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Arctic microorganisms respond more to elevated UV-B radiation than CO₂

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Surface ultraviolet-B radiation and atmospheric CO₂ concentrations have increased as a result of ozone depletion and burning of fossil fuels12. The effects are likely to be most apparent in polar regions where ozone holes have developed and ecosystems are particularly sensitive to disturbance4. Polar plant communities are dependent on nutrient cycling by soil microorganisms, which represent a significant and highly labile portion of soil carbon (C) and nitrogen (N). It was thought5 that the soil microbial biomass was unlikely to be affected by exposure of their associated plant communities to increased UV-B. In contrast, increasing atmospheric CO₂ concentrations were thought to have a strong effect as a result of greater below-ground C allocation6. In addition, there is a growing belief that ozone depletion is of only minor environmental concern because the impacts of UV-B radiation on plant communities are often very subtle7. Here we show that 5 years of exposure of a subarctic heath to enhanced UV-B radiation both alone and in combination with elevated CO₂ resulted in significant changes in the C:N ratio and in the bacterial community structure of the soil microbial biomass.

We used an established experiment situated close to the Abisko Scientific Research Station, Swedish Lapland (68.35°N, 18.82°E, 360 m above sea level) in a subarctic heath. The site has an open canopy of Betula pubescens ssp. czerepanovii and a dense dwarf shrub layer with scattered herbs and grasses. Plots were exposed to factorial combinations of UV-B radiation (simulating 15% ozone depletion under clear sky conditions) and elevated CO₂ (600 ± 50 p.p.m.). We determined soil microbial biomass C (Cmic) and N (Nmic) using the fumigation-extraction procedure8 and the patterns of C source utilization using extractable bacteria in customized Biolog plates containing a range of ecologically relevant C sources9.

Cmic decreased significantly from 3.1 mg C per g soil dry weight in the control to 1.5 mg C per g soil dry weight in the UV-B treatment (Table 1) but remained unaffected by the application of elevated CO₂ in combination with increased UV-B. This apparent ameliorative effect may reflect differences in the quality and quantity of C entering the soil in the UV-B only and UV-B with CO₂ treatments. In contrast, Nmic increased from approximately 0.1 mg N per g soil dry weight in the control to 0.3 mg N per g soil dry weight in the CO₂ + UV-B treatment (Table 1). The overall main effect of the UV-B treatment was to significantly increase Nmic by over 100% from 0.12 to 0.27 mg N per g soil dry weight (Table 1). These changes were reflected in the microbial biomass C:N ratio (Cmic:Nmic) which decreased significantly by 320% in the plots receiving enhanced UV-B, but was not influenced by exposure to elevated CO₂ (Table 1).

The average well colour development (AWCD; see Methods) of all C sources in the Biolog plates was significantly lower (P < 0.05) in all of the treatments compared to the controls (Table 1), suggesting either a lower or less active population of bacteria. Multivariate analysis of the sole C source utilization tests showed significant discrimination (P = 0.019) between the treatments (Fig. 1) indicating that the soil microbial community structure had also been affected by the treatments. The plots receiving either ambient or elevated CO₂, regardless of UV-B, tended to be separated primarily by the first canonical variate, while the combined addition of increased UV-B, resulted in separation owing to both the first and second canonical variates (Fig. 1). Thus, the combination of elevated CO₂ and UV-B resulted in a population structure different to that from the individual treatments. These substantial shifts in patterns of C utilization among the four treatments will almost certainly have resulted from a change in the dominant bacterial species extracted from this soil. These observations are independent of changes in the abundance of microorganisms, as reflected by AWCD and Cmic (Table 1), and further demonstrate the sensitivity of the microbial component of the ecosystem.

The results from our experiments demonstrate that, unlike the plant community, the soil microbial biomass is highly sensitive to elevated UV-B radiation and CO₂ concentrations. More importantly, the impacts of the UV-B treatment on the accumulation of N in the microbial biomass may have far-reaching implications for the supply of N to plants, because the productivity of many semi-natural ecosystems is limited by N (ref. 11). We are uncertain whether these changes reflect either increased microbial...
Table 1 Microbial responses to elevated UV-B and CO₂

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Cmax</th>
<th>Nmax</th>
<th>Cmax/Nmax</th>
<th>AWCD</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>2.7 ± 0.38</td>
<td>0.13 ± 0.26</td>
<td>35.7 ± 10.5</td>
<td>0.20 ± 0.07</td>
</tr>
<tr>
<td>CO₂</td>
<td>3.1 ± 0.56</td>
<td>0.10 ± 0.28</td>
<td>36.7 ± 7.6</td>
<td>0.12 ± 0.06</td>
</tr>
<tr>
<td>UV-B</td>
<td>1.0 ± 0.24</td>
<td>0.22 ± 0.42</td>
<td>4.8 ± 1.4</td>
<td>0.15 ± 0.06</td>
</tr>
<tr>
<td>CO₂ + UV-B</td>
<td>3.7 ± 0.32</td>
<td>0.31 ± 0.21</td>
<td>11.1 ± 1.6</td>
<td>0.12 ± 0.06</td>
</tr>
</tbody>
</table>

Main effect of ambient and increased UV-B

Ambient UV-B: 2.9 ± 0.47
Increased UV-B: 2.4 ± 0.28

Microbial biomass (mg per g soil dry weight) of carbon (Cmax) and nitrogen (Nmax) Cmax/Nmax ratio and average well colour development (AWCD). Values sharing a letter within columns are not significantly different (P > 0.05).

Individual treatments and main effects are compared separately.

Soil microbial biomass carbon and nitrogen

Duplicate cores (4 cm diameter, 6 cm deep) were extracted from each plot, the surface litter removed and the bulk soil sieved (2 mm). Microbial carbon (Cmic) and N (Nmic) were determined in 5-gram subsamples using the fumigation-extraction procedure 44. Total organic C (TOC) in the fumigated (24 h) sample (exposed to fumigation-free CHCl₃) was measured six times with distilled water and unfumigated extracts (0.5 M K₂SO₄) were determined by potassium peridate/ultra violet absorption (Lab-TOC, Pollution and Process Monitoring). For Nmic, 2-ml subsamples of the extracts were acid-digested 44 and the total N determined 45. Both Cmic and Nmic were calculated using the formula: Cmic or Nmic = (Cmic or Nmic)/Xₐ Xl, where X₀ and Xₐ are the C or N concentrations in fumigated and unfumigated extracts, respectively, and Xₐ is the proportion of microbial C (0.38; ref. 43) or N (0.54; ref. 9) extracted from soil. The Cmic and Nmic data sets were combined to produce a microbial biomass C:N ratio.

Soil carbon source utilization

Direct inspection of soil suspensions in Biolog microtitre plates containing different carbon sources in individual wells was used to determine (1) changes in the potential rate of C-source utilization, and (2) changes in relative and absolute rates of utilization of individual substrates to discriminate between soil microbial communities 28,29. We tested 30 ecologically relevant C sources using customised Biolog MT type plates in which the wells contained six amino acids, two carbohydrates, eight carboxylic acids, nine phenolic acids, and four long-chain aliphatic acids.

We analysed data using two different approaches. In the first, absolute rates of carbon development measured as absorbance at 590 nm (A₅₉₀) were compared for individual C sources. The average well colour development (AWCD) during the initial 96 h of incubation was compared using two-way analysis of variance (ANOVA) and least significant difference (LSD) multiple comparison tests. In the second, multivariate analysis of the A₅₉₀ values at equivalent AWCD from different times of incubation were compared. They were also transformed by dividing by the AWCD to avoid bias between samples with different inoculum density 46. The absorbance data were analysed by canonical variate analysis, after first reducing the dimensionality by principal component analysis and by comparison of mean intergroup Mahalanobis distances with simulated confidence limits and Monte-Carlo testing of significance 47. Simulated confidence limits for four groups (treatments) with eight replicates were 2.26 and 2.57 at the 95% and 99% confidence limits, respectively. All ANOVA, regression and multivariate analyses were conducted using Genstat 5.4 (NAG).

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Competing interests statement

The authors declare that they have no competing financial interests.

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