

## **Reduction of the Ambient UV-B Radiation in the High-Arctic Increases Fv/Fm in *Salix arctica* and *Vaccinium uliginosum* and Reduces Stomatal Conductance and Internal CO<sub>2</sub> Concentration in *Salix arctica***

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# Reduction of the Ambient UV-B Radiation in the High-Arctic Increases $F_v/F_m$ in *Salix arctica* and *Vaccinium uliginosum* and Reduces Stomatal Conductance and Internal $\text{CO}_2$ Concentration in *Salix arctica*

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## Abstract

This study investigates effects of reducing the ambient UV radiation on gas exchange and chlorophyll fluorescence of two shrub species, *Salix arctica* and *Vaccinium uliginosum*, in a high arctic heath in Northeast Greenland in July and August. On two sites films, Mylar and Lexan, were used to reduce UV-B radiation and UV-B + A radiation, respectively. A UV transparent film, Teflon, and no film were used as controls. Field measurements showed that the plants under Teflon, Mylar, and Lexan received approximately 91, 39, and 17% of the ambient UV-B irradiance, respectively. Reduced UV radiation increased maximal photochemical efficiency ( $F_v/F_m$ ) in both species. The responses varied in significance according to species, sites and time of growing season. Net assimilation ( $P_n$ ), measured as net  $\text{CO}_2$  uptake, was not significantly affected. But over the whole growing season stomatal conductance and intercellular  $\text{CO}_2$  concentration were decreased by both UV treatments. The underlying mechanisms for these results are discussed. PAR-irradiance had a negative influence on the absolute values of  $F_v/F_m$ . A positive correlation was found between  $F_v/F_m$  and  $P_n$  measured at ambient  $\text{CO}_2$ -level. It is concluded that it cannot be excluded, that the observed short-term effects could result in long-term negative effects on growth and survival for the investigated species.

## Introduction

A depletion of stratospheric ozone has occurred over the last 25 yrs. (Searles et al., 2001) and concurrently the irradiance of ultraviolet-B (UV-B, 280–315 nm [CIE, 1999]) radiation has increased on the earth's surface (Herman et al., 1996; Dahlback, 2002). Effects of UV-B, both direct and indirect and on different organizational levels, on sensitive vegetation and ecosystems have been reported (see e.g., Sullivan and Rozema, 1999; Björn, 2002). At high latitudes not only the relative increase in UV-B has been occurring most rapidly but also the absolute net depletion of ozone has been highest resulting in the potentially highest impact on the vegetation there (Björn et al., 1999; Pyle, 1997; Paul, 2001). The longevity of arctic plants makes them adapt only slowly (Callaghan and Jonasson, 1995) for which reason acclimation is of special importance when facing changes in the environment. Because of the short growing season and low temperatures arctic plants are already extremely acclimated to climate (e.g., Bliss, 1997). Furthermore, some of these acclimations increase the sensitivity to UV-B, such as a fast spring growth rate, a high ratio of unsaturated against saturated fatty acids and a slow photo reactivation (Rousseaux et al., 2001; Li et al., 2002; Björn, 2002). As an overall result, effects of even small changes in the UV-B level are likely to occur in arctic vegetation.

In this experiment we wanted to investigate effects of the present ambient UV radiation on high arctic vegetation and to study possible seasonal variation of these effects. The manipulative approach chosen was to reduce the UV-radiation dose on the vegetation by means of filters. As photosynthetic processes integrate many of the proposed direct and indirect UV effects (see e.g., Sullivan and Rozema, 1999), the investigations were focused on the effect of these treatments on the photosynthetic apparatus. As nondestructive measurements were

needed, measurements were concentrated on net leaf photosynthesis and fast kinetics chlorophyll fluorescence. Thus, effects on maximal photochemical efficiency ( $F_v/F_m$ ) and ambient and potential net photosynthesis, measured as  $\text{CO}_2$  flux, were studied. The overall hypothesis was that if the vegetation has not been fully acclimated to the present UV radiation, reductions in the irradiance load would improve the photosynthetic performance of the plants.

## Materials and Methods

### EXPERIMENTAL SITE

The fieldwork was carried out in a High Arctic heathland (Zackenbergs Research Station, Northeast Greenland, 74°N; 21°E) in July and August 2001. The mean air temperature was 4.9 and 5.8°C in July and August, respectively. The annual precipitation was 236 mm w.eq., falling mostly as snow during winter (DPC, 2003).

The plant species investigated were *Salix arctica* Pall. and *Vaccinium uliginosum* L., ssp. *microphyllum* Lge., comprising ca. 20 and 60% of the vegetation cover, respectively, and having broad, flat leaves well suited for physiological measurements.

### EXPERIMENTAL SET-UP AND TREATMENTS

The aim was to establish plots where parts of the UV spectrum in natural daylight were reduced with ambient UV irradiance as reference. Reductions were achieved by filtering the solar radiation through two different filters, Mylar® (type D. DuPont Teijin Films, Wilmington, Delaware, USA) and Lexan® (RIAS, Roskilde, Denmark). As control Teflon® filter (Fluoretek AB, Knivsta, Sweden.) was adopted. Teflon is

TABLE 1

Percentages of ambient UV-B and PAR that reached the plant canopy under the frames with Mylar, Teflon, and Lexan filters using a UV-B sensor (Scintec) and PAR sensor (LiCor). Measurements at a 45° angle to the sun correspond to measurements on a horizontal surface as the mean solar elevation is approximately 45° over the horizon

Angle to sun	Filter	UV-B (%)	PAR (%)
45°	Teflon (Filter Control)	90.6	96.8
	Mylar (-UV-B)	36.3	88.8
	Lexan (-UV-AB)	13.5	90.2
90°	Teflon (Filter Control)	91.1	97.9
	Mylar (-UV-B)	42.3	91.7
	Lexan (-UV-AB)	20.1	92.2

referred to as “filter control,” Mylar as “-UV-B,” and Lexan as “-UV-AB”. A fourth treatment was a control without any filter.

Two sampling sites were chosen, in the following named site 1 and 2, and filters were placed parallel to the soil surface 5 cm above canopy by means of 40 cm × 60 cm aluminium frames. The experiment was designed as a randomized block design where each site consisted of four experimental plots (replicates) of each treatment, in total 16 plots per site. Both sites were south-facing slopes, chosen to maximize the incoming amount of radiation and to make possible that the plots could benefit from uphill precipitation. Site 1 was marginally sloping (approx. 5°) while the inclination of site 2 was much steeper (approx. 45°).

## MEASUREMENTS

Filter transmittance for UV-A and UV-B was analyzed by a spectrophotometer (Cary 50, Varian Inc.). Measurements in the experimental area were done with a broadband cosine corrected UV-B sensor (UV-S-310-T, Scintec, Atmosphärenmesstechnik GmbH, Tübingen, Germany—now manufactured as UV-S-B-T by Kipp & Zonen B.V., Delft, The Netherlands).

During the sampling period measurements of maximal photochemical efficiency, measured as chlorophyll fluorescence ( $F_v/F_m$ ), were at each site done every third day and weekly on *S. arctica* and *V. uliginosum*, respectively. Measurements of net photosynthesis ( $P_n$ ), measured as leaf gas exchange, were done weekly at site 1 on *S. arctica*.

After dark adaptation for a minimum of 25 min (most often 30–40 min) of the leaves, chlorophyll fluorescence was measured with a Handy PEA (Hansatech Instruments, Ltd. King’s Lynn, Norfolk, UK) at 650 nm light (Tsimili-Michael and Strasser, 2001) with an intensity of 2500  $\mu\text{mol m}^{-2} \text{s}^{-1}$ . Measurements on *S. arctica* were done *in situ* whereas leaves of *V. uliginosum* were excised and immediately brought to the laboratory to be measured. This procedure was tested, and the detachment did not affect the response.

Leaf gas exchange was measured with a CIRAS-1 connected to an automatic broad leaf cuvette (PLC(B)) (PP Systems, Hertfordshire, UK) and done at leaf temperature optimum (20°C) and saturating photon irradiance (1200  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) at two CO<sub>2</sub> levels: Ambient (364 ppm) and saturated (1800 ppm). In cases where the leaf did not fill out the cuvette of the PLC (B) (2.5 cm<sup>2</sup>), a digital picture was taken of the cuvette with the leaf inserted and data was recalculated with the actual area, obtained by image analysis.

Possible plot edge effects were taken into account by preferentially avoiding measurements on leaves near the edges of the plots. Diurnal variations of responses were also taken into account by measuring chlorophyll fluorescence within the same time interval each day (1300–1800 h). Gas exchange measurements, taking longer time,

were done between 1100 and 2200 h. Data showed that the time of the day did not influence  $P_n$  (data not shown). Weekly, computer controlled CIRAS measurements were done to obtain  $P_n$  response curves of temperature, light, and CO<sub>2</sub> on leaves of *S. arctica* plants growing outside the laboratory.

During two days in August, series of measurements were performed, where  $F_v/F_m$  and gas exchange were measured on the same *S. arctica* leaf consecutively in order to compare the two physiological parameters directly on leaf basis.

The following climatic parameters were measured continuously on both sites by means of two identical data loggers (CR 10X, Campbell Scientific, Ltd., Loughborough, UK). At each site close to the plots relative air humidity and air temperature were measured (Vaisala 50Y probe) and PAR was measured perpendicular to the slope (GaAsP photodiode [Pontailier, 1990]). In four plots at each site soil moisture in 0 to 30 cm depth were measured (CS615 Water Content Reflectometer, Campbell Scientific). In all plots air and soil temperature in 3 cm depth were measured with epoxy (air) or rubber (soil) coated thermocouples connected to an AM25T Solid State Multiplexer (Campbell Scientific). Surface volumetric soil moisture content in 0 to 6 cm depth was measured weekly in all plots (Theta-probe type ML2x, Delta-T Devices Ltd). UV-B data was obtained from the meteorological station (no. 641) about 1 km from the sites (Asiaq (Greenland Survey)), unpublished).

## STATISTICAL ANALYSIS

Statistical analyses were conducted using the GLM procedure (SAS Institute, 2002). The effects of UV treatments, block and growing season (date) were tested with a three-way ANOVA. This was done for each species and each site. We used a four-way ANOVA to test the effects of species and sites, respectively. Each sampling day was also separately tested in a two-way ANOVA with treatment and block as factors. In cases of significant treatment effects these analyses were followed by tests of treatment differences using Tukey’s test. In addition, a repeated measures approach was also carried out, with treatment and block as main factors and with day repeated within each plot. This was to take into account that the same experimental unit (the plot) was measured several times during the season. Data from  $F_v/F_m$  and  $P_n$  measurements on the same day were tested to examine the connection between the two physiological parameters done with a multiple regression.

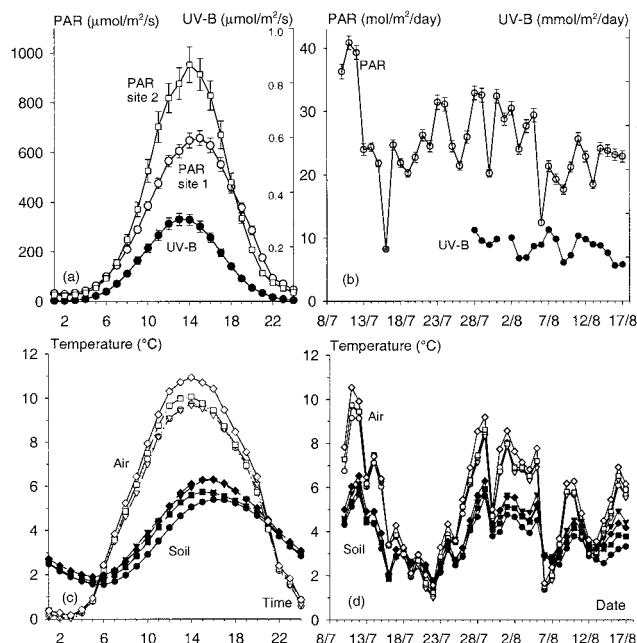
Levene’s test was used to test for homogeneity of variance. Where necessary parameters were transformed in order to meet the assumptions of ANOVA. All values presented here are non-transformed. Unless otherwise noted, differences are considered at the  $P < 0.05$  level.

In the following, analyses are referred to as “effect of treatments” when the tests included all four treatments and “effect of UV reduction” when only the treatments with filters (UV-B, UV-B + A and filter control) were included in the tests.

## Results

### FILTER PROPERTIES

Laboratory spectrophotometer measurements of the transmittance of the films showed that the Teflon, Mylar, and Lexan transmittance of UV-A (315–400 nm) averaged 88.6, 77.6, and 29.3% and for UV-B (280–315 nm) averaged 83.4, 0.7, and 8.0%, respectively. The field measurements with the Scintec sensor showed that the plant canopy under Teflon, Mylar, and Lexan, respectively, were exposed to approx. 91, 39, and 17% of the clear sky UV-B irradiance, slightly depending on the exposure angle to the sun (Table 1). Some of the measured



**FIGURE 1.** Seasonal fluctuations of PAR and temperature at site 1, UV-B from the climate station and diurnal fluctuations of PAR at site 1 and 2. (a) Mean diurnal PAR and UV-B  $\pm 1$  SE. (b) Daily accumulated PAR  $\pm 1$  SE and UV-B throughout the experimental period. (c) Mean diurnal temperatures of soil (black) and air (white). For both:  $\circ$  = control.  $\nabla$  = filter control.  $\square$  = -UV-B.  $\diamond$  = -UV-AB. (d) Mean daily temperatures throughout the measurement period. Signatures as in (c). (a) and (c) cover the period 10 July to 8 August. (b) and (d) are 24-h means.

irradiation is supposed to be due to diffuse and reflected radiation reaching the UV-B sensor from the open sides not covered with filters.

## MICROCLIMATE

Overlying large fluctuations, the overall irradiance and air and soil temperatures were declining during the experimental period (Fig. 1). The low PAR and temperatures 13–22 July were due to a very cloudy period. As can be seen on Figure 1a the PAR irradiance was highest on the site sloping most perpendicular to the midday solar irradiance (site 2). Midday refers to the time where the irradiance is highest which was around 1400 h (Fig. 1a). Correlations between radiation on the less sloping site 1 and on the nearby meteorological station were very good (all  $r > 0.94$ ,  $P < 0.0001$  for PAR,  $n = 479$ ) for which reason the UV-B data is expected to be comparable to radiation at site 1.

Mean relative air humidity was  $78\% \pm 0.5$  (diurnal) and  $67\% \pm 0.9$  (1300–1800 h) at Site 1. Soil moisture contents at both 0–6 and 0–30 cm depth were significantly lower at site 2 than at site 1 (mean values around 0.3 and 0.45  $\text{m}^{-3} \text{m}^{-3}$ , respectively). During the experimental period soil moisture hardly decreased and the soil moisture did not differ substantially between the treatments within the sites. No significant differences or tendencies in surface soil moisture content (0–6 cm depth) were seen during the season or between treatments within the sites.

## CHLOROPHYLL FLUORESCENCE

At both sites and for both species there was an overall effect of treatment (all  $P < 0.0001$ ) and of UV reduction on  $F_v/F_m$  (all  $P < 0.0001$  at site 2.  $P = 0.0002$  for *S. arctica* and  $P = 0.0023$  for *V. uliginosum* at site 1). Table 2 shows the details. It can also be seen that the values of  $F_v/F_m$  in the filter control were somewhat higher than 0.7,

**TABLE 2**

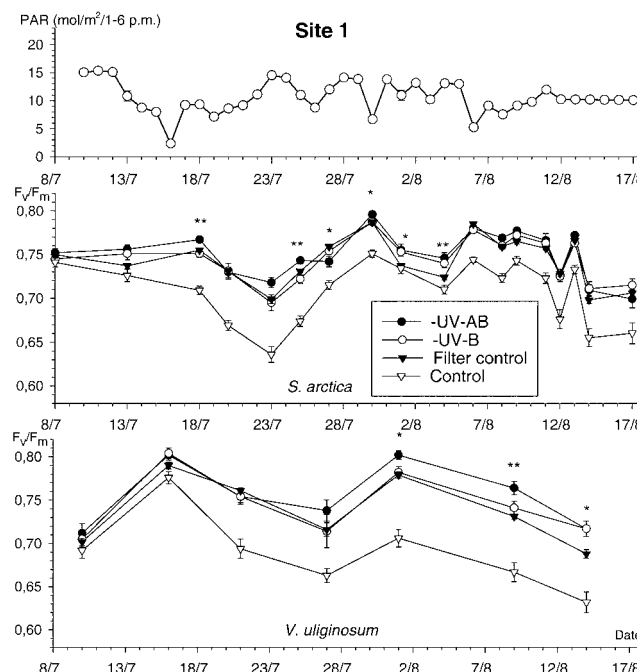
Mean  $F_v/F_m$  in the period 8 July–17 August. Letters are to be read per site per species. If different, the means are statistically different,  $P < 0.05$

Site	Treatment	<i>S. arctica</i>			<i>V. uliginosum</i>		
		N	Mean	SE	N	Mean	SE
1	-UV-AB	705	0.751 a	0.002	202	0.754 a	0.004
	-UV-B	700	0.746 b	0.002	207	0.744 ab	0.004
	Filter control	693	0.744 b	0.002	204	0.737 b	0.004
	Control	704	0.707 c	0.002	197	0.689 c	0.005
2	-UV-AB	621	0.733 b	0.002	204	0.726 a	0.004
	-UV-B	614	0.745 a	0.002	203	0.698 b	0.005
	Filter control	621	0.736 b	0.002	205	0.727 a	0.004
	Control	612	0.685 c	0.003	204	0.687 b	0.005

thus indicating a generally low stress level in the leaves of the two species. The levels of  $F_v/F_m$  were similar at the two sites but, aided by the large number of samplings ( $n = 6896$ ), the overall  $F_v/F_m$  proved to be significantly lower at site 2 than at site 1 ( $P < 0.001$ ). At site 1, the overall  $F_v/F_m$  did not differ significantly between the two species, but at site 2, *V. uliginosum* had a significantly lower overall  $F_v/F_m$  than *S. arctica* ( $P < 0.001$ ).

Figures 2 and 3 show the results of all measurements. For *S. arctica* the effects were pronounced in the middle of the sampling period with values of  $F_v/F_m$  being significantly higher after UV-B + A reduction at site 1 and after UV-B reduction at site 2. For *V. uliginosum* significantly positive effects of mainly UV-B+A reduction was seen on  $F_v/F_m$  in the end of the growing season at site 1 (higher values). This trend was not observed at site 2.

Mean values of  $F_v/F_m$  correlated negatively with PAR (1300–1800 h) at each site ( $r = -0.80$ ,  $P < 0.0001$ ,  $n = 20$  and  $r = -0.74$ ,  $P = 0.001$ ,  $n = 16$  at site 1 and 2, respectively) (Fig. 4). Tested on site 1 this



**FIGURE 2.** Mean  $F_v/F_m$  per treatment per sampling day and mean PAR at site 1 showing when significant differences between the filter treatments were found (2-factor ANOVA, filter treatments only). Days with significance are marked with \* when  $P < 0.05$ , \*\* when  $P < 0.01$ , or \*\*\* when  $P < 0.001$ .

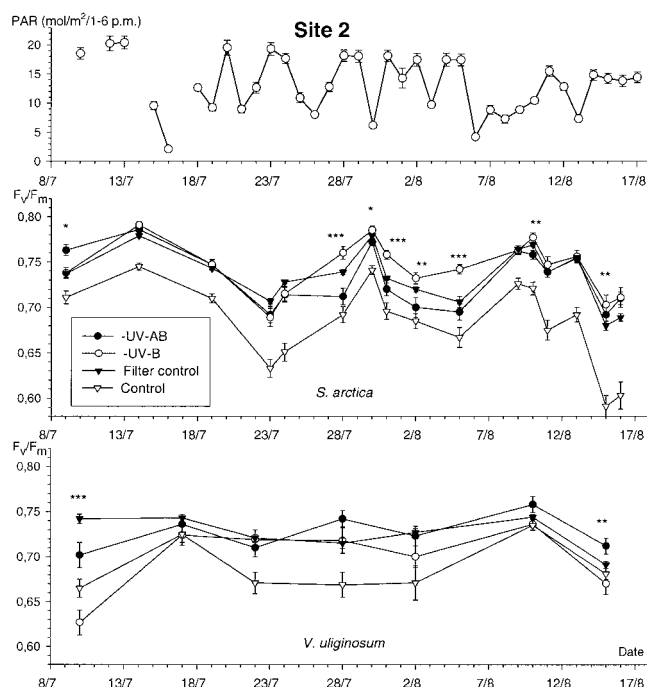


FIGURE 3. Mean  $F_v/F_m$  per treatment per sampling day and mean PAR at site 2. See Figure 2 legend. PAR data on 11, 14, and 17 July are omitted because of errors in noon PAR data.

correlation was even stronger in the first half of the sampling period (10–27 July) ( $r = -0.93$ ,  $P = 0.0003$ ,  $n = 9$ ) but less at the end of the period (30 July–17 August) ( $r = -0.72$ ,  $P = 0.02$ ,  $n = 10$ ).

#### GAS EXCHANGE

Figure 5 shows the seasonal variation of net photosynthesis at saturating light intensity in *S. arctica*. Comparing the treatments, the overall mean values of  $P_n$ , measured as net  $\text{CO}_2$  uptake, did not show any significant influence of UV reduction (Table 3). Despite this, both UV reduction treatments resulted in significantly lower overall values of stomatal conductance ( $g_s$ ) and intercellular  $\text{CO}_2$  concentration ( $C_i$ ) (all  $P < 0.002$ ). This was the case at both ambient and saturating  $\text{CO}_2$  level (Table 3). Apparently  $C_i$  did not show any particular seasonal variation whereas  $g_s$  showed same seasonality as  $P_n$ .

From the simultaneous measurements on the same *S. arctica* leaves, a correlation between  $P_n$  and  $F_v/F_m$  (all treatments) was found

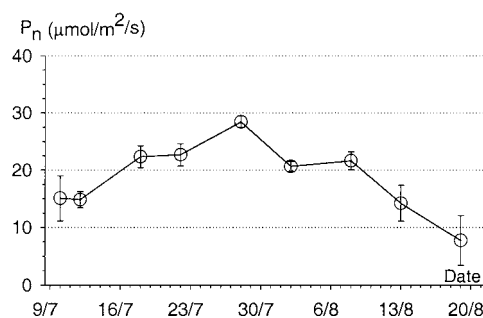


FIGURE 5. Net photosynthesis ( $P_n$ ) at  $1200 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ ,  $360 \text{ ppm CO}_2$ , and  $20^\circ\text{C}$  throughout the season. Data are mean  $\pm 1$  SE.

when  $P_n$  was measured at ambient  $\text{CO}_2$  level ( $r = 0.35$ ,  $P = 0.006$ ) but not at saturating level (Fig. 6).

## Discussion

### CHLOROPHYLL FLUORESCENCE

This experiment showed significantly higher values of  $F_v/F_m$  at reduced UV levels. This is in contrast to other UV-B exclusion experiments on natural vegetation at high latitudes (Xiong and Day 2001; Lud et al., 2001) where no changes in maximal photochemical efficiency were observed. Levels of and differences in  $F_v/F_m$  represent not only plant stress caused by UV-B. The influence of PAR on  $F_v/F_m$  was so large that plant stress caused by PAR and interactions between PAR and UV-B were considerable. In agreement with Xiong and Day (2001) this could be due to PSII being more affected by the large changes in PAR than the relatively small changes in UV-B (energetically).

The fact that PSII is more stressed on days with high PAR (negative correlation) is likely to be due to an irradiance that has been higher than the light saturating level for the plants. There were no days in the season where mean PAR (1300–1800 h) were more than  $900 \mu\text{mol m}^{-2} \text{s}^{-1}$  and light response curves showed that in general leaves

TABLE 3

Mean  $\pm 1$  SE of net photosynthesis ( $P_n$ ), stomatal conductance ( $g_s$ ) and inter-cellular  $\text{CO}_2$  ( $C_i$ ) per treatment at site 1, *S. arctica* in the period 20 July–17 August. P refers to ANOVA for all four treatments. P, filter treatment refers to ANOVA within the three filter treatments. Different letters show significant differences at  $\alpha = 0.05$  (Tukey, all treatments). Letters are to be read per dependent variable per  $\text{CO}_2$  level

Treatment	N	$P_n$ (mmol/m <sup>2</sup> /s)	$g_s$ (mmol/m <sup>2</sup> /s)	$C_i$ (mmol/mol)
Ambient $\text{CO}_2$ level				
P	181	0.0601	0.0006	< 0.0001
P, filter treatm.	135	0.2230	< 0.0001	< 0.0001
–UV-AB	47	$22.0 \pm 0.8$ a	$304 \pm 21$ b	$208 \pm 4$ b
–UV-B	45	$21.2 \pm 0.7$ a	$305 \pm 21$ b	$210 \pm 6$ b
Filter control	43	$21.9 \pm 0.7$ a	$350 \pm 25$ a	$224 \pm 4$ a
Control	46	$20.4 \pm 0.8$ a	$344 \pm 21$ ab	$232 \pm 5$ a
Saturating $\text{CO}_2$ level				
P	177	0.2308	0.0007	0.0043
P, filter treatm.	133	0.0620	< 0.0001	0.0014
–UV-AB	45	$73.3 \pm 2.3$ a	$318 \pm 21$ c	$1271 \pm 22$ c
–UV-B	44	$70.0 \pm 1.5$ a	$326 \pm 23$ bc	$1297 \pm 23$ bc
Filter control	42	$72.3 \pm 2.2$ a	$388 \pm 29$ a	$1356 \pm 18$ a
Control	46	$71.9 \pm 2.5$ a	$371 \pm 24$ ab	$1335 \pm 21$ ab

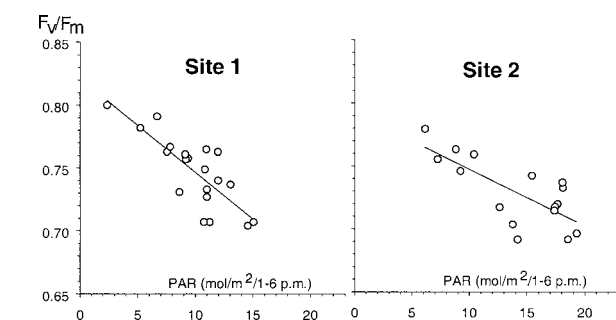


FIGURE 4. Correlation between accumulated (1300–1800 h.) daily PAR and mean daily  $F_v/F_m$  (filter treatments). Site 1:  $r = -0.80$  ( $n = 20$ ; days where either one or both of the species were measured on). Site 2:  $r = -0.74$  ( $n = 16$ ).

of *S. arctica* were saturated at  $1200 \mu\text{mol m}^{-2} \text{s}^{-1}$ . However, it should be taken into account that the light response curves were measured at  $20^\circ\text{C}$  leaf temperature while the ambient leaf temperature probably has been lower. On days with high PAR it is thus likely that the plants have been stressed by PAR as well as by UV-B.

Correlations between PAR and  $F_v/F_m$  declined during the season. As mean temperatures also declined during the season this could partially explain the response, but the primary cause is likely that  $F_v/F_m$  became increasingly influenced by senescence. Senescence starts already at the beginning of August, past the middle of the experimental period. This is in agreement with seasonal  $P_n$  peaking already during the end of July (Fig. 5) and was also confirmed by observations on the leaves, where changes in color were detected only short time after the peak of  $P_n$ .

The  $F_v/F_m$ -effects on *S. arctica* are most prominent in the middle of the sampling period (beginning of August) (Figs. 2, 3). The reason for this is presumably a combined effect of first, that the plants had experienced some weeks with UV-B reduction, and second, that there was still a relatively high incoming solar radiation at that time. According to the different slopes of the two sites, the high dependence on the solar radiation also explains why the effects on  $F_v/F_m$  differ between the sites. The site with highest incoming solar radiation (site 2) showed effects of the lowest UV-B reduction (-UV-B) while significant effects at site 1 only was found with the highest UV-B reduction (-UV-AB). The latter treatment does not reveal significant higher values of  $F_v/F_m$  at site 2. This indicates some interactions with UV-A effects when solar radiation is high as at site 2 in the beginning of August. These interactions could both involve the need for UV-A to contribute to photoreactivation and protection by flavonoids (Turunen et al., 1999; Jenkins et al., 2001) but also negative effects of UV-A (Cooley et al., 2000).

The effects on *V. uliginosum* appear later in the sampling period than those of *S. arctica* (Fig. 2). This could be due accumulative effects, but Phoenix et al. (2001) found no effects on *V. uliginosum* of 5 yr UV-B treatment. Instead the later appearance of effects in *V. uliginosum* at site 1 probably should be linked with interactions between the effects of senescence and UV-B. *Vaccinium uliginosum* at site 2 did not show any marked effects of reduced UV-B, nor is seen as prominent day to day fluctuations than on *V. uliginosum* at site 1 and on *S. arctica* on both sites (Figs. 2, 3)—except for 10 July, where initial methodological difficulties with *V. uliginosum* at site 2 are supposed to have affected the results that day. Phoenix et al. (2001) concluded a general UV-B tolerance but also interaction between precipitation and UV-B effects in *V. uliginosum*. Our results from the drier site 2 could be attributed to this. It is likely that  $F_v/F_m$  has been governed by factors other than the solar radiation on *V. uliginosum* at site 2.

#### REDUCED $g_s$ AND $C_i$ BUT NOT $P_n$

The significantly higher  $g_s$ —but not  $P_n$ —in the filter control plots (near-ambient UV-B) could be due to direct effects of UV-B. Direct effects on stomates have been reported from UV-B supplemental experiments (Nogués et al., 1999; Cooley et al., 2000). In contrast to this study other experimenters have shown that supplemental UV-B resulted in reduced  $g_s$ , but their results on  $C_i$  were inconsistent: Correia et al. (1999) also found an increased  $C_i$  while Nogués et al. (1999) found that the decrease in  $g_s$  was not followed by a similar decrease in  $C_i$ . As more closed stomates make changes in  $C_i$  more dependent on internal  $\text{CO}_2$  exchanges among the mesophyll cells, we believe that the reduced  $C_i$  found in this study is more determined by effects on respiration and/or rates of carboxylation/oxygenation of RuBisCO rather than being a direct result of reduced  $g_s$ . This is in accordance with the absence of effects on  $P_n$ , which, in case of  $C_i$  having been

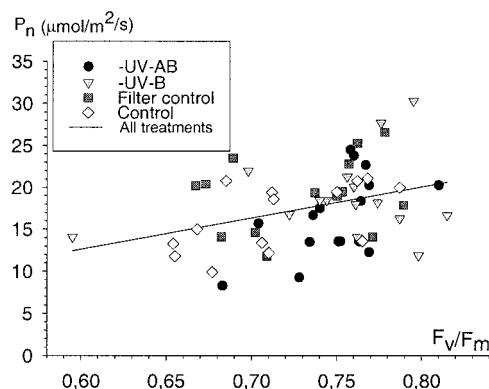


FIGURE 6.  $F_v/F_m$  and net photosynthesis ( $P_n$ ) at ambient  $\text{CO}_2$  level.  $r = 0.35$  ( $P = 0.0006$ ) for all treatments together. Each dot corresponds to one measurement ( $n = 59$ ). Omission of the  $F_v/F_m < 0.65$  does not change neither slope nor y axis intersection of the regression line.

determined only by  $g_s$ , would have been expected to have decreased too. If the lower  $g_s$  in the plants treated with UV reduction has limited the gross  $\text{CO}_2$  uptake at ambient  $\text{CO}_2$  level, the unaffected  $P_n$  could be explained by a lower respiration. If the amount of damage caused by UV-B was lower in the plants treated with UV reduction, the respiration needed for repair and protection would also be lower. Since reduction of UV-B resulted in positive effects on  $F_v/F_m$  and since UV-B in general causes the D1 polypeptide in PSII to become more unstable (Mackerness et al., 1997; Mattoo et al., 1999) it is also likely that UV-B reduction resulted in a lower turnover rate of D1 and thus a lower maintenance respiration. The assumption of lowered respiration is in agreement with Gwynn-Jones (2001) who found leaf respiration to be higher with enhanced UV-B. UV-B effects on respiration are in general not well investigated (Rozema et al., 1997) and our experiment reveals a need for further research.

The effects of UV-B may seem of less importance in the perspective of short-time climate variability or global change (e.g., Björn et al., 1999). Our results are in agreement with this. However, the impact of ambient UV-B may have been larger than we detected, at least for some of the leaves. In our experiment block effects and especially different angles of the leaves to the solar irradiance have caused large variation in data. This, together with the fact that accumulating effects of ambient UV-B have been found in Antarctic (Day et al., 2001; Robson et al., 2003) and that a continuous increase of the ambient UV-B level is presumed (Taalas et al., 2000), suggests that further investigations of the effects of ambient UV-B radiation on vegetation at high latitudes is necessary.

## Conclusion

The net depletion of the stratospheric ozone layer has increased the UV-B radiation in the High Arctic in such an order that a reduction of the UV-B irradiance on *S. arctica* and *V. uliginosum* resulted in frequent increases in  $F_v/F_m$  and reductions of  $g_s$  and  $C_i$  without affecting  $P_n$ . It cannot be excluded, that the observed short-term effects could result in long-term negative effects on growth and survival for the investigated species.

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