

Arctic mosses govern below-ground environment and ecosystem processes

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Received: 10 November 2005 / Accepted: 24 May 2007 / Published online: 6 July 2007
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Abstract Mosses dominate many northern ecosystems and their presence is integral to soil thermal and hydrological regimes which, in turn, dictate important ecological processes. Drivers, such as climate change and increasing herbivore pressure, affect the moss layer thus, assessment of the functional role of mosses in determining soil characteristics is essential. Field manipulations conducted in high arctic Spitsbergen (78° N), creating shallow (3 cm), intermediate (6 cm) and deep (12 cm) moss layers over the soil surface, had an immediate impact on soil temperature in terms of both average temperatures and amplitude of fluctuations. In soil under deep moss, temperature was substantially lower and organic layer thaw occurred 4 weeks later than in other treatment plots; the growing season for vascular plants was thereby reduced by 40%. Soil moisture was also reduced under deep moss, reflecting the influence of local heterogeneity in moss depth, over and

above the landscape-scale topographic control of soil moisture. Data from field and laboratory experiments show that moss-mediated effects on the soil environment influenced microbial biomass and activity, resulting in warmer and wetter soil under thinner moss layers containing more plant-available nitrogen. In arctic ecosystems, which are limited by soil temperature, growing season length and nutrient availability, spatial and temporal variation in the depth of the moss layer has significant repercussions for ecosystem function. Evidence from our mesic tundra site shows that any disturbance causing reduction in the depth of the moss layer will alleviate temperature and moisture constraints and therefore profoundly influence a wide range of ecosystem processes, including nutrient cycling and energy transfer.

Keywords Ecosystem processes · Soil temperature · Soil moisture · Nitrogen availability · Moss depth

Communicated by Allan Green and Sven Jonasson.

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Introduction

Mosses constitute one of the most important facets of tundra ecosystems, forming the dominant vegetation in terms of both biomass and productivity (Sonesson and Bergman 1980; Viereck et al. 1986; Oechel and Van Cleve 1986; Longton 1997). The moss layer is important in determining soil characteristics, such as temperature (Luthin and Guymon 1974) and moisture (Zimov et al. 1995), that in turn control carbon and nitrogen cycling within the rhizosphere (Van Cleve and Yarie 1986; Hobbie 1996; Hobbie et al. 2000). Recently, the effects of the presence or absence of mosses on the thermal and hydrological regimes of arctic soils were incorporated into Land Surface Models (Beringer et al. 2001) to predict more accurately the effects

of climate and vegetation changes. However, mosses do not grow as a homogeneous layer throughout tundra ecosystems, but form mats that vary both temporally and spatially. Here, we address how such variation in the depth of the moss layer influences the functioning of arctic ecosystems through its effect on the soil environment.

Factors that influence growing conditions for mosses result in large spatial variation in moss depth. Since most mosses are poikilohydric, moisture is an important growth determinant and is more limiting to moss productivity than are nutrients (Skre and Oechel 1979, 1981). In the wide range of arctic ecosystems where the majority of precipitation falls as snow, moisture regimes are controlled by topography through its influence on snow-melt patterns (Webber 1978; Miller 1982; Walker et al. 1993). Although moisture is an important determinant of moss growth, several other key factors influence the extent and depth of arctic moss layers. Recent studies have demonstrated that herbivory plays a key role in regulating moss cover and growth in tundra ecosystems (Van der Wal 2006). For instance, on Spitsbergen, mosses constitute a large part of the diet of reindeer (*Rangifer tarandus platyrhynchus*; Van der Wal 2006), which, in combination with trampling (Olofsson et al. 2001) and faecal deposition (Van der Wal et al. 2004; Gornall 2005), can lead to dramatic reduction of the depth of the moss layer. Climate change may also affect growing conditions for mosses. Many studies simulating climate change have highlighted that deterioration of moss cover occurs under conditions of increased temperature and nutrient availability (Molau and Alatalo 1998; Press et al. 1998; Robinson et al. 1998; Jónsdóttir et al. 2005; Walker et al. 2006).

The presence of a moss layer has been shown to affect soil characteristics in a wide range of northern ecosystems. In boreal forests, dense *Sphagnum* blankets caused water logging and a reduction of soil pH, lowering decomposition rates and thus nutrient availability (Longton 1992). In Alaskan forests, experimental removal of the moss layer increased soil temperatures (Luthin and Guymon 1974) and maximum depth of thaw (Dyrness 1982). Similarly, depth of the moss layer was observed to influence soil temperature across a wide range of high arctic tundra sites (Van der Wal and Brooker 2004) as well as in subarctic tundra heath (Olofsson et al. 2004). High moss cover also reduces evapotranspiration, which aids moisture retention in the soil (Zimov et al. 1995). The influence of mosses on the temperature and moisture regime of soils has implications for carbon and nitrogen cycling within the system. For example, large differences in soil temperature, depth and progression of soil thaw, and soil moisture content were thought to be responsible for the variability in plant-available ammonium, nitrate and phosphate measured in six arctic ecosystems along a toposequence in Alaska (Giblin et al.

1991; Shaver et al. 1990). Also, low soil temperature and poor drainage restrict decomposition (Hobbie et al. 2000), causing an accumulation of organic carbon in the soil.

It is thus apparent that the presence of mosses affects soil characteristics that control important soil processes. In this study, we aimed to quantify the effects of the depth of the moss layer on the physico-chemical environment of tundra soil and, consequentially, on soil nutrient availability and microbial activity, thereby clarifying the relative importance of soil moisture and temperature as controls of soil biological activity.

To achieve these aims, moss mats of different depths were created in an arctic tundra ecosystem in Spitsbergen. Soil temperature, moisture and nitrogen availability were monitored throughout two growing seasons. The implication of moss-mediated changes in soil characteristics, specifically temperature and moisture, for microbial biomass and activity were investigated in a controlled-environment soil incubation experiment.

Methods

Field study

Experimental set-up

To determine moss layer effects on soil characteristics, a field experiment was established in Adventdalen, a wide valley on Spitsbergen, Svalbard (78°10' N 16°07' E). Our study was conducted at a mesic site located on the outermost part of an alluvial fan. Yearly average temperatures during the course of this study were around -5°C. The monthly averages were observed to be highest during the growing season, reaching about 6°C; were around -7°C in November and December; and dropped to -15°C in January and February. Most precipitation (yearly average 185 mm) falls as snow in Adventdalen, and the winter snow depth is low and variable (10–15 cm) compared with surrounding areas due to strong winds that pass down the valley. It is therefore one of the first areas within the region to become snow free. Soil thaw begins after the site becomes snow free in May. By mid-June, the permafrost has reached its lowest depth, which is around 50 cm. Low summer precipitation (4–27 mm per month) means that the site dries over the season. The growing season for vascular plants lasts from early June to mid August. The soil has a shallow organic horizon of between 3 and 5 cm and a pH of around 5.9. Vegetation at the site is dwarf shrub-grass heath, in which dominant vascular plant species include *Salix polaris* and *Alopecurus borealis*, with some *Luzula confusa* and *Polygonum viviparum* (nomenclature follows Rønning 1996). Vascular plant biomass ranges from 67 to

103 g m⁻² above ground and 290–360 g m⁻² below ground (Gornall 2005). The site has continuous moss cover, the dominant moss species in the area being *Tomentypnum nitens* and *Sanionia uncinata*. Total live moss biomass ranges from 169 to 304 g m⁻², and depth of the moss layer ranges from 2 to 6.5 cm.

At the beginning of the growing season in June 2002, shallow (3 cm), intermediate (6 cm) and deep (12 cm) moss turfs were placed on plots with a bare soil surface from which vegetation had been previously stripped using a soil knife. All plots were 75 × 75 cm and were covered with nine adjacent 25 × 25 cm intact moss turfs placed out at natural density. For each of the treatments, moss turfs of approximately target depths were collected and trimmed to exactly 3, 6 and 12 cm by removing lower decomposing layers of the turfs. The moss *Tomentypnum nitens* dominated selected turfs. To avoid differences in evapotranspiration between turfs caused by different vascular plant cover, the vascular plants were weeded out.

Experimental plots were laid out in five blocks of three randomly assigned treatments (3, 6 and 12-cm deep moss). Due to constraints of a centrally placed soil moisture logger with 5 m long cables, blocks were arranged in a circle of 5 m radius around the data-logger but were all at least 2 m apart. Measurements were taken in the central 25 × 25 cm of each plot to avoid edge effects.

Soil temperature

Temperature sensors attached to loggers (RS[®] Temperature Logger, Northants, UK) were buried 2 cm below the soil surface at the centre of each plot. Spot measurements to the nearest 0.1°C of temperature were taken every 6 h during the period from 25 June 2002 to 1 September 2003. Prior to deployment temperature, sensors were calibrated in water of a known temperature.

Soil thaw depth

Soil thaw depth was measured underneath each moss turf throughout the 2003 growing season. For this, the central moss turf was carefully lifted, a metal rod inserted into the soil and depth (below soil surface) at which it reached the frozen soil layer recorded. Five measurements were taken per plot and then averaged. Measurements were taken every week throughout June and July and then every 2 weeks for the remainder of the field season.

Soil moisture

Moisture probes (Theta Probe type ML1, ΔT, Cambridge, UK) were buried such that moisture was measured in the soil volume between depths of 2 and 6 cm. The probes

were attached to a data-logger (DL300, ΔT, Cambridge, UK) that took spot measurements every 6 h. Measurements were taken over two growing seasons from 18 June to 23 August in 2002 and from 6 June to 2 September in 2003, and the frost-sensitive probes and logger were removed at the end of each growing season. During the second field season, soil under the deep moss mats was frozen for longer than that in other treatment plots; the delayed measurements in these plots commenced on the 2nd July once the soil had thawed.

There is a close, known relationship between moisture probe output (V) and soil dielectric constant (ϵ). Calibration entailed measurement of dry and damp soil (of known volumetric water content, θ) from the field site to enable calculation of constants (a_0 , a_1) using the equation describing the relationship between dielectric constant and volumetric water content ($\sqrt{\epsilon} = a_0 + a_1 \theta$; Whalley 1993).

Soil nitrogen availability

In order to determine whether altering the depth of the moss layer affected nitrogen availability, ion-exchange membranes were inserted in the soil for the 2002 growing season. This method uses anion and cation exchange membranes (BDH, UK #551642S and #551652U), which accumulate nitrate and ammonium ions, respectively (Weih 1998). Strips of 4 × 1 cm were cut, and string was attached at one end to aid relocation in the soil. The strips were rinsed in deionised water for 24 h; anion strips were then saturated in 2 M NaCl and cation strips saturated in 0.1 M H₂SO₄. In the central 25 × 25 cm of each plot, three pairs of ion-exchange membranes were placed in a slit made in the soil at a 45° angle to a depth of 4 cm. The slit was closed ensuring contact was made between the soil and the membrane, which remained in place from 15 June to 23 August 2002. The nitrate and ammonium ions were extracted by shaking in 2 M NaCl in 0.1 M HCl for 2 h. The resin strips were then removed and the remaining solution analyzed for NH₄⁺ and NO₃⁻ with a FIA-Star autoanalyser (FIA, Norway).

Ion-exchange membranes provide qualitative information on seasonally available nitrogen. To obtain quantitative data on actual soil nitrogen content and N-mineralization potential, soil cores (5 cm diameter) were taken from each plot, to a depth of 5 cm from the soil surface, at the end of the growing season in late August 2003 and stored at 2°C. To extract NH₄⁺ and NO₃⁻, 10 g of fresh soil was shaken with 25 ml 1 M KCl for 30 min on an orbital shaker. The resulting suspension was filtered through Whatman no. 42 paper and the concentration of NH₄⁺-N and NO₃⁻-N in the extracts determined using autoanalyser procedures (Bran and Luebbe continuous flow AA3, Delavan, USA; Ross 1992).

The net nitrogen mineralization potential was measured as the release of mineral N ($\text{NH}_4^+\text{-N}$ and $\text{NO}_3^-\text{-N}$) after incubation. Samples of 10 g (fresh soil) were incubated in the laboratory for 14 days at 15°C (Ross 1990). After incubation, soil samples were extracted and analyzed as above. The difference between total nitrogen in incubated and initial samples was used as a measure of potential net N mineralization rate, which was expressed on a per day basis.

Microbial biomass C and N

Microbial biomass C and N were determined in samples collected as above using the fumigation–extraction technique (Vance et al. 1987). From each sample, 5 g of fresh soil was fumigated with CHCl_3 for 24 h at 25°C under vacuum. After flushing out the CHCl_3 from the vacuum, soil samples were extracted for soluble C. Fumigated and unfumigated soil samples were extracted by adding 25 ml 0.5 M K_2SO_4 and placing on an orbital shaker for 30 min. Total organic C in filtered extracts was determined using an organic carbon analyzer (Shimadzu TOC 5000, Columbia, USA). The difference between extractable C from fumigated and unfumigated samples was converted to microbial biomass C using a k_{EC} factor of 0.35 (Sparling et al. 1990). Soil microbial N was measured in the extracts from fumigated and unfumigated soil by adding $\text{K}_2\text{S}_2\text{O}_8$, using the methodology of Ross (1992) followed by auto-analysis (Bran and Luebbe continuous flow AA3, Delavan, USA). The difference between extractable N from fumigated and unfumigated samples was converted to microbial biomass using a k_{EN} factor of 0.54 (Brookes et al. 1985).

Potential microbial activity was measured as basal respiration. Soil samples (1 g dry weight equivalent) were incubated for 24 h at 15°C in universal bottles sealed with a no. 37 Subaseal cap. The concentration of CO_2 in a 1-ml sample of headspace gas was subsequently measured using an infrared gas analyzer (Analytical Development Co., Series 225, Mk. 3).

Soil incubation experiment

An incubation experiment was undertaken to investigate further the relative influence of temperature and moisture on soil biological properties. The experiment employed three temperature and two moisture levels in factorial combination.

Experimental methods

Soil cores (5 cm diameter, 8 cm deep) were collected from undisturbed tundra at the field site in Adventdalen in September 2003. The cores were kept cold and transported

back to the laboratory in Aberdeen for experimentation. Vegetation was removed and the cores were trimmed from below to obtain the top 5 cm of soil. Initial core weight was recorded. Each soil core was placed inside a plastic tube (6 cm diameter, 6 cm deep), which was sealed at either end with parafilm, allowing gas exchange and minimising moisture loss. Each core was randomly assigned to a treatment. Temperature treatments were set at 5, 9 and 13°C, representing the natural temperature range observed during the growing season within the field experimental plots. Average soil temperature in the field during the period July–August was 5°C, and 13°C was the maximum soil temperature recorded on several occasions. The experiment also compared ‘ambient’ and ‘elevated’ soil moisture conditions. For the ambient treatment, cores were maintained in the moisture condition in which they were collected from the field at the end of the growing season (volumetric water content $0.44 \text{ m}^3 \text{ m}^{-3} \pm 0.01 \text{ SE}$). The elevated moisture treatment involved bringing the soil cores to field capacity ($0.53 \text{ m}^3 \text{ m}^{-3} \pm 0.02 \text{ SE}$), equivalent to soil moisture content at the beginning of the growing season in the field. Cores were incubated for 8 weeks. The experiment was fully factorial and replicated nine times.

Soil parameters

Five cores were extracted at the beginning of the experiment to give an initial N concentration. Net nitrogen mineralization was measured as the release of mineral N ($\text{NH}_4^+\text{-N}$ and $\text{NO}_3^-\text{-N}$) after incubation. Concentrations of soil mineral N, microbial biomass C and microbial biomass N were determined using the extraction and analysis methods detailed above.

Statistical analysis

Data were analysed using SAS for Windows V. 8.1 with generalised linear mixed models. Models for field data included ‘experimental block’ as the random effect. The models were fitted using the method of residual maximum likelihood (REML). Denominator degrees of freedom were estimated using Satterthwaite’s approximation (Littell et al. 1996). Data were log-transformed where appropriate, and the residual variances were modelled as constant to the mean using PROC MIXED. Autocorrelation between weeks within plots were modelled as a first-order autoregressive (AR 1) process (i.e. repeated measures) in the analysis of soil temperature, moisture and thaw depth data.

To determine the impact of experimental moss depth on soil temperature across the whole experimental period, data were averaged on a monthly basis, with treatment, month and their interaction as fixed effects in the model. Investigations of treatment effects and seasonality on soil

moisture across the summer period of 2002 and 2003 were conducted on weekly averages, with week and week \times week as fixed effects fitted before the effect of treatment and interaction terms. To inspect diurnal patterns, data from summer 2002 were averaged for each 6-hourly measurement period; and time, time \times time, treatment and their interactions were fitted as fixed effects. Thaw depth data had been collected on a weekly basis and were analysed accordingly with week, treatment and their interaction as fixed effects. Soil nutrients were analysed, with treatment as fixed effect. Soil incubation data were analysed, with soil temperature, moisture and their interaction as fixed effects in the model. Differences between individual treatments were inspected on the basis of post-hoc contrasts within the appropriate model structure.

Results

Field experiment

Temperature

Seasonal trends Depth of the moss turf had an immediate impact on soil temperature. Throughout the growing season in both the first and second experimental year, soil temperature was significantly higher in the plots with shallow moss mats (Fig. 1). In both years, the greatest difference in monthly soil temperature averages, ranging from 2.0 to 2.7°C, was between shallow and deep treatments in June and July. In October the pattern was reversed, with soil under deeper moss mats being warmest on average, whilst throughout the winter into May no significant differences between treatments were observed. Over the measurement

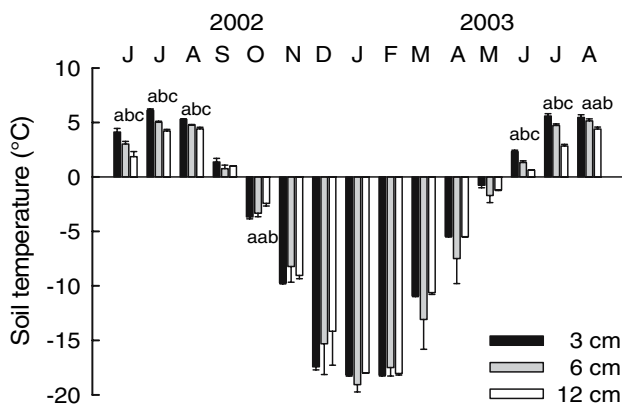


Fig. 1 Soil temperatures in plots with shallow (3 cm), intermediate (6 cm) and deep (12 cm) moss mats. Data are monthly averages for each treatment (\pm SE) from June 2002 until August 2003 ($n = 5$). Significant results within each month are indicated using letters; values not sharing a common letter differ significantly ($P < 0.05$)

period, soil temperature under the deepest moss turf was rarely above 5°C, whereas that under shallow moss frequently exceeded 9°C (on average 115 ± 8 h SE) and occasionally exceeded 12°C (on average 34 ± 4 h SE). The temperatures under shallow moss were over 5°C for the equivalent of 57 days longer than those under deep moss.

Diurnal fluctuations Diurnal temperature data during the growing season show that, in addition to the clear influence of moss depth on absolute soil temperature ($F_{2,47} = 313.8$, $P < 0.001$), there is a strong effect of increasing moss depth decreasing the amplitude of diurnal fluctuations (time² \times treatment: $F_{2,47} = 14.53$, $P < 0.001$; Fig. 2). Under deep moss, soil temperatures remained fairly constant, with an average maximum of 4.4°C; under intermediate and shallow moss, however, average soil temperatures showed diurnal fluctuation of 0.6 and 1.1°C, respectively.

Thaw depth

Measurements of thaw depth taken throughout the second experimental growing season (Fig. 3) showed that depth of the moss turf significantly affected patterns of soil thaw (week \times treatment: $F_{2,117} = 8.57$, $P < 0.001$). Thinner moss resulted in earlier thaw of the organic layer where the majority of roots are situated; the soil organic layer under the deep moss mats remained frozen for 1 month longer than in the other plots. Despite differences in the onset and progression of soil thaw, the maximum thaw depth of roughly 50 cm was similar for all treatments.

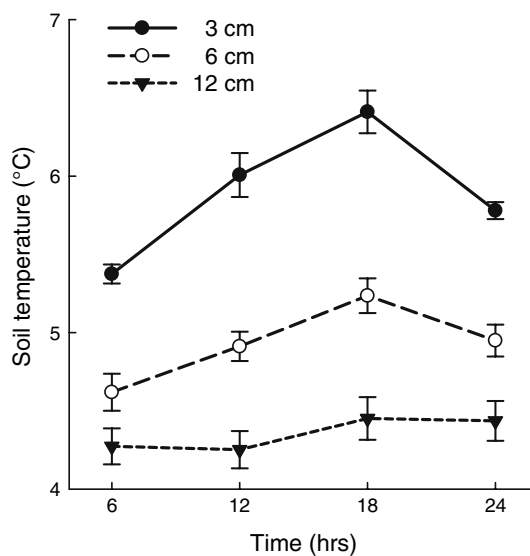


Fig. 2 Diurnal soil temperature patterns in plots with shallow (3 cm), intermediate (6 cm) and deep (12 cm) moss mats. Data shown are treatment averages (\pm SE) at each 6-hourly recording point from the 2002 growing season (25 June–28 August) ($n = 5$)

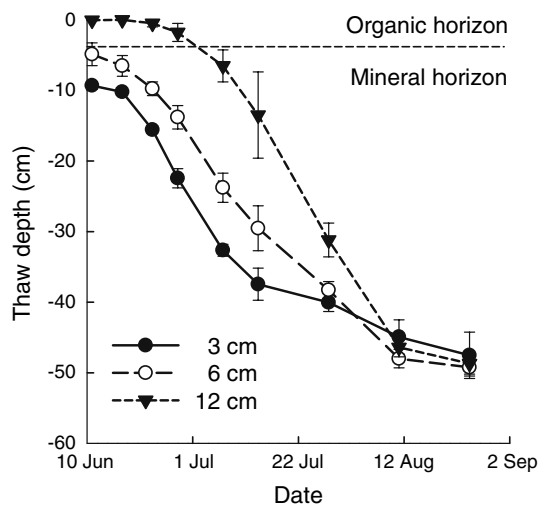


Fig. 3 Soil thaw depth measured during the growing season in 2003 in soil under shallow (3 cm), intermediate (6 cm) and deep (12 cm) moss mats. Data are weekly treatment averages (\pm SE) ($n = 5$)

Soil moisture

During the first summer, following snow melt, all plots exhibited a significant decrease in soil water content ($F_{1,104} = 125.9$, $P < 0.001$), which was most marked within the first 3 weeks of measurement. Subsequent drying of the soil was slow and minimal. During the second summer, the plots under shallow and intermediate moss turfs followed a similar pattern, again with the majority of drying occurring within the first 3 weeks ($F_{1,68} = 68.63$, $P < 0.001$). The soil under the deep moss mat was still frozen during this period, making measurement early in the growing season impossible.

Varying the depth of the moss turf had no significant effect on the moisture content of the soil in the first summer ($F_{2,7} = 1.05$, $P = 0.40$; Fig. 4a). Patterns in the data suggest that soil was driest under the shallow moss mats. However, treatment differences were insufficient to overcome background variation. During the second summer, the pattern was reversed (Fig. 4b) with significantly higher soil water content in plots under shallow moss turfs than under intermediate and deep moss ($F_{2,9} = 5.22$, $P = 0.03$).

Soil nitrogen availability and microbial activity

Moss depth affected the relative amounts of ammonium ions in the soil over the first growing season ($F_{2,12} = 29.26$, $P < 0.001$; Fig. 5a), with significantly greater ammonium availability in soil under shallow moss mats than under the other two treatments. There were similar patterns for nitrate ions; although differences were not significant ($F_{2,12} = 12.10$, $P = 0.07$; Fig. 5b) they were close to the threshold value of $P = 0.05$.

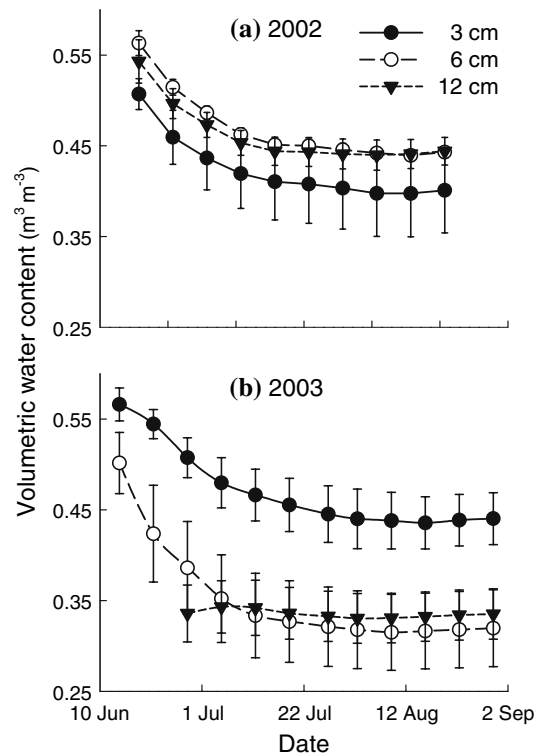


Fig. 4 Soil water content over the growing season in 2002 (a) and 2003 (b) in plots with shallow (3 cm), intermediate (6 cm) and deep (12 cm) moss mats. Data are weekly treatment averages (\pm SE) ($n = 5$)

Soil extractable nitrate differed significantly with moss depth (Table 1). Amounts of nitrate were higher in soils underneath shallow and intermediate moss treatments. There was no significant effect of moss depth on extractable ammonium or net nitrogen mineralization rate. Microbial biomass C differed significantly among treatments and was highest in soil under plots with shallow and intermediate moss depth (Table 1). Microbial biomass N followed a similar pattern, but differences were only marginally significant. Whereas microbial C to N ratio did not differ among treatments, soil under shallow moss turfs had higher potential microbial activity, measured through basal respiration rate, than soil under deep moss turfs.

Soil incubation experiment

The soil incubation experiment showed that, of the two soil variables investigated, the range of soil biological properties determined was more affected by soil temperature than by soil moisture (Table 2, Fig. 6).

Net N mineralization rate (Fig. 6b) and extractable soil ammonium were significantly higher in soil incubated at 9 and 13°C than in soil incubated at 5°C. Elevated soil moisture caused weakly significant increases in both mineralization (Fig. 6b) and ammonium availability

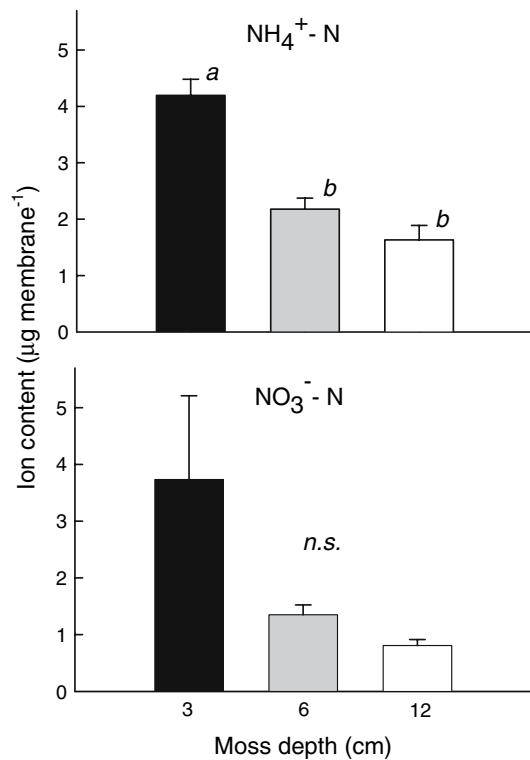


Fig. 5 Ammonium and nitrate availability, as determined using the ion-exchange membrane technique, in soils under shallow (3 cm), intermediate (6 cm) and deep (12 cm) moss mats. Data shown are treatment averages (\pm SE) ($n = 5$). Significant results are indicated using letters; bars not sharing a common letter differ significantly ($P < 0.05$)

(‘ambient’ = $36.7 \pm 5.5 \mu\text{g N g dw soil}^{-1}$, ‘elevated’ = $48.9 \pm 6.4 \mu\text{g N g dw soil}^{-1}$). Average nitrate concentration was lower than ammonium concentration, and no treatment effect was detected.

Microbial biomass C was significantly increased in soil incubated at 9 and 13°C (Table 2, Fig. 6a). Values in soil incubated at 5°C were comparable with those found in

soil under deep moss, whilst amounts in soil incubated at 9°C were similar to those in soil under shallow and intermediate turfs. Microbial biomass C also responded strongly and positively to increased soil moisture. Microbial biomass N and C:N did not differ significantly among treatments (Table 2).

Discussion

Field manipulations of the moss layer at an arctic site underlain by permafrost had an immediate impact on soil temperature, in terms of both average temperatures and amplitude of diurnal fluctuations. Soil temperature decreased with increased moss depth, and underneath the deepest moss this resulted in a 4-week delay to thaw of organic soil in spring. Soil moisture was reduced under deep moss turfs. Data from our field and laboratory experiments show that changes to soil temperature and moisture have major implications for soil chemical and biological properties.

Mosses alter the soil environment

The insulating properties of the moss layer have been highlighted in several studies (Luthin and Guymon 1974; Miller et al. 1980; Hinzman et al. 1991; Sharratt 1997; Beringer et al. 2001, Van der Wal and Brooker 2004). For example, Matthews et al. (1997) identified the insulating properties of moss as the causal factor in the creation of permafrost mounds in Southern Norway. These insulating properties are largely due to three factors. First, the moss acts as a physical barrier to incoming radiant energy (Shulgin 1957). Second, live shoots absorb energy to use in photosynthesis, thus preventing it reaching the soil surface (Miller et al. 1980). Third, moss has a much lower (4 \times) thermal conductivity than soil due to the presence of large

Table 1 Soil parameters (mean \pm SE, $n = 5$) measured in samples collected from under shallow (3 cm), intermediate (6 cm) and deep (12 cm) moss mats in August 2003 after 2 years of “treatment”

	Moss depth			Statistics	
	Shallow	Intermediate	Deep	$F_{2,8}$	P
Extractable $\text{NH}_4^+\text{-N}$ ($\mu\text{g N g}^{-1}$ dry soil)	13.9 ± 4.4	11.3 ± 2.6	18.3 ± 4.5	0.99	0.41
Extractable $\text{NO}_3^-\text{-N}$ ($\mu\text{g N g}^{-1}$ dry soil)	25.9 ± 3.1^a	22.5 ± 3.2^a	12.3 ± 3.5^b	5.36*	0.03*
N-mineralization ($\mu\text{g N g}^{-1}$ dry soil day^{-1})	0.52 ± 0.43	0.37 ± 0.35	0.92 ± 0.35	0.52	0.62
Microbial biomass C ($\mu\text{g C g}^{-1}$ dry soil)	938.4 ± 118.2^a	901.9 ± 140.7^a	567.6 ± 119.3^b	5.70*	0.03*
Microbial biomass N ($\mu\text{g N g}^{-1}$ dry soil)	317.4 ± 41.9	363.5 ± 39.5	214.5 ± 45.0	3.88	0.06
Microbial C:N	3.14 ± 0.48	2.42 ± 0.19	3.05 ± 0.67	0.73	0.51
Basal respiration ($\mu\text{l CO}_2 \text{ g}^{-1} \text{ h}^{-1}$)	6.31 ± 0.87^a	$5.04 \pm 1.07^{a,b}$	4.91 ± 0.28^b	4.39*	0.05*

Statistics (F , P values) refer to results of a GLMM. Significant results are indicated using letters; values not sharing a common letter differ significantly (* $P < 0.05$)

Table 2 Results of GLMM analysis of extractable ammonium and nitrate, net N-mineralization, microbial C, microbial N and microbial C to N ratio in response to temperature and moisture treatments ($n = 9$)

	Temperature	Moisture	Temperature \times moisture
Degrees of freedom	$F_{2,48}$	$F_{1,48}$	$F_{2,48}$
$\text{NH}_4^+\text{-N}$ ($\mu\text{g N g}^{-1}$ dw soil)	9.28***	2.87 [†]	0.60
$\text{NO}_3^-\text{-N}$ ($\mu\text{g N g}^{-1}$ dw soil)	0.26	0.90	0.90
N-mineralization ($\mu\text{g N g}^{-1}$ day ⁻¹)	7.27**	3.58 [†]	0.90
Microbial biomass C ($\mu\text{g C g}^{-1}$ dw soil)	3.33*	5.38*	0.50
Microbial biomass N ($\mu\text{g N g}^{-1}$ dw soil)	0.90	0.67	2.10
Microbial C:N	0.16	0.15	0.01

Figures are F values with significance demonstrated with a superscript: *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, [†] $P < 0.1$

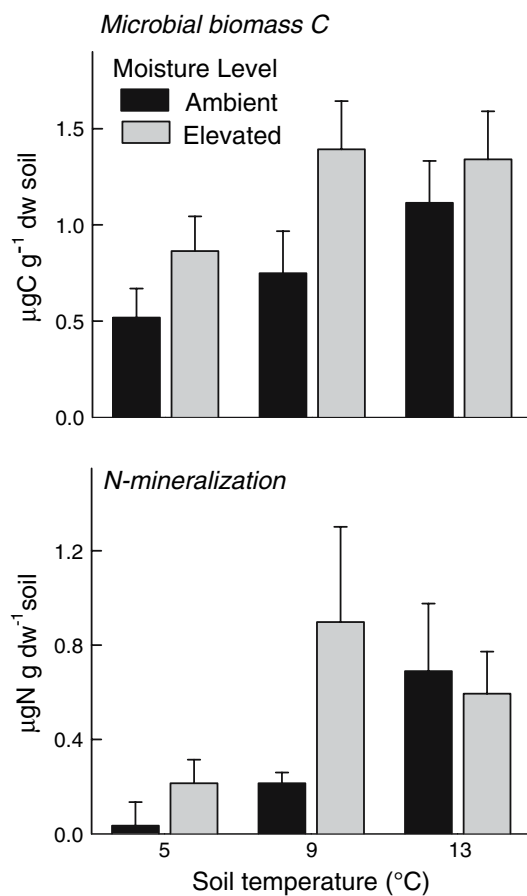


Fig. 6 Effects of soil temperature and moisture on microbial biomass carbon and net nitrogen mineralization. Data shown are treatment averages (\pm SE) ($n = 9$). Statistics are presented in Table 2

airspace, as opposed to water-filled spaces, inside the moss mat (Hinzman et al. 1991; Beringer et al. 2001). The effects of moss depth on soil temperature may be

influenced by variation in the moisture status of the moss layer. Moisture in the moss layer would increase thermal conductivity across it (Hinzman et al. 1991); thus, any effects of moss mat depth on moisture retention may influence heat loss or gain to the soil.

Our study confirms that soil temperature varies with moss depth, with a thicker moss layer resulting in both lower soil temperatures during the growing season and a decreased amplitude of diurnal soil temperature fluctuations. As well as buffering from high temperature in summer, deeper moss also buffered soil against low temperatures during a month at the beginning of the cold season, before a permanent snow cover developed.

One of the major findings of this study was that deeper moss delayed the onset of soil thaw for several weeks. The organic horizon, which contains the majority of vascular plant roots (Brooker and Van der Wal 2003), was frozen for 1 month longer in soil under deep moss. Such an effect may delay the onset of vascular plant growth early in summer, shortening their growing season by as much as 40%. This, in combination with lower soil temperatures throughout the growing season, is likely to constrain vascular plant root growth (Brooker and Van der Wal 2003) and consequently their total productivity. Compensation by the delay in soil freeze that occurs under deep moss at the end of the season is unlikely, because other factors including photoperiod cause the onset of senescence well before the soil freezes.

Soil under the deep and intermediate moss turfs was drier than that under shallow moss during the second summer. It is possible that deeper moss mats prevent infiltration of precipitation to the soil. However, during the growing season, inputs of water from precipitation are low (4–27 mm per month). The largest inputs of moisture to the soil are during snow melt. Thus, the delayed soil thaw is the more likely explanation for the significant differences in soil moisture observed in the second experimental year. During snow melt, soil under the deeper moss was still frozen. Initially, the melt water refreezes when it contacts the colder soil, which in effect seals any pores and greatly limits potential infiltration, restricting melt water movement into the frozen soil (Hinzman et al. 1991) and resulting in drier soil once thaw takes place. Thus, our observation may be an experimental artefact reflecting the small patch size of our turfs (75×75 cm), creating small areas of frozen soil. This may imitate natural hummock-hollow variation in soil moisture or the results of local disturbance to the moss layer.

In a situation of continuous moss carpet of even depth, soil would be likely to retain more moisture under thicker moss. Indeed, in the first year of our experiment, soil moisture tended to be greater under deeper moss layers. A deep moss layer retains water within its structure and

reduces evaporation from the soil surface. At a tundra site in Barrow, Alaska, only thin moss layers of less than 2 cm acquired water through capillary movement from the soil (Miller et al. 1980). With movement of water from the soil into the moss restricted in areas with deeper moss, evaporation from the moss surface is less likely to reduce soil moisture than in shallow moss areas. It may, however, be that the impact moss depth has on soil moisture at the landscape scale is fairly limited, and that the association between deeper moss layers and wetter soils, commonly observed in low lying areas throughout the Arctic, largely indicates how topography determines soil moisture which in turn sets the conditions for moss growth. Therefore, at the landscape scale, the moss layer may exert relatively more control over soil temperature than soil moisture.

Thus, the most significant effects of decreasing depth of the moss layer on the tundra soil environment are earlier active layer thaw, increased soil temperatures throughout the growing season and greater amplitude of soil temperature fluctuation. At a local scale, a reduction in moss layer depth also results in increased soil moisture. All these factors may influence biological activity in the soil.

Influence of mosses on below ground processes

Both field and soil incubation data in our study showed that the effects of moss depth on soil temperature influenced microbial biomass and activity and resulted in warmer soil under thinner moss layers containing more plant available nitrogen. Several studies have investigated the effects of soil temperature on soil processes, especially in arctic systems where temperature might be expected to limit biological activity (Van Cleve and Yarie 1986; Hobbie 1996; Hartley et al. 1999). Generally, such relationships are strongly non-linear, with the greatest increase in activity at higher soil temperatures (Nadelhoffer et al. 1991). In our study, the existence of a deep moss layer not only reduced average soil temperature, but also dampened the diurnal soil temperature fluctuation, thereby largely preventing the occurrence of soil temperatures higher than 5°C. In comparison, soil under shallow moss mats frequently exceeded 9°C and sometimes 12°C, at which temperatures biological activity will be greatly increased. Consequently, microbial biomass C under deep moss layers was 40% lower than under shallower moss. Microbial activity, measured as respiration in soil from the field experiment incubated at constant temperature in the laboratory, was reduced by 25%. An even greater suppression of microbial activity under deep moss might be expected in the field, where both average soil temperature and diurnal fluctuations are suppressed.

Soil nitrogen followed a similar pattern, with less inorganic nitrogen under deep moss. N-mineralization rates measured by incubation at 15°C did not vary with moss layer thickness, but field rates are likely to have varied with soil temperature and thus have been lower under deep moss. The delay in soil thaw may also have reduced total N-mineralization by reducing the duration of soil activity within the growing season.

We note that microbial C to N ratios in soils sampled at the end of the growing season were invariably low across all treatments. This may be partly due to the fact that competition for soil N with vascular plants could not occur due to their removal from the plots. However, the low microbial C to N ratio is also in line with its generally observed seasonal decline in both high alpine and high arctic ecosystems (Jaeger et al. 1999; Bardgett et al. 2002), suggesting that microbes become progressively less N limited as the growing season progresses. Importantly, microbes appear to be similarly C limited under moss of different depths despite contrasting soil temperature and nutrient availability.

Moisture is an important determinant of soil carbon and nitrogen cycling (Robinson et al. 1995; Fisk et al. 1998), and this was reflected in our laboratory study. Soils incubated at field capacity had approximately 50% more microbial carbon (averaged across temperatures) than cores incubated at ambient moisture. Thus, it is possible that elevated microbial biomass C in soil with shallow moss cover is a response to the higher soil moisture observed. Across the range of the incubation conditions we imposed, the response of microbial C to moisture was of similar magnitude to the response to temperature. N-mineralization responded much more strongly to the temperature than to the moisture treatments, which may suggest that the influence the moss layer exerts over soil biological activity arises more from its effect on soil temperature than on soil moisture. However, the differences between the temperature treatments are greater than the mean temperature differences observed under the different moss depths in the field, whereas the difference between the moisture treatments is more representative of the field variation. Thus, the N-mineralization responses to soil temperature and moisture under different moss depths in the field may be more similar.

At a local scale, the moss layer influences soil biological activity through its effect on both the soil temperature and moisture environment. Any decrease in the thickness of the moss layer results in a longer active season, with warmer soil of higher moisture content, all giving rise to greater soil biological activity. At a landscape scale, with topography being the main control of soil moisture, the influence of the moss layer on soil microbial activity is primarily through its influence on soil temperature.

Conclusions

We have demonstrated that in a high arctic mesic ecosystem the moss layer influences mean soil temperature, the amplitude of soil temperature fluctuation, the progression of soil thaw and, to a lesser extent, soil moisture. These key environmental parameters in turn constrain soil biological activity, which is fundamental to ecosystem processes including plant production, organic matter decomposition and carbon flux. Many arctic ecosystems are currently influenced by ecological drivers, which threaten the integrity of the moss layer, for example climate change and increasing herbivory and trampling. We show that any reduction in the depth of the moss layer will alleviate constraints imposed by both temperature (magnitude and duration) and moisture, and therefore profoundly influence a wide range of ecosystem processes including nutrient cycling, productivity and energy transfer.

Acknowledgments We are grateful to Hera Sengers and Anne-Mette Pedersen for invaluable help with field and laboratory work and Chris Mullins for providing essential equipment. We also thank Richard Bardgett for allowing laboratory work to be undertaken within the Ecology Research group at Lancaster University. This work was funded by NERC (NER/S/A/2001/05958).

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