

Six years of solar UV-B manipulations affect growth of *Sphagnum* and vascular plants in a Tierra del Fuego peatland

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Summary

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Received: 12 June 2003

Accepted: 17 July 2003

doi: 10.1046/j.1469-8137.2003.00898.x

- Tierra del Fuego is subject to increases in solar UV-B radiation in the austral spring and summer due to ozone depletion.
- Plastic films were used to filter solar UV-B radiation over peatland plots through six field seasons, resulting in near-ambient (c. 90%) and reduced (c. 17%) solar UV-B treatments.
- As in the first three field seasons of treatments, near-ambient UV-B caused reduced height growth but had no effect on biomass production of the moss *Sphagnum magellanicum*. It reduced leaf and rhizome growth of *Tetroncium magellanicum*. Height growth and morphology of *Empetrum rubrum* and *Nothofagus antarctica* were only affected by solar UV-B during the fourth to sixth field seasons. There was also a decrease in *Tetroncium* leaf nitrogen under near-ambient UV-B.
- Growth of *Sphagnum* was less affected than that of most emergent vascular plants. This enabled the *Sphagnum* mat to engulf more *Nothofagus*, and limit the escape of *Empetrum* under near-ambient UV-B. Yet, differences in the response of species to solar UV-B were not expressed as changes in plant community composition.

Key words: ozone depletion, UV-B radiation, *Sphagnum*, peatland, plant community, Tierra del Fuego, climate change, long-term ecological study.

© *New Phytologist* (2003) **160**: 379–389

Introduction

A stratospheric ‘ozone hole’ has formed above Antarctica during the austral spring (September–November) every year since the late 1970s (Farman *et al.*, 1985). This depletion of the ozone layer often extends beyond Antarctica to Tierra del Fuego, along with the associated increased ultraviolet-B radiation (UV-B) (Frederick *et al.*, 1994; Díaz *et al.*, 2000).

In Antarctica, solar UV-B was shown to reduce the rate of vegetative growth and leaf expansion of a native grass, *Deschampsia antarctica* Desv., and a forb, *Colobanthus quitensis* (Kunth) Bartl., compared with plants under filters that blocked much of the UV-B (Ruhland & Day, 2000; Day *et al.*, 2001; Xiong *et al.*, 2002). In short experiments with mosses, solar UV radiation had no effect on *Bryum argenteum* Hedw. (Green

et al., 2000) and *Sanionia uncinata* (Hedw.) Loeske (Montiel *et al.*, 1999; Lud *et al.*, 2003). However, significant changes in pigmentation due to short-term UV-B fluctuations have been detected in Antarctic mosses (Newsham *et al.*, 2002).

Tierra del Fuego, situated at the most southerly tip of South America, experiences the greatest increase in UV-B radiation as a consequence of ozone depletion of any region outside Antarctica (Díaz *et al.*, 1996; Cede *et al.*, 2002). This is most pronounced during October, when the ‘ozone hole’ can sometimes pass directly over Tierra del Fuego. Consequently, short-term increases in UV-B radiation of up to 50% from day to day can occur at Ushuaia, Argentina (55° S) (Díaz *et al.*, 2001). Also, the subsequent break-up of the Antarctic vortex (November–early December) allows pockets of ozone-depleted air to pass over this region later in the growing season.

High latitudes have historically received little UV-B radiation (Caldwell *et al.*, 1980). Thus, current decreases in the thickness of the ozone layer cause large relative increases in UV-B flux, although compared to lower latitudes, especially the tropics, total UV-B flux remains small. Since organisms have evolved under low background UV-B flux, they may be sensitive to a large relative increase in UV-B radiation. The location of Tierra del Fuego presents an opportunity to study more diverse plant communities than occur in Antarctica and yet still experience the effects of increased solar UV-B radiation (Díaz *et al.*, 2000, 2001).

Interspersed among mature *Nothofagus* forest stands, along stream and lake margins, peatlands form an important component of the landscape of southern Tierra del Fuego (Roig, 2000). The composition of the Tierra del Fuego peatlands is comparable to those of the Northern Hemisphere; *Sphagnum magellanicum* is a widespread peatland species (Daniels & Eddy, 1985), whilst *Empetrum rubrum* is a dominant vascular plant, similar to *Empetrum hermaphroditum* in the Northern Hemisphere.

The overall objective of the investigation was to follow changes in the peatland plant community through 6 years of solar UV-B manipulation. This paper concentrates on the last 3 years. After the first 3 years of UV-B manipulation in this peatland, Searles *et al.* (1999, 2002) observed a small reduction in *Sphagnum* height growth (*c.* 15%), and a decrease in size of the largest leaf of *Tetroncium* (*c.* 14% in November), but no growth responses of *Empetrum* or *Nothofagus* to the solar UV-B manipulations. Based on these findings, we continued with another 3 years of more intensive investigation into plant responses to solar UV-B treatments. We aimed to assess whether longer-term UV-B treatments would result in more conspicuous responses of the *Sphagnum* and emergent vascular plants to solar UV-B manipulations. Furthermore, we examined whether changes in growth and morphology of *Sphagnum* and the vascular plant species would be evident as shifts in species composition and density within the plant community.

Materials and Methods

The study site is a peatland of approximately 1500 × 500 m. It is located in Tierra del Fuego National Park (54°51' S 68°36' W) to the north of a small lake (Laguna Negra) and stream, otherwise surrounded by mature *Nothofagus* forest. The peatland derives all its water from precipitation, and has a pH of 4.5–6.5. The groundwater level drops to *c.* 40-cm depth when the peatland is driest in late summer. This peatland was chosen because it has relatively high plant diversity, homogeneously distributed over its area.

The peatland receives 500–600 mm precipitation annually. Precipitation over the 5-month growing season (October–February) was approximately 260 mm (1999–2000), 312 mm (2000–2001) and 269 mm (2001–2002) (T. M. Robson, unpublished data). The mean annual temperature is 5–6.5°C, reflecting the oceanic climate.

The peatlands of Tierra del Fuego have been well characterized by Mark *et al.* (1995) and Roig (2000). *S. magellanicum* (Brid.) forms an almost continuous mat, with occasional hummocks and small pools bordered by *Sphagnum fimbriatum* Wils. Of the emergent vascular plants, *Nothofagus antarctica* (Forster f) Oersted (Nothofagaceae) (southern beech) is most abundant along the forest border. This species usually grows as a small tree, but is severely stunted in the peatland, typically reaching only a few cm above the *Sphagnum* mat. *Empetrum rubrum* Vahl ex Willd (Empetraceae) (crowberry) is a creeping evergreen woody perennial, which dominates on the drier tops and sides of the hummocks; *T. magellanicum* Willd (Juncaginaceae) (arrow-rush) grows in the wetter hollows and depressions between hummocks. In addition, *Nanodea muscosa* Banks ex C. F. Garertner, a hemiparasite of *Sphagnum* peatlands, *Juncus scheuchzerioides* Gavdich, and *Pernettya pumila* (cf.) Hooker are found at lower density throughout the site (Moore, 1983). Most of the vascular plant species are visible as ramets emerging from the *Sphagnum* mat. Nearby ramets are often part of the same genet divided beneath the peatland surface.

Treatment plots

Ten pairs of 1.4 × 2-m experimental plots were selected during October of 1996 in level and homogeneous areas of the *Sphagnum* mat (Searles *et al.*, 1999). Near-ambient and reduced UV-B treatments were randomly assigned within the pairs of plots. Plastic-film filters were suspended horizontally from frames (*c.* 40 cm) above the plots to create the UV-B treatments (see photo, Ballaré *et al.*, 2001). A uniform pattern of slits was melted into the filters producing a matrix of small louvres (2 × 25 mm) distributed over the entire filter that enabled water from precipitation to penetrate evenly to the *Sphagnum* mat. Also, we did not wish to totally exclude UV-B in the reduced UV-B treatment. The reduced UV-B treatment was achieved using perforated polyester filters (100-µm thick, optically equivalent to 'Mylar-D', Dupont Co., Wilmington, Delaware, USA) that attenuate *c.* 83% of the short wavelength UV-B radiation and transmit most of the UV-A radiation (Searles *et al.*, 2002). Near-ambient UV-B plots were covered by perforated polyfluorine filters ('Aclar' type 22A, 38-µm thick, Honeywell, Pottsville, Pennsylvania, USA) that block *c.* 10% of the UV-B (Searles *et al.*, 2002; Zaller *et al.*, 2002).

The precipitation passing through the two filter types was found to be approximately equal. Photosynthetically active radiation (PAR, total quantum flux in the 400–700 nm waveband) was measured with a quantum sensor (LiCor, Lincoln, Nebraska, USA) at the study site in Tierra del Fuego National Park. This showed that 83–95% PAR radiation was transmitted through both filter types (data not shown).

Filters were installed in late September to coincide with snow melt in the peatland, and remained in place until late March in each of the three field seasons (1999–2002), following the same protocol as Searles *et al.* (1999, 2002). Broken

filters were replaced within a day, and a complete replacement of filters was made after three months, in late December. Filter attenuation remained unchanged over this time period (Searles *et al.*, 2002).

For the duration of the experiment, under both of the UV-B treatments, air, surface and below-surface temperatures, precipitation, and UV-B radiation were monitored (21× data-logger, Campbell Scientific, Logan, Utah, USA) and compared with ambient values (data not shown).

Growth measurements

Growth measurements were continued on *Sphagnum*, *Empetrum*, *Tetroncium* and *Nothofagus*, the same plant species studied during the first 3 years of the experiment (Searles *et al.*, 2002). For continuity and comparability, growth was measured in the same way as during the first 3 years of the project. Because *Sphagnum* peatlands are known to exhibit considerable inherent microsite variability (Gerdol, 1996; Mitchell *et al.*, 2000; Phoenix *et al.*, 2003), and responses to UV-B in the first 3 years of this project were subtle (Ballaré *et al.*, 2001; Searles *et al.*, 2002), we increased the sample size to include 12 ramets of each species per plot.

Sphagnum growth

Ten new colour-coded cranked wires (Clymo, 1970) were inserted into each plot in February of 1999 to allow time for the *Sphagnum* to recover from any associated disturbance (Searles *et al.*, 2002) before the first measurements in September 1999. The vertical growth of the *Sphagnum* mat up these wires (and two existing wires) was measured four times through each growing season to determine seasonal growth patterns. Existing wires were used to compare height growth of *Sphagnum* under the filters and in the open, to determine the influence of the plot microclimate on growth during the fourth and fifth field seasons. These measurements showed that *Sphagnum* height growth was greater under the near-ambient UV-B filter than in the open (data not shown).

At the beginning and end of the sixth field season, *Sphagnum* capitulum density was measured nondestructively. The number of *Sphagnum* capitula in a 120 × 120-mm area was counted, and six randomly assigned counts per plot were taken. *Sphagnum* capitulum mass was sampled at the same time that density was censused and height growth was measured.

Annual *Sphagnum* biomass production and volumetric density of capitula were calculated from height growth, density, and biomass data. To calculate biomass increase per stem, a capitulum correction factor was used following Gehrke (1998). A random sample of 14 *Sphagnum* capitula were removed from each plot and cut into two 5-mm lengths, 0–5 mm and 5–10 mm from the apex (for calculation of the capitulum correction factor). Samples were oven dried at 65°C for at least 72 h and subsequently weighed to obtain dry mass.

Tetroncium measurements

Tetroncium leaf length (second to fifth leaves produced), and total number of green and senescent leaves were measured during November, December and towards the end of the growing season every year. In March 2002, 12 ramets per plot were harvested for measurement of rhizome growth. *Tetroncium* grows sympodially from a rhizome, branching from the leaf axil. Each leaf produced leaves a scar around the rhizome's circumference allowing retrospective growth measurements to be taken. Tightly packed leaf scars correspond to late season growth, allowing annual rhizome growth to be determined as in other rhizomous plants (Duarte *et al.*, 1994; Moen & Walton, 1996). Total rhizome elongation over each of the last 7 years was measured, as was the distance between each of the most recent 13 leaf scars, to reveal the seasonal pattern of elongation over the year. Frequency of rhizome division and root production from the rhizome were also noted.

Twelve leaves per plot were harvested in February of 2001, air-dried, pooled, ground, and sealed in aluminium foil for analysis of their carbon and nitrogen composition. This analysis was carried out at Utah State University Analytical Laboratories, using a CHN1000 analyser (LECO Corporation, St Joseph, Michigan, USA).

Empetrum measurements

Annual stem elongation of *Empetrum* was measured as the distance from an annual terminal bud scar on the stem to the shoot apex (Searles *et al.*, 1999, 2002). Growth measurements of the same plants were taken once every field season in March, as was distance from the shoot apex to the *Sphagnum* mat. These plants had 3–4 years of growth above the *Sphagnum* mat when first selected in September 1999.

Annual terminal bud scars were used to carry out a retrospective analysis of *Empetrum* growth. Twelve ramets of various sizes were harvested from each plot every field season for more detailed measurements of the number of leaves, branching frequency, and total annual stem and branch growth (up to seven branches) following Shevtsova *et al.* (1997). A comparison was made between the last three field seasons (1999–2002), and the first three field seasons (1996–1999, ramets harvested in February 2000). The harvest of a range of ramets allowed the treatment effects on ramets differing in their years of growth above the *Sphagnum* mat to be assessed independently.

Nothofagus measurements

Nothofagus ramets with at least 3 years of stem growth visible above the *Sphagnum* mat were selected in September 1999. Stem growth and leaf production were measured twice during each field season. Expansion of the first and third true leaves produced was followed through each field season.

Terminal bud scars were used to determine the years of *Nothofagus* stem growth above the *Sphagnum* mat, retrospective annual stem extension, and branching frequency, in the same manner used with *Empetrum*. The vertical height of each stem above the *Sphagnum* mat was measured at the end of each season, and compared to the previous field season to calculate the rate of engulfment by *Sphagnum*.

Community composition

Community composition was assessed by placing a quadrat over a 120 × 60-cm area in the centre of the plot. The area was divided into 50 equal squares. All the *Nothofagus* ramets and at least two-fifths of the more abundant *Empetrum* ramets in the quadrat were censused. The number of years of growth of each ramet above the *Sphagnum* mat was assessed using annual terminal bud scars. Ramets were recruited into 'apparent age' classes dependent on whether they were outpacing or being engulfed by the *Sphagnum* mat. This allowed changes in the 'apparent age' structure of the *Nothofagus* and *Empetrum* populations to be assessed. The number of *Tetroncium* individuals and the less abundant *N. muscosa*, *J. scheuchzerioides* and *P. pumila* were counted at the end of the fifth and sixth field seasons of the project.

Statistical analysis

To allow for hydrological gradients and heterogeneity of vegetation across the site, each pair of plots was considered as a block. However, where between-block variability was low, block was omitted from model.

The effect of UV-B treatment on cumulative stem growth, distance between leaf scars on the *Tetroncium* rhizome, morphological characteristics of *Sphagnum* and *Empetrum*, and *Tetroncium* leaf carbon and nitrogen, was assessed using an ANOVA in a one-way factorial, randomized complete block design. The effect of UV-B treatment on *Tetroncium* leaf expansion was assessed using an ANOVA in a one-way factorial, completely randomized design. The effects of UV-B treatment and year on annual stem and rhizome growth, *Tetroncium* and *Nothofagus* morphological characteristics, change in height growth, and plant population size were assessed using an ANOVA in a two-way factorial, blocked split-plot-in-time

design. Year and UV-B treatment were fixed-effects factors, and blocks (where used) were a random-effects factor. The effects of UV-B treatment and apparent age on annual stem growth of *Empetrum* were likewise assessed using an ANOVA in a two-way factorial, blocked split-plot-in-time design. *Tetroncium* rhizome elongation data were Log_e or square-root transformed as appropriate before analysis to better meet assumptions of normality and homogeneity of variance. Back-transformed means and standard errors are presented.

We tested various covariance matrix structures: based on the assumption that growth in the peatland at any sampling time was most strongly correlated with growth at the next sampling time, together with Schwarz Bayesian information statistics, we determined that the first-order autoregressive structure was most appropriate for analysis of growing plants; and that the compound symmetry structure was most appropriate for repeatedly harvested samples. Growth responses of the *Tetroncium* rhizome, and *Sphagnum* capitulum were regressed against temperature, precipitation, and daily UV-B radiation data.

All computations were performed in SAS version 8.2 (SAS Institute Inc., Cary, North Carolina, USA). *P*-values, where given in the text or with figures in ANOVA tables, are accompanied by numerator and denominator degrees of freedom, and *F*-values.

Results

Sphagnum growth

Sphagnum height growth was consistently slightly less (*c.* 9%) under near-ambient than under reduced UV-B throughout the experiment (Fig. 1). Measurements throughout the growing season showed that most height growth occurred from October to January when the groundwater level is relatively high (data not shown), although this also coincides with maximum ozone depletion.

Capitulum density was slightly increased (*c.* 5%) under near-ambient compared with under reduced UV-B, and together with a tendency (*P* = 0.062) for increased capitulum mass (*c.* 8%), contributed to an increase (*c.* 32%) in volumetric density under near-ambient UV-B (Table 1). This offset the reduction in *Sphagnum* height growth seen under near-ambient UV-B (Fig. 1), and resulted in no change in *Sphagnum* biomass production between UV-B treatments (Table 1).

Table 1 *Sphagnum magellanicum* morphological parameters

Parameter	Capitulum mass (mg mm ⁻¹ stem length)	Density (stems m ⁻²)	Volumetric density (g dm ⁻³)	Biomass production (g m ⁻²)
Near-ambient	1.38 (± 0.06)	13 169 (± 396)	8.06 (± 0.75)	199.2 (± 10.9)
Reduced	1.27 (± 0.05)	12 588 (± 380)	6.10 (± 0.69)	191.7 (± 14.5)
<i>P</i> -value	0.062	0.006	0.056	0.625

Samples taken during field season 2001–2002. Mean of 10 plots per UV-B treatment (±1 se).

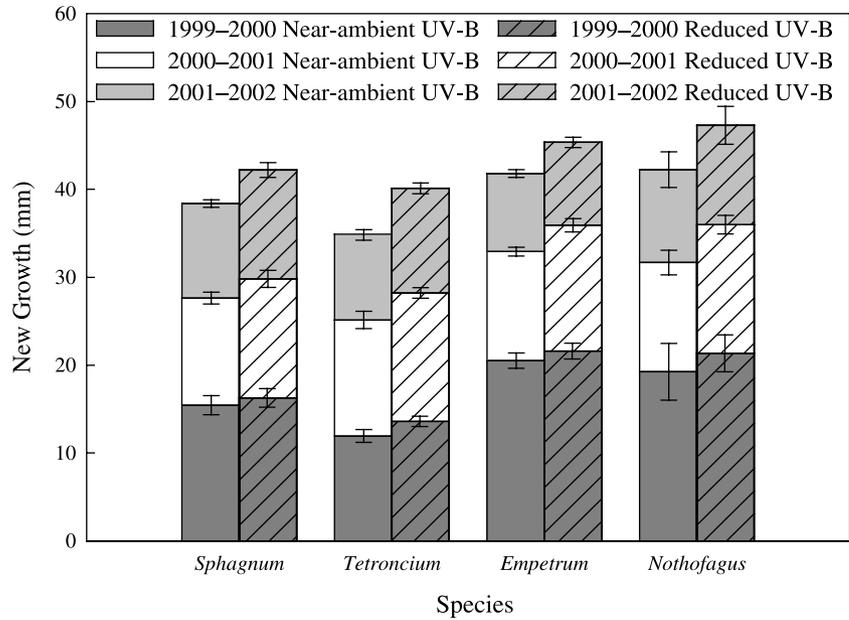


Fig. 1 Cumulative annual growth increments over three field seasons for the *Sphagnum*, *Empetrum* and *Nothofagus* stems, and the *Tetroncium* rhizome. Each field season mean is for 10 plots per UV-B treatment (± 1 SE). Back-transformed data are shown for *Tetroncium*.

	Source of variation	Split-Plot ANOVA				One-way ANOVA			
		Num	Den	F	P	Num	Den	F	P
		df	df			df	df		
<i>Sphagnum</i> growth	UV-B	1	9	4.97	0.027	1	9	5.95	0.037
	Year	2	36	8.95	<0.001				
	UV-B \times Year	2	36	0.05	0.951				
<i>Tetroncium</i> growth	UV-B	1	9	6.98	0.022	1	9	6.54	0.031
	Year	2	36	8.15	0.001				
	UV-B \times Year	2	36	1.68	0.201				
<i>Empetrum</i> growth	UV-B	1	9	3.66	0.072	1	9	6.28	0.028
	Year	2	36	118	<0.001				
	UV-B \times Year	2	36	1.10	0.319				
<i>Nothofagus</i> growth	UV-B	1	9	0.63	0.449	1	9	1.74	0.203
	Year	2	36	16.1	<0.001				
	UV-B \times Year	2	36	0.12	0.900				

***Tetroncium* growth**

Annual rhizome elongation was reduced (*c.* 13%) under near-ambient UV-B (Fig. 1). There was no difference ($F_{1,18} = 0.44$, $P = 0.516$) in the magnitude of UV-B effect over the course of the experiment (Fig. 2a).

Each ramet measured produced 5–6 leaves per growing season. By measuring elongation between individual leaf scars, we determined that the treatment effect was highly seasonal, most pronounced during periods of rapid growth and not apparent late in the season (Fig. 2b). No effect on annual root production or the frequency of clonal division was found from rhizome or ramet analysis (data not shown). *Tetroncium* growth response to the near-ambient UV-B treatment was significantly negatively correlated with rainfall ($R^2 = 0.894$), but not with other climatic variables (temperature and net radiation) (data not shown).

All measured leaves expanded more slowly under near-ambient UV-B, and reached a smaller final size (*c.* 13%) than under

reduced UV-B (only Leaf 3 is shown; Fig. 3). The number of leaves produced and the rate of leaf senescence were not affected by UV-B treatment (data not shown). There was no change in leaf carbon content (*c.* 43% carbon, both treatments; $F_{1,9} = 0.06$, $P = 0.813$), but there was significantly ($F_{1,9} = 8.51$, $P = 0.017$) less leaf nitrogen under near-ambient ($2.6 \pm 0.1\%$, mean ± 1 SE) than under reduced UV-B ($3.0 \pm 0.1\%$).

***Empetrum* growth**

Annual stem growth of a repeatedly measured cohort of ramets was consistently reduced from 1999 to 2002 under near-ambient UV-B (Fig. 1). This trend was more pronounced in harvested ramets, representing a range of sizes, over the same period (*c.* 10%; Table 2). There was also a slight tendency for less frequent branching and less branch growth under near-ambient UV-B from 1999 to 2002 (Table 2). *Empetrum* stem growth outpaced height growth of the *Sphagnum* mat

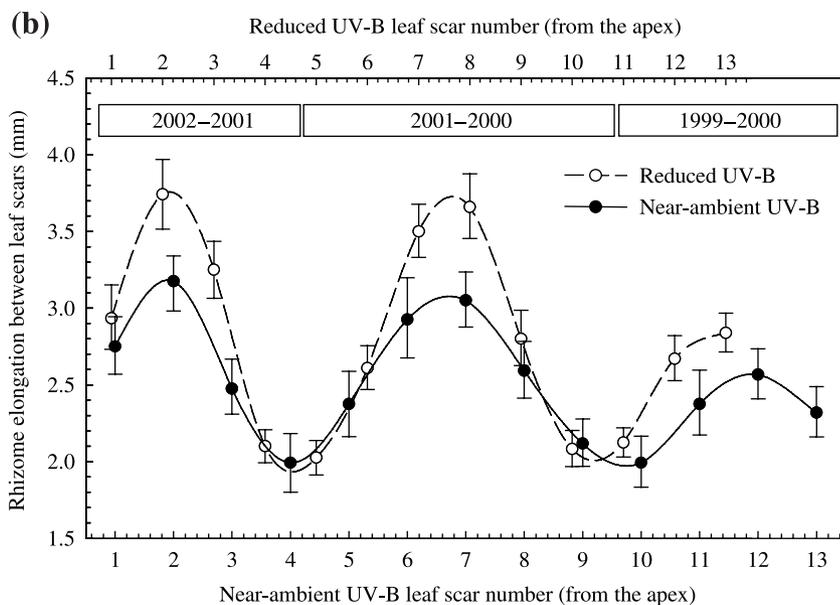
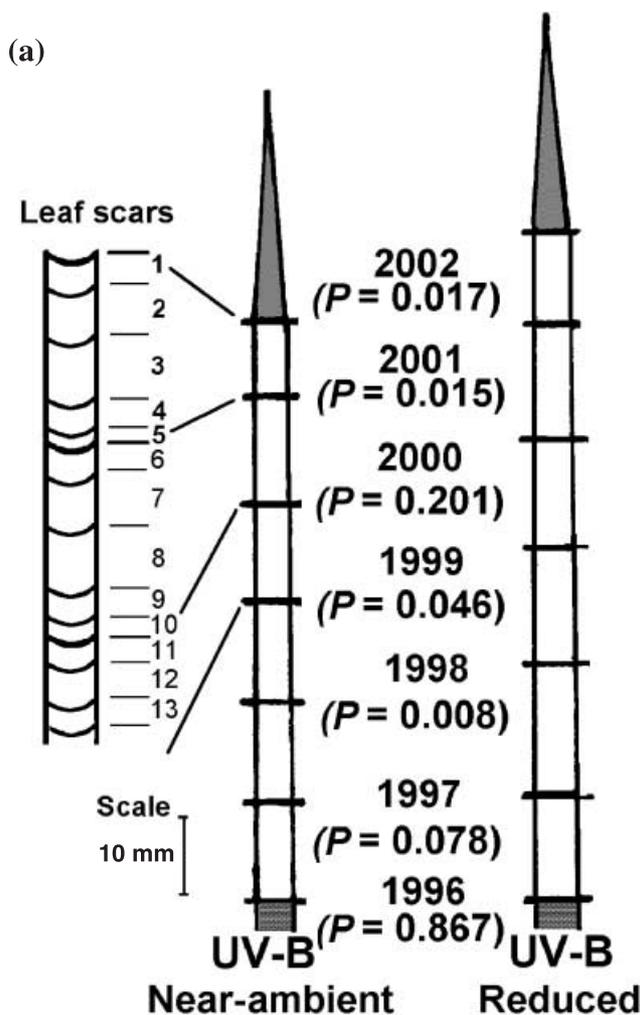


Fig. 2 *Tetroncium* rhizome growth. (a) Back-transformed mean annual growth is depicted. Annual elongation was calculated as the distance between tightly clustered leaf scars produced in the autumn of each year. The grey shaded area before 1996 designates growth before the UV-B treatments. Inset shows an impression of each individual leaf scar. (b) Rhizome elongation between the most recent 13 leaf scars produced before harvest in March 2002. Back-transformed means of 10 plots per UV-B treatment (± 1 SE) are plotted on two x-axes to allow for differential leaf production under the two treatments. Elongation was significantly reduced under near-ambient UV-B ($P < 0.05$) during the period of maximum growth in each field season.

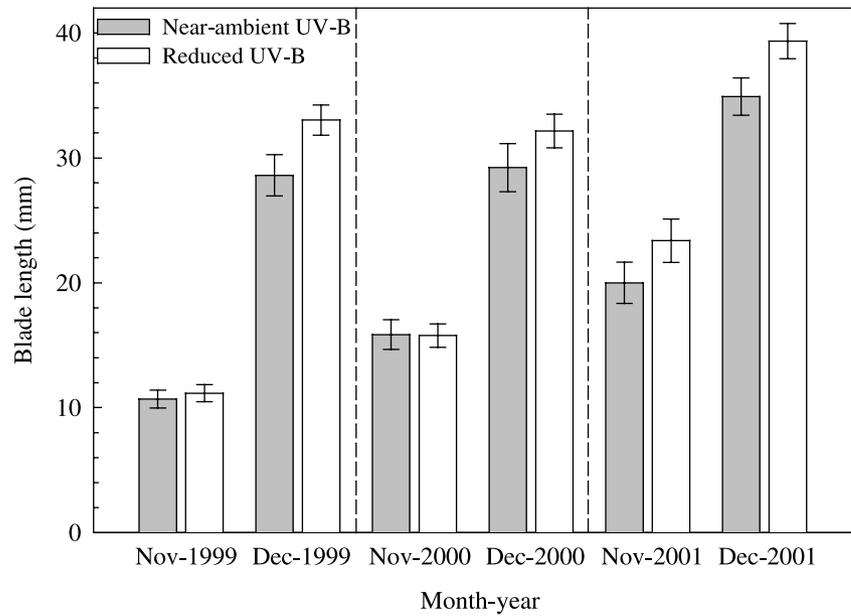


Fig. 3 *Tetroncium* blade length of the third leaf produced. There was a 2-wk interval between the November and December measurement in each year. Mean of 10 plots per UV-B treatment (± 1 SE).

	Source of variation	Num df	Den df	F	P
<i>Tetroncium</i> leaf 3 (Nov)	UV-B	1	9	1.22	0.298
	Year	2	36	72.1	< 0.001
	UV-B \times Year	2	36	2.79	0.075
<i>Tetroncium</i> leaf 3 (Dec)	UV-B	1	9	5.76	0.040
	Year	2	36	0.91	0.412
	UV-B \times Year	2	36	0.69	0.510

Table 2 Retrospective analysis of annual stem and leaf growth and morphology of *Empetrum* ramets

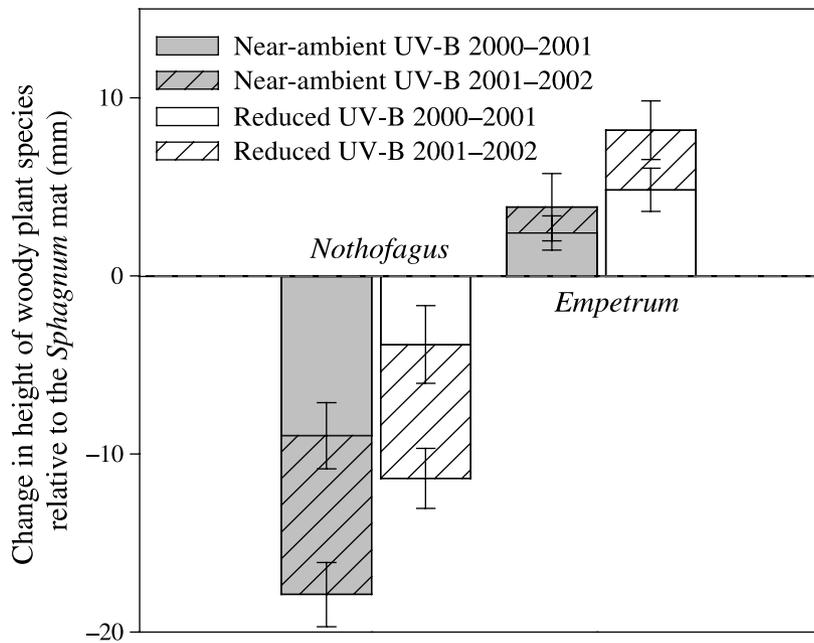
Retrospective analysis of harvested plants (1999–2002)				
UV-B treatment	New growth of main stem (mm)	New growth of stem and branches (mm)	Branching frequency (Branches year ⁻¹ growth)	Number of leaves (year ⁻¹ growth)
Near-ambient	12.4 (± 0.4)	29.0 (± 1.8)	1.2 (± 0.2)	25.8 (± 0.7)
Reduced	13.7 (± 0.5)	34.5 (± 2.2)	1.5 (± 0.1)	28.3 (± 1.3)
P-value	0.044	0.062	0.062	0.114
Retrospective analysis of harvested plants (1996–1999)				
	New growth of main stem (mm)	New growth of stem and branches (mm)	Branching frequency (Branches year ⁻¹ growth)	Number of leaves (year ⁻¹ growth)
Near-ambient	19.0 (± 1.0)	26.1 (± 1.4)	0.7 (± 0.1)	31.1 (± 1.4)
Reduced	19.4 (± 0.9)	27.9 (± 1.9)	0.8 (± 0.1)	34.9 (± 1.9)
P-value	0.664	0.214	0.634	0.124

1999–2002 ramets harvested in February of 2002. 1996–1999 ramets harvested in February of 2000. Data for three field seasons are pooled. Mean of 10 plots per UV-B treatment (± 1 SE).

under reduced UV-B (Fig. 4). However, the increase in *Empetrum* height above the growing *Sphagnum* mat was *c.* 53% less under near-ambient than under reduced UV-B (Fig. 4).

The apparent age structure of the ramet population above the *Sphagnum* mat also underwent some change due to the

UV-B treatments. Ramets with ≥ 4 years of growth above the *Sphagnum* exhibited much slower growth than those with fewer years of growth above the mat. The net result of slow growth of the ‘older’ ramets, and the consistently depressed growth of ‘younger’ ramets under near-ambient UV-B (data



	Source of variation	Num df	Den df	F	P
<i>Nothofagus</i> engulfment	UV-B	1	9	9.63	0.004
	Year	1	18	1.05	0.314
	UV-B × Year	1	18	1.08	0.308
<i>Empetrum</i> escape	UV-B	1	9	8.89	0.006
	Year	1	18	0.65	0.427
	UV-B × Year	1	18	0.03	0.873

Fig. 4 Cumulative annual changes in the height of *Nothofagus* and *Empetrum* ramets relative to the *Sphagnum* mat under near-ambient UV-B and reduced UV-B. Mean of 10 plots per UV-B treatment (± 1 se).

not shown), resulted in 20% of these 'older' ramets being partially engulfed by the *Sphagnum* between the 2001 and 2002 growing seasons (data not shown).

Nothofagus growth

Nothofagus stem growth was highly variable among shoots, and there was no statistically significant effect of UV-B treatment on stem growth (Fig. 1). When measured in the sixth field

season, there was a decrease in branching frequency (*c.* 35%) under near-ambient compared to reduced UV-B (Table 3).

Annual measurements of vertical height show that *Nothofagus* ramets were outpaced by the *Sphagnum* mat. Under near-ambient UV-B *Nothofagus* ramets were engulfed by the *Sphagnum* mat *c.* 57% more rapidly than under reduced UV-B (Fig. 4).

The UV-B treatments had no effect on *Nothofagus* leaf size or number in November, but in December when fully

Table 3 Leaf production and branching frequency of *Nothofagus* ramets

UV-B treatment	Number of leaves on new stem growth (Nov)	Number of leaves on new stem growth (Jan)	Leaf Area – Nov (mm ²)	Leaf Area – Dec (mm ²)	Branching frequency (Branches year ⁻¹ growth)
Near-ambient UV-B	3.3 (± 0.2)	4.2 (± 0.2)	1913 (± 123)	3135 (± 123)	1.3 (± 1.1)
Reduced UV-B	3.5 (± 0.2)	4.7 (± 0.3)	2313 (± 236)	3543 (± 186)	1.6 (± 1.1)
P-value					
UV-B	0.355	0.057	0.203	0.044	0.007
Year	0.0001	0.0001	0.0001	0.0001	
UV-B × Year	0.488	0.384	0.271	0.014	

Split-plot ANOVA on data for three field seasons, except branching frequency (2001–2002 only; one-way ANOVA). Mean of 10 plots per UV-B treatment (± 1 se).

Table 4 Annual population of peatland plant species, as total number of ramets above the *Sphagnum* mat per plot over the final two field seasons

Field season	Species UV-B treatment	<i>Nothofagus</i>	<i>Empetrum</i>	<i>Tetroncium</i>	<i>Pernettya</i>	<i>Nanodea</i>	<i>Juncus</i>
2000–01	Near-ambient	124 (± 20)	925 (± 175)	434 (± 87)	15 (± 5)	12 (± 4)	29 (± 14)
	Reduced	106 (± 26)	936 (± 142)	443 (± 120)	14 (± 7)	16 (± 3)	17 (± 5)
2001–02	Near-ambient	108 (± 20)	972 (± 179)	350 (± 85)	7 (± 2)	17 (± 6)	19 (± 8)
	Reduced	93 (± 14)	1059 (± 154)	327 (± 97)	10 (± 3)	16 (± 3)	9 (± 3)
<i>P</i> -value	UV-B	0.360	0.591	0.761	0.766	0.531	0.334
	Year	0.048	0.010	< 0.001	0.056	0.347	0.019
	UV-B × Year	0.555	0.269	0.863	0.759	0.055	0.722

Mean of 10 plots per UV-B treatment (±1 SE).

expanded, the first leaf produced annually was smaller (*c.* 15%) under near-ambient than under reduced UV-B (Table 3). There was also a tendency (*P* = 0.057) for fewer leaves (*c.* 10%) under near-ambient UV-B (Table 3).

Like *Empetrum*, the growth of *Nothofagus* ramets declined with years above the *Sphagnum* mat (Fig. 1). When broken down into apparent age classes, many *Nothofagus* ramets (*c.* 50%) had only one year of growth above the *Sphagnum* mat. No changes in the apparent age structure of *Nothofagus* due to solar UV-B treatment occurred during the last 2 years of the study (data not shown).

Community composition

Sphagnum annual height growth was greater than that of *Nothofagus* (Fig. 4) and *Tetroncium* (Fig. 1), but less than that of *Empetrum* in both treatments (Fig. 4). Irrespective of the UV-B treatments, *Empetrum* increased (*c.* 8%), whilst *Tetroncium* (*c.* 23%) and *Nothofagus* (*c.* 13%) decreased in ramet density from the fifth to the sixth field season (Table 4). However, there were no overall changes in the species composition of the plant community due to the UV-B treatments at the end of the sixth field season (Table 4).

Discussion

Overall, growth of *Sphagnum* and the vascular plant species was reduced by near-ambient UV-B over the last 3 years of our study. The effects, although small, were generally consistent over time. Many of the trends in measured parameters were not significant when taken in any one year, but were when repeatedly measured over several years.

A reduction in *Sphagnum* height growth and increase in volumetric density to due solar UV-B occurred during the fourth to sixth field seasons and is comparable to that reported during the first three field seasons (Searles *et al.*, 2002). There was no evidence of an incrementally greater treatment effect accumulating with time. A similar change in the growth and morphology occurred in *Sphagnum fuscum* growing under supplemental UV-B lamp treatments (*c.* 30% greater than

ambient) in a sub-Arctic (68° N) peatland (Gehrke, 1998). In a peatland microcosm study under similarly enhanced UV-B, there was no effect of the supplemental UV-B on *Sphagnum angustifolium*, and, if anything, a slight decrease in *Sphagnum balticum*, capitulum mass (Niemi *et al.*, 2002a, 2002b).

The most responsive species to UV-B radiation in our study was *Tetroncium*, which exhibited reduced rhizome growth and leaf expansion during the 6 years of treatments (also see Searles *et al.*, 2002). In other experiments in Tierra del Fuego, near-ambient UV-B similarly reduced summer root-growth in a *Carex* fen (Zaller *et al.*, 2002), and leaf expansion of perennial herb *Gunnera magellanica*, and fern *Blechnum penna-marina* (Rousseaux *et al.*, 1998, 2001). On the Palmer Peninsula, Antarctica, solar UV-B also reduced leaf expansion of *Deschampsia antarctica* (Day *et al.*, 2001) and *Colobanthus quitensis* (Xiong *et al.*, 2002).

Tetroncium favours the wettest areas of the peatland, and in high rainfall years the reduction in rhizome growth under near-ambient UV-B was less pronounced. The UV-B effect was apparently dampened by the greater annual growth under both treatments during wetter years. *Tetroncium* leaf nitrogen concentration was lower under near-ambient than under reduced UV-B. It is possible that these two effects were symptomatic of reduced nutrient availability in low rainfall years. Nutrient limitation is often considered to be the most important stress restricting growth of vascular plants in peatland competition (Aerts *et al.*, 1999; Bridgman, 2002). Even under long-term nitrogen deposition, *S. magellanicum* monoliths were able to capture and retain most nitrogen in the capitulum, and exhibited reduced height growth and increased density. This, in turn, limited nitrogen availability for the emergent vascular plants (Heijmans *et al.*, 2002a, 2002b).

Empetrum stem growth was consistently reduced by near-ambient solar UV-B during the fourth to sixth field seasons of the experiment. This treatment effect was not apparent during the first three field seasons of the research (Table 2; also see Searles *et al.*, 2002). Generally, *Empetrum* species have been found to be quite unresponsive to climate change factors (Shevtsova *et al.*, 1995; Press *et al.*, 1998; Tybirk *et al.*, 2000; Weltzin *et al.*, 2000). In contrast to our study, there were no

long-term effects of supplemental UV-B treatments (*c.* 30% greater than ambient) on growth or morphology of *E. hermaphroditum* in a sub-Arctic heath (Gehrke *et al.*, 1996; Phoenix *et al.*, 2001).

In our study, both *Empetrum* and *Nothofagus* were less competitive against the *Sphagnum* mat under near-ambient UV-B. *Empetrum* was less successful at escaping from the *Sphagnum* mat, and *Nothofagus* was engulfed by *Sphagnum* to a greater extent under near-ambient than under reduced UV-B. These trends can only partially be explained by reduced stem growth due to solar UV-B, and it is likely that the concurrent reduction in branching frequency and growth were also contributing factors. Indeed, changes in the production and orientation of branches are known to affect competition between *Sphagnum* and emergent peatland vascular plants (Svensson, 1995). In a comparable study of the effects of solar UV-B on a sub-Arctic heath community, a reduction in branching frequency was the only significant treatment effect on *E. hermaphroditum*, perhaps due to high within-treatment growth variation (Phoenix *et al.*, 2003).

After six field seasons of treatments, changes in growth and competition between *Sphagnum* and vascular plant species were still not reflected at the community level. This is similar to the results of other solar UV-B manipulation experiments of shorter duration (Day *et al.*, 2001; Phoenix *et al.*, 2003). The only population-level change was the partial engulfment by *Sphagnum* of 'older' *Empetrum* ramets subject to near-ambient UV-B for five and six field seasons of treatments. This may indicate that six field seasons is insufficient time for growth effects to be expressed at the community level in such a slow growing system, particularly when many other confounding environmental variables affect growth and competition (Shevtsova *et al.*, 1995; Press *et al.*, 1998).

Our reduced-UV-B treatment is lower than solar UV-B levels in this region before ozone depletion occurred (Searles *et al.*, 2002); therefore, our differences in UV-B treatments were substantially larger than the difference between normal solar UV-B before and with ozone depletion. Yet growth responses of *Sphagnum* and vascular plants to the solar UV-B manipulations were still rather subtle. If ozone depletion in this region substantially ameliorates within the next few decades, it is unlikely that significant changes in the structure of the Tierra del Fuego peatland plant community will occur. In our experiment, *Sphagnum* gained a competitive advantage over emergent vascular plants under near-ambient UV-B, but this was not substantial enough to alter the community composition between the fourth and sixth field seasons of this study. Biomass production of *Sphagnum* was unaffected by UV-B treatments, but hypothetically the change in *Sphagnum* morphology could alter carbon storage by affecting peatland hydrology (van Breemen, 1995), since the denser capitulum layer could retain more water, reducing decomposition in the acrotelm (Malmer *et al.*, 1994). To become meaningful in a broader context, the long-term effects of UV-B radiation

should be studied together with other climatic changes and this has received little attention (Björn *et al.*, 1999; Phoenix *et al.*, 2001; Sonesson *et al.*, 2002).

Acknowledgements

Funding was provided by the United States National Science Foundation Terrestrial Ecology and Global Change grants (95-24144 and 98-14357). We are particularly grateful to the Argentinean National Park Service (Administración de Parques Nacionales) for allowing us to use Parque Nacional de Tierra del Fuego to perform our experiments. We gratefully acknowledge the vital collaboration with CADIC-CONICET (Centro Austral de Investigaciones Científicas), Ushuaia (Dir. Eduardo Olivero), including access to the NSF UV monitoring station data (Susana Díaz), and weather data for Ushuaia (Rodolfo Iturraspe). Technical support and field assistance in Tierra del Fuego was provided by Nicolás Garibaldi, Ricardo Saenz-Samaniego, and Florencia Díaz. We also appreciate Peter Searles, Carla Giordano, Renato Gerdol and Hans Zaller for research advice, and Susan Durham's substantial statistical input. Two anonymous reviewers gave valuable suggestions on an earlier version of this manuscript.

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