman, J.F., Reuber, S., Cen, Y.-P. and Weissenböck, G. (1998) In: *Plant and UV-B. Responses to Environmental Change* (Ed. by P.J. Lumsden), pp. 157–170. Cambridge University Press, Cambridge.
- Bredahl, L., Ro-Poulsen, H. and Mikkelsen, T.N. (2004) *Arct. Antarct. Alp. Res.* **36**, 363–368.
- Caldwell, M.M. and Flint, S.D. (1994) *Climatic Change* **28**, 375–398.
- Caldwell, M.M., Robberecht, R. and Billings, W.D. (1980) *Ecology* **61**, 600–611.
- Callaghan, T.V., Björn, L.O., Chernov, Y., Chapin, T., Christensen, T.R., Huntley, B., Ims, R.A., Johansson, M., Jolly, D., Jonasson, S., Matveyeva, N., Panikov, N., et al. (2004a) *Ambio* **33**, 474–479.

- Callaghan, T.V., Björn, L.O., Chernov, Y., Chapin, T., Christensen, T.R., Huntley, B., Ims, R.A., Johansson, M., Jolly, D., Jonasson, S., Matveyeva, N., Panikov, N., *et al.* (2004b) *Ambio* **33**, 418–435.
- Callaghan, T.V., Björn, L.O., Chernov, Y., Chapin, T., Christensen, T.R., Huntley, B., Ims, R.A., Johansson, M., Jolly, D., Jonasson, S., Matveyeva, N., Panikov, N., *et al.* (2004c) *Ambio* **33**, 398–403.
- Callaghan, T.V., Björn, L.O., Chapin, T., Chernov, Y., Christensen, T.R., Huntley, B., Ims, R.A., Johansson, M., Riedlinger, Jolly, D., Jonasson, S., Matveyeva, N., Oechel, W., *et al.* (2005) In: *ACIA, Arctic Climate Impact Assessment* (Ed. by C. Symon, L. Arris and B. Heal), pp. 243–352. Cambridge University Press, New York.
- CIE (1999) *134/1:TC 6–26 report: Standardization of the terms UV-A1, UV-A2 and UVB*. Commission Internationale de l'Éclairage (CIE). Collection in Photobiology and Photochemistry, Vienna, Austria CIE 134–1999 ISBN 3 900 734 94 1.
- Day, T.A., Ruhland, C.T., Grobe, C.W. and Xiong, F. (1999) *Oecologia* **119**(1), 24–35.
- Day, T.A., Ruhland, C.T. and Xiong, F.S. (2001) *J. Photoch. Photobio. B* **62**, 78–87.
- de la Rosa, T.M., Julkunen-Tiitto, R., Letho, T. and Aphalo, P.J. (2001) *New Phytol.* **150**, 121–131.
- Farman, J.C., Gardiner, B.G. and Shanklin, J.D. (1985) *Nature* **35**, 207–210.
- Flint, S.D., Ryel, R.J. and Caldwell, M.M. (2003) *Agr. Forest Met.* **120**, 177–189.
- Gabeščík, A., Voňcina, M., Trost, T., Germ, M. and Björn, L.O. (2002) *J. Photoch. Photobiol. B* **66**, 30–36.
- González, R., Wellburn, A.R. and Paul, N.D. (1998) *Physiol. Plantarum* **104**, 373–378.
- Gröebner, J., Albold, A., Blumthaler, M., Cabot, T., de la Casiniere, A., Lenoble, J., Martin, T., Masserot, D., Müller, M., Philipona, R., Pichler, T., Pougatch, E., *et al.* (2000) *J. Geophys. Res.* **105**, 26991–27003.
- Gwynn-Jones, D., Lee, J.A. and Callaghan, T.V. (1997) *Plant. Ecol.* **128**, 242–249.
- Harborne, J.B. and Grayer, R.J. (1993) In: *The Flavonoids: Advances in Research since 1986* (Ed. by J.B. Harborne), pp. 589–618. Chapman & Hall, London.
- Hughes, K.A., Scherer, K., Svenøe, T., Rettberg, P., Horneck, G. and Convey, P. (2006) *Soil Biol. Biochem.* **38**, 1488–1490.
- Håkansson, K.B. (2006) *Påvirker det nuværende niveau af ultraviolet-B stråling Salix arctica? - Et eksklusions forsøg fra Nordostgrønland*. M.Sc. thesis, Department of Terrestrial Ecology, Biological Institute, University of Copenhagen.
- Johanson, U., Gehrke, C., Björn, L.O. and Callaghan, T.V. (1995a) *Funct. Ecol.* **9**, 713–719.
- Johanson, U., Gehrke, C., Björn, L.O., Callaghan, T.V. and Sonesson, M. (1995b) *Ambio* **24**, 106–111.
- Johnson, D. (2003) *Res. Microbio.* **154**, 315–320.
- Johnson, D., Campbell, C.D., Lee, J.A., Callaghan, T. and Gwynn-Jones, D. (2002) *Nature* **416**, 82–83.
- Jokela, K., Leszcynski, K. and Visuri, R. (1993) *J. Photoch. Photobiol. B* **58**, 559–566.
- Jones, M.H., Macdonald, S.E. and Henry, G.H.R. (1999) *Oikos* **87**, 129–138.
- Lehrner, G., Delatorre, J., Lütz, C. and Cardemil, L. (2001) *J. Photoch. Photobiol. B* **64**, 36–44.
- Madronich, S., McKencie, R.L., Björn, L.O. and Caldwell, M.M. (1998) *J. Photoch. Photobiol. B* **46**, 5–19.
- Paul, N. (2001) *New Phytol.* **150**, 1–8.
- Phoenix, G.K. and Lee, J.A. (2004) *Ecol. Res.* **19**, 65–74.

- Phoenix, G.K., Gwynn-Jones, D., Lee, J.A. and Callaghan, T.V. (2000) *Plant Ecol.* **146**, 67–75.
- Phoenix, G.K., Gwynn-Jones, D., Callaghan, T.V., Sleep, D. and Lee, J.A. (2001) *J. Ecol.* **89**, 256–267.
- Phoenix, G.K., Gwynn-Jones, D., Lee, J.A. and Callaghan, T.V. (2002) *Plant. Ecol.* **165**, 263–273.
- Rinnan, R., Keinänen, M.M., Kasurinen, A., Asikainen, J., Kekki, T.K., Holopainen, T., Ro-Poulsen, H., Mikkelsen, T.N. and Michelsen, A. (2005) *Global Change Biol.* **11**, 564–574.
- Robberecht, R., Caldwell, M.M. and Billings, W.D. (1980) *Ecology* **61**, 612–619.
- Robson, T.M., Pancotto, V.A., Flint, S.D., Ballaré, C.L., Sala, O.E., Scopel, A.L. and Caldwell, M.M. (2003) *New Phytol.* **160**, 379–389.
- Rousseaux, M.C., Ballaré, C.L., Giordano, C.V., Scopel, A.L., Zima, A.M., Szwarcberg-Bracchitta, M., Searles, P.S., Caldwell, M.M. and Diaz, S.B. (1999) *P. Natl. Acad. Sci. USA* **96**, 15310–15315.
- Rousseaux, M.C., Julkunen-Tiitto, R., Searles, P.S., Scopel, A.L., Aphalo, P.J. and Ballaré, C.L. (2004a) *Oecologia* **138**, 505–512.
- Rousseaux, M.C., Flint, S.D., Searles, P.S. and Caldwell, M.M. (2004b) *Photoch. Photobiol. B* **80**, 224–230.
- Rozema, J., Björn, L.O., Bornman, J.F., Gaberscik, A., Häder, D.-P., Trost, T., Germ, M., Klisch, M., Gröniger, A., Sinha, R.P., Lebert, M., He, Y.-Y., *et al.* (2002) *J. Photoch. Photobiol. B* **66**, 2–12.
- Rozema, J., Boelen, P. and Blokker, P. (2005) *Environ. Pollut.* **137**, 428–442.
- Rozema, J., Boelen, P., Solheim, B., Zielke, M., Buskens, A., Doorenbosch, M., Fijn, R., Herder, J., Callaghan, T., Björn, L.O., Gwynn-Jones, D., Broekman, R., *et al.* (2006) *Plant. Ecol.* **182**, 121–135.
- Ruhland, C.T. and Day, T.A. (2000) *Physiol. Plantarum* **109**, 244–351.
- Ruhland, C.T., Xiong, F.S., Clark, W.D. and Day, T.A. (2005) *Photoch. Photobiol. B* **81**, 1086–1093.
- Searles, P.S., Flint, S.D. and Caldwell, M.M. (2001a) *Oecologia* **127**, 1–10.
- Searles, P.S., Kropp, B.R., Flint, S.D. and Caldwell, M.M. (2001b) *New Phytol.* **152**, 213–221.
- Semerdjieva, S.I., Sheffield, E., Phoenix, G.K., Gwynn-Jones, D., Callaghan, T.V. and Johnson, G.N. (2003a) *Plant Cell Environ.* **26**, 957–964.
- Semerdjieva, S.I., Phoenix, G.H., Hares, D., Gwynn-Jones, D., Callaghan, T.V. and Sheffield, E. (2003b) *Physiol. Plantarum* **117**, 289–294.
- Sigsgaard, C., Petersen, D., Grøndahl, L., Thorsøe, K., Meltofte, H., Tamstorf, M. and Hansen, B.U. (2006) In: *Zackenberg Ecological Research Operations, 11th Annual Report, 2005* (Ed. by M. Rasch and K. Caning), pp. 11–35, Danish Polar Center, Ministry of Science, Technology and Innovation, Copenhagen.
- Solheim, B., Johanson, U., Callaghan, T.V., Lee, J.A., Gwynn-Jones, D. and Björn, L.O. (2002) *Oecologia* **133**, 90–93.
- Strasser, R.J., Tsimilli-Michael, M. and Srivastava, A. (2004) In: *Chlorophyll a Fluorescence: A signature of photosynthesis*, Advances in Photosynthesis and Respiration (Ed. by G.C. Papageorgiou and Godwinjee), pp. 321–363. Volume 19.
- Wardle, D.A. (2002) *Monographs in Population Biology* **34**. Princeton University Press, Princeton, New Jersey.
- Webb, A.R. (1997) In: *Plants and UV-B: Responses to Environmental Change* (Ed. by P.J. Lumsden), pp. 13–30. Cambridge University Press, United Kingdom.
- Weatherhead, B., Tanskanen, A., Stevmer, A., Andersen, S.B., Arola, A., Austin, J., Bernhard, G., Browman, H., Fioletov, V., Grewe, V., Herman, J.,

- Josefsson, W., *et al.* (2005) In: *ACIA, Arctic Climate Impact Assessment* (Ed. by C. Symon, L. Arris and B. Heal), pp. 151–182. Cambridge University Press, Cambridge.
- WMO (2003) *Scientific Assessment of Ozone Depletion: 2002. Global Ozone Research and Monitoring Project*. Report no. 47, World Metrological Organization, Geneva.
- Xiong, F.S. and Day, T.A. (2001) *Plant Physiol.* **125**, 738–751.
- Zaller, J.G., Caldwell, M.M., Flint, S.D., Scopel, A.L., Osvaldo, E.S. and Ballaré, C.L. (2002) *Global Change Biol.* **8**, 867–871.
- Zelles, L. (1999) *Biol. Fert. Soils* **29**, 111–129.