

Jake F. Weltzin · Calvin Harth · Scott D. Bridgham
John Pastor · Mark Vonderharr

Production and microtopography of bog bryophytes: response to warming and water-table manipulations

Received: 12 July 2000 / Accepted: 7 March 2001 / Published online: 26 April 2001
© Springer-Verlag 2001

Abstract Boreal peatlands, which contain a large fraction of the world's soil organic carbon pool, may be significantly affected by changes in climate and land use, with attendant feedback to climate through changes in albedo, fluxes of energy or trace gases, and soil carbon storage. The response of peatlands to changing environmental conditions will probably be dictated in part by scale-dependent topographic heterogeneity, which is known to interact with hydrology, vegetation, nutrients, and emissions of trace gases. Because the bryophyte community can contribute the majority of aboveground production in bogs, we investigated how microscale topography affects the response of bryophyte species production and cover to warming (using overhead infrared lamps) and manipulations of water-table height within experimental mesocosms. We removed 27 intact peat monoliths (2.1-m² surface area, 0.5–0.7 m depth) from a bog in northern Minnesota, USA, and subjected them to three warming and three water-table treatments in a fully crossed factorial design. Between 1994 and 1998, we determined annual production of the four dominant bryophyte taxa within three microtopographic zones (low, medium, and high relative to the water table). We also estimated species cover and calculated changes in topography and roughness of the bryophyte surface through time. Total production of all bryophytes, and production

of the individual taxa *Polytrichum strictum*, *Sphagnum magellanicum*, and *Sphagnum* Section *Acutifolia*, were about 100% greater in low microtopographic zones than in high zones, and about 50% greater in low than in medium zones. Production of bryophytes increased along the gradient of increasing water-table heights, but in most years, total production of bryophytes was negatively correlated with height above the set water table only for the wettest water-table treatment. Although bryophyte production was unaffected by the warming treatments, the bryophyte surface flattened in proportion to the degree of warming. These results indicate that production of bryophytes is driven most strongly by the absolute and relative height of the bryophyte surface above the water table. Predicted changes in water-table height commensurate with changes in surface temperature may thus affect both production and superficial topography of bryophyte communities.

Keywords Bryophyte bog · Climate change · Microtopography · Production · Water table

Introduction

Boreal peatlands comprise about half of the total global wetland area (Matthews and Fung 1987; Bridgham et al., in press), contain a large fraction of the world's soil organic carbon pool (Sampson et al. 1993), and have many functional attributes valued by society (Parkyn et al. 1997). As for other ecosystems, the structure and function of peatlands may be significantly affected by changes in historic and potential future climate and land use (Gorham 1991; Bridgham et al. 1995; Öquist and Svensson 1996; Oldfield et al. 1997). Peatlands may be particularly vulnerable to climate change because current low temperatures constrain biological activity, and most models of global climate change predict greater-than-average temperature increases at higher latitudes (Körner and Larcher 1988; Kattenberg et al. 1996). They may also embody positive or negative feedback mechanisms

J.F. Weltzin (✉)
Department of Ecology and Evolutionary Biology,
569 Dabney Hall, University of Tennessee, Knoxville, TN 37996,
USA
e-mail: jweltzin@utk.edu
Tel.: +1-865-9745218, Fax: +1-865-9743067

C. Harth · J. Pastor
Natural Resources Research Institute, University of Minnesota,
Duluth, MN 55811, USA

S.D. Bridgham
Department of Biological Sciences, University of Notre Dame,
Notre Dame, IN 46556, USA

J.Pastor · M. Vonderharr
Biology Department, University of Minnesota, Duluth,
MN 55811, USA

to anthropogenic climate change through changes in surface roughness, albedo, trace gas flux, or soil carbon storage (Bridgman et al. 1995, 1999; Harte et al. 1995; McFadden et al. 1998).

Most peatlands are characterized by considerable topographic heterogeneity at several scales, ranging from tens of centimeters (i.e., microscale hummocks, lawns, and hollows), to tens of meters (in the form of mesoscale ridges, pools, and lawns), up to landforms measured across many kilometers (macroscale) (Ivanov 1981; Glaser 1992). At each of these scales, characteristics of hydrology, vegetation, nutrients, and emissions of trace gases may exhibit differential responses to future environmental conditions (Gorham 1991; Bridgman et al. 1995; Waddington and Roulet 1996).

In particular, considerable interest has focused on the microtopographic features of hummocks – mounds of peat 30–50 cm above the water table, hollows – depressions where the water table is often close to the surface, and where water may pond during wet periods, and lawns – relatively level zones at intermediate heights (Sjörs 1948). Hummock-hollow topography has been well-described (Tansley 1939; Barber 1981), but the ultimate mechanisms underlying this widespread pattern are not well understood. The formation of microscale topography has been attributed to species-specific differences in production and decomposition and subsequent interactions between vegetation, hydrology, pH, and nutrient and water availability (Clymo 1965; Rydin 1985; Andrus 1986; Vitt 1990; Johnson and Damman 1991; Belyea 1996; Belyea and Clymo 1998).

Peatland microhabitats are often characterized by different assemblages of *Sphagnum* species (Tansley 1939; Andrus et al. 1983). Hummocks and hollows may differ in terms of oxygenation, redox potential, pH, and nutrient availability (Malmer 1962; Damman 1978; Pakarinen 1978; Zobel 1986). In addition, microtopographic variations have important ramifications for thermal regimes (Chapin et al. 1979), hydrologic regimes (Lindholm and Markkula 1984; Swanson and Grigal 1988), structure and function of plant communities (Andrus et al. 1983; Moore 1989; Malmer 1986), and emissions of trace gases (Kim and Verma 1992; Bubier 1995; Waddington and Roulet 1996; Waddington et al. 1998). However, the response of these microhabitats to changes in environmental conditions, particularly climate change, is not well known.

The objective of this research was to investigate the role of microscale topography in mediating the response of a bog bryophyte community, in terms of production and composition of the dominant bryophyte taxa, to experimental warming and water-table manipulations. Research was conducted within the context of a field-scale climate change experiment in northern Minnesota, USA. The overall objective of the experiment is to examine interactions among plant communities, the energy balance, carbon and nutrient cycling, and trace gas emissions in response to potential scenarios of climate change (Bridgman et al. 1999; Weltzin et al. 2000; Updegraff et al., in press; Northern Peatlands Soil Warming Project 2001).

Materials and methods

Source site

We selected a bog in the township of Toivola in northeastern Minnesota (47°N, 92°W) as our source site because it is typical of other bogs in the region, and has been described in detail (Bridgman et al. 1998, 1999; Chapin 1998). The peat at Toivola bog is approximately 3.5 m deep with a basal radiocarbon date of $10,040 \pm 70$ years B.P. The upper 60 cm is derived largely from *Sphagnum* moss, with increasing herbaceous remains below that point, and frequent woody inclusions throughout the profile (Bridgman et al. 1998). Vegetation is dominated by short (<10-cm height), ericaceous shrubs [*Chamaedaphne calyculata* (L.) Moench., *Andromeda glaucophylla* Link., *Kalmia polifolia* Wang., *Vaccinium oxycoccos* L., *Ledum groenlandicum* Oeder.], bryophytes [*Sphagnum fuscum* (Schimp.) Klinggr., *S. capillifolium* (Ehrh.) Hedw., *S. magellanicum* Brid., *Polytrichum strictum* Brid.], and black spruce [*Picea mariana* (Mill.) BSP].

Experimental design

We extracted intact peat monoliths from the central, treeless portion of the source site bog, and constructed a mesocosm facility to manipulate energy (infrared radiation) inputs and water-table levels within an experimental framework. The experimental design consisted of all combinations of three water-table treatments and three infrared loading treatments randomly assigned to three replicate plots. Details of mesocosm construction, infrared loading and water-table treatments, and biotic and abiotic response to these treatments are provided by Bridgman et al. (1999), Weltzin et al. (2000), and Northern Peatlands Soil Warming Project (2001). A summary is provided below.

The mesocosm facility was constructed between autumn 1993 and spring 1994 at the University of Minnesota Fens Research Facility (FRF), approximately 70 km north of Duluth, Minn. Twenty-seven intact cylindrical peat monoliths (2.1-m² surface area, 0.5–0.7 m depth) were removed from the bog, transported to the FRF, and placed in insulated plastic tanks of similar dimensions that had been sunken into an open field. The peat monoliths were removed in winter while frozen with minimal surface disturbance to vegetation (Bridgman et al. 1999).

We extracted our monoliths from the central, treeless portion of the bog, which had few deep hollows typical of other bog ecosystems (e.g., Crum 1988). As such, the majority of the surface of each monolith was characterized by bryophyte species associated with hummocks or lawns (i.e., *Sphagnum fuscum*, *S. capillifolium*, *S. magellanicum*). Cover of *S. recurvum* P. Beauv., a species associated with typical bog hollows, was visually estimated as <1% within our plots. However, there was considerable intra- and inter-plot variation in bryophyte surface topography (Fig. 1).

We used infrared heat lamps (Kalglo Electronics, Bethlehem, Pa.), identical to those used by Harte et al. (1995), to augment infrared loading starting in July 1994. Specifically, we mounted a single lamp approximately 130 cm above the mean surface height of 18 of the plots. The lamps were set at either half-power ('medium') or full-power ('high') outputs, and were left on continuously. The remaining nine plots were unheated ('ambient'). Heat treatments increased mean monthly soil temperatures by 1.7–4.5°C at 15-cm depth during the growing season (May–October). During the 1995 growing season, small patches (~100 cm²) of the bryophyte surface became desiccated, so we re-set the infrared lamps slightly higher above the plots to the current 130 cm height (Bridgman et al. 1999).

Water-table levels in peatlands are typically measured relative to surface depressions or hollows. We designated a datum hollow in each mesocosm from which we set water-table levels to approximately +1 cm (= 'wet'), –10 cm (= 'intermediate'), and –20 cm (= 'dry') relative to its surface. Water levels in each plot were maintained using a PVC-pipe manostat and a small adjacent sump bucket. We allowed the surface elevation of each plot to change

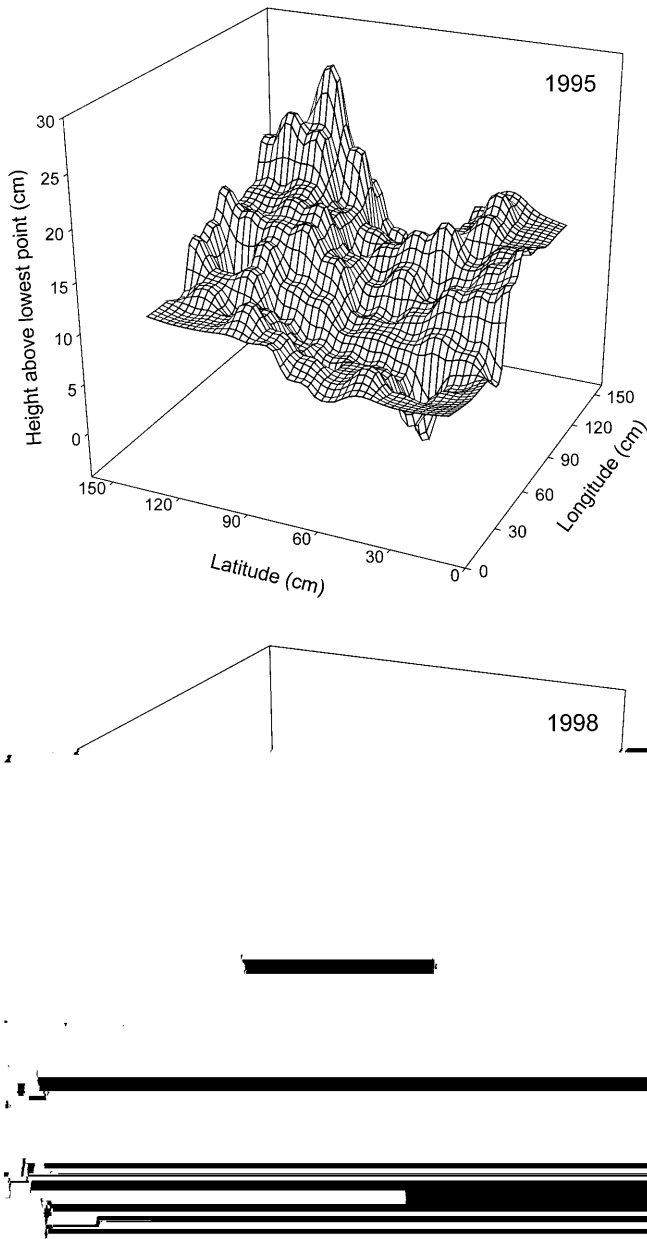


Fig. 1 Microtopography of the plot (no. 54) that exhibited the greatest change in surface heterogeneity between 1995 and 1998

relative to the water table as a treatment response. In 1996, the average water-table depths for the three hydrology treatments were at -11 , -19 , and -26 cm (Bridgham et al. 1999).

Water-table control of the mesocosms was maintained only during the growing season (May–October) to prevent ice damage to the PVC manostat assemblies. Water was replenished by natural rainfall and, during dry periods, by weekly additions of water pumped from a ditch draining a bog. Water was added to the bottom of each plot using a standpipe installed during construction of the mesocosms. The ditch water had a pH, electrical conductivity, and nutrient status similar to that of the porewater in the bog source site (Bridgham et al. 1999).

Bryophyte production, cover, and surface topography and roughness

Bryophyte production was based on measurements of basal cover (%), linear shoot growth (cm), shoot density (no./dm²), and

species-specific shoot mass/shoot length relationships. Bryophyte basal cover was determined in July or August of 1995–1997 from subplots within each mesocosm. Subplots were positioned using a removable sampling grid. The sampling grid was constructed to form an open square, with taut line strung from side to side at right angles to form a grid of intersecting points at a spacing of 12.5 cm. The grid was leveled at about 20 cm above the median surface height of each plot, and was held rigidly by supports bolted to the tank. We lowered a plumb bob from each grid point down to the bryophyte surface to establish our sample points. The number of sample points per plot ranged from 100 to 118 (mean=110) because small portions of the plot surface were deemed unsuitable for measurement (e.g., because they contained a micrometeorological sensor or a root in-growth core). To minimize edge effects, we did not establish sample points within 15 cm of the plot edge. We placed a round, 3-cm-diameter quadrat at each point, and calculated the percentage cover for each bryophyte species within the quadrat as the mean of visual estimates made by two or three observers. Bryophyte cover in 1994 was estimated visually for the entire plot.

Microtopographic zones within each plot were defined based on the vertical distance between the bryophyte surface and the removable sampling grid. In each year, we ranked the vertical distances for all ~2,970 points (=27 plots with ~110 points/plot), and then divided this dataset into three equal-sized subsets: points with the greatest vertical distance between the bryophyte surface and the frame were defined as representing low microtopographic zones in their respective plots. Similarly, points with the least vertical distance represented high microtopographic zones, and the remainder of the points represented intermediate zones. This approach allowed the proportion of each zone to vary among plots by year. Because our zones were not strictly equivalent to hummocks, lawns, and hollows, per se, we termed them as 'high,' 'medium,' and 'low,' respectively.

Shoot growth of bryophytes was estimated using the cranked-wire method, wherein stainless steel wires set vertically into the bryophyte surface act as static datum points for measuring bryophyte shoot extension (Clymo 1970). A total of nine cranked wires were installed in each plot. Wires were installed before determination of microtopographic zones, but each zone contained between one and six wires. Wires were treated as subsamples (i.e., averaged) within each microtopographic zone. Because we did not start using the removable sampling frame until 1995, we applied the 1995 cranked wire designations of microtopographic zone to the 1994 data. Vertical height of bryophyte growth relative to the top of the cranked wire was measured monthly during the growing season in 1994 through 1997; monthly measurements were summed to obtain total linear shoot growth within each microtopographic zone.

In October 1994 we collected three 10×10×4 cm (length, width, depth) samples of *Polytrichum strictum*, *Sphagnum capillifolium*, *S. fuscum*, *S. magellanicum*, and *S. recurvum* from different mono-specific populations at the bog source site. Samples were stored frozen until they were processed. For each species-specific sample, we determined shoot density (no./dm²). In addition, we established shoot mass/length relationships for individual shoots by clipping the top 1 cm for *P. strictum*, and 2 cm excluding the capitula for *Sphagnum* spp., drying them at 60°C, weighing them to the nearest milligram, and calculating shoot mass/shoot length ratios (Weltzin et al. 2000).

To determine whether bulk density of peat in the mesocosm plots changed over time in response to the different treatments, in winter of 2000 we extracted three frozen cores of peat (6-cm diameter, 15 cm deep) as subsamples from random locations within each plot. Similarly, to determine whether bulk density differed between the mesocosm plots and the Toivola bog source site, we used a serrated knife to extract cubes of peat (5 cm long, 6 cm wide, 14 cm deep) from ten locations selected at random near the original source area of the monoliths. For both sets of samples, we extracted roots by hand, and calculated bulk density (g mass/cm³) on an oven-dry basis.

Annual production of bryophytes was calculated for each species within each zone using species-specific stem mass/length re-

relationships and shoot densities developed in 1994, shoot growth estimates for that zone, and the cover of each species within that zone (Weltzin et al. 2000). *Sphagnum fuscum* and *S. capillifolium* were difficult to differentiate after 1994 because of organic staining from water applications, so were lumped into *Sphagnum* Sect. *Acutifolia* for all analyses. Plotwise production of bryophytes was determined by weighting zonal production of bryophytes by the relative areal proportion of each microtopographic zone within each plot (Weltzin et al. 2000).

For each plot in each year between 1995 and 1998, we calculated an index of surface roughness equal to the standard error of the vertical distance between the lowest point on the bryophyte surface and the balance of the points on the bryophyte surface. To further investigate the mechanism underlying changes in moss topography, we determined the relationship between the initial height of a given point in 1995 relative to its change in height between 1995 and 1998.

Statistical analysis

We analyzed bryophyte production and cover for main and interactive effects of microtopographic zone, water-table setting, infrared loading, and year with repeated-measures analyses of variance in a multivariate framework (MANOVA; Pillai's Trace in SAS procedure GLM; SAS Institute 1989; Von Ende 1993). We used Pearson product-moment correlation to determine correlations between total bryophyte production in each microtopographic zone versus the nominal height of that zone above the set water table. Water-table heights are nominal as they were reset weekly by additions of water, as necessary, but were allowed to vary otherwise.

We analyzed mesocosm peat bulk density in 2000 for main and interactive effects of water-table setting and infrared loading using an ANOVA model. We used a two-sample *t*-test to compare bulk density of peat in the mesocosms to bulk density of peat at the bog source site. Plot-wise surface roughness was analyzed for main and interactive effects of water-table setting, infrared loading and year using a MANOVA model. We used least-squares regression to determine plot-wise relationships between height of each point in 1995 and its net change in height between 1995 and 1998. Slopes differed from zero ($P < 0.07$) for all but one plot ($P = 0.73$) that we excluded from subsequent analysis. We used an ANOVA model to evaluate main and interactive effects of water-table setting and infrared loading on rates of change in height (i.e., the magnitude of the slope for each plot) between 1995 and 1998.

All data were tested for normality with the Shapiro-Wilk *W*-statistic (Shapiro and Wilk 1965). Data not normally distributed ($P < 0.05$) were log-transformed prior to analysis. We used Fisher's protected LSD (Fisher 1960) a posteriori mean separation tests to compare levels within factors for significant ($P < 0.05$) main effects

and first-order interactions not including year. We used paired *t*-tests (Zar 1996) to compare years for surface roughness. Water table, infrared loading, and year were treated as fixed effects in all ANOVA models. Means of subsamples within plots were used as appropriate.

Mechanical controls on the infrared heaters began to fail during the winter of 1995–1996, which caused the medium infrared loading treatments to become high infrared loading treatments before this problem was corrected in 1996 (Bridgham et al. 1999). Because the switches probably failed at different, unknown times, we included all three infrared loading treatments as part of our statistical analyses of 1996 data. This effectively reduced the sensitivity of our analyses to main and interactive effects of infrared loading.

Results

Bryophyte production within zones

Total production of all bryophytes, and production of the dominant bryophyte taxa, differed among microtopographic zones (Table 1). In particular, total production of all bryophytes, and production of *Polytrichum strictum*, *Sphagnum magellanicum*, and *Sphagnum* Sect. *Acutifolia* were each about 100% and 50% greater in low microtopographic zones than in high and medium microtopographic zones, respectively (Table 2).

Total production of bryophytes was dependent on interactive effects of infrared loading and water table (Table 1). At ambient infrared loading, production did not differ among water-table treatments (Table 3). Under medium infrared loading, production increased along the gradient of increasing water-table heights, but under high infrared loading, production did not differ between dry and wet plots, and was least at intermediate water-table heights. This pattern was similar for *Sphagnum* Sect. *Acutifolia* (data not shown), which contributed 84% of total bryophyte production.

The topographic heterogeneity of the surface of the bryophyte community contributed to considerable variation in mean surface height above the set (i.e., nominal) water table (see Fig. 1). Consequently, in 2 of 3 years,

Table 1 MANOVA *P*-values for annual production (g/m^2) of three bryophyte taxa, and total production of these taxa (plus *S. recurvum*), for effects of water-table setting (dry, intermediate, wet), infrared loading (ambient, medium, high), microtopographic zone (low, medium, high), and year (1994–1997)

Source	<i>Polytrichum strictum</i>	<i>Sphagnum</i> Sect. <i>Acutifolia</i>	<i>Sphagnum magellanicum</i>	Total
Water	0.47	0.01	0.32	0.02
Infrared	0.06	0.03	0.71	0.12
Water × Infrared	0.27	0.02	0.30	0.03
Zone	0.0002	<0.0001	0.003	<0.0001
Water × Zone	0.91	0.67	0.77	0.59
Infrared × Zone	0.71	0.17	0.85	0.15
Water × Infrared × Zone	0.87	0.14	0.91	0.09
Year	<0.0001	<0.0001	<0.0001	<0.0001
Year × Water	0.08	0.47	0.26	0.36
Year × Infrared	0.01	0.0002	<0.0001	0.0007
Year × Water × Infrared	0.95	0.65	0.01	0.50
Year × Zone	0.90	0.98	0.14	0.98
Year × Water × Zone	0.96	0.98	0.79	0.98
Year × Infrared × Zone	0.97	0.99	0.95	0.99
Year × Water × Infrared × Zone	0.99	0.99	0.90	0.99

Table 2 Annual production ($\text{g/m}^2 \pm 1$ SE) of three bryophyte taxa, and total production of these taxa (plus *S. recurvum*), in three microtopographic zones between 1994 and 1997. Means in rows with different lower-case letters differed ($P < 0.05$; Fisher's protected LSD)

Taxon	Microtopographic zone		
	Low	Medium	High
<i>Polytrichum strictum</i>	48 \pm 5 ^a	35 \pm 4 ^b	25 \pm 3 ^c
<i>Sphagnum</i> Sect. <i>Acutifolia</i>	299 \pm 15 ^a	229 \pm 15 ^b	157 \pm 11 ^c
<i>Sphagnum magellanicum</i>	12 \pm 2 ^a	7 \pm 1 ^b	5 \pm 1 ^c
Total bryophyte	359 \pm 18 ^a	271 \pm 17 ^b	187 \pm 12 ^c

Table 3 Total annual bryophyte production (g/m^2) between 1994 and 1997 in three water-table treatments and three infrared loading treatments. Means in rows with different lower-case letters, and in columns with different upper-case letters, differed ($P < 0.07$; Fisher's protected LSD)

Water-table setting	Infrared loading treatment		
	Ambient	Medium	High
Dry	253 \pm 24 ^{Aa}	223 \pm 27 ^{Ab}	263 \pm 22 ^{Aa}
Intermediate	297 \pm 41 ^{Aa}	269 \pm 24 ^{Ba}	220 \pm 27 ^{Bb}
Wet	309 \pm 29 ^{Aa}	350 \pm 34 ^{Cb}	268 \pm 31 ^{Ac}

Table 4 Pearson correlation coefficients (top value) and associated P -values (bottom value) for $\ln(\text{total bryophyte production})$ in each microtopographic zone versus the nominal height of that zone above the set water table, for each of three water-table settings between 1995 and 1997, and for all years combined. Significant coefficients after sequential Bonferroni correction (Rice 1989) are in boldface

Year	Water-table setting		
	Dry	Intermediate	Wet
All years	-0.23	-0.10	-0.52
	0.04	0.35	<0.0001
1995	-0.005	-0.02	-0.70
	0.98	0.91	<0.0001
1996	-0.12	-0.29	-0.46
	0.56	0.14	0.02
1997	-0.33	0.03	-0.59
	0.10	0.89	0.001

and when years were combined, total production of bryophytes was correlated with height above the set water table only for the wettest water-table treatment (Table 4, Fig. 2).

Total production of bryophytes did not differ among infrared loading treatments in 1994, 1996, or 1997 ($P > 0.83$) but was greater in ambient (451 g/m^2) and medium (407 g/m^2) infrared treatments than in high (231 g/m^2) infrared treatments in 1995 (year \times infrared loading interaction, $P < 0.0001$; Table 1). Similarly, in 1995 *Sphagnum* Sect. *Acutifolia* produced about twice as much biomass in ambient (395 g/m^2) and medium (329 g/m^2) treatments than in high (174 g/m^2) infrared

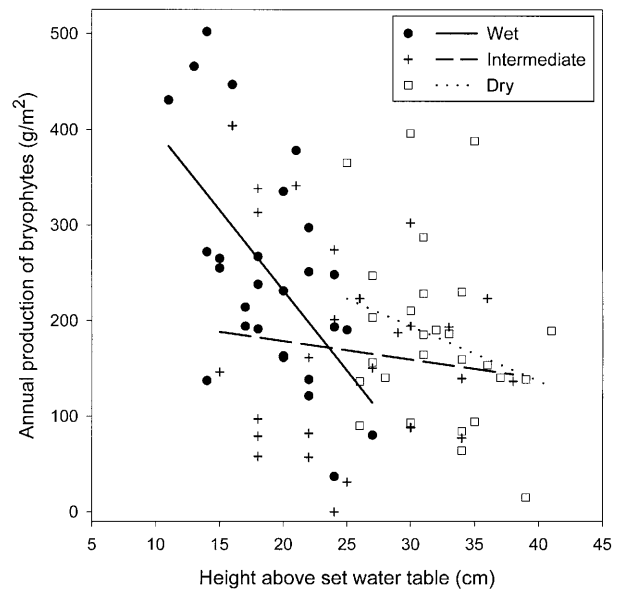


Fig. 2 Regressions of total bryophyte production (g/m^2) in 1997 for each microtopographic zone versus the height of that zone above the set water table ($n=27$); intercepts and coefficients for the wet, intermediate, and dry zones are 581 and -17.5 ($P=0.0009$), 214 and -1.8 ($P=0.59$), and 360 and -5.5 ($P=0.20$), respectively. All intercepts differed from zero ($P < 0.02$).

treatments ($P < 0.0001$), and *S. magellanicum* produced about three times as much biomass in ambient and medium (both 14 g/m^2) than in high (5 g/m^2) infrared treatments ($P=0.008$). In contrast, production of *P. strictum* was about 2 times greater in high than ambient infrared treatments in 1996 (96 g/m^2 vs 52 g/m^2 , respectively; $P=0.0006$) and 1997 (10 g/m^2 vs 5 g/m^2 , respectively; $P=0.04$).

Bryophyte production within plots

When production in each zone was scaled to the entire plot, production of bryophytes was greatest in the wet treatment (313 g/m^2), and did not differ between intermediate (257 g/m^2) or dry (247 g/m^2) treatments (Weltzin et al. 2000). In contrast, production of bryophytes was unaffected by infrared loading treatment. Production was also strongly year-dependent, ranging from 197 g/m^2 in 1994 to 363 g/m^2 in 1995 and 330 g/m^2 in 1996, and back down to 199 g/m^2 in 1997. Production tended to be highly correlated with growing season (May through October) precipitation between 1995 and 1997 ($r=0.98$, $P=0.12$, $n=4$), although this relationship was attenuated if 1994 was included ($r=0.40$, $P=0.60$, $n=3$) (cf. Backèus 1988; Moore 1989; Thormann and Bayley 1997a, 1997b).

Bulk density of peat in the top 15 cm of mesocosm plots did not differ among treatments in 2000, 6 years after treatment initiation ($P > 0.71$; mean \pm 1 SE=0.022 \pm 0.001 g dry mass/cm^3). Further, this value did not differ from bulk density of peat in the top 15 cm at the bog

Table 5 Bryophyte surface roughness between 1995 and 1998. Surface roughness is the standard error of vertical distance between the reference datum hollow and ~110 points on the bryophyte surface within each plot. Means with the same lower-case letter were not different ($P>0.05$; Fisher's protected LSD)

Year	Mean surface roughness
1995	0.38±0.02 ^a
1996	0.35±0.02 ^{bc}
1997	0.34±0.01 ^b
1998	0.36±0.01 ^{ac}

source site ($P>0.41$; 0.024 ± 0.001 g dry mass/cm³). These results indicate that bryophyte shoot production on a unit area basis can be determined based on linear extension of shoots.

Cover

Cover of *P. strictum*, *S. magellanicum*, and *Sphagnum* Sect. *Acutifolia* was not affected by microtopographic zone or its interactions with either treatment or year ($P>0.29$; data not shown). However, cover of *Sphagnum* Sect. *Acutifolia* was 7% and 13% lower in the high compared to the ambient infrared loading treatments in 1995 and 1996, respectively (year × infrared loading; $P<0.0001$). In contrast, cover of *P. strictum* was greater in high than in ambient infrared treatments in 1995 (13% vs 5%) and 1996 (17% and 10%) (year × infrared loading; $P<0.0001$). Cover of *S. magellanicum* was greater in high compared to the ambient infrared loading treatments in 1996 (year × infrared loading; $P=0.04$). Other species-specific changes in cover were not interpretable in relation to the treatments applied.

Changes in topography and roughness of the bryophyte surface

The majority (88%) of the points on the bryophyte surface increased in height relative to the grid frame between 1995 and 1998. This indicated an increase in peat volume in all plots over this 3-year period. However, slopes of plot-wise relationships between the height of each point in 1995 and its net change in height between 1995 and 1998 were all negative ($P<0.07$), which indicated that low points rose at a faster rate than high points, which was consistent with the results for production. Further, slopes were steepest in the high infrared loading treatment (−0.64), intermediate in the medium infrared treatment (−0.48), and least in the ambient infrared treatment (−0.35; $P<0.05$). This indicated that the bryophyte surface tended to flatten through time (Fig. 1), and that the rate of change in height relative to the initial height was proportional to the infrared loading.

In contrast, the roughness of the bryophyte surface, when averaged over the entire plot, was unaffected by main or interactive effects of water table or infrared

loading, or the interaction of these factors with year ($P>0.08$; data not shown). Although roughness differed among years ($P=0.008$), it did not change directionally between 1995 and 1998 (Table 5).

Discussion

Bryophyte production

Total production of bryophytes, and production of individual bryophyte species, decreased as height of the bryophyte surface increased above the set water table. Although our low, medium, and high microtopographic zones correspond only roughly to the classic designations of hollow, lawn, and hummock, respectively, our results are supported by similar findings that production of bryophytes in ombrotrophic systems is greater in topographic lows compared to topographic highs (Clymo and Reddaway 1971; Pederson 1975; Pakarinen 1978; Grigal 1985; Rochefort et al. 1990; Vitt 1990). In fact, zone had the dominant effect on production, surpassing effects of our infrared loading and water-table treatments.

Differences in production among hummocks, hollows, and lawns are often confounded by differences in species composition of these habitats (see reviews by Andrus 1986; Vitt 1990). However, our topographic zones did not differ in species cover, which suggests that differences in production were related more to differences in microenvironmental conditions associated with each topographic position than to inherent, species-specific rates of production.

In particular, depth to water table appears to form the major constraint on bryophyte production in this study. The importance of water-table position to bryophyte production is well documented (e.g., Clymo 1973, 1984;; Clymo and Hayward 1982; Vasander 1982; Andrus et al. 1983; Rydin 1985, 1993; Rydin and McDonald 1985; Wallén et al. 1988; Rochefort et al. 1990). Moreover, there appears to be an important threshold effect. Within each of our three water-table treatments, there existed considerable variation in the distance between the bryophyte surface and the water table. When water tables were relatively close to the surface (i.e., in the wet treatment), production was inversely correlated with depth to water table. However, when water tables were relatively deep, as in the intermediate and dry treatments, production of bryophytes was uncorrelated with depth to water table. This suggests that the height of the water table has a relatively narrow range of influence on production of bryophytes, i.e., within 20–25 cm below the bryophyte surface.

Temporary reductions in the production (in 1995) and cover (in 1995 and 1996) of *Sphagnum* Sect. *Acutifolia* in the high infrared loading treatment suggest that this taxon was negatively impacted by the relatively low position of the infrared lamps. Concomitant but temporary increases in the cover and production of *Polytrichum*

strictum in the same plots suggest that *P. strictum* was favored either directly by the increased infrared loading and/or indirectly by reductions in competition by *Sphagnum* Sect. *Acutifolia*. Differential effects of competition on species-specific growth rates have been observed to structure composition of *Sphagnum* communities in the field (Clymo and Hayward 1982).

Bryophyte surface topography and roughness

A priori, differential production of bryophytes in topographic lows and highs should contribute to a decrease in microtopographic heterogeneity over time (e.g., Clymo and Hayward 1982; Hayward and Clymo 1983). In other words, relatively high rates of production should fill topographic depressions, which would cause the bryophyte surface to become more level through time. This is in fact what we observed, but the response of a given point on the surface depended on the infrared loading treatment. In particular, as infrared loading increased, the plots tended to become flatter due to differential rates of bryophyte growth at both low and high points. The lack of a concomitant decrease in overall surface roughness suggests that small-scale (i.e., within zone) topographic heterogeneity did not change over the course of this study.

Although the bryophyte surface flattened in response to infrared loading, we did not observe a cyclic succession of low and high microtopographic zones in any plots. This observation was supported by several lines of evidence, which are nonetheless tempered by the duration of this experiment. First, mean (± 1 SD) linear growth of bryophytes (between 1995 and 1997 in all microtopographic zones) was 3.1 ± 2.0 cm, less than one-third of the range in height within each plot (11.2 ± 5.2 cm) over the same time period. Second, the majority (i.e., 88%) of points on each bryophyte surface increased in height during the course of the study. Third, a number of other studies have indicated that cyclic succession of hummocks and hollows is unlikely to occur, even on time scales as long as 60 years (Backéus 1972; Barber 1981; Svensson 1988).

Differences in the decay rates of different *Sphagnum* species may initiate and maintain hummock and hollow microtopography (Johnson and Damman 1991; Belyea 1996; Belyea and Clymo 1998). In particular, it is thought that patches dominated by *Sphagnum* species that decay slowly accumulate peat through time (i.e., form a hummock), whereas patches characterized by species that decay at faster rates would eventually form hollows. In contrast, other studies have found that species characteristic of hummocks and hollows decay at comparable rates (e.g., Clymo 1965; Rosswall et al. 1975). In addition, decay rates may be further constrained by microenvironmental conditions such as anoxia caused by high water tables (Coulson and Butterfield 1978; Belyea 1996). In our study, observations that (1) production was greater in wetter microtopographic

zones, (2) relatively high growth rates caused infilling of topographic depressions, and (3) species composition did not differ among zones suggest that peat accumulation is constrained by environmental conditions characteristic of the different microtopographic zones, in addition to possible species-specific differences in production and decomposition.

Bryophyte communities in changing climates

Biotic processes in northern ecosystems are usually directly or indirectly constrained by low temperatures and short growing seasons (e.g., Van Cleve et al. 1991). Accordingly, increases in surface temperatures are predicted to affect these ecosystems by alleviating temperature constraints (Gorham 1991; Apps et al. 1993; Bridgman et al. 1995). In this experiment, increases in soil temperature commensurate with model predictions of global warming did not affect bryophyte production, although infrared loading modified the topography of the bryophyte surface. In contrast, bryophyte production was driven strongly by the absolute and relative height of the bryophyte surface above the water table. These results suggest that changes in water-table height, independent of or commensurate with changes in surface temperature (Roulet et al. 1992; Rouse 1998), may affect the productivity and structure of bryophyte communities. Alternatively, changes in the abundance or production of associated lifeforms more sensitive to changes in climatic or environmental conditions (e.g., shrubs; Weltzin et al. 2000) may serve as the ultimate constraint on bog bryophyte communities.

Acknowledgements We thank the St. Louis County Land Department for use of their land; C. Chapin, B. Dewey, J. Janssens, K. Johnson, J. Keller, T. Malterer, C. Maly, K. Updegraff, P. Weishampel, and numerous undergraduate students for help in the field; the Bridgman laboratory group and R.S. Clymo and H. Rydin for comments on the manuscript; and the National Science Foundation for financial support (DEB9496305, DEB9707426, DEB9629415).

References

- Andrus RE (1986) Some aspects of *Sphagnum* ecology. *Can J Bot* 64:416–426
- Andrus RE, Wagner DJ, JE Titus (1983) Vertical zonation of *Sphagnum* mosses along hummock-hollow gradients. *Can J Bot* 61:3128–3139
- Apps MJ, Kurz WA, Luxmoore RJ, Nilsson RO, Sedjo RA, Schmidt R, Simpson LG, Vinson TS (1993) Boreal forests and tundra. *Water Air Soil Pollut* 70:39–53
- Backéus I (1972) Bog vegetation remapped after 60 years. *Oikos* 23:384–393
- Backéus I (1988) Weather variables as predictors of *Sphagnum* growth on a bog. *Holarct Ecol* 11:146–150
- Barber KE (1981) Peat stratigraphy and climatic change: a paleoecological test of the theory of cyclic bog regeneration. Balkema, Rotterdam
- Belyea LR (1996) Separating the effects of litter quality and microenvironment on decomposition rates in a patterned peatland. *Oikos* 77:529–539

- Belyea LR, Clymo RS (1998) Do hollows control the rate of peat bog growth? In: Standen V, Tallis JH, Meade R (eds) Patterned mires and mire pools: origin and development; flora and fauna. British Ecological Society, London, pp 55–65
- Bridgham SD, Johnston CA, Pastor J, Updegraff K (1995) Potential feedbacks of northern wetlands on climate change. *BioScience* 45:262–274
- Bridgham SD, Updegraff K, Pastor J (1998) Carbon, nitrogen, and phosphorus mineralization in northern wetlands. *Ecology* 79: 1545–1561
- Bridgham SD, Pastor J, Updegraff K, Malterer TJ, Johnson K, Harth C, Chen J (1999) Ecosystem control over temperature and energy flux in northern peatlands. *Ecol Appl* 9:1345–1358
- Bridgham SD, Ping C-L, Updegraff K, Richardson JL, Pastor J (in press) Soils of peatlands: histosols and gelsols. In: Richardson JL, Vepraskas MJ (eds) Wetland soils: their genesis, hydrology, landscape and separation into hydric and nonhydric soils. Ann Arbor Press, Ann Arbor, Mich.
- Bubier J (1995) The relationship of vegetation to methane emission and hydrochemical gradients in northern peatlands. *J Ecol* 83:403–420
- Chapin CT (1998) Plant community response and nutrient dynamics as a result of manipulations of pH and nutrients in a bog and fen in northeastern Minnesota. Ph.D. Dissertation. University of Notre Dame, Notre Dame, Indiana
- Chapin FS III, Van Cleve K, Chapin MC (1979) Soil temperature and nutrient cycling in the tussock growth form of *Eriophorum vaginatum*. *J Ecol* 67:169–189
- Clymo RS (1965) Experiments on breakdown of *Sphagnum* in two bogs. *J Ecol* 53:747–758
- Clymo RS (1970) The growth of *Sphagnum*: methods of measurement. *J Ecol* 58:13–49
- Clymo RS (1973) The growth of *Sphagnum*: some effects of environment. *J Ecol* 61:849–869
- Clymo RS (1984) The limits to peat bog growth. *Philos Trans R Soc Lond B* 303:605–654
- Clymo RS, Hayward PM (1982) The ecology of *Sphagnum*. In: Smith AJE (ed) Bryophyte ecology. Chapman and Hall, London, pp 229–289
- Clymo RS, Reddaway EJF (1971) Productivity of *Sphagnum* (bog-moss) and peat accumulation. *Hidrobiologia* 12:181–192
- Coulson JC, Butterfield J (1978) An investigation of the biotic factors determining the rates of plant decomposition on blanket bog. *J Ecol* 66:631–650
- Crum H (1988) A focus on peatlands and peat mosses. University of Michigan Press, Ann Arbor, Mich.
- Damman AWH (1978) Distribution and movement of elements in ombrotrophic peat bogs. *Oikos* 30:480–495
- Fisher RA (1960) The design of experiments, 7th edn. Hafner, New York
- Glaser (1992) Ecological development of patterned peatlands. In: Wright Jr HE, Coffin BA, Aaseng NE (eds) The patterned peatlands of Minnesota. University of Minnesota Press, Minneapolis, pp 27–42
- Gorham E (1991) Northern peatlands: role in the carbon cycle and probable responses to climatic warming. *Ecol Appl* 1:182–195
- Grigal DF (1985) *Sphagnum* production in forested bogs of northern Minnesota. *Can J Bot* 63:1204–1207
- Harte J, Torn MS, Chang FR, Feifarek B, Kinzig AP, Shaw R, Shen K (1995) Global warming and soil microclimate: results from a meadow-warming experiment. *Ecol Appl* 5:132–150
- Hayward PM, Clymo RS (1983) The growth of *Sphagnum*: experiments on, and simulation of, some effects of light flux and water-table depth. *J Ecol* 71:845–863
- Ivanov KE (1981) Water movement in mirelands. Academic Press, London
- Johnson LC, Damman AWH (1991) Species-controlled *Sphagnum* decay on a south Swedish raised bog. *Oikos* 61:234–242
- Johnson LC, Damman AWH (1993) Decay and its regulation in *Sphagnum* peatlands. *Adv Bryol* 5:249–296
- Kattenberg A, Giorgi F, Grassl H, Meehl GA, Mitchell JFB, Stouffer R J, Tokioka T, Weaver AJ, Wigley TML (1996) Climate models – projections of future climate. In: Houghton JT, Meira Filho LG, Callander BA, Harris N, Kattenberg A, Maskell K (eds) Climate change 1995: the science of climate change. Cambridge University Press, Cambridge, pp 285–357
- Kim J, Verma SB (1992) Soil surface CO₂ flux in a Minnesota peatland. *Biogeochemistry* 18:37–51
- Körner C, Larcher W (1988) Plant life in cold climates. *Symp Soc Exp Biol* 42:25–57
- Lindholm T, Markkula I (1984) Moisture conditions in hummocks and hollows in virgin and drained sites on the raised bog Laaviosuo, southern Finland. *Ann Bot Fenn* 21:241–255
- Malmer N (1962) Studies on mire vegetation in the Archaean area of southwestern Gotland (south Sweden). I. Vegetation and habitat conditions on the Åkhult mire. *Opera Bot* 7:1–322
- Malmer N (1986) Vegetational gradients in relation to environmental conditions in northwestern European mires. *Can J Bot* 64: 375–383
- Matthews E, Fung I (1987) Methane emission from natural wetlands: global distribution, area, and environmental characteristics of sources. *Global Biogeochem Cycles* 1:61–86
- McFadden JP, Chapin III FS, Hollinger DY (1998) Subgrid-scale variability in the surface energy balance of arctic tundra. *J Geophys Res* 103:28,947–28,961
- Moore TR (1989) Growth and net production of *Sphagnum* at five fen sites, subarctic eastern Canada. *Can J Bot* 67:1203–1207
- Northern Peatlands Soil Warming Project (2001) University of Notre Dame, Notre Dame, Indiana <http://www.nd.edu/~soil-warm>
- Oldfield F, Thompson R, Crooks PRJ, Gedye SJ, Hall VA, Harkness DD, Housley RA, McCormac FG, Newton AJ, Pilcher JR, Renberg I, Richardson N (1997) Radiocarbon dating of a recent high-latitude peat profile: Stor Amyran, northern Sweden. *Holocene* 7:283–290
- Öquist MG, Svensson BH (1996) Non-tidal wetlands. In: Watson RT, Zinyowera MC, Moss RH (eds) Climate change 1995: impacts, adaptations and mitigation of climate change: scientific-technical analyses. Cambridge University Press, Cambridge, pp 215–239
- Pakarinen P (1978) Distribution of heavy metals in the *Sphagnum* layer of bog hummocks and hollows. *Ann Bot Fenn* 15: 287–292
- Parkyn L, Stoneman RE, Ingram HAP (eds) (1997) Conserving peatlands. CAB International, Wallingford, Oxon
- Pederson A (1975) Growth measurements of five *Sphagnum* species in south Norway. *Norw J Bot* 22:277–284
- Rice WR (1989) Analyzing tables of statistical tests. *Evolution* 43:223–225
- Rocheffort L, Vitt DH, Bayley, SE (1990) Growth, production, and decomposition dynamics of *Sphagnum* under natural and experimentally acidified conditions. *Ecology* 71:1986–2000
- Rosswall T, Veum A, Kärenlampi L (1975) Plant litter decomposition at Fennoscandian tundra sites. In: Wiegolaski FE (ed) Fennoscandian tundra ecosystems. I. Plants and microorganisms. Springer, Berlin Heidelberg New York, pp 268–277
- Roulet NT, Moore T, Bubier J, Lafluer P (1992) Northern fens: methane flux and climatic change. *Tellus* 44B:100–105
- Rouse WR (1998) A water balance model for a subarctic sedge fen and its application to climatic change. *Clim Change* 38:207–234
- Rydin H (1985) Effect of water level on desiccation of *Sphagnum* in relation to surrounding *Sphagna*. *Oikos* 45:374–379
- Rydin H (1993) Mechanisms of interactions among *Sphagnum* species along water-level gradients. *Adv Bryol* 5:153–185
- Rydin H, McDonald AJS (1985) Photosynthesis in *Sphagnum* at different water contents. *J Bryol* 13:579–584
- Sampson RN, Apps M, Brown S, Cole CV, Downing J, Heath LS, Ojima DJ, Smith TM, Solomon MA, Wisniewski J (1993) Workshop summary statement: terrestrial biospheric carbon fluxes – quantification of sinks and sources of CO₂. *Water Air Soil Pollut* 70:3–15

- SAS Institute (1989) SAS/STAT user's guide, Version 6, 4th edn. SAS Institute, Cary, N. C.
- Shapiro SS, MB Wilk (1965) An analysis of variance test for normality (complete samples) *Biometrika* 52:591–611
- Sjörs H (1948) Myrvegetation in Bergslagen. *Acta Phytogeogr Suec* 21:1–299
- Svensson G (1988) Fossil plant communities and regeneration patterns on a raised bog in south Sweden. *J Ecol* 76:41–59
- Swanson DK, DF Grigal (1988) A simulation model of mire patterning. *Oikos* 53:309–314
- Tansley AG (1939) *The British islands and their vegetation*. Cambridge University Press, London
- Thormann MN, Bayley SE (1997a) Aboveground net primary production along a bog-fen-marsh gradient in southern boreal Alberta, Canada. *Écoscience* 4:374–384
- Thormann MN, Bayley SE (1997b) Aboveground plant production and nutrient content of the vegetation in six peatlands in Alberta, Canada. *Plant Ecol* 131:1–16
- Updegraff K, Bridgman SD, Pastor J, Weishampel P, Harth C (in press) Ecosystem respiration response to warming and water-table manipulation in peatland mesocosms. *Ecol Appl*
- Van Cleve K, Chapin III FS, Dyrness CT, Viereck LA (1991) Element cycling in taiga forests: State-factor control. *BioScience* 41:78–88
- Vasander H (1982) Plant biomass and production in virgin, drained and fertilized sites in a raised bog in southern Finland. *Ann Bot Fenn* 19:103–125
- Vitt DH (1990) Growth and production dynamics of boreal mosses over climatic, chemical and topographic gradients. *Bot J Linn Soc* 104:35–59
- Von Ende CN (1993) Repeated measures analysis: growth and other time-dependent measures. In: Scheiner SM, Gurevitch J (eds) *Design and analysis of ecological experiments*. Chapman and Hall, New York, pp 113–137
- Waddington JM, Roulet NT (1996) Atmosphere-wetland carbon exchanges: scale dependency of CO₂ and CH₄ exchange on the developmental topography of a peatland. *Global Biogeochem Cycles* 10:233–245
- Waddington JM, Griffis TJ, Rouse WR (1998) Northern Canadian wetlands: net ecosystem CO₂ exchange and climatic change. *Clim Change* 40:267–275
- Wallén B, Falkengren-Grerup U, Malmer N (1988) Biomass, productivity, and relative rate of photosynthesis of *Sphagnum* and different water levels on a south Swedish peat bog. *Holarct Ecol* 11:70–76
- Weltzin JF, Pastor J, Harth C, Bridgman SD, Updegraff K, Chapin CT (2000) Response of bog and fen plant communities to warming and water-table manipulations. *Ecology* 81:3464–3478.
- Zar JH (1996) *Biostatistical analysis*. Prentice Hall, Upper Saddle River, New Jersey
- Zobel M (1986) Aeration and temperature conditions in hummock and depression peat in Kikepera bog, southwestern Estonia. *Suo* 37:90–99