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Epidermal UV-screening in vascular plants from Svalbard (Norwegian Arctic)

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Abstract Stratospheric ozone depletion is most pronounced at high latitudes, and the concurring increased UV-B radiation might adversely affect plants from polar areas. However, vascular plants may protect themselves against UV-B radiation by UV-absorbing compounds located in the epidermis. In this 3-year study, epidermal UV-B (λ_{max} 314 nm) and UV-A (λ_{max} 366 nm) screening was assessed using a fluorescence method in 12 vascular species growing in their natural environment at Svalbard. The potential for acclimation to increased radiation was studied with artificially increased UV-B, simulating 11% ozone depletion. Open-top chambers simulated an increase in temperature of 2–3°C in addition to the UV-B manipulation. Adaxial epidermal UV-B transmittance varied between 1.6 and 11.4%. Artificially increased UV-B radiation and temperature did not consistently influence the epidermal UV-B transmittance in any of the measured species, suggesting that they may not have the potential to increase their epidermal screening, or that the screening is already high enough at the applied UV-B level. We propose that environmental factors other than UV-B radiation may influence epidermal UV-B screening.

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Introduction

The stratospheric ozone layer has become locally depleted during the last decades, with multiple possible effects on terrestrial and aquatic ecosystems. Major depletions of ozone have been documented, not only in the Antarctic (Farman et al. 1985; Solomon 1990; Newman 1999) but also in arctic regions (Taalas et al. 1996; Hansen et al. 1997; Rex et al. 1997; Shindell et al. 1998). One model predicts that March values of the ozone column in the Arctic will be reduced to one-third of the natural level before recovery starts around 2010–2015, and that the ozone losses might partly be a result of increased concentrations of greenhouse gases (Shindell et al. 1998). A weakened protecting ozone shield exposes the Arctic to increased ultraviolet-B (UV-B) radiation (280–320 nm) (Kerr and McElroy 1993; Jokela et al. 1995; Madronich et al. 1995). In the past, arctic areas have received little UV-B radiation compared with lower latitudes, due to the low solar zenith angle and the increasing thickness of the ozone layer from the equator towards the poles. This implies that the relative increase of UV-B radiation will be high in these areas. A large change in relative UV-B might be more important than absolute radiation levels (Björn et al. 1997).

UV-B radiation can damage the DNA and the photosynthetic apparatus of plants, as reviewed by, for example, Bornman and Teramura (1993), Jordan (1996), Jansen et al. (1998) and Caldwell et al. (1998). Caldwell et al. (1998) summarized studies from the last 3 decades, with 600 publications, and concluded that about one-third of the species studied are deleteriously affected by UV-B. The majority of tested species are, however, annual agricultural species. Responses to UV-B radiation might also have been exaggerated in many growth-chamber experiments, as UV-B has been applied at unrealistically low levels of PAR (Warner and Caldwell 1983; Mirecki and Teramura 1984; Fiscus and Booker 1995; Caldwell et al. 1998; Sullivan and Rozema 1999).

Plants have a range of UV-B protecting strategies, among them screening of potentially damaging radiation by UV-B absorbing compounds located in the epidermis (Schnitzler et al. 1996; Bornman et al. 1997; Schmitz-Hoerner and Weissenböck 2003). Hydroxycinnamic acids and flavonoids are known as important screening compounds in higher plants. Hydroxycinnamic acids absorb primarily in the UV-B-range, while many flavonoids have a second major absorption band in the UV-A. Accumulation of flavonoids and other phenolic compounds is induced by UV-B radiation (Tevini et al. 1991; Beggs and Wellmann 1994; Dixon and Paiva 1995; Bornman et al. 1997; Cooper-Driver and Bhattacharya 1998; Meijkamp et al. 2001; Searles et al. 2001; Tegelberg et al. 2001). The amount of incident UV-B that is not absorbed by these compounds and eventually reaches the mesophyll can be measured (Bornman and Vogelmann 1988; Day et al. 1993). Bilger et al. (1997) have developed a method for assessment of epidermal transmittance of UV-B based on chlorophyll fluorescence, which is non-intrusive and rapid compared to traditional methods such as transmittance measurements through epidermal peels and measurement of internal radiation using fibre-optic microprobes.

Some studies have demonstrated that plants that grow in environments with naturally low levels of UV-B radiation show a lower tolerance to UV-B than plants occuring in high irradiance areas (Robberecht and Caldwell 1986; Sullivan et al. 1992). One might therefore expect arctic plants to be vulnerable to elevated UV-B levels. Since the production of protective screening compounds represents a metabolic cost (Hessen 1996), one could also hypothesize that arctic plants, growing under extreme conditions, have a relatively low screening capacity for UV-B radiation.

Robberecht et al. (1980) measured the transmittances of epidermal peels of 11 species collected at Barrow, Alaska, and found a mean of about 5%, with values ranging from 0.4 to 24.4%. This means that about 75–99.5% of the incident UV-B radiation is attenuated by the epidermis of the arctic species investigated. In comparison, the mean transmittance in species collected from high UV-B radiation zones, e.g. at high altitudes (2,500–4,000 m a.s.l.) in equatorial and tropical regions, was 2% (Robberecht et al. 1980). In a growth-chamber study, an arctic provenance of *Oxyria digyna* was found to have an epidermal transmittance for UV-B radiation of about 12%, compared with 7% for an alpine ecotype (Caldwell et al. 1982). Barnes et al. (1987) observed significant increases in the level of whole-leaf UV-absorbing compounds in response to UV-B supplementation in Alaskan populations of *Lupinus*, which might indicate a potential for increased protection with enhanced UV-B irradiance in these plants. Apart from these few studies, data on epidermal UV protection are very limited for arctic angiosperms.

The main aim of this study was to measure epidermal transmittance to assess UV-B protection in arctic plants from Svalbard. By using fluorescent UV-B lamps to simulate an 11% depletion of the ozone layer, and so-called Open Top Chambers (OTC) to enhance temperature, we also wanted to study the acclimation potential of arctic plants to the suspected increase in UV-B irradiation, and to investigate the effects of possible future climatic warming on UV-B acclimation.

Materials and methods

Study area

All parts of this study were carried out at the arctic archipelago of Svalbard, on the main island Spitsbergen, near Longyearbyen (78°12′N, 15°32′E) and in the nearby Adventdalen valley, during the field seasons of 1999, 2000 and 2001. One uncommon species, *Salix reticulata* L., was collected near the Polish research station at Hornsund (77°00′N, 15°31′E) in 2001.

The Longyearbyen and Adventdalen area belongs to the middle-arctic tundra zone sensu Bliss (1981) (Elvebakk 1997). The vegetation on slopes and ridges is dominated by *Cassiope tetragona* (L.) D. Don, while snowbeds are characterized by *O. digyna* (L.) Hill and *Ranunculus* species. On the valley floor, *S. polaris* Wahlenb. and the mosses *Polytrichum hyperboreum* R. Br. and *Sanionia uncinata* (Hedw.) Loeske are the dominant species. Long-term mean temperature for the warmest month (July) is 6.5°C for Longyearbyen (Førland et al. 1997). Mean temperatures for the three summer months during the three study years are given in Table 1. The 2001 season was somewhat warmer than the two other years, while 2000 was especially cold in June. The long-term mean annual precipitation for Longyearbyen is 203 mm (Førland et al. 1997).

Investigation of epidermal transmittance in arctic plants from Svalbard

Leaves from 12 different species (*Bistorta vivipara* L., *C. tetragona*, *Dryas octopetala* L., *O. digyna*, *Papaver dahlianum* Nordh., *Salix polaris*, *Salix reticulata*, *Saxifraga cernua* L., *Saxifraga cespitosa* L., *Saxifraga nivalis* L., *Saxifraga oppositifolia* L. and *Silene acaulis* (L.) Jacq.) were collected during the last week of July and the 1st week of August, in all three field seasons.

Each sample consisted of one preferentially young but mature leaf from ten different individuals of the species, growing in the same microhabitat (normally within 1 m^2, with the same exposure). Six samples, each from one of six different plots in the Longyearbyen-Adventdalen area, were taken for each species during the three field seasons if available. In general, the plots were identical each year. The plants within plots were not necessarily the same in different years. Leaves were collected in plastic bags and measurements of epidermal UV-transmittance were carried out indoors within 1 h of sampling.

UV- and temperature-enhancement experiment

Two previously established experimental sites in the valley of Adventdalen (78°10.50′N, 16°0.39′E) were used in the study of UV-B

Table 1 Mean monthly summer temperatures (°C) at Longyearbyen Airport, measured by the Norwegian Meteorological Institute

	June	July	August	Mean
1999	2.7	6.4	4.9	4.7
2000	2.1	6.1	5.2	4.5
2001	3.4	6.4	6.5	5.4

acclimation in Svalbard plants. The sites were established in 1996 as described by Solheim et al. (2002). Site I is situated on the valley floor (approx. 5 m a.s.l.) on glaciofluvial and fluvial deposits, mainly sandur, with *Salix polaris* and *Polytrichum hyberboreum* as the dominant species. Site II is situated on a mountain slope (approx. 30 m a.s.l.) on marine deposits, with a more dense, and higher canopy, with *C. tetragona*, *D. octopetala* and *Salix polaris* as the dominant species and a large variety of other herbs and grass species such as *O. digyna*, *Stellaria crassipes* Hult., *B. vivipara* and *Luzula confusa* (Hartm.) Lindeb. Five species were included in the UV-enhancement experiment: *S. polaris* and *B. vivipara* from site I, *O. digyna*, *D. octopetala* and *C. tetragona* from site II.

The experimental site had a factorial design with four replicates of each treatment (ambient and enhanced UV-B, total of eight plots), each consisting of a metal frame (2.5×1.3 m) holding six UV-B fluorescent tubes 1.5 m above the vegetation. A simulation of 11% ozone depletion under clear sky conditions was achieved by enhancing the ambient UV-B radiation with UV-B radiation from the fluorescent tubes (Q-PANEL, UVB-313, Cleveland, Ohio). The daily supply of UV-B radiation was calculated based on the estimated daylight-UV-B from a clear sky, without any corrections for clouds or measured PAR. The middle 70-cm section of the two central lamps in each frame was covered with aluminium foil to obtain an even distribution within the plots. A single sheet of preburned cellulose diacetate (0.13 mm, Courtaulds, Derby, UK) was used to eliminate ecologically irrelevant ultraviolet-C (UV-C, <280 nm) from the lamps, for the UV-B treatment. The filters were changed every 2nd week. When used in combination with a cellulose diacetate filter, the UVB-313 lamps have a ratio of UV-A (315–400) to UV-B (280–315) of 0.78 in unweighted units of energy (W m^{-2}) (McLeod 1997). A squarewave UV-B supplement system was applied, where the daily irradiation occurred around noon. This was controlled by timers that switched on and off three lamps at a time to get a stepwise increase or decrease of the daily UV-exposure. The daily exposure time was adjusted every 2nd week to match the seasonal change in natural UV-B radiation. See Johanson et al. (1995) and Björn et al. (1997) for further details of the UV-B radiation-enhancement system. The ambient and enhanced biologically effective UV-B radiation ($UV\text{-}B_{BE}$), on a clear day in early July at this latitude are 1.40 and 1.85 kJ m^{-2} day^{-1}, respectively, as calculated by the model of Björn and Murphy (1985) and the generalized plant action spectrum (Caldwell 1971), and normalised at 300 nm. For all 3 years, the UV-B radiation enhancement started at the end of snow melt in the middle of June and ended when senescence was in progress in early September (Solheim et al. 2002).

At site I, one Open Top Chamber, a small hexagonal greenhouse, made of UV-B transparent Plexiglas (Röhm, Darmstadt, Germany) was placed in each UV-B and control plot, to study possible mutualistic effects of global warming and enhanced UV-radiation. Each OTC was 27 cm high and covered a basal area of 0.42 m^2. The OTCs were in place during the same period as the UV-B enhancement was applied, and were then removed during winter to avoid any adverse effects on the duration of snow cover. Temperature loggers (Tinytag *Plus*, Intab, Stenkullen, Sweden), with sensors at approximately plant height, were out during the season of 1999. They showed that the temperature inside the OTCs was about 2–3°C higher than the ambient air temperature (data not shown). The species studied inside the OTCs were *B. vivipara* and *S. polaris*.

Each sample consisted of one leaf from ten different specimens, and transmittance was measured on both leaf sides. The plants sampled were not necessarily the same every year. One sample was taken from all the UV-B and control plots, both inside and outside the OTCs.

Measurement of UV-transmittance

Epidermal UV-transmittance was determined as described by Burchard et al. (2000), using an Xe-PAM fluorometer (Walz, Effeltrich, Germany). This method is based on the fact that irradiance absorbed by the chloroplasts in the mesophyll induces emission of chlorophyll fluorescence. Fluorescence was excited consecutively with three different excitation beams in the UV-B (λ_{max} 314 nm), UV-A (λ_{max} 366 nm) and blue-green spectral (400–550 nm) regions. In some experiments, a red measuring beam was used additionally, as defined by an interference filter (Balzers B-20, λ_{max} 665 nm, HBW 5 nm). The majority of the UV-radiation is absorbed by UV-absorbing substances located in the epidermis, whereas blue-green light (BG) reaches the chloroplasts largely undiminished. The intensity of the fluorescence emitted by the chloroplasts is dependent on the amount of light they absorb. The ratio of fluorescence intensity induced by the two beams, $F(UV)/F(BG)$, provides a relative measure of how much UV radiation is transmitted through the epidermis and, hence, the quantity reaching the uppermost layer of chloroplasts. All signals are normalized with respect to those obtained upon excitation of a blue plastic filter with emission properties similar to those of chlorophyll (fluorescence standard, Walz). This same standard has also been used in other studies (Burchard et al. 2000; Markstädter et al. 2001).

Anthocyanins in the epidermis, which absorb in the blue part of the solar spectrum, may complicate this method (Barnes et al. 2000). Visibly anthocyanin (red-) coloured leaves, which were observed with *O. digyna* and *B. vivipara*, were not used for the measurements. In 2000 and 2001, a red reference beam was used in addition to the blue one with *O. digyna*, as red light is not absorbed by anthocyanins. The ratio $F(BG)/F(R)$ did not vary systematically in the investigated leaves (data not shown).

The relative fluorescence ratios obtained are still dependent on the relative intensity of the excitation beams. A method for estimating actual epidermal UV-transmittance involves a comparison of $F(UV)/F(BG)$ in leaves that have had the epidermis stripped off, with the same ratio in intact leaves. Epidermal transmittance of UV-A and UV-B can then be estimated by normalizing $F(UV)/F(BG)$ of intact leaves to $F(UV)/F(BG)$ from epidermis-free leaves (assumed to represent 100% transmittance) (Markstädter et al. 2001),

$$T\% = 100 * \left[F(\mathrm{UV})/F(\mathrm{BG})_{\mathrm{ep}}/F(\mathrm{UV})/F(\mathrm{BG})_{\mathrm{mes}}\right]$$

where $T\%$ denotes the transmittance in percent, and $F(UV)/F(BG)_{ep}$ and $F(UV)/F(BG)_{mes}$ denote fluorescence ratios for leaves with and without (mesophyll only) epidermis, respectively. For most species, it is only possible to remove the abaxial epidermis and, hence, measurements of leaves without epidermis were taken on the abaxial side. Unfortunately, the only species where the abaxial epidermis could be stripped off using a scalpel and a pair of tweezers was *O. digyna*. Mean $F(UV)/F(BG)_{mes}$ values for this species ranged from 0.93 to 1.18 (UV-B) and from 1.49 to 1.96 (UV-A). In the UV-B especially, these data are considerably lower than values determined with the same apparatus in epidermis-free leaves of six different species (*Pisum sativum* L., *Vicia faba* L., *Brassica napus*, *Brassica rapa*, *Cucumis sativus* and *Arabidopsis thaliana* L.) grown at 21°C in a greenhouse. With these species, the mean values for epidermis-free abaxial sides ranged from 1.66 to 2.39 and from 1.41 to 1.78 for UV-A and UV-B, respectively. The mean values over these data were 2.283 (standard deviation, 0.121) and 1.674 (SD, 0.207). These last values were used as estimates of $F(UV\text{-}A)/F(BG)_{mes}$ and $F(UV\text{-}B)/F(BG)_{mes}$, respectively, for all plants in the current study.

All plants included in this study (except *Bistorta vivipara*) and plants used as reference for epidermis-free leaves have more or less horizontally oriented leaves, i.e. the adaxial epidermis is most exposed to the sun. Both adaxial and abaxial transmittance were measured for all leaves, but only the results for the adaxial side are shown due to space limitations. Generally, the abaxial transmittance is higher than the adaxial.

Statistical analysis

For the survey of epidermal UV transmittance of Svalbard plants, the mean values for all samples of all 12 species measured all 3 years were tested using a 2-way ANOVA. The effect of UV-B and

temperature enhancement was tested with a 2-way and a 3-way GLM repeated measurements ANOVA, respectively, using plot as replicate. The statistical software applied was Systat 10 for Windows (SPPS, Chicago, Ill).

The number of species sampled varied for the following reasons: some problems with the setting of the Xe-PAM fluorometer occurred in 2000 and were not immediately identified. Consequently, some results from 2000 were rejected, including data on *Silene acaulis*, *Saxifraga cespitosa* and *Cassiope tetragona*. *Saxifraga nivalis* and *Salix reticulata* were not always measured due to limited availability.

Results

Epidermal UV-transmittance of untreated Svalbard plants

In the survey of adaxial epidermal UV-transmittance in 12 Svalbard species, percentage transmittance of UV-A varied from 3.8 (*Salix reticulata*, 2001) to 11.6% (*Saxifraga oppositifolia*, 2000). UV-B transmittance ranged from 1.6 (*Saxifraga cespitosa*, 2001) to 11.4 % (*Bistorta vivipara*, 2000). All transmittance results are summarized in Fig. 1. Ten out of 12 species consistently had a UV-B transmittance lower than 9%; 5 species never had a mean above 6%. There was a significant effect of year ($P < 0.001$ for both UV-A and UV-B), and the ANOVA tests also indicated that there was an interaction among species and years ($P < 0.001$ for both UV-A and UV-B).

UV-B supplementation experiment

In addition to the general survey of Svalbard plants, five species were investigated that were grown under increased UV-B irradiation corresponding to 11% ozone depletion. The treatment did not consistently affect the epidermal UV-A or UV-B transmittance for any of the five species tested (Fig. 2 and Table 2 for results from the statistical analysis). However, Fig. 2 suggests that effects of the UV-treatment were apparent in some species and some years, but the direction of change sometimes varied between years.

Temperature-enhancement experiment

An increase in temperature of 2–3°C, as a result of OTC treatment, did not have any consistent effect on UV-A or UV-B transmittance for *Bistorta vivipara* (Fig. 3) ($P = 0.348$ and 0.331, respectively). Enhanced temperature slightly increased UV-A transmittance in *Salix*

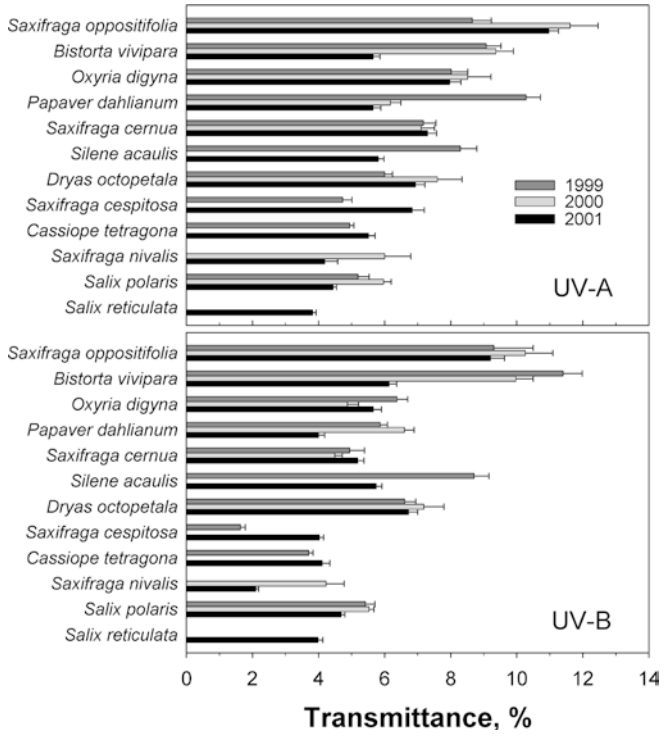

Fig. 1 Epidermal UV-A and UV-B transmittance (+SE) of 12 Spitsbergen plant species measured during 3 growth seasons, 1999, 2000 and 2001. The species are sorted according to the mean over 3 years of UV-A transmittance. Some species are not represented all years due to instrument problems in 2000 (*Saxifraga cespitosa* and *Cassiope tetragona*) and availability (*Salix reticulata* and *Saxifraga nivalis*)

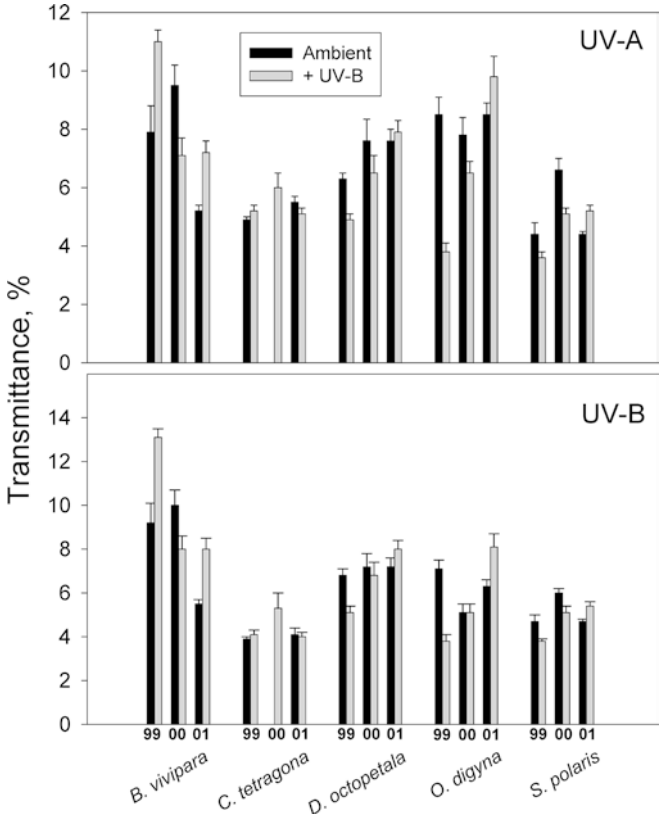

Fig. 2 Epidermal UV-A and UV-B transmittance (+SE) of five Spitsbergen plant species subjected to enhanced UV-B, simulating an 11% depletion of the ozone layer, with controls (*Ambient*). The experiment was carried out during the three growth seasons, 1999, 2000 and 2001

Table 2 Results from the two-way repeated measurements ANOVA for species included in the UV-B enhancement experiment (see also Fig. 2)

Species	UV-treatment						Year						Year*UV-treatment					
	UV-A transm.			UV-B transm.			UV-A transm.			UV-B transm.			UV-A transm.			UV-B transm.		
	df	*F*	*P*-value	*df*	*F*	*P*-value	*df*	*F*	*P*-value	*df*	*F*	*P*-value	*df*	*F*	*P*-value	*df*	*F*	*P*-value
Bistorta vivipara	1	0.299	0.639	1	0.604	0.518	2	0.141	0.873	2	0.370	0.712	2	1.220	0.386	2	1.230	0.383
Dryas octopetala	1	0.768	0.445	1	0.463	0.463	2	1.531	0.290	2	1.939	0.224	2	0.099	0.907	2	0.392	0.692
Cassiope tetragona	1	0.384	0.562	1	0.208	0.667	1	3.324	0.128	1	3.101	0.139	1	0.016	0.904	1	0.004	0.951
Oxyria digyna	1	2.961	0.183	1	2.108	0.242	2	4.209	0.072	2	1.912	0.228	2	3.925	0.081	2	3.640	0.090
Salix polaris	1	0.002	0.969	1	0.070	0.816	2	4.092	0.108	2	2.726	0.179	2	2.222	0.224	2	1.702	0.292

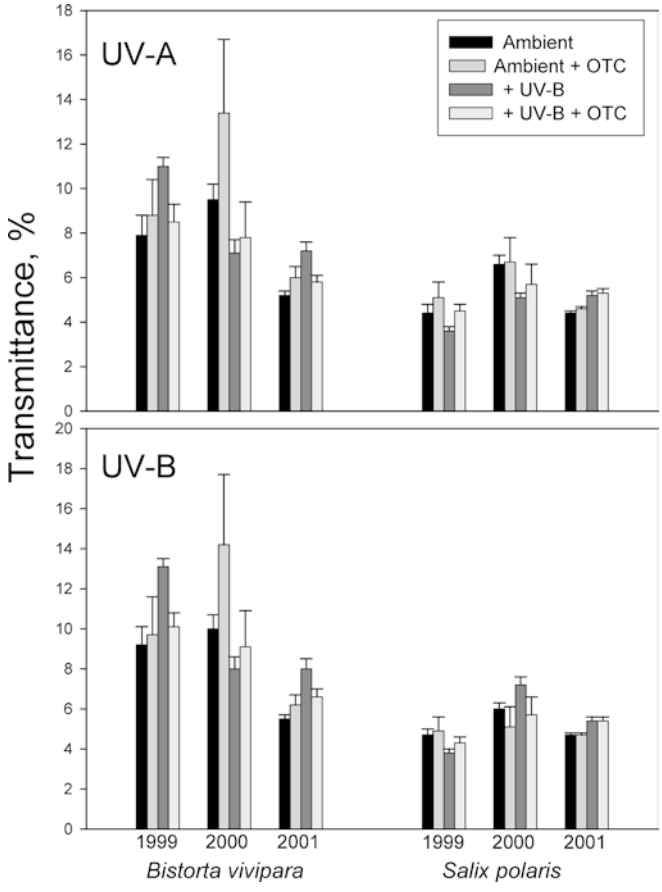

Fig. 3 Transmission of UV (+SE) through the adaxial epidermis of UV-treated and control specimens (*Ambient*) of the two Spitsbergen plant species grown in Open Top Chambers (*OTC*s) or in open air. The experiment was carried out during the three growth seasons, 1999, 2000 and 2001

polaris ($P = 0.032$), but this was not significant for UV-B ($P = 0.064$). Again, trends observed for 1 year were absent or sometimes even opposite in other years.

Discussion

Our measurements indicated that 88–98% of the incident UV-B radiation was absorbed by epidermal screening compounds in arctic plants. The observed transmittance values are lower than we initally expected, and within a narrower range than what was recorded for 11 arctic species collected at Barrow, Alaska (0.4–24.4%) (Robberecht et al. 1980). For the only species common to these two studies, *O. digyna*, Robberecht et al. (1980) observed a UV-B transmittance of 3.2%, which is substantially lower than what we measured (around 6%). Caldwell et al. (1982) cultivated an arctic provenance of *O. digyna* in a growth chamber and reported the epidermal UV-B transmittance to be 12%. However, their growth conditions might have caused less production of protecting compounds than under natural field exposure. The observed transmittance values are in a similar range as those found for angiosperms from a temperate mountain region by Day et al. (1992), but considerably lower than the data reported in the same study for seven herbaceous dicots. One may conclude that the majority of the investigated species from Svalbard are not less protected by epidermal screening than plants at lower latitudes, in spite of the comparatively lower UV-B radiation at Svalbard. However, epidermal screening is only one part of the protection of plants against the adverse effects of UV-B radiation. Therefore, plants at Svalbard may still be more susceptible to UV-B-induced DNA damage or oxidative stress than plants grown at lower latitudes.

The observed transmittance values are influenced by the choice of the reference for 100% transmittance. We chose to use epidermis-free leaves of six different broadleaved, mostly crop, species grown at conditions that minimized epidermal transmittance as a reference, instead of those obtained from *O. digyna* grown under field conditions (see Materials and methods). The choice of the latter would have increased UV-B transmittance values by about a factor of 1.5. In the crop species, low UV/BG fluorescence ratios for epidermis-free leaves could also be observed when they were grown under conditions that enhanced epidermal screening (data not shown, see also Markstädter et al. 2001). There was a consistent correlation for all investigated species between $F(\mathrm{UV})/F(\mathrm{BG})$ ratios with and without epidermis, which the data from *O. digyna* also fitted. The reason for the decrease in $F(\mathrm{UV})/F(\mathrm{BG})_{\mathrm{mes}}$ could be a contamination of the mesophyll, with UV-absorbing com-

pounds lost from destroyed epidermal cells during removal of the epidermis, or increased screening capacity of the uppermost cell walls of the mesophyll. In both cases, total UV protection of the mesophyll is only assessed when $F(UV)/F(BG)_{ep}$ values are related to the maximal possible values from epidermis-free leaves, which were only available from the mentioned crop species.

Epidermally located anthocyanins in *O. digyna* and *Bistorta vivipara* may have contributed to epidermal screening of the blue reference beam, thereby causing a too-high value for UV transmittance (Barnes et al. 2000). Since we selected leaves that were not red coloured, and since measurements with a red reference beam gave no indication for a screening of the blue beam, we believe that anthocyanins caused no problem. However, chosing green leaves may have selected against leaves with high flavonoid production. In any case, we would have recorded transmittance values higher than actually true.

The considerable screening in the UV-A spectral region (Fig. 1), which is of the same order of magnitude as that in the UV-B, suggests that flavonols, and possibly also flavones, play an important role in UV screening. The approximately linear relationship between UV-A and UV-B transmittance varied to some extent between species (data not shown), which is probably due to a species-specific composition of absorbing compounds.

Numerous studies have shown that the concentration of UV-absorbing phenolic compounds in leaves, especially flavonoids, increases with increasing UV-B radiation (e.g. Tevini et al. 1991; Beggs and Wellmann 1994; Dixon and Paiva 1995; Bornman et al. 1997; Cooper-Driver and Bhattacharya 1998; Meijkamp et al. 2001; Tegelberg et al. 2001). In contrast to the apparently general rule is a recent report on a UV-exclusion experiment with a subarctic heath community (Phoenix et al. 2002). Here, exclusion of UV-B and UV-A radiation resulted in an increase of UV-B-absorbing compounds in *Vaccinium vitis-ideae* and *V. uliginosum*. Variable responses of UV-B screening to elevated UV-B have also been reported for *Betula pendula* (Tegelberg et al. 2001). For the five species investigated in our study, epidermal screening increased with enhanced UV-B radiation in only some of them, and then only in some years (Fig. 2). The reason for inconsistent responses to UV-B radiation is unclear, and a higher number of replicates in the experiment would perhaps have given a clearer result. Possibly, a large proportion of UV-screening compounds in the investigated plants is constitutive. The UV-B radiation already naturally present at Svalbard, together with the actual PAR, is apparently sufficient to induce, and may possibly also saturate, synthesis of UV-B screening compounds. However, de la Rosa et al. (2001) reported that synthesis of important UV-B-protecting flavonoids in birch is not saturated by natural levels of UV-B + PAR. However, arctic, and possibly also subarctic growth conditions, may influence the sensitivity to UV-B radiation, or even induce synthesis of phenolic compounds. Drought, mineral-nutrient status, low temperature and wounding/herbivory are factors that have been shown to increase synthesis of UV-absorbing secondary metabolites in plants (Murali and Teramura 1985; Sullivan and Teramura 1990; Balakumar et al. 1993; Lavola and Julkunen-Tiitto 1994; Musil and Wand 1994; Dixon and Paiva 1995; Hakulinen et al. 1995; Solecka and Kacperska 1995; Chaves et al. 1997; Hunt and McNeil 1998; Keinänen et al. 1999; Levizou and Manetas 2001; de la Rosa et al. 2001; Tosserams et al. 2001; Awad and de Jager 2002). One may assume that natural variation in such factors could explain some of the interannual variation of screening. Low temperatures may induce anthocyanin production (e.g. Saure 1990; Shvarts et al. 1997), and maybe also the synthesis of other flavonoids (Christie et al. 1994; Solecka and Kacperska 1995). Hence, we speculate that low temperatures may be one of the causes for the generally low transmittances observed on Svalbard. However, increased temperature is a predicted global change (IPCC 2001) that could possibly reduce induction of UV-B-absorbing compounds if low temperatures are important. However, the temperature-enhancement by OTCs (Fig. 3) did not produce any clear trends; an increase of 2–3°C does not seem sufficient to change the UV-B protection of investigated species. In a similar study of Antarctic vascular plants, a temperature increase of 1.3–2.3°C had no effect on leaf concentration of soluble UV-B-absorbing compounds (Day et al. 1999).

Sullivan and Rozema (1999) summed up three decades of research by concluding that under field and realistic experimental conditions (e.g. natural spectral balance of UV-B, UV-A and PAR), most plants appear to be well protected from extensive damage due to exposure to enhanced UV-B radiation. Our study of epidermal UV-screening in arctic plants from Svalbard supports this conclusion, as does also a study by Johanson (unpublished work), who measured growth and reproductive output of the vegetation from the same experimental facilities as used for plants in Fig. 2. In most cases, they found no significant responses of the UV-enhancement on the plants. However, there exists no study of photosynthesis or DNA damage on these plants, and it may of course be that other parts of the plants may be more vulnerable than the leaves.

In conclusion, it seems possible that UV-B radiation is only one of several factors controlling epidermal UV transmittance of plants at Svalbard. Alternatively, today's UV + PAR-levels are already high enough to saturate synthesis of absorbing compounds. Such a conclusion is based on: (1) the relatively low transmittance in most plants; (2) the failure to consistently induce higher screening by artificial UV-B radiation; (3) the high variability from year to year, which may be governed by some unknown condition. It is not possible to decide which factors are important in induction of UV-B screening, but the prevailing low temperature may possibly be important.

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