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Depletion of stratospheric ozone over the Antarctic and Arctic: Responses of plants of polar terrestrial ecosystems to enhanced UV-B, an overview

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Polar plant responses to UV-B may be different in the Arctic than Antarctic regions.

Abstract

Depletion of stratospheric ozone over the Antarctic has been re-occurring yearly since 1974, leading to enhanced UV-B radiation. Arctic ozone depletion has been observed since 1990. Ozone recovery has been predicted by 2050, but no signs of recovery occur. Here we review responses of polar plants to experimentally varied UV-B through supplementation or exclusion. In supplementation studies comparing ambient and above ambient UV-B, no effect on growth occurred. UV-B-induced DNA damage, as measured in polar bryophytes, is repaired overnight by photoreactivation. With UV exclusion, growth at near ambient may be less than at below ambient UV-B levels, which relates to the UV response curve of polar plants. UV-B screening foils also alter PAR, humidity, and temperature and interactions of UV with environmental factors may occur. Plant phenolics induced by solar UV-B, as in pollen, spores and lignin, may serve as a climate proxy for past UV. Since the Antarctic and Arctic terrestrial ecosystems differ essentially, (e.g. higher species diversity and more trophic interactions in the Arctic), generalization of polar plant responses to UV-B needs caution.

Keywords: Antarctic; Arctic; UV-B; Terrestrial polar ecosystems; Tundra; Stratospheric ozone; *Deschampsia antarctica*; *Salix polaris*

1. Introduction and outline of the paper

For the last 30 years an annual ozone hole has occurred over the Antarctic and since about a decade ago ozone depletion has occurred over the north pole during the Arctic spring. During Antarctic spring 50–60% ozone depletion has occurred uninterruptedly with marked increases in surface UV-B fluxes as a result.

We briefly consider the development of the ozone hole over the south and north polar regions, current knowledge of stratospheric ozone and surface UV-B and possibilities to reconstruct past UV regimes. We mainly focus on the (few) field studies on effects of (enhanced) solar UV-B radiation on plant species in the (sub)antarctic and (sub)arctic climate zones.

This is not an in-depth review, but a selective overview highlighting relevant results and research lines for the future. For more detailed reviews we refer the reader to the following: Caldwell and Flint (1994), Rozema et al. (1997), Caldwell et al. (1998), Huttunen et al. (1998), Sullivan and Rozema (1999) and Rozema (1999) review effects of increased UV-B radiation on plants of terrestrial ecosystems; Day (2001); Paul (2001) and Paul and Gwynn-Jones (2003) review the ecological

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role of UV-B; Searles et al. (2001a,b) comprises a meta-analysis of UV-B field studies; Flint et al. (2003) evaluate methodologies; Robinson et al. (2003), Robson et al. (2003), Rozema et al. (in press) and Boelen et al. (in press) review UV-B field research in the (sub)antarctic and (sub)arctic. The two main methodologies used for manipulation of UV-B radiation in the field are compared (Table 2): UV-B (lamp) supplementation and UV-B (filter) exclusion or screening. Not only climate differs between the Antarctic and Arctic, but also their terrestrial ecosystems. Here we evaluate UV-B effects on polar plants species and discuss consequences of these differences (Table 1).

2. Ozone depletion over the Antarctic and Arctic

Since 1974 the thickness of the stratospheric ozone layer has decreased by about 0.5% per year for all latitudes, the tropical zones excepted, mostly as a result of ozone breakdown by chlorine released from emitted chlorofluorocarbons (Farman et al., 1985). Accordingly, surface UV-B radiation has increased by about 5% (Madronich et al., 1998; WMO, 2003). The Antarctic polar vortex obstructs the supply of ozone from other latitudes, leading to severe ozone breakdown at the surface of cold (−78 °C) polar stratospheric clouds (PSCs): the Antarctic ozone hole. Although complete breakdown of stratospheric ozone may occur during some days, ozone depletion is 50–60% on average. The ozone hole has occurred uninterruptedly every Antarctic spring for 30 years. Since 1995–1996 severe depletion of stratospheric ozone has also occurred over the Arctic (Dahlback, 2002; Rex et al., 2004). The Arctic is climatically less isolated and less cold than the southern polar region. The critical temperature of −78 °C, required for ozone breakdown by chlorine at the surface of polar stratospheric cloud crystals, did not occur earlier until warming of lower layers of the atmosphere as a result of the greenhouse problem led to lower stratospheric temperatures at the north pole in recent years (Shindell et al., 1998).

Table 1
Comparison of antarctic and arctic terrestrial ecosystems in terms of climate, geographical and climatical degree of isolation, evolutionary and biogeographical history, species diversity and ecosystem structure and trophic relationships

	Antarctic	Arctic
Climate and plant life	Extremely cold, polar vortex Annual precipitation 350–500 mm Mean air temperature warmest summer month –continental antarctic: below 0 °C, no terrestrial plant life –maritime Antarctic: 0–2 °C, limited terrestrial plant life –subantarctic: 5–10 °C, abundant terrestrial plant life Turner et al., 1997; Smith, 2003; Convey and Smith, in press	Less extreme cold (Gulfstream), no polar vortex Annual precipitation 200–350 mm Mean air temperature warmest summer month –arctic areas: below 0 °C, no terrestrial plant life –maritime arctic: 0–6.5 °C (Svalbard, Longyearbyen), abundant terrestrial plant life –subarctic 8–12 °C (Abisko) abundant terrestrial plant life including numerous vascular plants Rønning, 1996; Callaghan and Jonasson, 1995
Isolation	Antarctic continent isolated from continents on southern hemisphere, subantarctic island (groups), also climatically isolated (polar vortex) Smith, 1984, 1996, 2003	No real arctic continent, terrestrial arctic ecosystems: northern tops of North America, Eurasia (Siberia) and scattered island groups. Climatically less isolated.
Species diversity of (flowering) plants	Low (empty ecosystems), 2 flowering species Smith, 1984, 1996, 2003	High (filled ecosystems), e.g. about 160 flowering plant species Svalbard archipelago Rønning, 1996
Impact of human disturbance	Low, but significant in subantarctic regions (islands), many plant and animal species introduced Smith, 1984	Comparatively low, also in subarctic, despite long-term human presence
Terrestrial ecosystems structure, Trophic relationships	Simple, less representative –e.g. no Arbuscular Mycorrhizal Fungi mutualism in the Antarctic –no large herbivore mammals Convey, 2001	Less simple, more representative –e.g. Arbuscular Mycorrhizal Fungi mutualism widely distributed –large herbivore mammals (reindeer, musk ox) Post and Forchhammer, 2002
Evolutionary, biogeographical history	Very young, *Colobanthus* and *Deschampsia* pollen in 5000 year old peat, but no other vascular plants Fabiszewski and Wojtun, 1997	Young, arctic tundra vegetation since last glacial period: Younger Dryas, 11,000 years ago Isarin and Bohncke, 1999

While as yet no signs of recovery have been reported and the Antarctic ozone hole in 2003 was the second largest ozone hole ever (WMO, 2003), recovery of the ozone layer and disappearance of the polar ozone holes are predicted by 2050–2060 (WMO, 2003).

There is limited vascular and cryptogamic plant growth during the Antarctic or Arctic spring. Ozone depletion is less in the polar summer, the main period for plant growth, but only limited data of ambient UV-B irradiance in the Antarctic and Arctic are available (Dahlback, 2002; Newsham, 2003).

3. Current, past and future stratospheric ozone and surface UV-B, possibilities to reconstruct past UV climates

Whilst chlorofluorocarbons, (CFCs) have been banned and recovery of the stratospheric ozone layer is foreseen, the sudden, unpredicted occurrence of the ozone hole of the Antarctic in 1974, and its persistence for many decades, leaves us with important questions. Has there been an earlier ozone hole? What was the cause of such an ozone hole, and how did the ozone hole disappear and: is there natural variation of stratosphere ozone and surface UV-B (Rozema et al., 2002b)?

Instrumental monitoring of stratospheric ozone started only in 1926 (Staehelin et al., 2002; Webb, 2003) using Dobson spectrometers. Despite marked fluctuation, a decline of stratospheric ozone in Staehelin's data measured at Arosa, Switzerland, between 1970–1980 is detectable. Reliable instrumental data from before 1920 do not exist.

Indirect evidence of past levels of stratospheric ozone and surface UV-B may be derived from records of solar activity. Unexpectedly, well documented records of sun spot counts dating from 1550–1600 exist and sun spots correlate strongly with solar activity (Lean et al., 1995; Lean, 2000; Rozema et al., 2002b).

Apparently, an 11-year sunspot cycle and possibly centennial and millennial scale variation of solar activity exist, relating to variation of the temperature of planet Earth. Cold winters in parts of atlantic Europe in the Little Ice Age (Maunder Minimum) correlate well with few sun spots and low solar activity (Rozema et al., 2002b; Rind et al., 2004).

Satellite measurements started after the occurrence of the Antarctic ozone hole have significantly increased our knowledge of stratospheric ozone and surface UV-B (Lean, 2000). At solar highs UV-B radiation is only slightly increased, while UV-C radiation is strongly increased, stimulating the formation of stratospheric ozone, and thus solar activity is predicted to anticorrelate with surface UV-B. Recent reports of WMO (2003) demonstrate the predicted 11-year sunspot driven variation of stratospheric ozone.

It appears that the anthropogenic, CFC based (50–60%) depletion of stratospheric ozone causing the Antarctic and Arctic ozone, strongly exceeds the 11 years based variation of stratospheric ozone (4–13%) or the centennial or millennium time scale variation (27%) (Rozema et al., 2002b).

Additionally it is being attempted to track historic surface UV-B (and stratospheric ozone) through measurement of UV-B absorbing compounds in plant parts such as para-coumaric acid in pollen and moss spores and monolignols in (sub) fossil wood and lignin, all of which are preserved in the fossil record (Rozema et al., 2001a,b, 2002a,b; Blokker et al., in press; Doorenbosch et al., in press). Using UV-B absorbing pigments (scytonemin) in blue-green algae inhabiting shallow Antarctic lakes as a proxy for past UV-B, Hodgson (2001) and Leavitt et al. (2003a,b) found evidence for increased surface UV-B radiation in a period with reduced solar activity during the late quaternary and argued that Antarctic lakes may have received twice as much UV-B prior circa 3000–4000 years ago than they do at present.

One of the most widespread products of the phenyl propanoid pathway is lignin, which is a peroxidase catalysed polymerization product of three possible precursors. Coniferyl alcohol is the major component of gymnosperm lignin, whereas lignin in angiosperms is mainly composed of both coniferyl- and sinapyl alcohol. Coumaryl units are abundant, e.g. in compression wood lignin and grass lignins (Humphreys and Chapple, 2002).

Despite the small amount of possible monomers, lignin has a complex chemical structure due to the wide variety of possible intermolecular linkages. This and the insoluble and non-hydrolysable nature of lignin make it hard to analyse it by conventional analytical techniques. A very useful tool is pyrolysis-GC/MS, especially when combined with thermally induced hydrolysis and methylation reagents such as tetramethyl ammonium hydroxide (TMAH) (Blokker et al., in press).

In Fig. 1 aromatic monolignol compounds have been identified in wood of the polar willow *Salix polaris,* e.g. guiacyl units and syringyl units. Syringyl units correspond to sinapyl alcohol and sinapic acid, guiacyl units refer to coniferyl alcohol and ferulic acid, and para-coumaryl units to coumaryl alcohol and para-coumaric acid. See also Blokker et al. (in press) for more detailed chemical and methodological information. The relationship between UV-B and these monolignols requires studies of responses of trees to elevated UV-B (cf. Laakso et al., 2000; Tegelberg et al., 2001), and currently we expose for this purpose *Quercus, Pinus, Salix, Alnus* and *Betula* trees to elevated UV-B (Rozema et al., unpublished).

The aromatic building blocks of lignin are induced by solar UV-B by affecting the key-enzymes of the phenyl

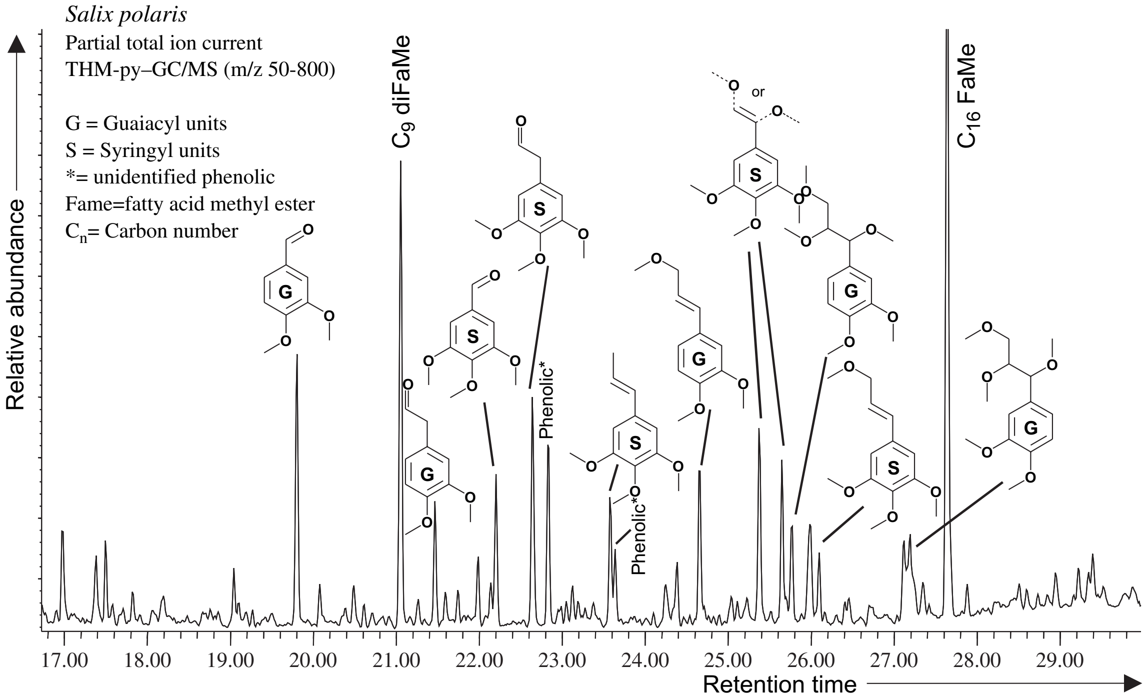

Fig. 1. Partial total ion current (16.80–30.00 min) of a TMAH-pyrogram of a 0.5× 1mm diameter piece of *Salix polaris* wood from Adventdalen, Longyearbyen, Spitsbergen, collected June 2003. Peaks indicate relative abundance of guiacyl (derived from coniferyl alcohol) and syringyl units, (derived from sinapyl alcohol). Retention time coniferyl alcohol: 24.66 min; retention time sinapyl alcohol: 26.10 min. See Blokker et al., in press for more analytical detail.

propanoid pathway (e.g. Hahlbrock and Griesebach, 1979; Meijkamp et al., 1999; Van de Staaij et al., 2002). The monolignol ratios of lignin of tree and plant species from various plant groups, latitudes and climate zones differ (Taiz and Zeiger, 1991). It is hypothesized that quantities or ratios of these monolignol compounds may contain signals of past climates.

By means of experimental manipulation of single climate factors (e.g. UV-B, PAR, atmospheric CO_2 and temperature) obtained correlative relationships may help to disentangle the complicated relation between monolignols and environmental interactions.

4. Differences between Antarctic and Arctic climates and terrestrial ecosystems

Stratospheric ozone depletion is most pronounced in the Antarctic and Arctic, as explained above. Ozone depletion at other than polar latitudes is less pronounced and subject to a variety of other factors such as horizontal and vertical transport of ozone (Stohl et al., 2003; WMO, 2003).

We refrain from defining in detail the geographical boundaries of the Arctic and Antarctic biome. Generally the area demarcated by the subantarctic islands is considered Antarctic in terrestrial Antarctic ecosystems studies (Convey, 2001), reaching to latitudes far away from the South Pole, e.g. Ile Crozet (47° S). Dependent on continental or maritime influences, southern limits of the Arctic biome also vary (Hessen, 2002).

Both in the Arctic and Antarctic there is terrestrial and aquatic animal and plant life (Hessen, 2002; Smith, 1984; Roberts, 1989; Convey, 2001a). However, terrestrial polar ecosystems in particular experience severe and harsh abiotic conditions, e.g. frost, wind, limited water availability, limited nutrient supply, short growing season. Thus polar plant life is at the physiological limits of survival (Robinson et al., 2003). Terrestrial polar plant life is restricted to relative mild maritime regions such as the Antarctic Peninsula and the Svalbard archipelago, which is influenced by the warm Gulfstream (Table 1). The Antarctic climate is, partly because of the polar vortex, more extreme than that of the Arctic. As a consequence vascular plants are few and cryptogamic plant species dominate the Antarctic terrestrial vegetation, with only two vascular plants (Smith, 1984) (Table 2), while in general plant life is more abundant in Arctic regions. For instance the high Arctic tundra of Svalbard contains more than 160 flowering plants including dwarf shrubs such as *Cassiope tetragona* and *Salix polaris* (Rønning, 1996). Arctic areas (e.g. Siberia, Alaska) are more or less contiguous with the sub-arctic Atlantic and temperate continents of Europe, Asia and North America and thus allowed exchange of plants and animals during periods

Table 2
Species composition of high arctic tundra vegetation at Adventdalen, Svalbard, the moss peat bank vegetation on Signy Island and Léonie Island, near Rothera base

Adventdalen, Arctic 78°55′ N, 11°56′ E	Signy Island, Antarctic 60°42′ S, 45°35′ W	Leonie Island/Rothera, Antarctic 67°35′ S, 68°2′ W
Flowering plants	**Flowering plants**	**Flowering plants**
Graminoids	Graminoids	Graminoids
Alopecurus borealis	*Deschampsia antarctica*	*Deschampsia antarctica*
Festuca rubra	*Colobanthus quitensis*	*Colobanthus quitensis*
Luzula confusa		
Carex misandra		
Woody dwarf shrubs/trees		
Salix polaris (deciduous)		
Cassiope tetragona (evergreen)		
Dryas octopetala		
Herbs		
Saxifraga hirculus		
Saxifraga oppositifolia		
Saxifraga hieracifolia		
Stellaria crassipes		
Oxyria digina		
Bistorta vivipara (=Polygonum viviparum)		
Hemiparasites		
Pedicularis hirsuta		
Equisetales		
Equisetum arvense		
Lycopodiaceae		
Huperzia selago		
Rønning, 1996; Rozema et al., in press	Boelen et al., in press	Smith, 1984; Newsham et al., 2002, 2003; Huiskes et al., 1999; Lud et al., 2001, 2002; Rozema et al., 2001a,b,c
Mosses	**Mosses**	**Mosses**
Sanionia uncinata	*Sanionia uncinata*	*Sanionia uncinata*
Polytrichum hyperboreum	*Chorisodontium aciphyllum*	*Cephaloziella*
	Polytrichum strictum	*Andraea regularis*
	Warnstorfia sarmentosa	
Rozema et al., in press	Boelen et al., in press	Lud et al., 2002; Newsham et al., 2002
Terrestrial algae		**Terrestrial algae**
Nostoc sp.		*Prasiola crispa* ssp. *antarctica*
Solheim et al., 2002		Lud et al., 2001
Lichens		**Lichens**
Peltigera aphtosa		*Turgidosculum complicatulum*
Stereocaulon alpinum		*Usnea antarctica*
Crustose lichen		
Solheim et al., 2002; Bjerke et al., 2003; Zielke, 2004		Lud et al., 2001

of climate change, including the glacial retreats during the Quaternary. This has led to a relatively high biodiversity in Arctic biomes in contrast with Antarctic regions (cf. Smith, 1984; Convey and Smith, in press). At Peary Land (northernmost Greenland, 84° N) about 100 species of vascular plants occur (Holmen, 1957). Abundant Arctic terrrestrial plant life, together with contiguity with northern hemisphere continents, has probably also allowed the existence of large herbivore mammals like musk ox and reindeer at the Arctic tundra (Post and Forchhammer, 2002).

It is therefore obvious that assessment of responses to enhanced UV-B is relevant in terrestrial polar ecosystems which face severe ozone depletion for up to 30 years.

Table 2 illustrates the marked difference in diversity of vascular plants by comparing the vegetation composition of the high Arctic tundra of Svalvard with that of the moss peat banks of Signy Island and the terrestrial vegetation of Léonie Islands. The cryptogamic plant species list in Table 2 is incomplete, it just refers to the species exposed to UV-B in our studies (Rozema et al., 2001a, in press; Lud et al., 2001; Boelen et al., in press). There are many more cryptogamic species in the maritime terrestrial Antarctic and Arctic environment (see e.g. Rønning, 1996; Elvebakk, 1994; Smith, 1984; Convey, 2001).

As a result of the low species diversity in the Antarctic, the structure and trophic relationships of terrestrial ecosystems are relatively simple. In this respect Antarctic terrestrial ecosystems will be less representative of ecosystems from lower latitudes than Arctic terrestrial ecosystems. The successful establishment of many introduced plant species, particularly in the subantarctic region, indicates that niches in terrestrial Antarctic ecosystems may have not been filled due to the geographical isolation (Smith, 1996; Frenot et al., 1997).

Although subantarctic (South Georgia) populations of *Deschampsia antarctica* and *Colobanthus quitensis* are mycorrhizal (Christie and Nicolson, 1983), roots of the perennial Antarctic hairgrass *Deschampsia antarctica* collected from Palmer station (Demars and Boerner, 1995) and from Léonie Island (cf. Rozema et al., 2001a; Rozema and van de Staaij, unpublished) were not infected by arbuscular mycorrhiza. However, in the greenhouse, roots of *Deschampsia antarctica* could be infected with *Glomus intraradices* and *Glomus etunicatum* to form typical arbuscular mycorrhizae structures (Demars and Boerner, 1995). Probably the geographical isolation has prevented natural transport of spores and fungal infection of *Deschampsia* root systems at Palmer and Léonie Island. In contrast a marked proportion of root samples of the perennial *Festuca rubra* collected at the high Arctic tundra on Spitsbergen contained mycorrhizal fungal hyphae, spores, arbuscules or vesicles.

Root samples of *Festuca rubra* from the high Arctic tundra at Svalbard were collected in June 2002 from experimental plots which had been irradiated with UV-B from fluorescent lamps since 1996. See Rozema et al. (in press) and Solheim et al. (2002) for more details on the methodology. The infection percentage of the UV-B irradiated plots (simulating 15% ozone depletion) was 45% and in the control plots, receiving ambient solar UV-B, 38% of the root sampled was infected by vesicular-arbuscular mycorrhizae, but the difference is not significant ($n = 4$, $p = 0.4$).

Both the north and south pole regions were free of terrestrial plant life during the last quaternary glacial period (Smith, 1984, 1996; Isarin, 1997) and current terrestrial plant communities must be evolutionary and biogeographically young. It is likely that invasion of vascular plants and their mycorrhizal fungi in the Arctic after quaternary glacial retreat was faster than at the Antarctic because of the geographical and climatic isolation of the latter. As a consequence of the marked differences between Antarctic and Arctic terrestrial ecosystems (Table 1), results of UV-B field experiments should be compared with caution.

5. Depletion of stratospheric ozone, does enhanced surface UV-B affect plant growth of polar terrestrial ecosystems?

Results of UV-B supplementation and UV-B exclusion studies in the field at high latitudes have been summarized in Table 3 (Antarctic) and Table 4 (Arctic). This is not a complete survey and review, for a more complete recent survey of effects of enhanced UV-B on terrestrial ecosystems see Caldwell and Flint (1994), Rozema et al. (1997), Searles et al. (2001a,b) and Robinson et al. (2003) (in particular for the Antarctic). Neither does the number of "no effect scores" or "negative response scores" express objective quantitative importance, it is a selective, qualitative survey.

We have selected polar UV-B field studies with (leaf) growth, photosynthetic rates or DNA damage as parameters, which may indicate plants to be sensitive or tolerant to elevated UV-B. In the case of UV-B exclusion studies we interpreted reduced growth of near ambient UV-B compared to below ambient UV-B as a negative response. We excluded UV field studies on UV-B absorbing compounds from the survey since concentrations of phenolics do not relate unambiguously to tolerance or sensitivity to UV-B (Searles et al., 2001a,b). Growth of the two phanerogamic Antarctic plants, *Deschampsia antarctica* and *Colobanthus quitensis,* appeared to be affected by manipulated surface solar UV-B levels during periods of severe ozone depletion in field experiments lowering ambient UV-B levels to below ambient UV-B levels (Day et al., 1999; Ruhland and Day, 2000; Xiong and Day, 2001). Leaf growth of *Deschampsia antarctica* decreased with elevated UV-B, but shoot density increased and relative growth rate was not affected (Rozema et al., 2001a).

Similar results have been obtained in field UV-B exclusion experiments running since 1996 at the subantarctic Tierra del Fuego by Ballaré et al. (2001), Rousseaux et al. (1999), Searles et al. (2001a,b) and Robson et al. (2003) for *Nothofagus* species, the herb *Gunnera* and *Sphagnum* species. So far such marked UV-B effects on polar plant growth have not been conclusively confirmed by UV-B supplementation experiments in the field, neither in the Antarctic (cf. Lud et al., 2001, 2002; Rozema et al., 2001c, nor in the (sub)Arctic (Björn, 2002; Rozema et al., in press; Phoenix et al., 2001).

Table 3
Effects of UV-B manipulation (exclusion, supplementation) on plant growth, photosynthesis, DNA damage or N fixation in Antarctic plants

Species	Location	Reference	UV-B treatment	Growth, photosynthesis, DNA damage	No effect	Negative	Positive
Flowering plants							
Deschampsia antarctica	Palmer	Day et al., 1999	UV-B exclusion	Shoot growth		+	
Deschampsia antarctica	Palmer	Day et al., 2001	UV-B exclusion	Leaf growth		+	
Deschampsia antarctica	Palmer	Ruhland and Day, 2000	UV-B exclusion	Leaf growth		+	
Deschampsia antarctica	Palmer	Xiong and Day, 2001	UV-B exclusion	Leaf growth area, biomass		+	
Deschampsia antarctica	Rothera	Lud et al., 2001	UV-B supplementation	photosynthesis	+		
Deschampsia antarctica	Controlled environment	Rozema et al., 2001a,b,c	UV-B supplementation	Leaf length		+	
Deschampsia antarctica	Controlled environment	Rozema et al., 2001a,b,c	UV-B supplementation	Shoot density			+
Deschampsia antarctica	Controlled environment	Rozema et al., 2001a,b,c	UV-B supplementation	RGR	+		
Colobanthus quitensis	Palmer	Xiong and Day, 2001; Day et al., 2001	UV-B exclusion	Leaf area, length, cushion biomass		+	
Colobanthus quitensis	Palmer	Xiong and Day, 2001	UV-B exclusion	RGR, NAR, shoot biomass, leaf area		+	
Mosses							
Sanionia uncinata	Rothera	Lud et al., 2002	UV-B exclusion	Biomass, branch length	+		
Sanionia uncinata	Rothera	Lud et al., 2002	UV-B exclusion	Branching			+
Sanionia uncinata	Rothera	Lud et al., 2003	UV-B supplementation	DNA damage		+	
Sanionia uncinata	Rothera	Lud et al., 2002, 2003	UV-B exclusion	Photosynthesis	+		
Sanionia uncinata	Rothera	Lud et al., 2002	UV-B supplementation	Photosynthesis	+		
Sanionia uncinata	Rothera	Newsham et al., 2002	Naturally elevated UV-B	Photosynthesis	+		
Cephaloziella aciphyllum	Rothera	Newsham et al., 2002	Naturally elevated UV-B	Photosynthesis	+		
Sphagnum magellanicum	Tierra del Fuego	Searles et al., 1999, 2002; Robson et al., 2003	UV-B	Height		+	
Sphagnum magellanicum	Tierra del Fuego	Searles et al., 1999, 2002; Robson et al., 2003	UV-B	Capitulum density			+
Sphagnum magellanicum	Tierra del Fuego	Searles et al., 1999, 2002; Robson et al., 2003	UV-B	Biomass per area	+		
Algae							
Prasiola crispa ssp. *antarctica*	Leonie Island	Lud et al., 2001	UV-B exclusion	Photosynthesis	+		
Lichens							
Usnea antarctica	Rothera	Lud et al., 2001	UV-B exclusion	Photosynthesis	+		

Table 4
Effects of UV-B manipulation (supplementation/exclusion) on plant growth, photosynthesis, DNA damage or N fixation in (high) arctic tundra plants

Species	Location	Reference	UV-B treatment	Parameter	No effect	Negative	Positive
Flowering plants							
Vaccinium uliginosum, vitis-idea *Empetrum hermaphroditum*	Abisko	Phoenix et al., 2001	UV-B supplementation	Growth	+		
Vaccinium myrtillus	Abisko	Phoenix et al., 2001	UV-B supplementation	Growth		+	
Salix polaris	Svalbard, Adventdalen	Rozema et al., in press	UV-B supplementation	Cover	+		
Salix polaris	Svalbard, Adventdalen	Rozema et al., in press	UV-B supplementation	DNA damage	+		
Dryas octopetala	Svalbard, Adventdalen	Rozema et al., in press	UV-B supplementation	Cover	+		
Salix polaris	Svalbard, Adventdalen	Rozema et al., in press	UV-B supplementation	Cover	+		
Cassiope tetragona	Svalbard, Adventdalen	Rozema et al., in press	UV-B supplementation	Cover	+		
Cassiope tetragona	Svalbard, Adventdalen	Rozema et al., in press	UV-B supplementation	DNA damage	+		
Pedicularis hirsuta	Svalbard, Adventdalen		UV-B supplementation	N plants/plot		+	
Mosses							
Polytrichum hyperboreum	Svalbard, Adventdalen	Rozema et al., in press	UV-B supplementation	Cover	+		
Polytrichum hyperboreum	Svalbard, Adventdalen	Rozema et al., in press	UV-B supplementation	Length male gametophytes		+	
Polytrichum commune	Abisko	Gehrke, 1999	UV-B supplementation	Growth length biomass	+	+	
Hylocomium splendens	Abisko	Phoenix et al., 2001	UV-B supplementation	Growth	+		
Dicranum elongatum	Abisko	Sonesson et al., 2002	UV-B supplementation	Growth	+		
Sanionia uncinata	Svalbard, Ny Ålesund	Lud et al., 2002	UV-B supplementation	DNA damage		+	
Sanionia uncinata	Svalbard, Adventdalen	Rozema et al., in press	UV-B supplementation	Cover	+		
Sphagnum fuscum	Abisko	Gehrke, 1999	UV-B supplementation	Thallus length, biomass			
Sphagnum fuscum	Abisko	Gehrke, 1999	UV-B supplementation		+		
Sphagnum fuscum	Abisko	Sonesson et al., 2002	UV-B supplementation	Growth	+		
Algae							
Nostoc	Svalbard, Adventdalen	Solheim et al., 2002	UV-B supplementation	N-fixation	+	+	
	Svalbard, Adventdalen	Zielke, 2004	UV-B supplementation	N-fixation	+	+	
	Svalbard, Adventdalen	Bjerke et al., 2003	UV-B supplementation	N-fixation	+	+	

Bryophytes form a significant component of both Arctic and Antarctic terrestrial vegetation, and are apparently well adapted to extreme polar climatic conditions. Where the Antarctic distribution of *Deschampsia antarctica* and *Colobanthus quitensis* stops, latitudes of the southern distribution limits of bryophytes are further south (Smith, 2003; Convey and Smith, in press). Some of the Arctic and Antarctic mosses are cosmopolites, i.e. *Bryum argenteum* (Smith, 1984, 1999), occurring outside the polar regions in open, exposed, urban microhabitats like rocks, walls, roofs. Other mosses are bipolar, e.g. *Sanionia uncinata* (Smith, 1984; Lud et al., 2001). Some polar bryophytes do sexually reproduce and form sporulating sporophytes, i.e. *Polytrichum hyperboreum* on the Svalbard tundra (Rozema et al., in press). Antarctic mosses tend to reproduce more sexually at higher Antarctic latitudes (Convey, 1996; Smith and Convey, 2002). From the limited number of field studies on polar bryophytes, it has been concluded that (partial) exclusion of solar UV-B in (sub)antarctic areas with significantly reduced stratospheric ozone does not affect growth, photosynthesis and DNA (Green et al., 2000; Huiskes et al., 1999; Lud et al., 2002, 2003; Newsham et al., 2002; Boelen et al., in press). Shoot length and shoot biomass of sub(ant)arctic *Sphagnum* species was slightly affected with enhanced UV-B in UV-B supplementation field studies, but biomass per ground area appeared to be unaffected (Gehrke, 1999; Searles et al., 2002; Robson et al., 2003). Length of male antheridium bearing gametophyte *Polytrichum hyperboreum* plants was reduced with enhanced UV-B, but not that of sporulating and non-sporulating moss plants in the high Arctic Svalbard tundra (Rozema et al., in press). Branching of the Antarctic moss *Sanionia uncinata* was reduced, shoot biomass and length were unaffected, DNA damage increased with enhanced UV-B during the day (PAR level 1000–1500 μmol $m^{-2} s^{-1}$) but was repaired during the (non-dark) night (PAR level 100 μmol $m^{-2} s^{-1}$) (cf. Lud et al., 2001).

Here we conclude, based on the low number of field studies in (sub)polar areas, that bryophytes are not significantly affected by enhanced UV-B levels simulating 15–30% stratospheric ozone depletion. Bryophytes, with relatively non-differentiated leaves, often consisting of one cell layer, are no more sensitive to enhanced UV-B than vascular plants.

With the notable exception of the results of Day and his group (Day et al., 1999, 2001; Xiong and Day, 2001), most UV-B supplementation and UV-B exclusion field studies indicate no UV-B or only small UV-B effects. This is in line with conclusions drawn for UV-B manipulation studies for terrestrial ecosystems from non polar latitudes (Caldwell and Flint, 1994; Rozema et al., 1997; Caldwell et al., 1998; Paul and Gwynn-Jones, 2003; Aphalo, 2003).

6. UV-B supplementation and UV-B exclusion field studies in (sub)polar regions

In Table 5 technical, practical and differences and research consequences of UV-B supplementation and UV-B exclusion field studies are listed. Recently Flint et al. (2003) surveyed and compared UV-B supplementation and UV-B exclusion field ecosystem studies. A major problem of non-modulated UV-B supplementation is the excessive supply of UV-B irradiance under cloudy conditions and the altered spectral weighting function in case of shading by lamp arrays, while UV-B exclusion with UV-B absorbing foils causes altered PAR, temperature and humidity.

Problems of UV-B supplementation field studies may consist of excessive irradiance of UV-B during periods of cloud cover in non-modulated systems (Flint et al., 2003) and irradiance of UV-A by the fluorescent tubes. The latter problem can be solved by application of a proper UV-A treatment control, by comparing lamps with UV-A blocking foil with lamps with UV-A and UV-B transmitting foil (Boelen et al., in press).

UV-B exclusion studies (Fig. 2b) do not require electrical power supply and allow near ambient solar UV-B and below ambient UV-B comparisons, by filtering UV-B wavelengths away with appropriate foils. These foils should be replaced regularly since the foils photodegrade. Thus natural solar UV-B is reduced. This may be particularly relevant at Antarctic sites with severely depleted stratospheric ozone and high ambient UV-B. However covering plants with filter foils alters the enclosed microenvironment, i.e. temperature may increase, humidity be altered (reduced during the day, increased by condensation during the night) and rainfall is intercepted. Attempts to prevent this by perforating the foil resulted in an uneven distribution of rainfall (Ballaré et al., 2001; Flint et al., 2003). Altered humidity within the foil or under foil may be limited in the year round windy environment of Tierra del Fuego (Robson et al., 2003), air temperature inside and outside the exclusion plots did not differ (Searles et al., 2002), but this seems to be the exception to the rule. In particular poikilohydric mosses are susceptible to changes in environmental humidity and increased humidity in the foil enclosed micro-environmental may have made the enclosed mosses (but also flowering plants) more responsive to elevated UV-B (cf. de Bakker et al., in preparation).

Well-planned studies in controlled environments exposing bryophytes to elevated UV-B and moisture will be relevant in this respect to analyse UV-B-humidity, temperature and PAR interaction. Photosynthetically active radiation (PAR, 400–700 nm) and infrared radiation are differentially transmitted by UV-B excluding and UV-B transmitting foils, which may affect photosynthesis and plant growth and thus

Table 5
Comparison of UV-B supplementation versus UV-B exclusion (filtering) field systems in terms of simulation of ozone depletion, methodology, costs, power supply, maintenance (see also Flint et al., 2003)

	UV-B supplementation	UV-B exclusion
UV-B and ozone depletion scenarios	Simulates various scenarios of stratospheric ozone depletion, compares ambient and elevated UV-B e.g. 15, 30, 50% ozone depletion. If possible modulated UV-B supplementation Caldwell et al., 1983; Sullivan et al., 1994; Boelen et al., in press	Compares ambient and below ambient solar UV-B fluxes, above ambient UV-B not possible. Particularly relevant in regions and period with ozone depletion and enhanced surface UV-B Flint et al., 2003
Method, controls	Ambient solar UV-B and (lamp) UV-A and UV-B emitted by fluorescent tubes (and not filtered away by mylar foil), non burning lamps, effigies	Ambient solar UV-B, UV-B transmitting foil and UV-B blocking foil (mylar)
Costs, power supply, maintenance	Expensive, requires electrical power supply, not always available at remote places. Frequent renewal of foils	Relatively inexpensive, no electrical power supply required, can be installed in remote places, less frequently renewal of foils
Errors, artefacts, problems	Lamps emit UV-A and UV-B, UV-A effect may be assessed by comparing Mylar foil treatment to lamp frame without output. However, UV-B effects cannot be assessed without UV-A effect	Differences in transmitted PAR, increased temperature, altered air humidity and reduced (not in Tierra del Fuego with year round strong winds) or altered (uneven) precipitation by interception by foil Effects attributed to UV-B interact with PAR, temperature and moisture Searles et al., 1999, 2001a,b, 2002; Robson et al., 2003
Application	Needs electrical power supply, has been applied in Antarctic and Arctic High arctic tundra, Svalbard: Gehrke, 1999; Björn, 2002; Solheim et al., 2002; Zielke, 2004; Rozema et al., in press Antarctic, Palmer station: Day et al., 1999 Antarctica: Rozema et al., 2001a,b,c; Lud et al., 2002; Boelen et al., in press	Maybe relevant in area of Antarctic ozone hole to compare naturally elevated and lower levels of surface UV-B. Long-term UV-B exclusion may imply marked year to year variation in absolute UV-B levels Sub(ant)arctic: Tierra del Fuego: Ballaré et al., 1999; Ballaré et al., 2001; Rousseaux et al., 1999 Abisko: Phoenix et al., 2003

the response to UV-B (Flint et al., 2003). The above observed altered microclimate inside foil enclosures may imply that no clear UV-B effects are assessed in UV-B exclusion studies, but interactions of UV-B with the changed environmental factors.

Reduced growth of Antarctic plants comparing below ambient and near ambient UV-B in field UV-B exclusion studies has not been confirmed by UV-B supplementation studies in polar areas, where ambient and above ambient UV-B irradiance levels are applied. At least in part this may be explained by UV-B irradiance dose response curves for (length) growth (Fig. 3). An ambient UV-Bbe (biologically available UV-B) level of 2.5 kJ $m^{-2}\,day^{-1}$ and 5.0 kJ $m^{-2}\,day^{-1}$ UV-Bbe, an above ambient UV-B level, and 0 kJ $m^{-2}\,day^{-1}$ as a below ambient UV-B level was chosen, see Rozema et al. (2001a) for more explanation. The curve in Fig. 3 indicates that growth reduction in response to increased UV-B levels from 2.5 to 5.0 kJ $m^{-2}\,day^{-1}$ (as with UV-B supplementation) is much less than increasing UV-B levels from below ambient (0 kJ $m^{-2}\,day^{-1}$) to (near) ambient 2.5 kJ $m^{-2}\,day^{-1}$(as with UV-B exclusion). UV-B exclusion studies, drastically reducing UV-B levels, may be more relevant for studying the ecological role of UV-B, rather than evaluating consequences of ozone depletion. UV-B supplementation studies in the field may help to assess consequences of enhanced UV-B as a result of stratospheric ozone depletion.

7. Conclusions

Based on the few available relevant polar UV-B field studies, there are only few and small effects of enhanced UV-B on plant species from polar ecosystems. The majority of the polar species and plant parameters related to growth and photosynthesis are not significantly affected by elevated UV-B (Tables 3 and 4). There are only few longer term field studies, consisting of UV-B exclusion (Ballaré et al., 2001; Rousseaux et al., 1999; Searles et al., 2001a,b; Robson et al., 2003), or UV-B supplementation studies (Phoenix et al., 2001; Solheim et al., 2002; Rozema et al., in press; Boelen

Fig. 2. a–d. UV-B supplementation set up with small UV lamp systems. (a) At the Antarctic: Leonie Island (Rozema et al., 2001a,b,c). (b) At Signy Island at a moss peat bank vegetation (Boelen et al., in press). (c) At the Arctic at the high arctic tundra of Adventdalen, Svalbard (Rozema et al., in press). (d) UV-B exclusion set up in a coastal dune grassland ecosystem (Rozema et al., 1999). The UV-B blocking or transmitting foil is supported by a frame and consists of overlying strips, transmitting precipitation to some extent. Ballaré et al. (2001), Searles et al. (2002) and Robson et al. (2003) use a similar UV-B exclusion set up in Tierra del Fuego terrestrial ecosystems, with perforated foil. Day et al. (1999, 2001) used vertical cylindric set-ups surrounding the antarctic hairgrass *Deschampsia antarctica*.

et al., in press). Comparison and interpretation of UV-B exclusion and UV-B supplementation field studies need to assess and quantify the possible errors and problems inherent to the two differing UV-B manipulation methodologies.

The finding that plants of polar terrestrial ecosystems are not markedly affected by enhanced solar UV-B, neither the flowering polar plants, nor the moss species studied, contradicts what several authors hypothesized: stressful harsh climatic and environmental polar conditions would make polar plants vulnerable to enhanced UV-B, and repair of UV-B induced damage could be hampered by low polar temperatures. In addition, polar moss plants have been assumed to be relatively sensitive to enhanced UV-B because of single cell layer leaves (cf. de Bakker et al., 2005, in preparation), lacking specialized epidermal cells with UV-B absorbing flavonoids as in many flowering plants.

An alternative hypothesis to explain their UV-B tolerance is that plants like mosses and lichens are

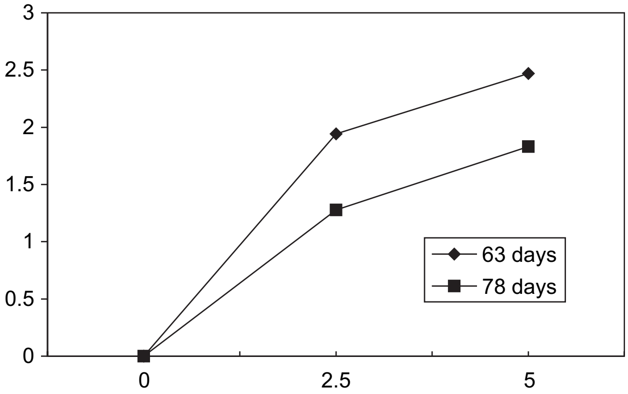

Fig. 3. Decreased leaf length (cm, *Y*-axis) of *Deschampsia antarctica* (relative to leaf length at 0 kJ m^{-2} day^{-1}) after 63 days and 78 days of plant growth exposed to 0, 2.5 or 5.0 kJ m^{-2} day^{-1} biologically effective UV-B (*X*-axis). Plants were grown in a climate room (4 °C, PAR 150 μmol m^{-2} s^{-1}, 75% relative humidity). Calculated after Rozema et al. (2001a,b,c). For more detailed description of experimental conditions, see Rozema et al. (2001a,b,c).

evolutionary older than flowering plants and may therefore have adapted to higher historic surface UV-B levels, than those occurring at present (Rozema et al., 2002a,b).

We discuss several possible causes and consequences of the responses of plants of polar terrestrial ecosystems to enhanced UV-B.

1. The scientific evidence so far is not conclusive and more and sufficiently replicated and longer term field experiments are needed (e.g. Niemi et al., 2002). There is considerable spatial variation in the polar terrestrial environmental (Solheim et al., 2002) and limited field plot replication and limited statistical power may have prevented significant UV-B effects to be detected (Robinson et al., 2003; Aphalo, 2003).
2. The UV-B exclusion and UV-B supplementation field approaches both provide useful information (Table 2), but differ essentially in the manipulated UV-B levels (Fig. 3).UV-B exclusion studies, reducing ambient UV-B levels will, be more relevant for studying the ecological role of UV-B, while UV-B supplementation studies may help to evaluate consequences of elevated UV-B during stratospheric ozone depletion despite methodological problems involved in both approaches.
3. Growth of terrestrial Antarctic and Arctic plants is not significantly affected by elevated UV-B simulating 15, 30 or may be higher (e.g. 50%) levels of ozone depletion. Assuming that experimental manipulation in the field (UV-B filtering or supplementation) does not contain insurmountable errors, and growth of polar plants has really occurred (polar plants grow slowly and the duration of the field experiment should allow observable growth), the absence of any significant overall UV-B effect implies that polar plants are adapted to high UV-B regimes and capable of preventing UV-B damage and or effectively repair UV-B damage. UV-B induced damage may occur in polar plants (Lud et al., 2002; Rozema et al., in press), but is repaired overnight by photoreactivation. In either case (prevention of UV-B damage or repair of UV-B damage), absence of significant UV-B effects may be interpreted as (terrestrial) polar plants being tolerant to enhanced UV-B. More generally this has been concluded for terrestrial plants and terrestrial ecosystems as a whole (Rozema et al., 1997; Caldwell et al., 1998; Paul and Gwynn-Jones, 2003; Aphalo, 2003). Also epidermal characteristics of (sub)arctic plants such as hairs and wax layers will contribute to protection against UV-B (Kinnunen et al., 2001). The tolerance to enhanced UV-B of higher and lower terrestrial polar plants to enhanced UV-B may also relate to the evolutionary history of terrestrial plants. Since the evolution of the planet Earth, algal plant life in the oceans and evolution of terrestrial plant life, some 500 millions years ago (Rozema et al., 1997, 2002a,b) the ozone layer developed and early land plants like mosses and lichens may have experienced significantly higher UV-B than current surface UV-B levels. Present-day terrestrial plants may still contain the UV-B tolerance acquired earlier (Rozema et al., 1997; Rozema and Björn, 2002).
4. There is considerable variation of surface UV-B in the terrestrial environment related to latitude, altitude, albedo, cloud cover, shading (Rozema et al., 1997; Caldwell et al., 1998; Paul and Gwynn-Jones, 2003). Surface UV-B levels in tropical and subtropical regions greatly exceed those of polar latitudes and it is likely that terrestrial plants have adapted to this marked variation. Polar plants are evolutionary young. The polar regions have become revegetated by tundra plants since the retreat of polar ice caps after the last glacial period: the Younger Dryas at the northern hemisphere some 11 000 years ago (Isarin, 1997). This implies that current tundra plants originated from plants growing at lower latitudes with naturally higher surface UV-B fluxes.
5. Antarctic and Arctic terrestrial ecosystems differ essentially in terms of climate, degree of isolation (geographically and climatically), evolutionary and biogeographical history, species diversity, impact of human disturbance, ecosystems structure and trophic relationships, so effects of UV-B on Antarctic and Arctic terrestrial ecosystems should be cautiously compared and interpreted.

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