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Reduction of solar UV-B mediates changes in the *Sphagnum* capitulum microenvironment and the peatland microfungal community

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Abstract The influence of near-ambient and reduced solar UV-B radiation on a peatland microfungal community was assessed by exposing experimental plots to UV-selective filtration. Replicate plots were covered with special plastic films to effect treatments of near-ambient and attenuated solar UV-B. The microfungal community from the top 1 cm of *Sphagnum* capitulum in a Tierra del Fuego peatland was censused throughout three growing seasons, between 1999 and 2002. *Sphagnum* capitula under near-ambient UV-B were more compressed and held more water than capitula under reduced UV-B. This water had a greater conductivity and was more acidic under near-ambient UV-B, as would be expected with increased leaching from the *Sphagnum* leaves. Nine regularly occurring hyphal fungi from the peatland were identified, at least to genus. Over three field seasons, no treatment effect on total fungal colony abundance was recorded, but individual species abundance was increased (*Mortierella alpina*), decreased (*Penicillium frequentans*), or was unaffected (*P. thomii, Aureobasidium*) by near-ambient UV-B. Species richness was also slightly lower under near-ambient UV-B. These treatment differences were smaller than seasonal or inter-annual fluctuations in abundance and species richness. In a growth chamber experiment, lamp UV-B treatments indicated that realistic fluxes of UV-B can inhibit fungal growth in some species. In addition to this direct UV-B effect, we suggest that changes in the peatland fungal community under near-ambient solar UV-B may also result from increased nutrient and moisture availability in the *Sphagnum* capitulum. The subtle nature of the responses of peatland fungi to solar UV-B suggests that most fungal species we encountered are well adapted to current solar UV-B fluxes in Tierra del Fuego.

Keywords Ozone depletion · *Sphagnum magellanicum* · Tierra del Fuego · *Penicillium* · *Mortierella*

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Introduction

Tierra del Fuego, at the southern tip of South America, has received increased UV-B radiation due to stratospheric ozone depletion for at least the last 20 years (Farman et al. 1985; Frederick et al. 1994). Whilst solar UV-B fluxes often remain low compared to those at low latitudes (about half of mid-summer values at 40° latitude), the relative increase in daily UV-B flux in Tierra del Fuego during the austral spring (October–November) can be up to twice that received prior to the occurrence of ozone depletion (Rousseaux et al. 1999; Searles et al. 1999). This substantial relative UV-B increase may influence community dynamics at different trophic levels in the forests and peatlands that dominate the region, e.g., slower decomposition rate (Pancotto et al. 2003), and changes in the extent of herbivory (Ballaré et al. 2001; Zaller et al. 2003).

Sphagnum mosses in peatlands create the hydrological conditions that allow carbon sequestration to occur through incomplete decomposition (van Breemen 1995; Clymo et al. 1998). Peatlands hold an estimated one-third of global soil organic carbon (Adams and Faure 1998; O'Neill 2000). The importance of peatlands in the global carbon cycle has spurred considerable research. In particular, the interaction of warming (Gerdol et al. 1998; Weltzin et al. 2001), increased N deposition (Berendse et al. 2001; Tomassen et al. 2003), increased atmospheric CO_2 (Heijmans et al. 2001, 2002), and changing precipitation (Weltzin et al. 2003) on rates of plant growth and decomposition in peatlands (O'Neill 2000) have been investigated. However, few studies have involved the influence of UV-B radiation on processes and

organisms associated with decomposition in heaths and peatlands (Johnson et al. 2002; Searles et al. 2001; Johnson 2003).

Water held between leaflets and in hyaline cells of the *Sphagnum* capitulum (dead water-filled cells of the uppermost *Sphagnum* leaflets) provides a niche for the peatland surface microfauna and fungi (Vitt 2000). *Sphagnum*-associated fungi in the acrotelm (Ingram 1978; Belyea 1996), the aerobic layer of the peatland, initiate most of the decomposition of *Sphagnum* (Thormann et al. 2002). Peatland microfungi are also important in the food web of the *Sphagnum* mat (Gilbert et al. 1998, 1999), and serve as a food source for some species of testate amoebae (Coûteaux and Dévaux 1983; Coûteaux and Pussard 1983).

Although the hydrology of the upper few centimeters of a peatland is largely dependent on environmental conditions (Bragazza et al. 2003), the volume of water held near the surface is influenced by *Sphagnum* capitulum size and density (Hayward and Clymo 1982). It is not known whether changes in *Sphagnum* capitulum growth and morphology under near-ambient UV-B (Robson et al. 2003) are expressed in the peatland microfungal community.

Microfungal communities are sensitive to changes in acidity and nutrient concentrations in *Sphagnum* capitulum water (Zabawski 1967; Thormann et al. 2003). Higher concentrations of solutes in the capitulum water, indicated by increased conductivity, under supplemental UV-B, were reported by Niemi et al. (2002a, b). As moss leaves are only one cell thick they are thought to be particularly susceptible to membrane damage, which leads to cytosolic leakage (Gerdol 1991). Nutrient-binding organochemicals, phenolics, and uronic acid, are excreted and leached by *Sphagnum* into the surrounding water (Rasmussen et al. 1995). These lower the pH of the peatland and are inhibitory to some microfungi (Heil et al. 2002), but are utilized by others (Flanagan and Scarborough 1974; Thormann et al. 2002).

From a preliminary microfungal sample in January of 1999, *Mortierella, Penicillium*, and *Mucor* were identified as the most abundant genera in the top 1 cm of the *Sphagnum* capitulum (Searles et al. 2001). Species of all three genera are known to respond to UV-B radiation. Supplemental UV-B treatments decreased the abundance of *Mucor* in decomposing leaf litter (Gehrke et al. 1995). Supplemental UV-B inhibited growth of *Mortierella parvispora*, compared to dark controls (Hughes et al. 2003). *Penicillium frequentans* was less abundant on senescent *Gunnera magellanica* leaves (Pancotto et al. 2003) under near-ambient compared to reduced UV-B.

We sampled the peatland microfungi during three field seasons of exposure to near-ambient and reduced UV-B (1999–2002), and concurrently measured plant growth and sampled water from the *Sphagnum* capitulum. We identified the different fungal species in the community where possible, and tracked changes in their abundance to assess the species specificity of response to UV-B. We examined the effect of solar UV-B on fungal diversity, as ubiquitous species were expected to have greater tolerance of UV-B than species native to Tierra del Fuego. We postulated that the combined effects of UV-B on fungal growth and the altered *Sphagnum* capitulum morphology with associated changes in capitulum water chemistry could act to alter the microfungal community. To test this hypothesis, we compared responses of cultured fungi in petri dishes with those of the peatland microfungal community under different UV-B treatments. We sampled *Sphagnum* capitula at depths of 0–5 and 5–10 mm from the peatland surface. Since solar radiation only penetrates a few millimeters into the *Sphagnum* mat, our goal was to contrast the microfungal community at the peatland surface where it is subject to direct solar radiation, with the community just below the surface where no solar radiation penetrates. We also observed whether the magnitude of response of the microfungal community to near-ambient UV-B followed a similar pattern during three field seasons.

Materials and methods

The study site is a *Sphagnum magellanicum* (Brid) dominated peatland in the Tierra del Fuego National Park (54°51′S 68°36′W).

A weather station and CS 21x datalogger at the site (Campbell Scientific, Logan, Utah) were used to record temperature, precipitation, wind speed, and UV-B radiation throughout each field season. Ambient UV-B (Table 1) and UV-B under the two filter types (data not shown) were measured using broadband global radiation sensors (Solar Light, Model PMA2102, Philadelphia, Penn.), calibrated to a double-monochromator spectroradiometer SUV-100 at the Ushuaia UV-monitoring station (Biospherical Instruments, San Diego, Calif.). Mean temperatures for the 5-month period, October–February, were 8.9°C (1999–2000), 7.9°C (2000–2001), and 9.7°C (2001–2002). Total precipitation for the same 5-month period was 260 mm (1999–2000), 312 mm (2000–2001), and 269 mm (2001–2002). Ground water was ca. 40 cm maximum depth below the surface. The *Sphagnum* mat remained frozen at 5-cm depth through the winter until at least the end of September (for more details of the climate and flora of the peatland see Robson et al. 2003).

Ten pairs of 1.4×2.0-m plots were established during October 1996. Plots were located within an area of relatively homogeneous vegetation without pronounced hummocks and hollows in the *Sphagnum* mat, between a small lake (Laguna Negra) and *Nothofagus* wood. These plots were maintained for the following six field seasons (September–March), and have been used in several long-term field experiments (Ballaré et al. 2001; Robson et al. 2003).

Plastic film filters were stretched (ca. 40-cm height) over the plots to create the near-ambient and reduced UV-B treatments (see photo Ballaré et al. 2001). A matrix of small louvred slits (ca. 25×2 mm) was melted into the filters prior to installation, to enable water from precip-

Table 1 Monthly averages of daily integrated solar UV-B radiation over three 5-month field seasons recorded at our peatland field site in Tierra del Fuego National Park (1999–2000, 2001–2002). Data from a nearby fen field site are presented from 2000–2001 courtesy of J.G. Zaller, because of instrument failure at the peatland. The daily UV-B values (kJ m^{-2} day^{-1}) are normalized to one at 300 nm and weighted with the generalized plant action spectrum (Caldwell 1971). Daily means for each month are shown ±1SD among days. Data from the NSF UV-monitoring station in Ushuaia (http://www.biospherical.com/nsf/login/update.asp) are given in parentheses for comparison

Month	1999–2000	2000–2001	2001–2002
October	2.38±0.68 (2.29)	3.36±2.31 (2.97)	3.22±1.37 (2.32)
November	3.99±1.22 (3.34)	2.57±1.41 (2.60)	2.78±0.99 (2.78)
December	4.48±1.21 (4.62)	4.11±1.97 (3.91)	4.41±1.24 (4.59)
January	4.26±1.10 (4.31)	3.68±1.74 (3.61)	5.75±1.80 (–)
February	2.91±1.00 (2.77)	2.17±0.91 (2.64)	4.11±1.12 (–)
March	–	–	2.23±1.19 (–)

itation to penetrate evenly to the *Sphagnum* mat (Searles et al. 2001). Field trials showed that almost all the precipitation passed equally through the two filter types (Robson et al., unpublished data). Polyester filters (100 μm thick, optically equivalent to Mylar-D, Dupont, Wilmington, Del.), that attenuate ca. 83% of short wavelength UV-B radiation (300 nm) were perforated (Searles et al. 2002), and were used to achieve the reduced UV-B treatment. Polyfluorine filters (Aclar type 22A, 38-μm thick, Honeywell, Pottsville, Penn.) that block ca. 10% of the UV-B (Searles et al. 2002), were used to create our near-ambient UV-B treatment. Both films are equally transparent to longer wavelengths (UV-A and visible), each blocking ca. 10% of visible radiation. The UV-B treatments were randomly assigned within each pair of plots ("block") and remained in place from late September–March each year. This period incorporates early spring when the ozone hole opens but the sun is low in the sky, through to autumn when UV-B again becomes very low (Díaz et al. 2001). During winter the peatland is usually covered by snow and ice.

The microfungal community, *Sphagnum* capitulum mass, and water held by the capitulum were sampled at four evenly spaced time intervals during the fourth (1999–2000) and sixth (2001–2002) field seasons, and three times during the fifth (2000–2001) field season of long-term UV-B treatments. To avoid edge effects, all samples were taken at least 20 cm from the edge of the area covered by the filters. To accommodate *Sphagnum* surface heterogeneity (Mitchell et al. 2000), a random sample of 28 *Sphagnum* capitula was removed from each plot using sterile forceps. *Sphagnum* capitula were maintained in isolated conditions and taken to the laboratory for immediate weighing and processing.

Under a laminar-flow hood, *Sphagnum* capitula from both near-ambient UV-B and reduced UV-B plots were cut into two 5-mm lengths, corresponding to the 0- to 5-mm and 5- to 10-mm depths beneath the surface of the *Sphagnum* mat. Previously, it was established that at least 99% of solar radiation is attenuated at 6-mm depth in the *Sphagnum* capitulum (Searles et al. 1999). The 28 capitula taken from each plot were pooled, weighed, and added to two tubes containing 6 ml of autoclaved deionized water. These tubes were agitated for 4 min, then 400-μl and 200-μl volumes were pipetted onto potato dextrose agar (PDA) under sterile conditions (following Dickinson 1982).

Agar plates were incubated in the dark at room temperature. The various fungal species grew at different rates, so it was necessary to monitor growth from 3 until 8 days after inoculation. Colony forming units (CFUs) of each species were counted to determine fungal abundance. Fungal species were identified using Domsch et al. (1980), and additional specific keys for *Mortierella* (Cabello 1997), and *Biverticillium* (Quintanilla 1985).

Ionic conductivity (DIST ATC dissolved solid tester, Cole Parmer, Chicago, Ill.) and pH (Corning pH-40 sensor, New York) of the 6 ml of water held by the *Sphagnum* capitulum were measured within 12 h after harvest. Samples were stored in the dark at 4°C until a second measurement of ionic conductivity was taken after 60 h. Ionic conductivity is considered a good relative indicator of ionic leaching from *Sphagnum* cells (Gerdol 1991). Ionic conductivity was adjusted for H^+ ions following Sjörs (1950). Tests using alcohol to sterilize the sample confirmed that microbial activity did not affect ionic conductivity after 60 h. On termination of the experiment, *Sphagnum* capitula were oven dried at 65°C for 72 h and dry mass determined. This allowed the initial water content to be calculated gravimetrically by subtracting dry mass from the initial fresh mass measured directly after capitula were removed from the peatland.

In February 2003, the most prominent fungal species were isolated from *Sphagnum* capitula. Fungi from near-ambient UV-B and reduced UV-B plots exhibited the same inherent growth rates when inoculated onto petri dishes containing PDA. Cultures were left untreated for 2 days to confirm that inoculation was successful before UV-B treatments were administered in a growth chamber equipped with a 6,000-W xenon lamp. Daily growth, changes in sporulation, sclerotia, hyphal density, and pigmentation were recorded. The different UV-B treatments were created by replacing most of the petri-dish lid with a plastic filter. As with the solar UV-B treatments in the peatland, polyester film was used to block most of the UV-B radiation, and polyfluorine film allowed the lamp UV-B radiation to pass. A cellulose diacetate filter was wrapped around the lamp to remove radiation <290 nm. The fungi were exposed to 3.5–4 kJ m^{-2} day^{-1} UV-B weighted with the generalized plant action spectrum normalized at 300 nm (Caldwell 1971), measured with a modified double-monochromator (Optronic, Orlando, Fla.). In Ushuaia, Tierra del Fuego, the average November–February UV-B dose from 1996–2002 was ca. 4 kJ m^{-2} day^{-1} (Table 1; and Searles et al. 2002), rising to in excess of 8 kJ m^{-2} day^{-1} on the four or five occasions each austral spring when the "ozone hole" passed over the site. Fungal cultures also received ca. 46.8 mol m^{-2} day^{-1} (800 μmol m^{-2} s^{-1} for 16 h) of photosynthetically active

radiation (total photon flux, 400–700 nm). These daily doses were calculated to approximately simulate our peatland radiation treatments in the field (Zaller et al. 2004).

Statistical analysis

Species occurrence was calculated as mean presence in the ten plots of each treatment type over the duration of the study (1999–2002). Unadjusted species richness was calculated at the 0- to 5-mm and 5- to 10-mm depths, and the Shannon-Weiner index was used to assess evenness of fungal distribution throughout the experiment. The effect of UV-B treatment on each fungal species occurrence, and on species richness was tested using a one-way factorial ANOVA.

To control for the influence of gradients in ground-water depth and pH, and floristic composition across the site, each pair of plots was considered as a block in the statistical models. The effect of UV-B treatment, depth, and month on *Sphagnum* dry mass, water, pH and conductivity, was assessed using an analysis of variance of a three-way factorial, blocked split-split-plot-in-time design. Ionic conductivity was only measured during the final field season of treatments. Hence, to allow for direct comparison between physical parameters, only results from the final field season are presented for *Sphagnum* capitulum mass, water, and pH.

The abundance of some fungi was low, and there were no distinct seasonal trends in abundance, so abundance data for each field season were pooled before analysis. The effect of UV-B treatment, depth and field season on abundance of each fungal species was assessed using an analysis of variance of a three-way factorial, blocked split-

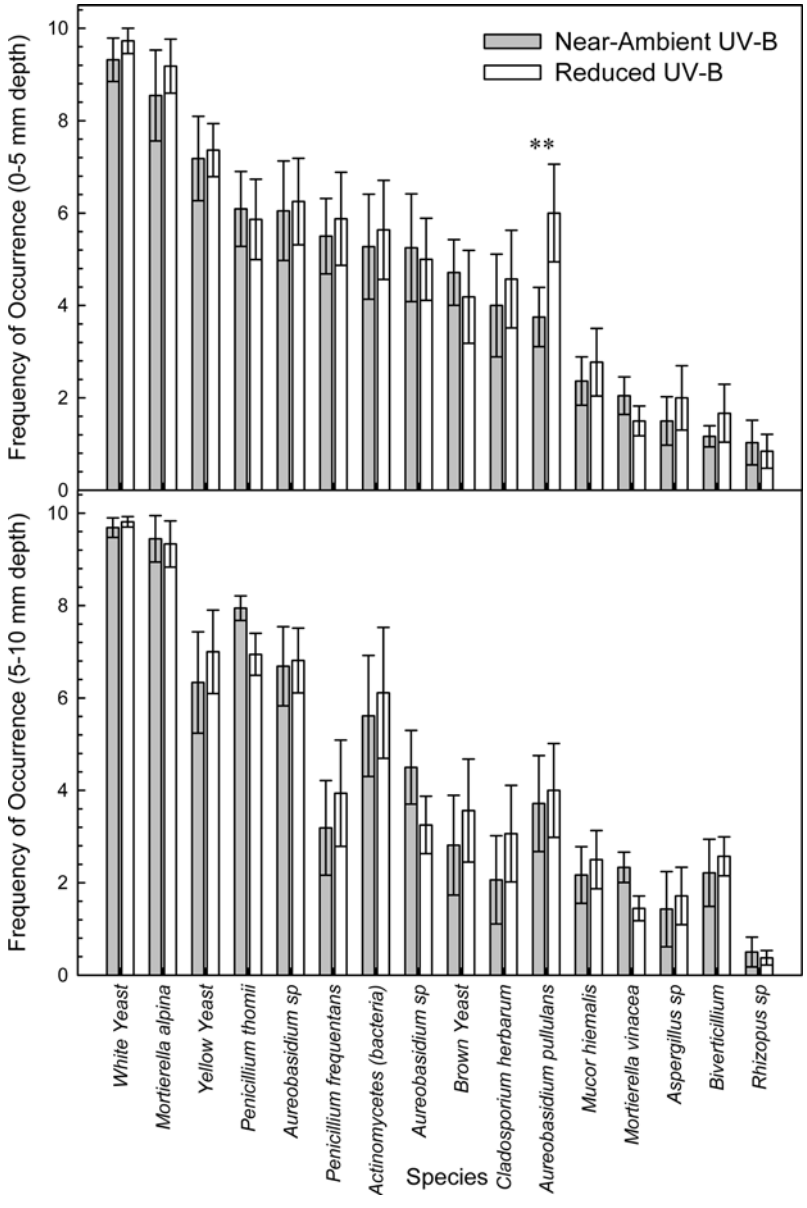

Fig. 1 Frequency of microfungal species occurrence in the *Sphagnum* capitulum, at 0- to 5-mm and 5- to 10-mm depths in the peatland. Mean (±1SE) number of plots with species present in each UV-B treatment of 11 samples over three field seasons. Species with less than 1-in-10 occurrence, on average, were not assessed. ** $P<0.01$

split-plot-in-time design. The UV-B, depth and field season ("year") were the fixed-effects factors and block, block × UV-B, block × UV-B × depth were the random-effects factors in the design (Aldworth and Hoffman 2002). A first order autoregressive variance/covariance structure for repeated-measures-in-time was determined to be most appropriate for the data (Keselman et al. 2002). To assess the relationships amongst species within the microfungal community, and between fungal species, *Sphagnum* capitulum water and climatic variables, correlations across the ten blocks over the two UV-B treatments, at two depths were used.

The growth chamber experiment was performed twice. Each fungal species was inoculated into four pairs of petri dishes, which were rotated daily under the lamp. Daily measurements of the colony diameter of fungi cultured showed fungal growth to be constant. Growth rate of each colony was calculated by linear regression, and the mean calculated for each species under lamp-UV-B and lamp-UV-B controls. The effect of lamp UV-B on the growth of cultured fungi was tested using a one-way factorial ANOVA in a completely randomized design. All computations were performed in SAS, Version 8.2 (SAS Institute, Cary, N.C.).

Results

Nine species of hyphal fungi were isolated from the *Sphagnum* capitulum (Fig. 1), of which *M. alpina* and *P. thomii* were the most common. Additionally, several forms of *Aureobasidium* (including *A. pullulans*) a filamentous bacteria *Actinomycetes* and white and colored yeasts, were isolated from the *Sphagnum* (Fig. 1). There were no significant UV-B effects on occurrence of individual fungal species, except *A. pullulans*, which was present in fewer plots under near-ambient UV-B than under reduced UV-B at the 0- to 5-mm depth (Fig. 1).

Species richness of the microfungal community was slightly lower under near-ambient than under reduced UV-B (Fig. 2). When averaged over the entire sampling period, species richness was significantly lower at 0- to 5-mm depth from the *Sphagnum* surface under near-ambient UV-B (Fig. 2a; $F_{1,9}$=8.53, P=0.017), but not at the 5- to 10-mm depth (Fig. 2b; $F_{1,9}$=1.98, P=0.193). Shannon-Weiner evenness (J') for the entire 0- to 10-mm depth was slightly less under near-ambient UV-B in mid-summer (January) during each of the three field seasons (Fig. 2c). This difference is statistically significant if the 11 samples over the 3-year period are considered ($F_{1,10}$=15.9, P=0.003).

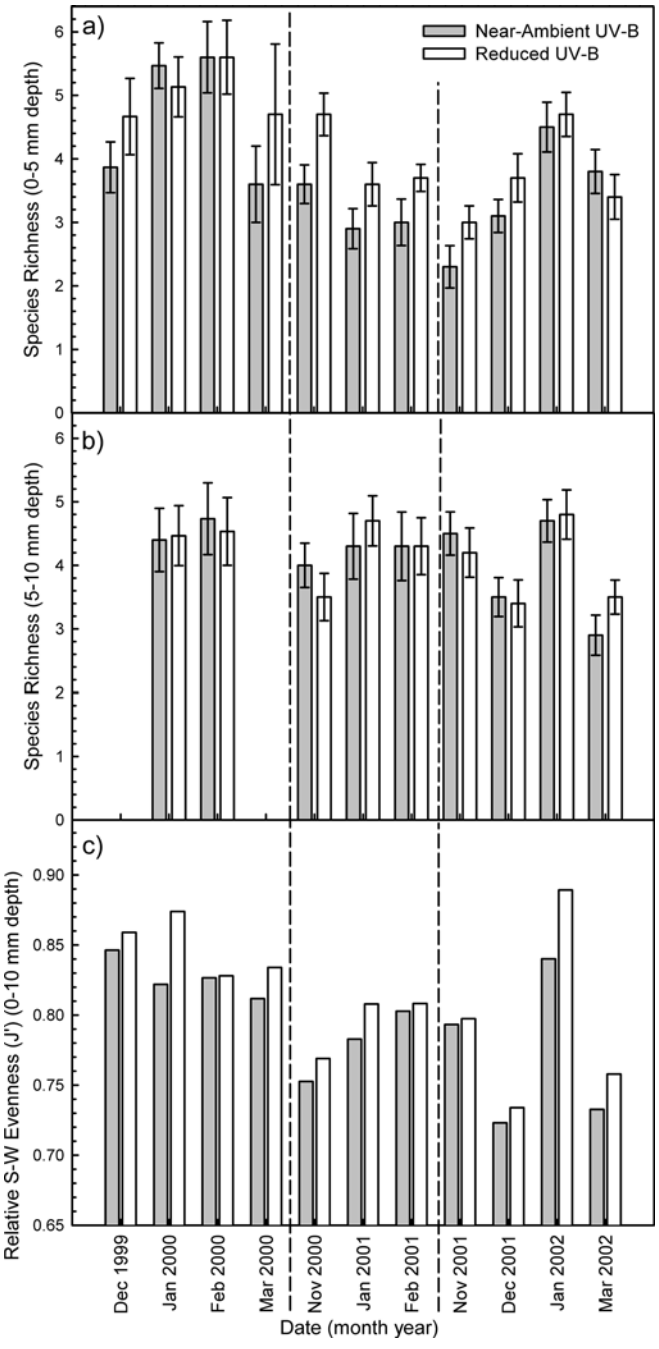

Fig. 2a–c Fungal diversity: mean species richness at **a** 0- to 5-mm and **b** 5- to 10-mm depths (±1SE), and **c** Shannon-Weiner evenness (J') at 0- to 10-mm depth, in the *Sphagnum* capitulum, of ten plots for each UV-B treatment. Diversity was calculated for each of 11 sample dates over three field seasons. In December 1999 and March 2000, only the 0- to 5-mm depth was assessed

Effects of UV-B on the *Sphagnum* microenvironment

Solar UV-B affected *Sphagnum* morphology and properties of the capitulum water (Fig. 3). The *Sphagnum* capitula under near-ambient UV-B held more water than did those under reduced UV-B in our January and March samples (Fig. 3d). This effect was significantly more apparent at the 0- to 5-mm than at the 5- to 10-mm depth (Fig. 3d). Higher capitulum dry mass at the 0- to 5-mm depth under near-ambient UV-B was maintained throughout the growing season (Fig. 3a). Water associated with the *Sphagnum* capitulum was more acidic under near-ambient UV-B in the November and December samples (Fig. 3c). The initial ionic conductivity of *Sphagnum*

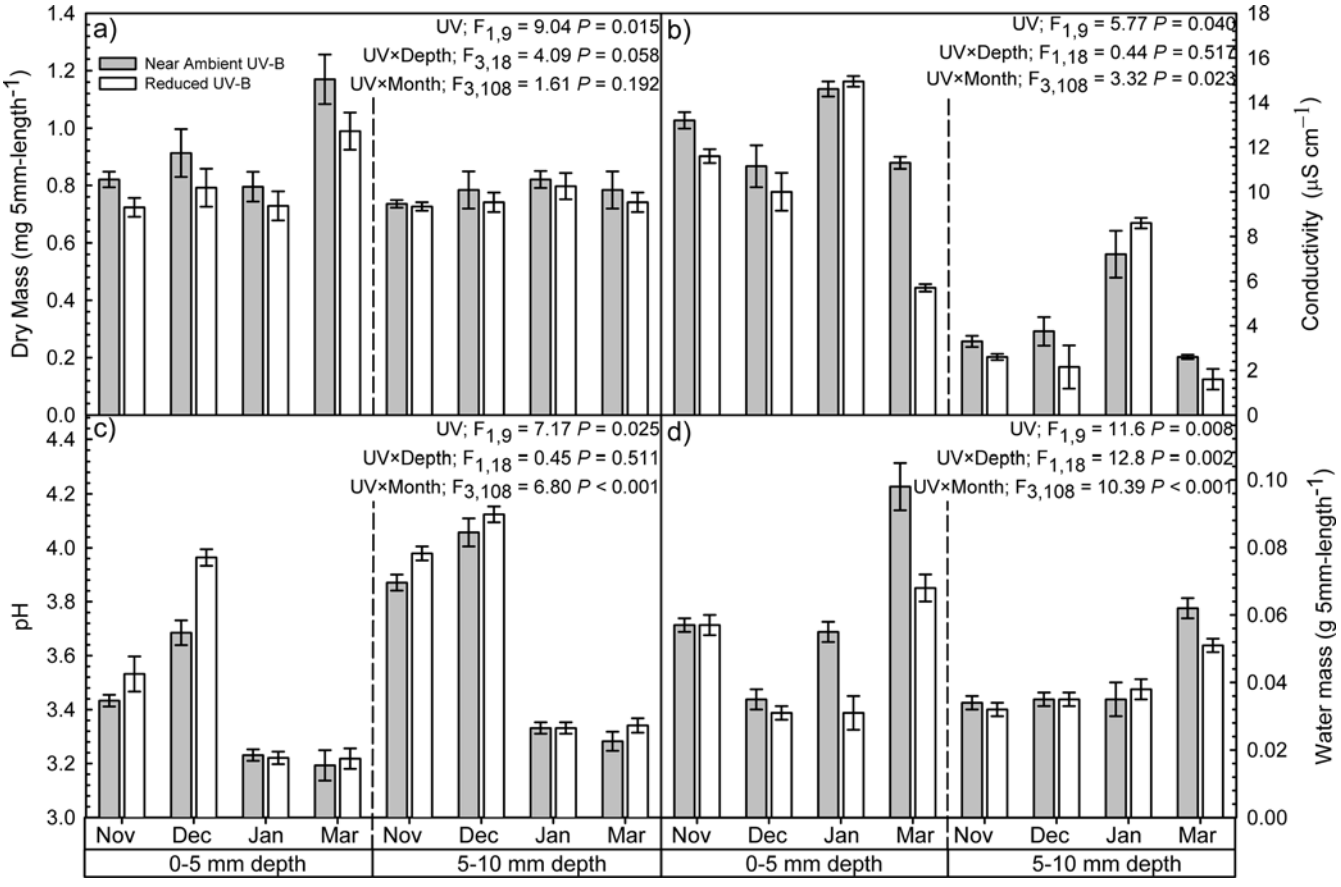

Fig. 3a–d Physical properties of the *Sphagnum* capitulum. All four of the dependent variables tested demonstrated a significant effect of month ($P<0.001$) and depth ($P<0.001$). Other sources of variation had insignificant effects. Monthly mean, 2001–2002 field season ±1SE: **a** *Sphagnum* capitulum dry-mass. **b** Change in the ionic concentration of water from the *Sphagnum* capitulum between 24 and 72 h after harvest. **c** pH of water from the *Sphagnum* capitulum 24 h after harvest. **d** Water held by the *Sphagnum* capitulum

capitulum water after harvest was greater under near-ambient UV-B (data not shown). The rate of increase in ionic conductivity between 24 and 74 h after harvest was also greater under near-ambient UV-B at three of the four sampling times (Fig. 3b).

Effects of UV-B on fungal species within the microfungal community

Despite a suggestion that abundance of hyphal fungi increased under near-ambient UV-B (Fig. 4, UV-B × Year), the abundance of hyphal fungi in the top 10 mm of the peatland was not significantly affected by solar UV-B when considered over the three field seasons (Fig. 4). However, the overall abundance of fungi did decrease over with time under both treatments (Fig. 4).

The unpigmented species *M. alpina* was more abundant under near-ambient than reduced UV-B (Fig. 5a), but only at the depth of 5–10 mm. At the 0- to 5-mm depth, no effect of near-ambient UV-B on *M. alpina* was apparent (Fig. 5a). There was no overall treatment effect on a related pigmented species *M. vinacea*, but it was more abundant under near-ambient UV-B in the 2000–2001 field season (Fig. 5b), suggesting a UV-B × field season

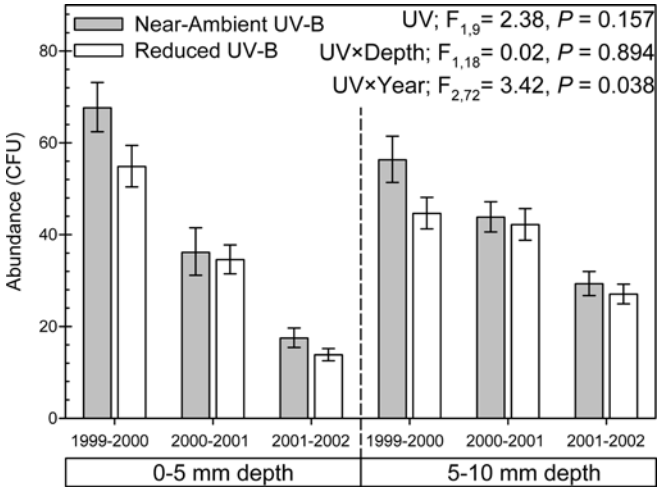

Fig. 4 Abundance of all species of hyphal fungi (colony-forming units). Data represent the back-transformed means (±1SE) of three or four samples pooled over each field season

interaction. However, when pure cultures of *M. alpina* and *M. vinacea* were subjected to lamp UV-B approximating that of solar UV-B at the peatland surface, there was a reduction of more than 20% in colony growth rate of both species (Table 2).

Table 2 Growth rates of fungal species in pure culture under lamp UV-B radiation

Species	Colony growth rate (mm h^{-1})		P (N=4)
	UV-B^-	UV-B^+	
Mortierella alpina	0.482	0.385	0.049
M. vinacea	0.375	0.286	0.024
Penicillium thomii	0.395	0.349	0.539
P. frequentans	0.495	0.370	0.032
Mucor hiemalis	1.354	0.815	0.037
Aureobasidium sp	0.432	0.168	0.034
Aspergillus sp	0.292	0.115	0.008
Cladosporium herbarum	0.234	0.193	0.049

Colony growth rate per hour was calculated by linear regression of colony diameter over 6 days (all R^2>0.90). The UV-B^+ treatment received 3.5–4.0 kJ m^{-2} day^{-1}. The UV-B^- treatment received minimal UV-B

Two other related species, *P. thomii* and *P. frequentans*, were affected in different ways by near-ambient UV-B. Whilst *P. frequentans* growth and abundance were reduced by both near-ambient UV-B in the peatland and by lamp UV-B in pure culture, *P. thomii* was not affected by UV-B in either experiment (Fig. 5c, d; Table 2). However, an increase in pink sclerotia typical of *P. thomii*, and an apparent decrease in conidial frequency were observed under lamp UV-B, whilst no difference in the conidia of *P. frequentans* was evident.

Abundance in the peatland of the unpigmented species *Mucor hiemalis* under near-ambient UV-B was significantly lower in the final field season of treatments, but unaffected by UV-B overall (Fig. 5e). In pure culture under lamp UV-B, *M. hiemalis* growth was reduced (ca. 40%; Table 2), and hyphal density was observed to increase. *Cladosporium herbarum* abundance in the peatland was highly variable amongst years and did not differ between near-ambient (mean CFU±1SE; 0–5 mm, 1.89±0.72, 5–10 mm, 1.89±0.59 mm) and reduced UV-B (0–5 mm, 2.58±0.54 mm; 5–10 mm, 1.82±0.50 mm; $F_{1,9}$=0.74, P=0.41). Colony growth of *C. herbarum* under lamp UV-B was less inhibited than most other species (ca. 18%; Table 2). *Aspergillus* isolated at the 0- to 5-mm depth in the final field season was less abundant in the peatland under near-ambient (mean CFU±1SE; 0.30±0.10) than under reduced UV-B (0.70±0.19, $F_{1,9}$=6.94, P=0.01), and in the growth chamber it was strongly inhibited by lamp UV-B (ca. 50%; Table 2). Overall, there was no consistent UV-B effect on white or colored yeasts in the peatland, but changes in yeast abundance under the UV-B treatments at the two depths lead to a significant interaction between UV-B and depth (Fig. 5g, h). At the 0- to 5-mm depth there was a tendency for more yeasts under near-ambient UV-B than under reduced UV-B, whilst at the 5- to 10-mm depth the opposite tendency was apparent (Fig. 5g, h). *Aureobasidium* abundance was unaffected by UV-B treatment in the peatland (Fig. 5f). Lamp UV-B inhibited *Aureobasidium* growth (Table 2) and accelerated sporulation by approximately 2 days.

Discussion

To the best of our knowledge, ours is the only Southern Hemisphere peatland microfungal community to have been studied (see also Searles et al. 2001). All the species we encountered are widespread and frequently isolated from Northern Hemisphere peatlands, e.g., in Sweden (Nilsson et al. 1992), Canada (Thormann et al. 2003), and Italy (Dal Vesco 1975). *Penicillium thomii* and *Mortierella* species often dominate microfungal communities near the *Sphagnum* surface (Zabawski 1967; Maciejowska-Pokacka 1971; Dickinson and Maggs 1974; Thormann et al. 2003), and this was also the case in our peatland. In line with Searles et al. (2001), *M. alpina* continued to be the most common species, despite favoring the less acidic areas of the peatland (see also Dal Vesco 1975; Fritze and Bååth 1993).

The response of fungi to our UV-B treatments was species specific (Figs. 4, 5). Overall fungal abundance was largely unaffected (Fig. 4), but diversity was slightly lower (Fig. 2) under near-ambient UV-B. These results may indicate that whilst some of the less common species declined under near-ambient UV-B, others, whose growth was relatively unaffected by UV-B, were able to compensate and proliferate (Fig. 5). Additionally, those species that were most abundant under near-ambient UV-B, particularly at the 5- to 10-mm depth, may have been able to exploit the increased ionic concentration and altered *Sphagnum* capitulum morphology.

Sampling of the microfungal community over three field seasons revealed more effects of near-ambient UV-B than did the initial census of Searles et al. (2001). Often long-term experiments show responses to UV-B that are not apparent in studies of shorter duration (Björn et al. 1999; Day et al. 2001; Phoenix et al. 2001; Pancotto et al. 2003). The detection of UV-B effects on microfungal community composition after several years of treatments is not surprising, given that more changes in the plant community were detected after 6 years of UV-B treatments (Robson et al. 2003) than during the first 3 (Searles et al. 1999, 2002). This is particularly true for those fungal species that may respond indirectly to changes in the *Sphagnum* microenvironment brought about by UV-B.

Effects of UV-B on the *Sphagnum* microenvironment and potential consequences for peatland fungi

More water was held at the *Sphagnum* surface under near-ambient than reduced UV-B (Fig. 3). We consider that this was due to the more compressed and densely packed *Sphagnum* capitula under near-ambient UV-B (Robson et al. 2003). Moisture is known to be an important influence on microfungal community composition in peatlands (Nilsson et al. 1992). Thus, the larger wetter capitula are

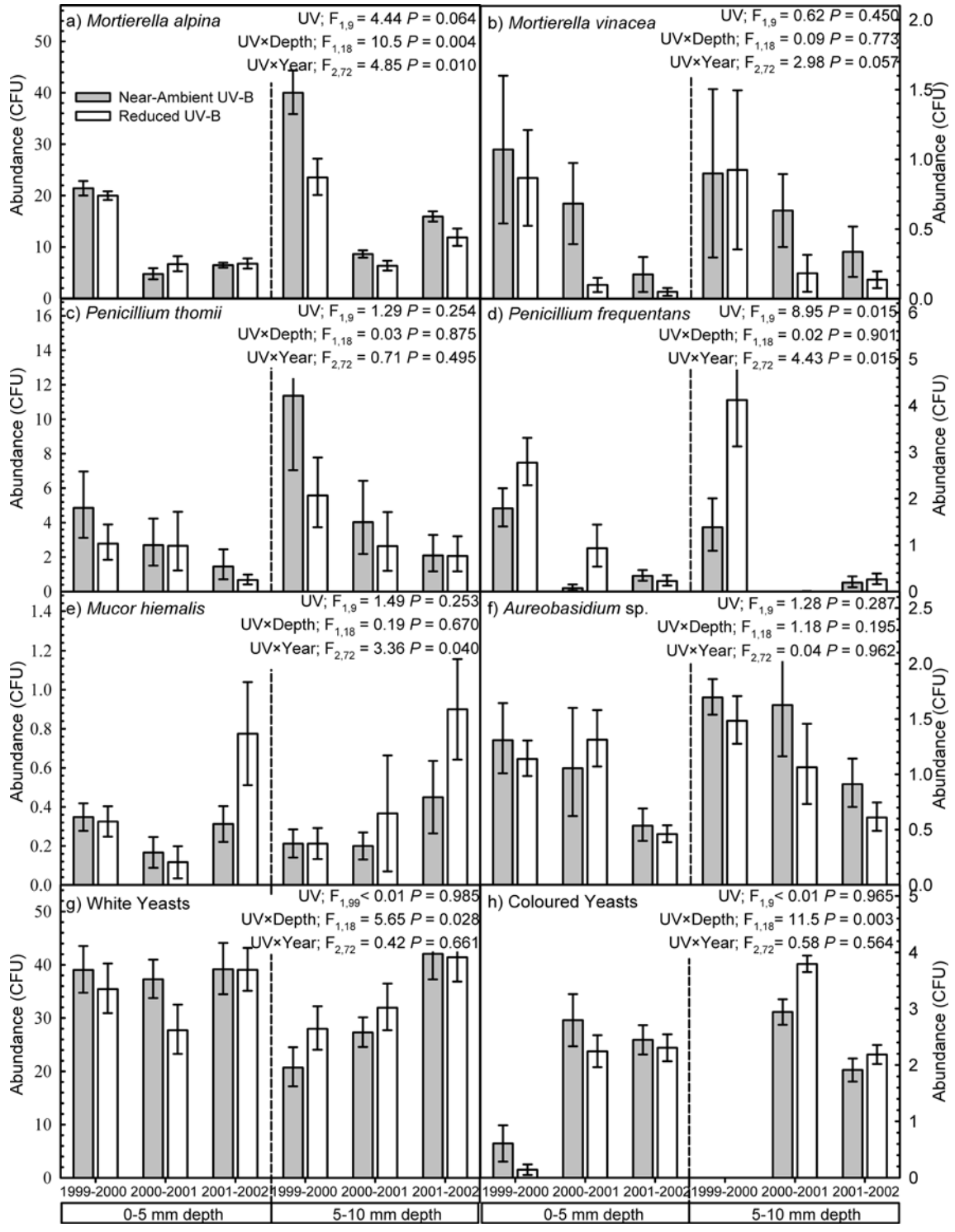

Fig. 5a–h Response of individual fungal species from the peatland microfungal community to near-ambient and reduced UV-B. **a** *Mortierella alpina*, **b** *M. vinacea*, **c** *P. thomii*, **d** *P. frequentans*, **e** *Mucor hiemalis*, **f** *Aureobasidium* sp, **g** White yeasts, and **h** Colored yeasts. The number of CFU per 200 ul from each 6-ml sample containing 14 *Sphagnum* capitula is shown. Back-transformed means (±1 SE) of multiple samples (3–4 occasions) for each field season. Three-way interaction terms were all non-significant, except for *P. frequentans*, $F_{2,72}$=3.60, P=0.032

likely to have provided greater opportunity for fungal colonization under near-ambient UV-B.

The capitulum water was more acidic and had greater ionic conductivity under near-ambient UV-B. These effects of UV-B were not detected over the entire field season, and were not correlated with the volume of water held by the capitulum. Increased ionic conductivity is typically correlated with the leaching of sodium, magne-

sium and calcium during the *Sphagnum* growing season, and release of nitrogen and phosphorus during *Sphagnum* senescence in the autumn (Gerdol 1991; Bragazza and Gerdol 1999). Niemi et al. (2002b) attributed increased concentration of calcium and magnesium ions to increased *Sphagnum* membrane permeability under supplemental UV-B radiation. The greater abundance of *M. alpina* and other species under near-ambient UV-B at 5- to 10-mm depth, and an amelioration of direct UV-B effects for *M. alpina* at 0- to 5-mm depth in our peatland (Fig. 5a), may be due to the nutritional benefit gained through increased *Sphagnum* membrane permeability under near-ambient UV-B. *Mortierella* are known to break down sugars in initial phases of decomposition in peatlands, and have been shown to respond positively to increased leaching from the *Sphagnum* capitula (Deacon 1997; Thormann et al. 2003).

Decreases in pH and increases in nutrient content in the acrotelm, where most decomposition occurs (Williams and Yabitt 2003), may provide a more favorable environment for the majority of peatland microfungi (Zabawski 1967; Szumigalski and Bayley 1996). Leaching from the *Sphagnum* capitulum is the most significant mass loss during the first phase of decomposition (Thormann et al. 2002), so increased leaching under near-ambient UV-B could have important implications for decomposition processes.

Effects of UV-B on fungal species within the microfungal community

The active decomposer species *P. thomii* (Thormann et al. 2002, 2003) was the second most abundant species in our microfungal community after *M. alpina*. Its abundance remained unchanged by UV-B during our three-field-season sampling period (1999–2002) and in the initial sample from the peatland in January 1999 (P.S. Searles, unpublished data). Similarly, *P. thomii* on senesced *Gunnera magellanica* leaves prior to decomposition in a nearby heath was equally abundant under near-ambient and reduced UV-B (Pancotto et al. 2003).

Several investigators have reported *Cladosporium herbarum* to be quite tolerant of UV-B. The occurrence of *C. herbarum* was not significantly reduced by supplemental UV-B (30% above ambient) on the lamina of living oak leaves (Newsham et al. 1997a), though it did decrease during their decomposition (Newsham et al. 1997b). In Tierra del Fuego, *C. herbarum* abundance was not affected by near-ambient UV-B on living *Carex* leaves (Searles et al. 2001), and it increased on *G. magellanicum* leaves under near-ambient UV-B prior to decomposition (Pancotto et al. 2003). In line with these results, the abundance of *C. herbarum* in our peatland was unaffected by near-ambient UV-B, and under lamp UV-B in a growth chamber its colony growth was less inhibited than most other species studied.

It has been suggested that dark pigmentation in *C. herbarum* and other fungi confers protection from UV-B (Pancotto et al. 2003). In Antarctica, pigmentation of some fungal species in isolated cultures increased in response to ambient UV radiation (Hughes et al. 2003). Also in Antarctica, fewer unpigmented mycelia and conidia were present in the open than under "closed plastic cloches" that reduced UV and increased temperature by 6°C, whereas there were no differences between treatments in the abundance of pigmented soil fungi (Onofri et al. 2000). However, increased solar and supplemental UV-B do not always favor pigmented species of fungi. Supplemental UV-B radiation shifted competitive advantage from unpigmented towards pigmented fungi in only two out of six pair-wise tests of soil fungal species (Duguay and Klironomos 2000). It is difficult to make generalizations about fungal species responses to UV-B as, even within genera, fungi are known to behave differently (Moody et al. 1999). This was the case with the two *Mortierella* species that we encountered (Fig. 5a, b). However, most species of *Penicillium* studied (apart from *P. frequentans*) appear to be tolerant of UV-B. This is illustrated by the apparent lack of effect of UV-B radiation on *P. thomii* abundance in our peatland, also of supplemental UV-B radiation from lamps on *P. brecompactum* in a sub-Arctic peatland (Gehrke et al. 1995), and on *Penicillium* species living on oak leaves (Newsham et al. 1997a). *Penicillium* are generally considered to have high tolerance of environmental stress (Zabawski 1967; Domsch et al. 1980). Some decomposer fungi have been shown to initially respond to UV-B, but these responses were transitory (Gehrke et al. 1995; Newsham et al. 1997a). This may indicate that some species are able to acclimate to higher UV-B radiation.

Conclusions

Changes in the peatland microfungal community under long-term near-ambient UV-B were small and species specific. This was surprising given that there were considerable reductions in growth of fungal cultures under our lamp UV-B treatments. Our peatland UV-B treatments did increase the ionic conductivity, acidity and the volume of water held by the *Sphagnum* capitulum. Perhaps, given that solar UV-B is attenuated quickly at the peatland surface, microenvironmental changes brought about by UV-B were an important influence on the peatland microfungal community. However, this remains to be explicitly tested.

Overall fungal diversity near the surface of the *Sphagnum* was low under both treatments, making subtle effects on community difficult to detect. The small decrease in richness recorded may be due to direct inhibition by solar UV-B of less common fungal species, or increased dominance of the most common species in the peatland near-surface microfungal community. This decrease in diversity did not influence the overall fungal abundance, and it appears that most of the fungal species at the peatland surface are sufficiently tolerant of, or protected against, current solar UV-B radiation in Tierra

del Fuego. All of the fungi encountered are relatively ubiquitous, and known to live in environments where the UV-B flux is significantly higher than it is in Tierra del Fuego. Alternatively, it is possible that these fungi in Tierra del Fuego have already adapted to the increased solar UV-B radiation that they receive after over 2 decades of ozone depletion in this region.

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References

Adams JM, Faure H (1998) A new estimate of changing carbon storage on land since the last glacial maximum, based on global land ecosystem reconstruction. Global Planet Change 16–17:3–24

Aldworth J, Hoffman WP (2002) Split-plot model with covariate: a cautionary tale. Am Stat 56:284–289

Ballaré CL, Rousseaux MC, Searles PS, Zaller JG, Giordano CV, Robson TM, Caldwell MM, Sala OE, Scopel AL (2001) Impacts of solar ultraviolet-B radiation on terrestrial ecosystems of Tierra del Fuego (southern Argentina): an overview of recent progress. J Photochem Photobiol B 62:67–77

Belyea LR (1996) Separating the effects of litter quality and microenvironment on decomposition rates in a patterned peatland. Oikos 77:529–539

Berendse F, van Breemen N, Rydin H, Buttler A, Heijmans M, Hoosbeek MR, Lee JA, Mitchell E, Saarinen T, Vasander H, Wallén B (2001) Raised atmospheric CO_2 levels and increased N deposition cause shifts in plants species composition and production in *Sphagnum* bog. Global Change Biol 7:591–598

Björn LO, Callaghan TV, Gehrke C, Gwynn-Jones D, Lee JA, Johanson U, Sonesson M, Buck ND (1999) Effects of ozone depletion and increased ultraviolet-B radiation on northern vegetation. Polar Res 18:331–337

Bragazza L, Gerdol R (1999) Hydrology, groundwater chemistry and peat chemistry in relation to habitat condition in a mire on the south-eastern Alps of Italy. Plant Ecol 144:243–256

Bragazza L, Gerdol R, Rydin H (2003) Effects of mineral and nutrient input on mire bio-geochemistry in two geographical regions. J Ecol 91:417–426

Breemen N van (1995) How *Sphagnum* bogs down other plants. Trends Ecol Evol 10:270–275

Cabello MN (1997) El genero Mortierella (Zygomycotima, Mucorales) en Tierra del Fuego (Argentina). Bol Soc Argent Bot 33:53–58

Caldwell MM (1971) Solar ultraviolet radiation and the growth and development of higher plants. In: Giese AC (ed) Photophysiology, vol 6. Academic, New York, pp 131–177

Clymo RS, Turunen J, Tolonen K (1998) Carbon accumulation in peatlands. Oikos 81:368–388

Coûteaux M-M, Dévaux J (1983) Effet d'un enrichissement en champignons sur la dynamique d'un peuplement thécamoebien d'un humus. Rev Ecol Biol Sol 20:519–545

Coûteaux M-M, Pussard M (1983) Nature du régime alimentaire des Protozoaires du sol. In: LeBrun P, André HM, De Medts A, Grégoire-Wibo C, Wauthy G (eds) New trends in soil biology. Proceedings of the VIII international colloquium of soil zoology. Dieu-Brichart, Ottignies-Louvain-la-Neuve, Louvain-La-Nueve, pp 179–195

Dal Vesco G (1975) Soil fungi from a mountain bog in the Cogne Valley. Allionia 20:81–92

Day TA, Ruhland CT, Xiong FS (2001) Influence of solar UV-B radiation on Antarctic terrestrial plants: results from a four-year field study. J Photochem Photobiol B 62:78–87

Deacon JW (1997) Modern mycology, 3rd edn. Blackwell, Oxford, pp 190–191

Díaz S, Deferrari G, Booth CR, Martinioni D, Oberto A (2001) Solar irradiances over Ushuaia (54.49°S, 68.19°W) and San Diego (32.45°N, 117.11°W) geographical and seasonal variation. J Atmos Sol-Terr Phys 63:309–320

Dickinson CH (1982) The phylloplane and other aerial plant surfaces. In: Burns RG, Slater JH (eds) Experimental microbial ecology. Blackwell, Oxford, pp 412–430

Dickinson CH, Maggs GH (1974) Aspects of the decomposition of *Sphagnum* leaves in an ombrophilous mire. New Phytol 73:1249–1257

Domsch KH, Gams W, Anderson T-H (1980) Compendium of soil fungi. Academic, London

Duguay KJ, Klironomos JN (2000) Direct and indirect effects of enhanced UV-B radiation on the decomposing and competitive abilities of saprobic fungi. Appl Soil Ecol 14:157–164

Farman JC, Gardiner BG, Shanklin JD (1985) Large losses of total ozone in Antarctica reveal seasonal ClO_x/NO_x interaction. Nature 315:207–210

Flanagan PW, Scarborough AM (1974) Physiological groups of decomposer fungi on tundra plant remains. In: Holding AJ, Heal OW, MacLean SFJ, Flanagan PW (eds) Soil organisms and decomposition in tundra. Tundra Biome Steering Committee, Stockholm, pp 159–181

Frederick JE, Díaz SB, Smolskaia L, Esposito W, Lucas T, Booth CR (1994) Ultraviolet solar radiation in the high latitudes of South America. J Photochem Photobiol 60:356–362

Fritze H, Bååth E (1993) Microfungal species composition and fungal biomass in coniferous forest soil polluted by alkaline deposition. Microbial Ecol 25:83–92

Gehrke C, Johanson U, Callaghan TV, Chadwick D, Robinson CH (1995) The impact of enhanced ultraviolet-B radiation on litter quality and decomposition processes in *Vaccinium* leaves from the Subarctic. Oikos 72:213–222

Gerdol R (1991) Seasonal variations in the element concentrations in mire water and in *Sphagnum* mosses on an ombrotrophic bog in the southern Alps. Lindbergia 16:44–50

Gerdol R, Bonora A, Marchesini R, Guanlandri R, Pancaldi S (1998) Growth response of *Sphagnum capillifolium* to night-time temperature and nutrient level: mechanisms and implications for global change. Arct Alp Res 30:388–395

Gilbert D, Amblard C, Bourdier G, Francez A-J (1998) The microbial loop at the surface of a peatland: structure, function and impact of nutrient input. Microb Ecol 35:83–93

Gilbert D, Francez A-J, Amblard C, Bourdier G (1999) The microbial communities at the surface of the *Sphagnum* peatlands: good indicators of human disturbances? Ecologie 30:45–52

Hayward PM, Clymo RS (1982) Profiles of water content and pore size in *Sphagnum* and peat, and their relation to peat bog ecology. Proc R Soc Lond B 215:299–325

Heijmans MPD, Berendse F, Arp WJ, Masselink AK, Klees H, De Visser W, van Breemen N (2001) Effects of elevated carbon dioxide and increased nitrogen deposition on bog vegetation in the Netherlands. J Ecol 89:268–279

Heijmans MMPD, Klees H, de Visser W, Berendse F (2002) Response of a *Sphagnum* bog plant community to elevated CO_2 and N supply. Plant Ecol 162:123–134

Heil M, Baumann B, Andary C, Linsenmair KE, McKey D (2002) Extraction and quantification of "condensed tannins" as a measure of plant anti-herbivore defence? Revisiting an old problem. Naturwissenschaften 89:519–524

Hughes KA, Lawley B, Newsham KK (2003) Solar UV-B radiation inhibits the growth of Antarctic terrestrial fungi. Appl Environ Microbiol 69:1488–1491

Ingram HPA (1978) Soil layers in mires: function and terminology. J Soil Sci 29:224–227

Johnson D (2003) Response of terrestrial microorganisms to ultraviolet-B radiation in ecosystems. Res Microbiol 154:315–320

Johnson D, Campbell CD, Lee JA, Callaghan TV, Gwynn-Jones D (2002) Arctic microorganisms respond more to elevated UV-B radiation than CO_2. Nature 416:82–83

Keselman HJ, Algina J, Kowlchuk RK (2002) A comparison of data analysis strategies for testing omnibus effects in higher-order repeated measures designs. Multivar Behav Res 37:331–357

Maciejowska-Pokacka Z (1971) Results of one year studies on the influence of various soils on the mycoflora under cocksfoot. Acta Mycol 7:31–40

Mitchell EAD, Buttler A, Grosvernier, Rydin H, Albinsson C, Greenup AL, Heijmans MMPD, Hoosbeek MR, Saarinen T (2000) Relationships among testate amoebae (Protozoa), vegetation and water chemistry in five *Sphagnum*-dominated peatlands in Europe. New Phytol 145:95–106

Moody SA, Newsham KK, Ayes PG, Paul ND (1999) Variation in the responses of litter and phylloplane fungi to UV-B radiation (290–315 nm). Mycol Res 103:1469–1477

Newsham KK, Low MNR, McLeod AR, Greenslade PD, Emmett BA (1997a) Ultraviolet-B radiation influences the abundance and distribution of phylloplane fungi on pedunculate oak (*Quercus robur*). New Phytol 136:287–297

Newsham KK, McLeod AR, Roberts JD, Greenslade PD, Emmett BA (1997b) Direct effects of elevated UV-B radiation on the decomposition of *Quercus robur* leaf litter. Oikos 79:592–602

Niemi R, Martikainen PJ, Silvola J, Sonninen E, Wulff A, Holopainen T (2002a) Responses of two *Sphagnum* moss species and *Eriophorum vaginatum* to enhanced UV-B in a summer of low UV intensity. New Phytol 156:509–515

Niemi R, Martikainen PJ, Silvola J, Wulff A, Turtola S, Holopainen T (2002b) Elevated UV-B radiation alters fluxes of methane and carbon dioxide in peatland microcosms. Global Change Biol 8:361–371

Nilsson M, Bååth E, Söderström B (1992) The microfungal communities of a mixed mire in northern Sweden. Can J Bot 70:272–276

O'Neill KP (2000) Role of bryophyte dominated ecosystems in the global carbon budget. In: Shaw AJ, Goffinet B (eds) Bryophyte biology. Cambridge University Press, Cambridge, pp 344–368

Onofri S, Fenice M, Cicalini AR, Tosi S, Magrino A, Selbmann L, Zucconi L, Vishniac HS, Ocampo-Friedmann R, Friedmann EI (2000) Ecology and biology of microfungi from Antarctic rocks and soils. Ital J Zool 67 [Suppl] 1:163–167

Pancotto VA, Sala OE, Cabello MN, López NI, Robson TM, Ballaré CL, Caldwell MM, Scopel AL (2003) Solar UV-B decreases decomposition in herbaceous plant litter in Tierra del Fuego, Argentina: potential role of an altered decomposer community. Global Change Biol 9:1465–1474

Phoenix GK, Gwynn-Jones D, Callaghan TV, Sleep D, Lee JA (2001) Effects of global change on a sub-Arctic heath: effects of enhanced UV-B radiation and increased summer precipitation. J Ecol 89:256–267

Quintanilla JA (1985) Three new species of *Penicillium* belong to Subgenus *Biverticillium* Dierckx, isolated from different substrates. Mycopathologia 91:69–78

Rasmussen S, Wolff C, Rudolph H (1995) Compartmentalization of phenolic constituents in *Sphagnum*. Phytochemistry 38:35–39

Robson TM, Pancotto VA, Flint SD, Ballaré CL, Sala OE, Scopel AL, Caldwell MM (2003) Six years of solar UV-B manipulations affect growth of *Sphagnum* and vascular plants in a Tierra del Fuego peatland. New Phytol 160:379–389

Rousseaux MC, Ballaré CL, Giordano CV, Scopel AL, Zima AM, Szwarcberg-Bracchitta M, Searles PS, Caldwell MM, Diaz SB (1999) Ozone depletion and UVB radiation: impact on plant DNA damage in southern South America. Proc Natl Acad Sci USA 96:15310–15315

Searles PS, Flint SD, Díaz SB, Rousseaux MC, Ballaré CL, Caldwell MM (1999) Solar ultraviolet-B radiation influence on *Sphagnum* bog *Carex* fen ecosystems: first field season findings in Tierra del Fuego, Argentina. Global Change Biol 5:225–234

Searles PS, Kropp BR, Flint SD, Caldwell MM (2001) Influence of solar UV-B radiation on peatland microbial communities of southern Argentina. New Phytol 152:213–221

Searles PS, Flint SD, Díaz SB, Rousseaux MC, Ballaré CL, Caldwell MM (2002) Plant response to solar ultraviolet radiation in a southern South America *Sphagnum* peatland. J Ecol 90:704–713

Sjörs H (1950) On the relation between vegetation and electrolytes in north Swedish mire waters. Oikos 2:241–258

Szumigalski AR, Bayley SE (1996) Decomposition along a bog to rich fen gradient in central Alberta, Canada. Can J Bot 74:573–581

Thormann MN, Currah RS, Bayley SE (2002) The relative ability of fungi from *Sphagnum fuscum* to decompose selected carbon substrates. Can J Microbiol 48:204–211

Thormann MN, Currah RS, Bayley SE (2003) Succession of microfungal assemblages in decomposing peatland plants. Plant Soil 250:323–333

Tomassen HBM, Smolders AJP, Lamers LPM, Roelofs JGM (2003) Stimulated growth of *Betula pubescens* and *Molinia caerulea* on ombrotrophic bogs: role of high levels of atmospheric nitrogen deposition. J Ecol 91:357–370

Vitt DH (2000) Peatlands: ecosystems dominated by bryophytes. In: Shaw AJ, Goffinet B (eds) Bryophyte biology. Cambridge University Press, Cambridge, pp 312–343

Weltzin JF, Harth C, Bridgham SD, Pastor J, Vonderharr M (2001) Production and microtopography of bog bryophytes: response to warming and water-table manipulations. Oecologia 128:557–565

Weltzin JF, Bridgham SD, Pastor J, Chen J, Harth C (2003) Potential effects of warming and drying on peatland plant community composition. Global Change Biol 9:141–151

Williams CJ, Yabitt JB (2003) Botanical composition of peat and degree of peat decomposition in three temperate peatlands. Ecoscience 10:85–95

Zabawski J (1967) Studies on the mycoflora of *Sphagnum* bog Zieleniec. Zesz Probl Postepow Nauk Roln 76:355–400

Zaller JG, Searles PS, Rouseaux MC, Caldwell MM, Flint SD, Sala OE, Ballaré CL, Scopel AL (2003) Solar ultraviolet-B radiation can affect slug feeding preference for some plant species native to a fen ecosystem in Tierra del Fuego, Argentina. Plant Ecol 159:43–51

Zaller JG, Searles PS, Caldwell MM, Flint SD, Scopel AL, Sala OE (2004) Growth responses to ultraviolet-B radiation of two *Carex* species dominating an Argentinean fen ecosystem. Basic Appl Ecol 5:153–162