

Solar UV-B influences microfaunal community composition in a Tierra del Fuego peatland

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Abstract

The peatlands of Tierra del Fuego are subject to increased solar ultraviolet-B radiation (UV-B) due to the influence of the Antarctic ‘ozone hole’. Research into the effects of climate change and ozone depletion on peatlands has predominantly focused on the higher plant community and neglected other organisms. In the second 3-year portion of a 6-year experiment, we intensified our investigations of the response of the peatland surface microfaunal community to current and attenuated solar UV-B, and assessed possible links to changes in the microenvironment. Near-ambient UV-B and reduced UV-B treatments were realised by stretching plastic film filters that differentially attenuate UV-B over peatland sample plots. We extracted the microfauna and analysed the dissolved nutrients held within *Sphagnum* capitula removed from the top 1-cm of the peatland. In line with previous findings in this system, testate amoebae were more abundant under near-ambient UV-B than under reduced UV-B. Populations of the most common genus, *Assulina*, and other less prominent amoebae species of *Heleopera* and *Euglypha*, were consistently increased under near-ambient UV-B. Overall diversity of testate amoebae was also higher under near-ambient UV-B than under reduced UV-B, whereas rotifers, nematodes and mites were less abundant under near-ambient UV-B. Concentrations of DOC and P were generally higher under near-ambient UV-B than under reduced UV-B. These changes, combined with the changes previously reported in the plant and fungal communities, have the potential to influence peatland C storage, and surface nutrient availability. The peatland microfaunal community under near-ambient solar UV-B may be regulated by the plant community through the leaching of nutrients from leaf cells, and changes in *Sphagnum* morphology that affect the capitulum microenvironment.

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1. Introduction

The peatlands of Tierra del Fuego are subject to increased solar ultraviolet-B radiation (UV-B) (Searles et al., 1999), due to the influence of Antarctic ozone depletion that extends over much of southern South America (Orce and Hebling, 1997; Cede et al., 2002). Solar UV-B is known to affect plant growth (Ballaré et al., 2001; Robson et al., 2003), litter decomposition (Pancotto et al., 2003), herbivory (Rousseaux et al., 1998, 2004; Zaller et al.,

2003) and peatland fungi (Robson et al., 2004) in Tierra del Fuego.

Peatland ecosystems play an important role in global C sequestration (Gorham, 1991). They have been studied in the context of general climate change (review: Oechel et al., 2000), and specifically ozone depletion (Gehrke, 1998; Björn et al., 1999; Searles et al., 1999, 2002; Sonesson et al., 2002), but research has focused largely on the peatland higher plant community. Like plants, micro-organisms influence the rates of biogeochemical cycling and peatland C storage. Testate amoebae, rotifers, and nematodes are readily observed in water held by the *Sphagnum* capitulum close to the peatland surface. Testate amoebae are abundant in peatlands, and are known to exhibit a more pronounced response than higher plants to small-scale environmental changes in conductivity, dissolved N and C, and water table depth (Mitchell et al., 2000a). Thus, they may provide an

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early indication of subtle effects on the peatland micro-environment before they are expressed by the higher plant community (Mitchell et al., 2003). Similarly, populations of nematodes (Schröter et al., 2003), rotifers, and peatland metazoa (Hampton, 2004) are known to fluctuate in response to biotic and abiotic environmental changes and trophic interactions.

During the first 3 years (1996–1999) of this long-term experiment, there were few changes to the peatland higher plant community (Searles et al., 1999, 2002), but the population of testate amoebae, sampled in late February, was larger in the top 1-cm of the peatland under near-ambient solar UV-B (Searles et al., 1999, 2001). Continued investigation during the following 3 years (1999–2002) of UV-B treatments revealed new effects on the peatland plant community (Robson et al., 2003). This raises the question of whether trends in the microfaunal community under the two UV-B treatments remained consistent over the entire 6-year period.

The microfungus community inhabiting the *Sphagnum capitula* in our peatland plots exhibited lower species richness and a change in species composition under the near-ambient UV-B compared to the reduced UV-B treatment (Robson et al., 2004). Peatland fungi and bacteria initiate the decomposition of *Sphagnum* and vascular plants, and themselves serve as food for testate amoebae and other microfauna (Gilbert et al., 2000; Mitchell et al., 2000a), so changes in their abundance due to UV-B may influence the peatland microfaunal community. Since the feeding relationships among groups of microfauna are also complex (Yeates and Foissner, 1995), we wanted to know whether different micro-organisms that comprise the various components of the peatland food web responded similarly to our UV-B treatments. To this end, we concurrently monitored populations of rotifers, nematodes, and, in the final field season, acari mites. We also identified the species of testate amoebae present at our peatland study site, and assessed their diversity under both UV-B treatments.

Under near-ambient UV-B, more-compressed *Sphagnum capitula* hold water of a lower pH and higher ionic conductivity than under reduced UV-B (Robson et al., 2004). This difference may be indicative of increased leaching from the *Sphagnum* leaflets (Moore et al., 1998). To test this, we measured ionic nitrogen (N), phosphorus (P), and dissolved organic carbon (DOC) concentrations in the *Sphagnum capitulum* water.

During the first 3 years of UV-B treatments (1996–1999), the microfaunal populations at two depths in the *Sphagnum capitulum* were sampled, the 0–5-mm depth that receives some solar radiation, and the 5–10-mm depth that does not (Searles et al., 2001). There were no significant differences in the effects of UV-B treatments on peatland microfaunal populations at the two depth increments (Searles et al., 2001). This seems to indicate that indirect changes, in nutrients or trophic interactions, were important factors in ameliorating any direct effect of solar UV-B on the

microfauna. We consider that the depth-dependent changes in fungal and yeast abundance during the second 3 years of UV-B treatments (Robson et al., 2004), may be reflected in the microfaunal population at the two depths.

The seasonal population dynamics of peatland microfauna in such a variable oceanic climate as Tierra del Fuego is not well known. Since fluctuations in UV-B are also highly seasonal, we decided to monitor the populations of testate amoebae, rotifers, and nematodes throughout the spring and summer, rather than only at the end of summer (Searles et al., 2001). The effects of relatively low doses of UV-B are often small, so by frequent and regular sampling we hoped to obtain more meaningful results and confirm that previous small treatment differences persisted through the season and were not simply the result of short-term climatic variability.

2. Methods

2.1. Experimental set-up and treatments

The study site is a *Sphagnum*-dominated peatland in Tierra del Fuego National Park (54°51'S 68°36'W), 20 km to the west of Ushuaia, at the southern tip of South America. Twenty sample plots (2×1.40 m) were installed in the peatland during October of 1996, and maintained through each 6-month period during the austral spring and summer over the subsequent 6 years (for more details see Robson et al., 2003). Two UV-B treatments were effected using special plastic-film filters that differentially attenuate the solar UV spectrum. A reduced-UV-B treatment was achieved using polyester film (optically equivalent to Mylar-D; DuPont Co., Wilmington, DE, USA), and a near-ambient-UV-B treatment was achieved using Aclar plastic film (type 22A, Honeywell Co., Pottsville, PA, USA). A pattern of small louvred slits (ca. 25×2 mm) was melted into every filter before it was stretched horizontally (ca. 40 cm) above each sample plot, allowing precipitation to reach the peatland surface. Field measurements showed that the temperature did not differ between the treatments and that almost all the precipitation passed equally through the two filter types (unpublished data). Aclar filters transmit ca. 90%, but polyester filters only ca. 17%, of the short wavelength UV-B spectrum, while both filter types are highly transparent to longer wavelengths (UV-A and visible) (Searles et al., 2002).

2.2. Sampling *Sphagnum capitula* and extraction of microfauna

Sphagnum magellanicum (Brid.) capitula were sampled from the peatland at three intervals, 6-weeks apart, during each field season (1999–2002): at the beginning of November; in mid-December; and late January.

Each sample comprised 28 *Sphagnum* capitula removed individually from the entire plot area, excluding a 20-cm strip around the perimeter of the plot to avoid edge effects (as in Robson et al., 2004). This number of capitula was considered sufficient to obtain a representative sample of the microfaunal community in each plot, encompassing micro-scale heterogeneity, based on the recommendations of Mitchell et al. (2000a), and our own field trials.

Sphagnum capitula were maintained in isolated conditions and taken to the laboratory for immediate processing. Searles et al. (1999) established that at least 99% of the solar radiation is attenuated at 6-mm depth in the *Sphagnum* carpet. In an attempt to segregate microfauna exposed to some radiation and to no radiation, *Sphagnum* capitula were cut into two sections corresponding to 0–5 and 5–10-mm depth increments from the upper tips of the *Sphagnum*. The 28 capitula from each depth were added to 12 ml of water, a small sub-sample of which was removed for fungal analysis (see Robson et al., 2004). To standardise our estimate of the microfaunal population among samples, a fixed number of exotic *Lycopodium*-spore markers suspended in warm water were added to each sample (Stockmarr, 1971, Lund University, Batches #938934, #124961). Individual samples were mechanically vibrated for 10 s and the solution was strained through a fine mesh. The procedure was repeated with a further 5 ml of water to maximise the extraction of micro-organisms. We consider this procedure adequate to disassociate the microfauna from the surface of the *Sphagnum* leaves, but it probably does not extract all of those individuals that live within the *Sphagnum* hyaline cells (Mitchell et al., 2003). Thus, our results are likely to be a slight underestimate of the total microfaunal population.

The strained solution was centrifuged (500g) for 15 min and the supernatant decanted for nutrient analysis. The residue was transferred to 2-ml Eppendorf tubes and re-centrifuged at high speed for 3 min to obtain a pellet containing the micro-organisms (adapted from Searles et al., 2001). The supernatant was removed down to 0.25 ml, and three drops of glycerol were added to slow evaporation under the microscope. One drop of the dye Rose Bengal (1% aqueous), which stains cytoplasm red, was added to the samples to aid observation of testate amoebae, rotifers, nematodes, and acari mites.

Microfaunal populations were counted under the microscope relative to the number of exotic *Lycopodium* spores, and adjusted per 10 mg of dry *Sphagnum* (Searles et al., 2001). At least four slides from every plot, each containing one drop of liquid, were counted for each sample.

Testate amoebae were identified to species level where possible. Bdelloid rotifers (Bdelloidea) were of fairly uniform size and physical characteristics. No distinction was made between different species of nematode. Acari mites and the less abundant amoebae species were only counted during the final field season.

2.3. Nutrient analysis

Nutrients were analysed during the 2001–2002 field season on microfaunal samples from November to January, and an additional late-season sample from March. Following centrifugation of the microfaunal samples, dilutions of the supernatant were prepared for nutrient analysis using deionised distilled water. These samples were kept frozen prior to their transport to Utah State University Biogeochemical Laboratory for analysis. The November N and P samples from 0–5 and 5–10-mm depths were pooled for analysis. DOC was determined using wet persulphate oxidation (100 °C), on an Oceanography International 700 total organic C analyser (Menzel and Vaccaro, 1964). N and P were determined using a DIONEX-500 ion chromatograph with suppressed conductivity detection (Hedin et al., 1998).

2.4. Diversity calculations

Two indices of diversity were calculated that incorporated species occurrence and richness of the testate amoebae population under the two treatment types. Simpson's index (D) measures the probability that two individuals drawn at random from a sample are of the same species, thus gives more weight to the more abundant species in the sampled population. The Reciprocal of Simpson's index was used to aid interpretation. The Shannon–Weiner index (H') measures the uncertainty with which the identity of a species drawn from the population can be predicted; as this value increases, species abundance and richness tend to increase. Both indices also allow the calculation of heterogeneity/evenness; sampled as a proportion of the (theoretical) maximum species occurrence. In both cases higher values reflect more even distribution of species in the population (Ludwig and Reynolds, 1988; Zar, 1996).

2.5. Statistical analysis

Gradients in ground-water depth, pH, and floristic composition across the site led to high spatial variability in microfaunal populations. To control for the influence of these factors, each pair of adjacent plots was considered as a block in the statistical models. Microfaunal counts were square-root transformed to better meet the assumptions of normality, and homogeneity of variance. The effect of UV-B treatment, depth and time on each micro-organism, and on nutrient concentrations, was assessed using an analysis of variance of a three-way factorial, blocked split-split-plot-in-time design, as appropriate for repeatedly sampled populations (Robson et al., 2004). All computations were performed in SAS, Version 8.2 (SAS Institute Inc., Cary, NC, USA). Numerator and denominator degrees of freedom are given in subscript with F and P values for each test. In a few instances, where the differences between UV-B treatments are consistent over many sampling dates,

we find it reasonable to consider a marginally non-significant effect of UV-B when our P -value falls between 0.05 and 0.10.

3. Results

The population of microfauna, particularly rotifers and nematodes, per dry mass of *Sphagnum* was higher under both UV-B treatments than that reported by Searles et al. (2001); but we suggest that this was due to improvements in the extraction procedure rather than an actual increase since the first 3-year of the experiment. In line with the findings of Searles et al. (2001), the population of testate amoebae was higher under near-ambient UV-B than under reduced UV-B (Figs. 1 and 2). Diversity of

testate amoebae was also slightly higher under near-ambient UV-B (Table 1). This was exhibited both as an increase in species richness and occurrence under near-ambient UV-B at 0–5-mm depth from the *Sphagnum* surface (Table 1).

The microfaunal community composition was similar to that reported for northern peatlands (Tolonen et al., 1992; Mitchell et al., 2000b). Twelve distinct testate amoebae taxa were identified, and the most common of these were consistent with those reported for this site by Searles et al. (2001). In order of abundance these were; *Assulina muscorum*; *Assulina semilunulum*; *Heleopera petroicola*; *Euglypha* species (*E. ciliata*, *E. compressa*, *E. rotunda*); *Diffugia oblonga*; *Nebela* species; *Corythion dubium*; *Cyclopyxis arcelloides*; *Centropyxis aerophila*; *Hyalosphenia* species; and *Heleopera sylvatica*.

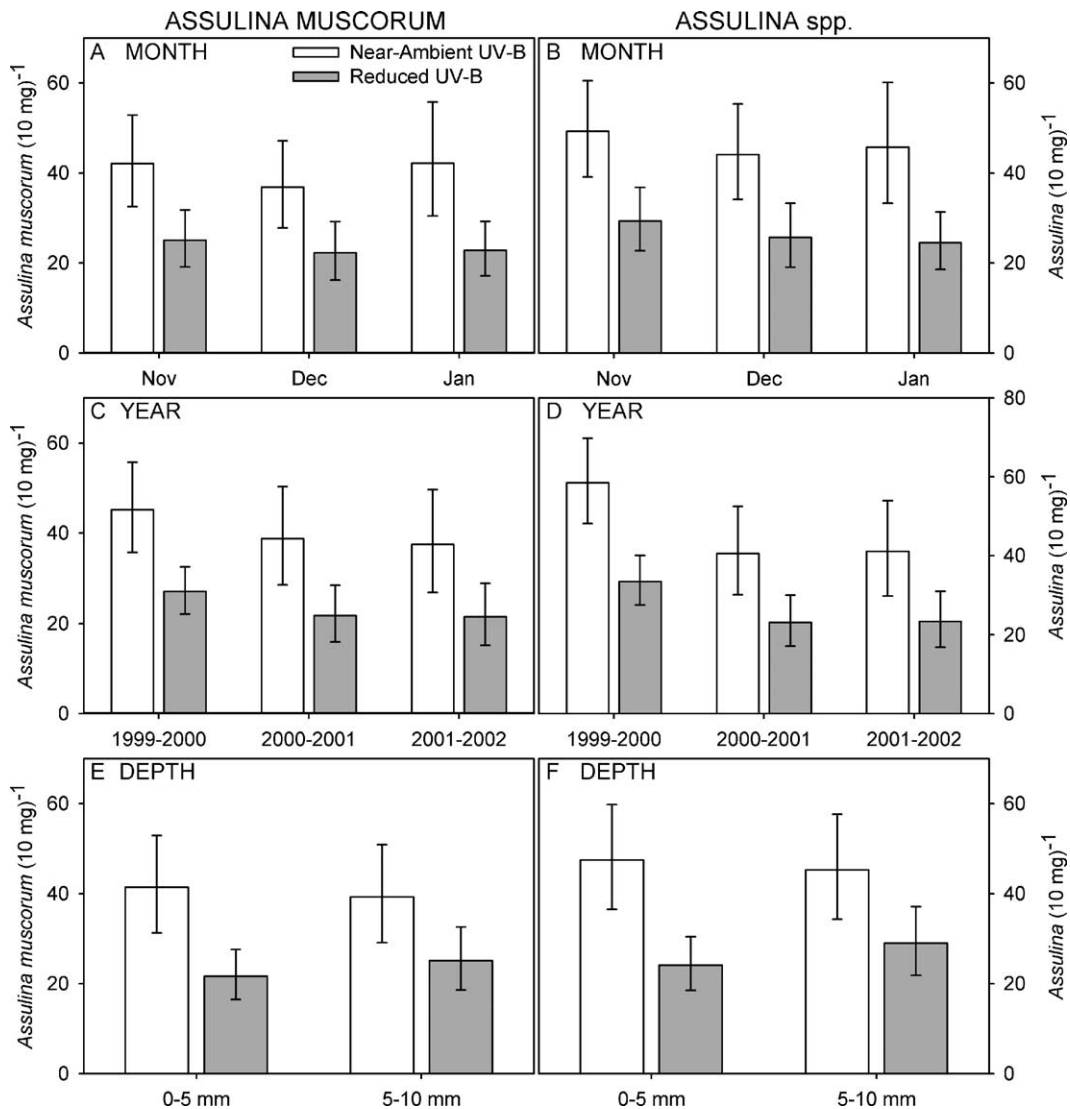


Fig. 1. Trends in the populations of *Assulina muscorum* (UV-B: $F_{1,9}=4.6$, $P=0.060$), and all *Assulina* species including empty tests (UV-B: $F_{1,9}=3.7$, $P=0.084$) under near-ambient and reduced UV-B. There were no significant interaction effects of UV-B with depth or time. The populations of *Assulina* under both UV-B treatments decreased between 1999–2000 and 2000–2001 (Year: $F_{2,213}=6.5$, $P=0.002$). Data are back-transformed means \pm 1 SE, of the number of testate amoebae per 10-mg dry mass of *Sphagnum* capitulum.

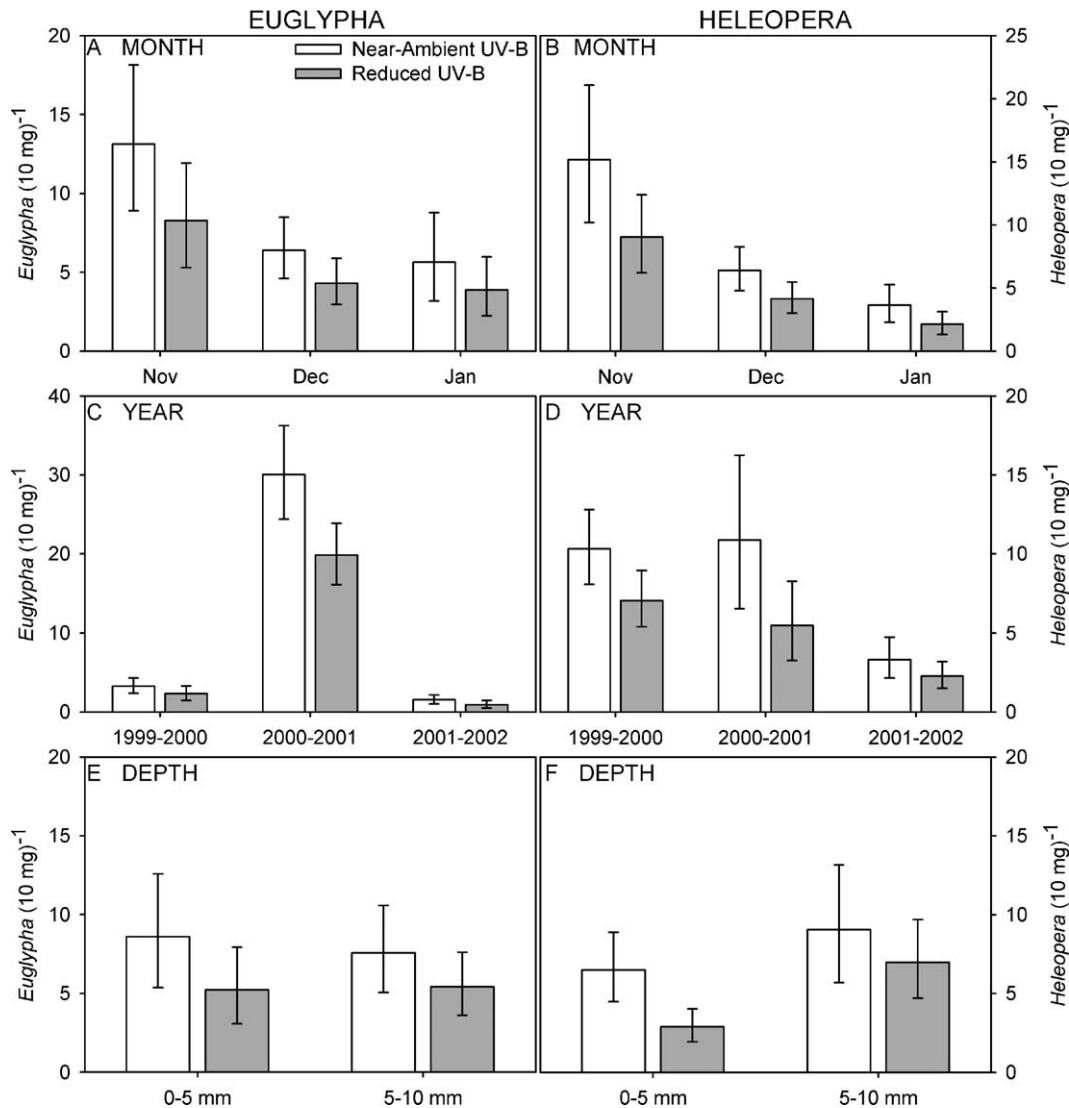


Fig. 2. Trends in the populations of *Euglypha* species, including *E. compressa*, *E. rotunda* and *E. cilata*, (UV-B: $F_{1,9}=4.3$, $P=0.067$), and *Heleopera* species (UV-B: $F_{1,9}=5.0$, $P=0.052$) under near-ambient and reduced UV-B. There were no significant interaction effects of UV-B on *Euglypha* with depth or time. Under both UV-B treatments *Euglypha* populations were highest during the 2000–2001 field season (Year: $F_{2,213}=215$, $P<0.001$), and decreased significantly after November (Month: $F_{2,213}=9.4$, $P=0.001$); as did *Heleopera* populations (Month: $F_{2,213}=26$, $P<0.001$). The UV-B effect on *Heleopera* was more evident at 0–5-mm depth (UV \times Depth: $F_{1,18}=3.4$, $P=0.082$), where they were less abundant overall (Depth: $F_{1,18}=28$, $P<0.001$). Data are back-transformed means ± 1 SE of the number of testate amoebae per 10-mg dry mass of *Sphagnum* capitulum.

Of the testate amoebae, members of the genus *Assulina* increased most consistently in response to near-ambient UV-B (Fig. 1). Though marginally statistically significant, the response of *Assulina* to UV-B was consistent throughout the experiment at both depths, particularly in the species *A. muscorum* (Fig. 1), and did not vary seasonally or annually. The proportion of empty tests of *Assulina* was very low (consistent with Heal, 1964; Mitchell et al., 2000a), and did not differ between treatments (data not shown).

Two other genera of testate amoebae, *Euglypha* and *Heleopera*, were also more abundant under near-ambient UV-B (Fig. 2). Small polyphagous *Euglypha* were significantly more abundant under both treatments during

the fifth field season (2000–2001) than during other field seasons ($F_{2,312}=215$, $P<0.001$). This may be a result of unusually wet cloudy weather conditions during the fifth field season (Robson et al., 2004). The largely predatory *Heleopera* were more common under both treatments at the lower depth increment of 5–10 mm ($F_{1,18}=28$, $P<0.001$), and tended to decrease in abundance over the field season ($F_{2,312}=15$, $P<0.001$). No effect of UV-B was apparent in the population of *D. oblonga*, which was also abundant in the peatland (data not shown). Other less common species of amoebae, counted only during the final field season, were highly heterogeneous across the site and largely failed to exhibit significant responses to UV-B (data not shown).

Table 1
Effect of UV-B on testate amoebal diversity

Species	0–5 mm depth		5–10 mm depth		P-value		
	Near-ambient UV-B	Reduced UV-B	Near-ambient UV-B	Reduced UV-B	UV-B _{1,8}	Depth _{1,16}	UV-B × depth _{1,16}
Species occurrence	72.2 (±3.2)	60.0 (±0.6)	74.1 (±3.8)	69.7 (±2.9)	0.073	0.068	0.195
Species richness (S)	16.7 (±0.2)	15.3 (±0.3)	14.7 (±0.4)	14.0 (±0.7)	0.021	0.002	0.029
<i>Shannon–Weiner diversity</i>							
SW Diversity (<i>H'</i>)	1.12 (±0.02)	1.08 (±0.02)	1.09 (±0.03)	1.08 (±0.03)	0.018	0.135	0.173
SW evenness (<i>J'</i>)	0.91 (±0.03)	0.86 (±0.03)	0.86 (±0.04)	0.86 (±0.04)	0.024	0.016	0.006
<i>Simpson's index</i>							
Simpson's diversity (<i>1/D</i>)	11.5 (±1.2)	10.5 (±1.2)	10.9 (±1.8)	10.9 (±1.1)	0.057	0.706	0.013
Simpson's equitability (<i>E_D</i>)	0.69 (±0.08)	0.68 (±0.05)	0.74 (±0.07)	0.78 (±0.04)	0.897	0.003	0.381

Diversity based on the mean species occurrence on nine sample dates over three field seasons (± 1 SE).

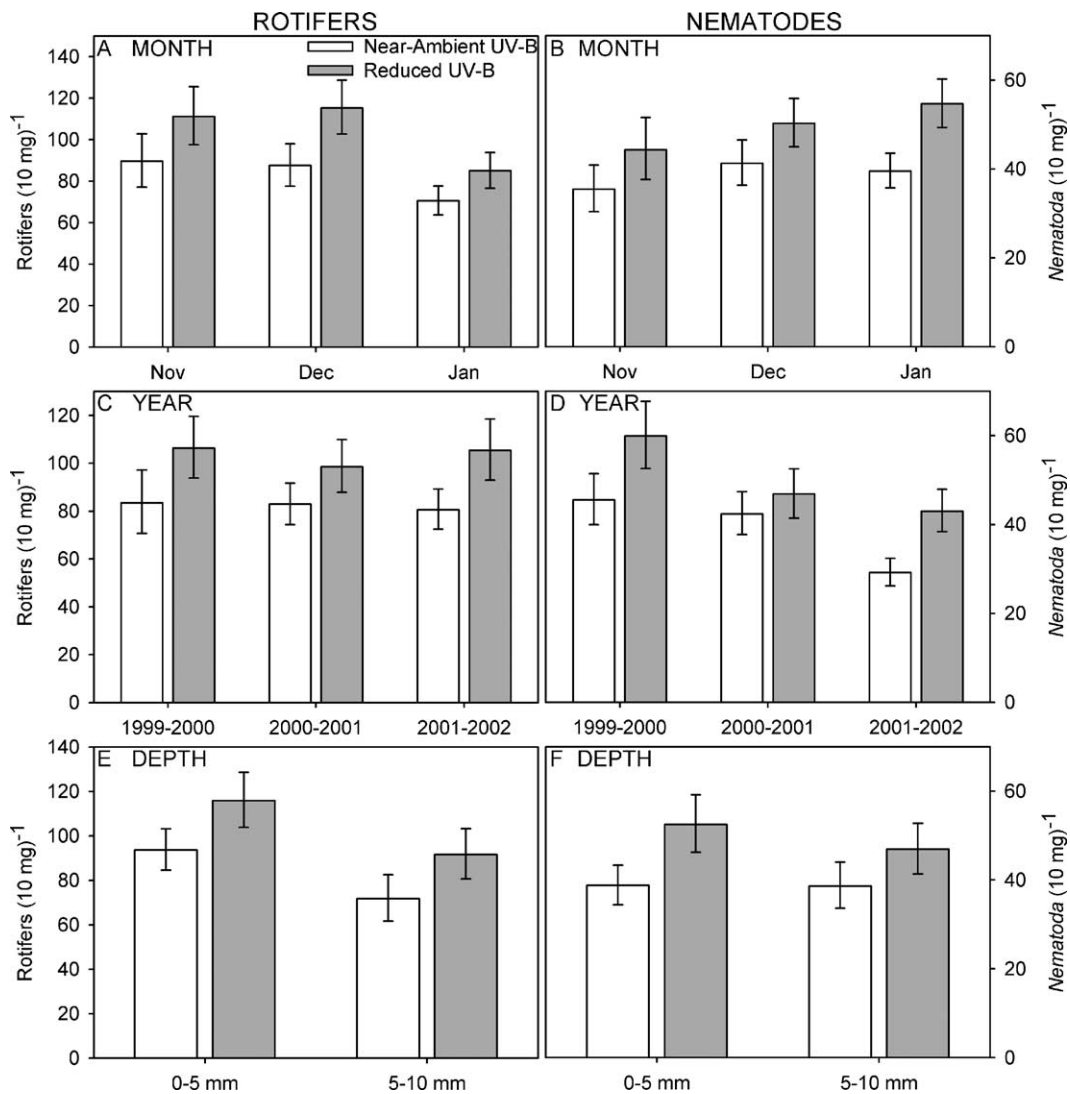


Fig. 3. Trends in the populations of rotifers (UV-B: $F_{1,9}=17.3$, $P=0.002$), and nematodes (UV-B: $F_{1,9}=15.6$, $P=0.003$) under near-ambient and reduced UV-B. The UV-B effect on rotifers was slightly more pronounced at 0–5-mm depth than at 5–10-mm depth (UV × Depth: $F_{1,18}=21$, $P<0.001$). The rotifer populations under both treatments decreased (Month: $F_{2,213}=9.3$, $P=0.001$), whereas the nematodes population increased (Month: $F_{2,213}=9.4$, $P=0.001$) during the field season. There were no other significant effects of UV-B with depth or time on either nematodes or rotifers. Data are back-transformed means ± 1 SE, of the number of micro-metazoa per 10-mg dry mass of *Sphagnum* capitulum.

Unlike the first 3-year experiment when no change, or a slight increase, was reported (Searles et al., 1999, 2001), the populations of nematodes and rotifers were significantly smaller under near-ambient UV-B compared to reduced UV-B (Fig. 3). The population of nematodes fluctuated significantly with time ($F_{2,312}=3.3$, $P<0.039$), without exhibiting clear seasonal or annual trends. Rotifers were most common closer to the surface (0–5-mm depth) under both UV-B treatments ($F_{1,18}=21$, $P<0.001$), and their population tended to decrease towards the end of each field season ($F_{2,312}=9.3$, $P<0.001$; Fig. 3). The population of acari mites was only recorded during the final field season, and as with nematodes and rotifers, was smaller under near-ambient UV-B (Fig. 4).

In general, peatland samples exhibited higher concentrations of DOC and P, but not N under near-ambient UV-B than under reduced UV-B during the final field season (Figs. 5 and 6). The difference in DOC between UV-B treatments was not apparent in the March sample at the end of the field season (Fig. 5). The concentration of DOC was higher closer to the peatland surface (0–5 mm) in both treatments ($P<0.001$), and there was no UV-B \times depth interaction for any of the nutrients (Figs. 5 and 6).

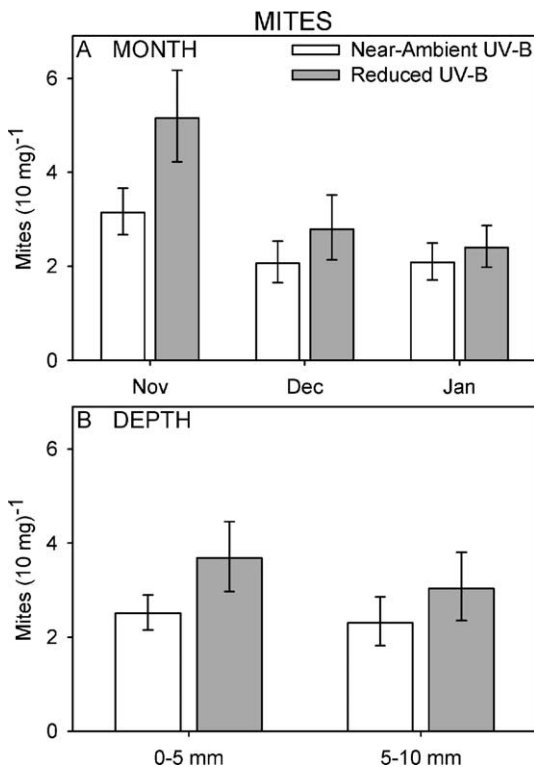


Fig. 4. Trends in the populations of acari mites (Acari: Oribatida) under near-ambient and reduced UV-B, during the sixth field season, 2001–2002 (UV-B: $F_{1,9}=4.7$, $P=0.58$). The mite population under both treatments was significantly higher during November than at other sampling times (Month: $F_{2,72}=5.9$, $P=0.004$). There were no significant interaction effects of UV-B with depth or month. Data are back-transformed means \pm 1 SE, of the number of acari mites per 10-mg dry mass of *Sphagnum* capitulum.

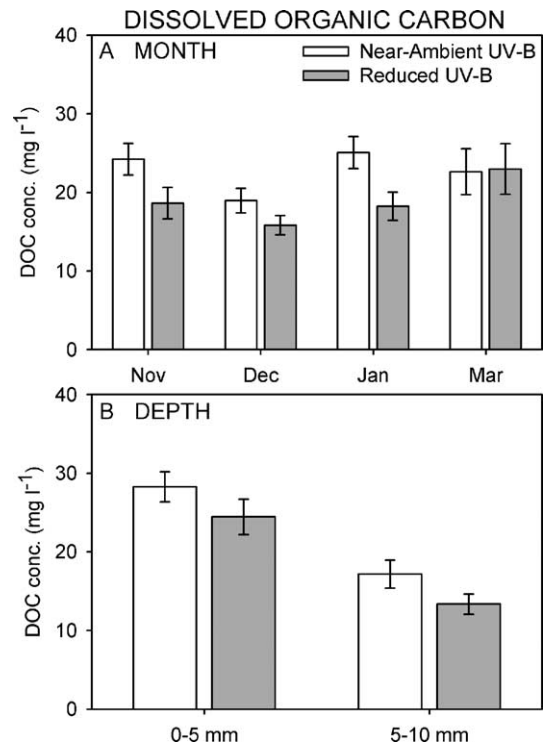


Fig. 5. Concentration of DOC in the *Sphagnum* capitulum water under near-ambient and reduced UV-B, during the sixth field season, 2001–2002 (UV-B: $F_{1,9}=10.19$, $P=0.011$). There were no significant interaction effects of UV-B on DOC concentration with depth or time. Under both treatments DOC was more concentrated closer to the surface ($F_{1,9}=90$, $P<0.001$). The concentration is calculated from standardised 1 ml water removed from each sample. Data are means \pm 1 SE, of the DOC concentration (mg l^{-1}) in each sample of 28 *Sphagnum* capitulum in 1-ml water for each plot.

4. Discussion

4.1. Effects of UV-B on peatland microfauna

Solar UV-B had a significant effect on the peatland surface microfauna. Abundance and diversity of testate amoebae were consistently promoted, but populations of rotifers, nematodes, and mites diminished under our near-ambient solar UV-B treatment. The effect on testate amoebae over the latter 3 years was consistent with the first 3 years of this study, but the change in rotifers and nematodes contrasted with that reported by Searles et al. (1999, 2001). The increases in DOC and P support our previous reports of higher ionic conductivity under near-ambient UV-B (Robson et al., 2004).

The composition of the testate amoebae assemblage under both UV-B treatments was similar but less diverse than commonly reported in *Sphagnum* peatlands (Tolonen et al., 1992; Gilbert et al., 1998a; Mitchell et al., 2000a), probably because only the top 1-cm of the peatland was sampled, and certain species only occur at greater depth (Mitchell et al., 2000b). This also supports the view that at

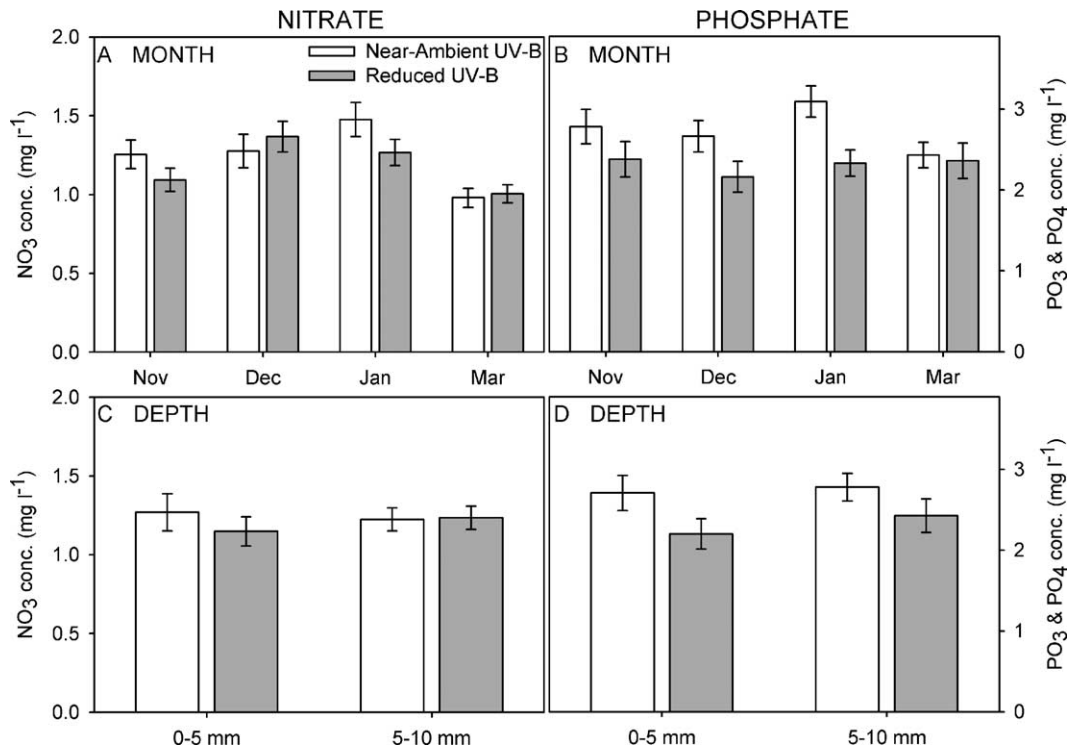


Fig. 6. Concentrations of N and P in the *Sphagnum capitulum* water under near-ambient and reduced UV-B, during the sixth field season (2001–2002). The concentrations of N in November ($F_{1,9}=3.6$, $P=0.09$) and January ($F_{1,9}=4.9$, $P=0.05$) alone were higher under near-ambient UV-B, but there was no overall difference between treatments (UV-B: $F_{1,9}=1.46$, $P=0.257$). P concentration was significantly higher overall under near-ambient UV-B than reduced UV-B (UV-B: $F_{1,9}=7.79$, $P=0.012$). There were no significant interaction effects of UV-B with depth or time on N and P concentration. The concentration is calculated from standardised 1 ml of water removed from each sample. Data are means \pm 1 SE, of the N and P concentrations (mg l^{-1}) in each sample of 28 *Sphagnum capitulum* in 1 ml water.

higher latitudes richness of testate amoebae declines, as proposed by Ledeganck et al. (2003), who linked testate amoebae species richness in grassland ecosystems with plant functional group diversity.

The responses of testate amoebae were species-specific, but overall they were more abundant under near-ambient UV-B. This appears counterintuitive since UV-B is generally considered to be deleterious to organisms. Thus, the increase in abundance is likely mediated by indirect effects of the UV-B treatments causing the microenvironment in the *Sphagnum capitulum* to be more favourable for testate amoebae under near-ambient UV-B than under reduced UV-B. Growth of the microfaunal community is primarily thought to be limited by the thickness of the water film around *Sphagnum capitulum* leaflets (Mitchell et al., 2003). The small species of testate amoebae that we encountered, *Assulina*, *Euglypha*, and *Cerastium dubium*, have flattened tests particularly well adapted to survive in very thin water membranes (Bobrov et al., 1995). *Sphagnum capitula* were wider and more compressed, and consequently held more water under near-ambient UV-B than reduced UV-B (Robson et al., 2003, 2004), so are likely to have provided more sites with a suitable microenvironment for testate amoebae.

The *Sphagnum capitulum* ecosystem is complex, and feeding relationships among micro-organisms are not well

known (Gilbert et al., 2003), but it has been suggested that predation pressure from the peatland metazoa can exert control over the testate amoebae populations in the *Sphagnum capitulum* (Mitchell et al., 2003). The reduction we report in the populations of predators such as mites and rotifers under near-ambient UV-B may lead to a relaxation of predation pressure. This release would allow the testate amoebae population to increase.

The *Sphagnum capitulum* pH remained low through the spring under near-ambient UV-B, compared to reduced UV-B (Robson et al., 2004), and DOC and P concentrations also exhibited the largest difference between UV-B treatments at this time of year. The trend in pH may be indicative of predominantly fungal production under near-ambient UV-B, compared to greater high-affinity nutrient uptake by bacteria under reduced UV-B. *Assulina* are thought to be mainly fungivores (Pejler and Běrzinš, 1993; Gilbert et al., 2000), whilst nematodes are mainly bacteriovores (Ruess et al., 1999), so their relative changes in abundance under the solar UV-B treatments would be consistent with these trends in their principal food sources.

Solar radiation is attenuated quickly near the surface of the peatland (Searles et al., 2001), and very little solar UV-B is thought to penetrate the *Sphagnum capitulum*. Any direct influence of UV-B would occur close to the surface of

the peatlands. While depth was unimportant in explaining the difference due to UV-B treatment in testate amoebae, the reduction in the rotifer population was greater at 0–5 than 5–10-mm depth. Testate amoebae of the genus *Assulina* exhibit pigmented and non-pigmented test (shell) phenotypes. Pigmented tests are physically weaker than unpigmented tests, but their pigmentation may impart some protection from UV-B (Schönborn and Peschke, 1990), suggesting that there is a trade-off. Other amoebae species (e.g. *Heleopera* and *Diffugia*) construct their tests from plant material and detritus; these materials may also confer some UV-B protection. Nematodes and rotifers are transparent to visible radiation and may be transparent to UV (Leech and Williamson, 2000), and thus more sensitive. Studies of the effects of UV-B on lakes and estuarine ecosystems have shown that the motility of ciliates and flagellates, which occupy a similar role in the food web as the peatland micro-metazoa, can be reduced by UV-B (Mostajir et al., 1999). Under supplemental UV-B, this reduction in activity was sufficient to allow increased abundance of their prey and other lower-trophic-level micro-organisms (Mostajir et al., 1999). Ciliates and flagellates were not encountered in our *Sphagnum* capitula, but if rotifer and nematode motility were similarly reduced, this would affect their ability to prey and to escape predation.

4.2. Effects of UV-B on peatland biogeochemistry

Higher DOC and P concentrations under near-ambient UV-B are probably predominantly due to greater leaching of nutrients from leaflets of the *Sphagnum* capitulum (Robson et al., 2004). Of the peatland microfauna, testate amoebae make the largest contribution to C and N mineralisation (Gilbert et al., 1998b). Thus, an increase in their populations in peatlands under near-ambient UV-B would also be expected to increase decomposition, and release more nutrients to the plant community. However, we were unable to consistently detect an increase in N content of the capitulum water under near-ambient UV-B. The availability of N in peatlands is limited (Malmer et al., 2003), particularly in the Southern Hemisphere where atmospheric deposition is low (Price et al., 2004), so any extra N may quickly be utilised, making it difficult to detect any effect.

DOC is important in the peatland carbon cycle and also as a primary food source for the microfauna, fungi, and bacteria. The higher concentration of DOC under near-ambient UV-B than under reduced UV-B may be related to the increase in testate amoebae in tandem with increased leaching from plant material or greater release during decomposition. Direct photochemical cleavage by UV-B may also play a small role in increasing DOC concentration (Tranvik and Bertilsson, 2001).

4.3. Conclusions

We conclude that populations of testate amoebae near the peatland surface are consistently increased by UV-B. This effect is probably mediated by the *Sphagnum* capitula through changes in the microenvironment and nutrient availability, as illustrated by the lower P and DOC concentrations under near-ambient UV-B. Given that testate amoebae are considered to be good early indicators of subtle changes in the peatland ecosystem, we expected them to exhibit a response to UV-B before the vascular plants. Testate amoebae were consistently increased under near-ambient UV-B over the full 6-year period, whereas changes in the vascular plants (Robson et al., 2003), rotifers and nematodes, became apparent only towards the end of the experiment.

The effect of solar UV-B on rotifers and nematodes in the latter 3 years of the experiment differed from that reported by Searles et al. (1999, 2001) during the first 3 years of UV-B treatments. This may be due to an accumulation of subtle effects, such as an increase in competition from testate amoebae; changes in the capitulum microenvironment, or even direct UV-B effects. These reduced populations of rotifers and nematodes may eventually feed back on their predators, such as acari mites.

Our results combined with the changes reported in the higher plant and fungal communities, show that solar UV-B can alter the peatland ecosystem at many levels. These changes have the potential to influence peatland carbon storage and plant nutrient availability.

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