

# Potential effects of warming and drying on peatland plant community composition

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## Abstract

Boreal peatlands may be particularly vulnerable to climate change, because temperature regimes that currently constrain biological activity in these regions are predicted to increase substantially within the next century. Changes in peatland plant community composition in response to climate change may alter nutrient availability, energy budgets, trace gas fluxes, and carbon storage. We investigated plant community response to warming and drying in a field mesocosm experiment in northern Minnesota, USA. Large intact soil monoliths removed from a bog and a fen received three infrared warming treatments crossed with three water-table treatments ( $n = 3$ ) for five years. Foliar cover of each species was estimated annually.

In the bog, increases in soil temperature and decreases in water-table elevation increased cover of shrubs by 50% and decreased cover of graminoids by 50%. The response of shrubs to warming was distinctly species-specific, and ranged from increases (for *Andromeda glaucophylla*) to decreases (for *Kalmia polifolia*). In the fens, changes in plant cover were driven primarily by changes in water-table elevation, and responses were species- and lifeform-specific: increases in water-table elevation increased cover of graminoids – in particular *Carex lasiocarpa* and *Carex livida* – as well as mosses. In contrast, decreases in water-table elevation increased cover of shrubs, in particular *A. glaucophylla* and *Chamaedaphne calyculata*. The differential and sometimes opposite response of species and lifeforms to the treatments suggest that the structure and function of both bog and fen plant communities will change – in different directions or at different magnitudes – in response to warming and/or changes in water-table elevation that may accompany regional or global climate change.

*Keywords:* climate change, global warming, peatlands, plant cover, soil warming, species composition, water-table, wetlands

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## Introduction

About 4% of the global land surface is occupied by wetlands, which contribute substantially to global pools and fluxes of carbon (Matthews & Fung, 1987; Aselmann & Crutzen, 1989). Boreal peatlands, which comprise about half of the total global wetland area (Bridgham *et al.*,

2001), store about one-third of the world's organic carbon in the form of living or partially decayed vegetation, or peat (Sampson *et al.*, 1993), and contribute 10% of global atmospheric methane flux (Bartlett & Harriss, 1993).

The structure and function of boreal peatlands may be significantly impacted by climate change (Gorham, 1991; Bridgham *et al.*, 1995) or changes in land use, because temperature regimes that currently constrain biological activity in these regions are predicted to increase substantially within the next century (Kattenberg *et al.*, 1996). Peatlands may also serve as positive or negative feedback mechanisms to anthropogenic climate change through

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changes in surface roughness, albedo, trace gas fluxes, or disturbance regimes (Bridgman *et al.*, 1995; Chapin *et al.*, 1997; Updegraff *et al.*, 2001; Weltzin *et al.*, 2001). Further, peatlands may cause feedbacks to local or regional climates through ecosystem control over energy fluxes, although the direction and magnitude of these potential feedbacks remains largely unexplored (Melillo *et al.*, 1996; Sellers *et al.*, 1997; but see Bridgman *et al.*, 1999).

Although all peatlands are defined by long-term accumulation of soil carbon, they are actually a heterogeneous group of ecosystems. In regions without permafrost, the most fundamental distinction is between bogs and fens, which have different plant community composition, hydrology, nutrient availability, and soil chemistry (Moore & Bellamy, 1974; Gore, 1983; Bridgman *et al.*, 1996, 1998, 2001). Bogs are ombrotrophic – i.e., they receive all their water and mineral inputs from precipitation, and consequently they have acidic soils, low basic cation content, less humified peat, and are often dominated by *Sphagnum* mosses, evergreen ericaceous shrubs, and black spruce (*Picea mariana* (Mill.) BSP). In contrast, fens are minerotrophic – i.e. they receive inputs of water and minerals from ground water and/or overland run-off, which causes more alkaline, higher pH soils and more humified peat; they tend to be dominated by graminoids (e.g. *Carex lasiocarpa* Ehrh., *C. livida* (Wahl.) Willd.), nonericaceous shrubs, and trees such as northern white cedar (*Thuja occidentalis* L.) and tamarack (*Larix laricina* (Du Roi) K. Koch). ‘Strings’, or raised linear features within fens, may include taxa typically representative of bogs.

Because of these differences in biotic and abiotic conditions, bogs and fens are likely to differ in their response to climate change. Results from an ongoing climate change experiment in northern Minnesota, USA, indicate that bogs and fens differ in their response to increased infrared loading (i.e. warming) and changes in water-table elevation in terms of above- and below-ground net primary production (Weltzin *et al.*, 2000, 2001), thermal energy flux and evapotranspiration (ET) (Bridgman *et al.*, 1999), atmospheric carbon flux and gross primary production (Updegraff *et al.*, 2001), and ecosystem carbon and nutrient budgets (unpublished data).

Differential responses of bogs and fens to experimental manipulations of heat and water-tables are likely mediated by differences in the composition, structure, and productivity of the resident plant communities. Moreover, if these structural and functional characteristics of the plant community change over time in response to shifts in climatic conditions, these changes may themselves mediate the response of the entire ecosystem to climatic forcing (cf. Harte *et al.*, 1995; Chapin *et al.*, 1997).

The objective of this paper is to describe the response of the bog and fen plant communities to ongoing manipulations in the aforementioned large-scale field experiment

in Minnesota, USA. We focus on the response of species dominance (i.e. cover), to a gradient of infrared warming and water-table elevations arranged in a fully crossed experimental design. We describe the response of all species and the dominant lifeforms (moss, shrub, graminoid, herbaceous dicot) to five years (i.e. 1994–1998) of experimental manipulation.

## Methods

### Sites

Source sites for the mesocosms consisted of a bog and a fen in the townships of Toivola and Alborn, respectively, in northeastern Minnesota (47°N, 92°W). The bog and fen source sites are typical of other northern bogs and fens, and have been described in detail (Bridgman *et al.*, 1998; Chapin, 1998; Bridgman *et al.*, 2001).

The peat at the bog site is approximately 3.5 m deep with a basal radiocarbon date of  $10\,040 \pm 70$  yr BP. 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). Source site vegetation is dominated by short (< 15-cm height) ericaceous shrubs (*Chamaedaphne calyculata* (L.) Moench., *Andromeda glaucophylla* Link., *Kalmia polifolia* Wang., *Vaccinium oxycoccos* L., *Ledum groenlandicum* Oeder.), mosses (*Sphagnum fuscum* (Schimp.) Klinggr., *S. capillifolium* (Ehrh.) Hedw., *S. magellanicum* Brid., *Polytrichum strictum* Brid.), and black spruce (*P. mariana* (Mill.) BSP). Source site pore-water pH was 3.8, and porewater  $[Ca^{+2}]$  and  $[Mg^{+2}]$  were  $2.3\text{ mg L}^{-1}$  and  $1.0\text{ mg L}^{-1}$ , respectively.

Bog monoliths were extracted from the central, treeless portion of the bog. Although bogs exhibit characteristic surficial microtopography (Watt, 1947; Crum, 1988), we a priori selected cores from a portion of the bog with relatively little microtopographic heterogeneity. The mean ( $\pm 1$  SD) range in elevation between high and low points within the bog plots in 1995 was  $11.6 \pm 5.6$  cm, although the moss surface tended to flatten during the course of the experiment at a rate proportional to experimental infrared loading (Weltzin *et al.*, 2001).

The fen has approximately 4.4 m of sedge peat overlying about 2 m of unconsolidated aquatic (limnic) peat, with a basal age of  $9730 \pm 70$  years BP (Bridgman *et al.*, 1998). To maximize the contrast with the bog, we extracted cores from low areas (flarks) that were dominated by graminoids (*Rhynchospora alba* (L.) Vahl, *R. fusca* (L.) Ait. f., *Carex limosa* L., *C. lasiocarpa* Ehrh., *C. livida* (Wahl.) Willd.) with minimal cover of mosses. Source site pore-water pH was 4.7, and porewater  $[Ca^{+2}]$  and  $[Mg^{+2}]$  were  $5.2\text{ mg L}^{-1}$  and  $2.3\text{ mg L}^{-1}$ , respectively.

### Experimental design

We extracted intact peat monoliths from the two source sites and constructed a mesocosm facility to manipulate heat inputs and water-table levels within an experimental framework. Treatment combinations were replicated three times and randomly assigned within each ecosystem type, yielding a full-factorial experimental design (2 ecosystems  $\times$  3 water-table treatments  $\times$  3 warming treatments  $\times$  3 replicates, 54 plots). Details of mesocosm construction, warming and water-table treatments, and abiotic response to these treatments are provided by Bridgham *et al.* (1999).

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, MN. Twenty-seven intact cylindrical peat monoliths (2.1-m<sup>2</sup> surface area, 0.5–0.7-m depth) were removed each from the bog and fen, transported to the FRF, and placed in insulated plastic tanks of similar dimensions that had been sunken into a large field. The peat monoliths were removed in winter while frozen with minimal surface disturbance to vegetation.

We used infrared heat lamps (Kalglo Electronics, Bethlehem, PA) to augment infrared loading starting in July of 1994. Specifically, we mounted lamps approximately 130 cm above the mean surface height of two-thirds of the plots. The lamps were set at either half-power (= 'medium') or full-power (= 'high') outputs, and were left on continuously. The remaining one-third of the plots were unheated (= 'ambient'). Heat treatments increased mean monthly soil temperatures by 1.6–4.1 °C at 15-cm depth during the growing season (May–October). The soil temperature response was strongly seasonal, with much greater effects during spring and autumn. Fen communities were on average 0.8–1.0 °C warmer than bog communities during the growing season due to ecosystem-dependent control over energy fluxes (Bridgham *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. However, we allowed the surface elevation of each plot to change relative to the water-table as the plots have gained or lost soil carbon as a treatment response. In 1996 in the bog plots, the average water-table depths for the three hydrology treatments were at –11, –19, and –26 cm, whereas the fens remained relatively close to their original set values with treatment means of 0, –10, and –19 cm (Bridgham *et al.*, 1999). The water-table

elevation at the natural source sites are on average approximately –21 and +2 cm in the bog and fen, respectively (Chapin, 1998). Consequently, the 'dry' and 'wet' treatments most closely reflect *in situ* conditions in the bog and fen, respectively.

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 and transported to the mesocosm facility for immediate use. The ditch water had a pH, electrical conductivity, and nutrient status similar to that of the pore water in the bog source site. We could find no readily available source of water with chemistry similar to the fen, so we used the bog ditch water for all mesocosms (Bridgham *et al.*, 1999). However, this is typical of many larger peatlands, where bogs occur on topographic highs and drain into fens (Glaser, 1992).

Obviously, use of mesocosms inevitably involves certain trade-offs of experimental control vs. 'ecological reality.' We chose mesocosms to facilitate control of water-table levels and determination of whole-ecosystem energy and nutrient budgets (unpublished data), which would otherwise be infeasible using plots in natural peatlands. Moreover, the size of the tanks provides a representative sample of both the upper portion of the peat column and the plant community. For example, the 60-cm depth of the peat monoliths in the mesocosms contains the entire rooting depth of constituent plant species (Weltzin *et al.*, 2000). In addition, the cross-sectional areas of the mesocosms (2.1 m<sup>2</sup>) are large enough to potentially contain all the plant species present at the bog or fen source sites (based on species-area curves constructed for these communities; Pastor, unpublished data). Although there is the potential for edge effects or invasions by species atypical of the natural sites, we avoided the edges of the plots when sampling (as described below), and have not observed any plant invasions. Finally, community composition and productivity in the mesocosms tend to mirror interannual variations in these variables at the source sites, probably, because of regional and seasonal variations in precipitation or growing season temperature (Chapin, 1998; Weltzin *et al.*, 2000; Chapin *et al.*, in press).

### Estimates of species cover

Canopy cover of each species of graminoid, herbaceous dicot (hereafter forb), and shrub was estimated visually within each plot in August and September of each year (1994–1998) at the estimated time of peak standing biomass. It was difficult to estimate cover of moss species in the fen mesocosms during the summer, because they

were obscured by green standing biomass, so we estimated fen moss covers in September after graminoids senesced. Moss cover data were not collected from the fen community in 1996, because of a relatively early snowfall.

Species-specific moss cover within bog plots was determined in July or August of 1995–1998 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 string 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 levelled 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 moss 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 ingrowth 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 moss species within the quadrat as the mean of visual estimates made by two to three observers. Moss cover in 1994 was estimated visually for the entire plot (Weltzin *et al.*, 2001).

#### Statistical analysis

We analysed total cover of graminoids, forbs, shrubs, and mosses within each plant community for main and interactive effects of water-table setting, heat treatment, and year with repeated-measures multivariate analyses of variance (MANOVA; Pillai's Trace in SAS procedure GLM; SAS Institute 1989). We did not analyse cover of forbs in the bog community, because it averaged < 1% across all years and treatments. We similarly analysed cover data for a total of 16 dominant taxa for bog or fen (defined as having cover > 4% averaged across all treatments and years within each community). For a total of the 14 most dominant taxa in 1998 (with > 4% across treatments and within community in that year), we examined main and interactive effects of water-table and warming with separate analysis of variance (ANOVA) models.

All data were tested for normality with the Shapiro-Wilk *W*-statistic (Shapiro & 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 all significant ( $P < 0.05$ ) main effects

and first-order interactions. Water-table, warming, plant community, and year were treated as fixed effects in all ANOVA models.

Principal components analysis (PCA) of the correlation matrix was used to analyse and display vegetation patterns for the bog and fen plots based on species cover for all years, and for 1998 only. We removed species present in less than 5% of the plots from each dataset before ordination (Gauch, 1982); this left 19 and 48 species for ordination in the bog and fen datasets, respectively. We analysed the correlation matrix, because it accentuates the distribution rather than the abundance of taxa (Noy-Meir *et al.*, 1975), and because it was more readily interpretable than PCA of the variance-covariance matrix. We also examined the datasets using detrended correspondence analysis (DCA), but did not use DCA, because there were no apparent arch effects in the PCA ordinations, and the results were no more interpretable than PCA.

## Results

The response of lifeform and species cover to water-table and heat treatments over time depended on the species composition of the bog and fen communities. Therefore, we discuss the results of each community separately.

#### *Bog community lifeforms*

In 1994, cover of mosses in the bog community was greater than 98%. Over the next 4 years, moss cover declined in all plots, but did not differ between treatments until 1998 (Table 1). In 1998, cover was greater in the wet treatment (mean  $\pm$  SE =  $95 \pm 1\%$ ) than in the intermediate ( $92 \pm 2\%$ ) or dry ( $89 \pm 2\%$ ) treatments, which did not differ. Further, cover was greater in the ambient heat treatment ( $95 \pm 1\%$ ) than in the medium ( $91 \pm 2\%$ ) or dry ( $90 \pm 2\%$ ) treatments, which did not differ.

Total cover of shrubs, averaged across years, was 30 and 50% greater in the medium ( $73 \pm 3\%$ ) and high ( $85 \pm 3\%$ ) heat treatments than in the ambient ( $57 \pm 2\%$ ) heat treatment, respectively (Table 1). Shrub cover was greater in the dry ( $77 \pm 3\%$ ) than wet ( $66 \pm 3\%$ ) treatment; shrub cover at intermediate water-table settings ( $72 \pm 4\%$ ) did not differ from either dry or wet treatments ( $P > 0.21$ ). Independent of treatment, shrub cover increased from about 56% in 1994 and 1995 to about 80% in 1996 through 1998.

Total cover of graminoids was greater in ambient heat treatments ( $17 \pm 2\%$ ) than in medium ( $10 \pm 1\%$ ) or high ( $9 \pm 1\%$ ) heat treatments, which did not differ. Graminoid cover was about 8% in 1994 and 1995, and increased to about 15% by 1996.

*Bog community taxa*

Between 1994 and 1998, covers of the dominant moss, shrub, and graminoid taxa in the bog mesocosms were not affected by water-table setting or, with the exception of *P. strictum*, its interactions with heat treatment or year (Table 2). Cover of *P. strictum* was greater in high than in ambient heat treatments in 1995 ( $13 \pm 1\%$  vs.  $5 \pm 1\%$ , respectively) and 1996 ( $17 \pm 2\%$  vs.  $10 \pm 2\%$ , respectively), and was greater in dry ( $16 \pm 2\%$ ) than wet ( $10 \pm 2\%$ ) plots in 1996 (data not shown). Cover of *P. strictum* in all plots dropped precipitously to  $< 3\%$  in 1997 and 1998, when it no longer differed between treatments ( $P > 0.05$ ).

Averaged across treatments throughout the experiment, and in 1998, cover of *A. glaucophylla*, a subdominant shrub in the bog community, was much greater in the high heat treatment than in the medium or ambient heat treatments (Tables 2 and 3). In contrast, cover of the subdominant shrub *K. polifolia* after 1995 was two to three times greater in the ambient heat treatment than in the medium or high heat treatments (Fig. 1). Cover of other shrubs increased from 20% (*L. groenlandicum*) to 50% (*C. calyculata*, *Vaccinium oxycoccus*) in all plots

between 1994 and 1998. Cover of *Eriophorum spissum* increased from  $7 \pm 2\%$  in 1994 to  $11 \pm 2\%$  in 1998.

Ordination of species and quadrat scores for all years did not reveal any particular pattern of bog community response relative to the heat or water-table treatments. However, quadrat scores for 1994 tended to cluster together along Axis I relative to other years, albeit with substantial spread along Axis II, which indicated the relative homogeneity of these plots at experiment initiation. Ordination of species and quadrat scores for 1998 did not contribute any information beyond patterns of species response elucidated by the univariate analyses.

*Fen community lifeforms*

Cover of graminoids in the fen mesocosms differed between water-table treatments, but the pattern was year-dependent (Table 1). In 1994, graminoid cover did not differ among water-table settings (Fig. 2a). By 1995 and thereafter, graminoid cover was greater in wet plots than in intermediate or dry plots, which did not differ. In all treatments, graminoid cover at least tripled between 1994 and 1996. However, graminoid cover declined between

**Table 1** MANOVA *P*-values for cover (%) of moss, forb, graminoid, and shrub lifeforms within bog and fen plant communities for effects of water-table setting (dry, intermediate, wet), infrared warming (ambient, medium, high), and year (1994–1998). Moss cover in fen communities was not determined in 1996 and were not included in this analysis

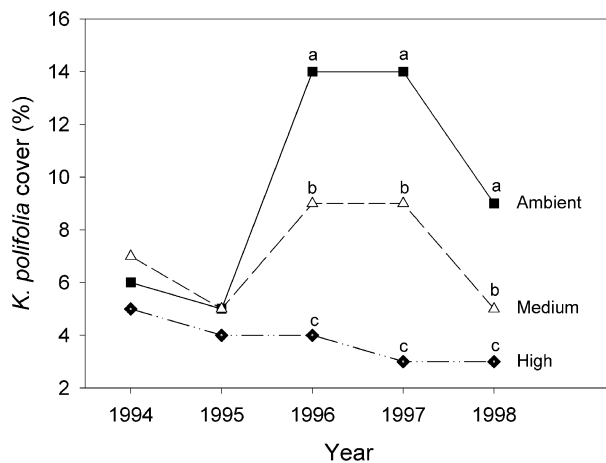
Source	Moss	Bog Graminoid	Shrub	Moss	Fen Forb	Graminoid	Shrub
Water	0.28	0.15	0.04	< 0.0001	0.23	< 0.0001	0.08
Infrared	0.12	0.03	< 0.0001	0.01	0.04	0.13	0.52
Water × Infrared	0.12	0.14	0.10	0.63	0.55	0.49	0.60
Year	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001
Year × Water	0.02	0.59	0.82	0.30	0.22	0.002	0.04
Year × Infrared	0.04	0.75	0.39	0.17	0.39	0.12	0.60
Year × Water × Infrared	0.13	0.99	0.16	0.22	0.20	0.33	0.68

**Table 2** MANOVA *P*-values for cover (%) of dominant shrub (S), graminoid (G), and moss (M) species within bog plots for effects of water-table setting (dry, intermediate, wet), infrared warming (ambient, medium, high), and year (1994–1998). Species codes are composed from the first four letters of the genus and species, except *Sphagnum* Section *Acutifolia*; full taxon names are in Table 3

Source	Taxon/Lifeform									
	Andrglau S	Chamcaly S	Kalmpoli S	Ledugroe S	Vaccocyc S	Eriospis G	Polystri M	SphaAcut M	Sphamage M	
Water	0.53	0.38	0.66	0.98	0.61	0.47	0.20	0.66	0.79	
Infrared	0.003	0.28	0.01	0.97	0.91	0.06	0.07	0.15	0.83	
Water × Infrared	0.61	0.21	0.93	0.61	0.99	0.15	0.42	0.38	0.82	
Year	0.02	< 0.0001	< 0.0001	< 0.0001	0.0006	0.0006	< 0.0001	< 0.0001	0.0009	
Year × Water	0.46	0.34	0.56	0.84	0.31	0.89	0.02	0.22	0.58	
Year × Infrared	0.54	0.10	0.02	0.69	0.73	0.86	0.03	0.09	0.10	
Year × Water × Infrared	0.28	0.18	0.37	0.72	0.14	0.97	0.77	0.76	0.23	

**Table 3** ANOVA *P*-values and means for cover (%) of common taxa within lifeforms in bog and fen plant communities in 1998. Taxa had cover >5% averaged across treatments in 1998. Water-table setting and infrared warming did not interact ( $P > 0.12$ ). Means in rows, within water-table setting and within infrared warming, with different lower-case letters differed ( $P < 0.05$ )

Community	Lifeform	Taxon	Mean cover (%)								
			Source ( $P > F$ )		Water-table setting			Infrared warming			
			Water	Infrared	Dry	Intermediate	Wet	Ambient	Medium	High	
Bog	Graminoid	<i>Eriophorum spissum</i>	0.21	0.19	8	12	15	15	12	7	
		Moss	<i>Sphagnum sect. Acutifolia</i>	0.31	0.04	80	81	85	87 a	81 ab	78 b
	Shrub	<i>Sphagnum magellanicum</i>	0.47	0.46	4	7	7	5	6	8	
		<i>Andromeda glaucophylla</i>	0.58	0.004	13	9	11	< 1 a	8 a	25 b	
		<i>Chamaedaphne calyculata</i>	0.31	0.18	51	46	40	38	49	49	
		<i>Kalmia polifolia</i>	0.84	0.005	6	6	5	9 a	5 ab	3 b	
		<i>Ledum groenlandicum</i>	0.86	0.90	7	5	6	7	5	6	
		<i>Vaccinium oxycoccus</i>	0.24	0.91	7	16	8	11	9	11	
Fen	Graminoid	<i>Carex lasiocarpa</i>	0.003	0.30	4 a	5 a	22 b	5	13	12	
		<i>Rhynchospora spp.</i>	0.19	0.17	14	20	31	31	17	16	
		<i>Scheuchzeria palustris</i>	0.004	0.04	4 a	11 b	12 b	6 a	9 ab	12 b	
	Shrub	<i>Andromeda glaucophylla</i>	0.01	0.39	16 a	4 b	4 b	11	7	7	
		<i>Chamaedaphne calyculata</i>	0.04	0.84	13 a	3 b	3 b	6	7	7	
		<i>Vaccinium macrocarpon</i>	0.78	0.59	4	10	6	2	11	7	



**Fig. 1** Cover (%) of *Kalmia polifolia* in mesocosm bog communities as affected by infrared warming (ambient, medium, high) between 1994 and 1997 ( $n = 9$ ). Within year, means with different lowercase letters were different ( $P < 0.05$ ).

1996 and 1998, particularly within the intermediate and dry plots, which by 1998 had cover values similar to 1994.

The cover of shrubs in fen mesocosms increased between 1994 and 1998, but the extent of this increase depended on water-table setting (Table 1). By 1998, shrub cover was nearly two times greater in dry treatments than in wet or intermediate treatments, which did not differ (Fig. 2b).

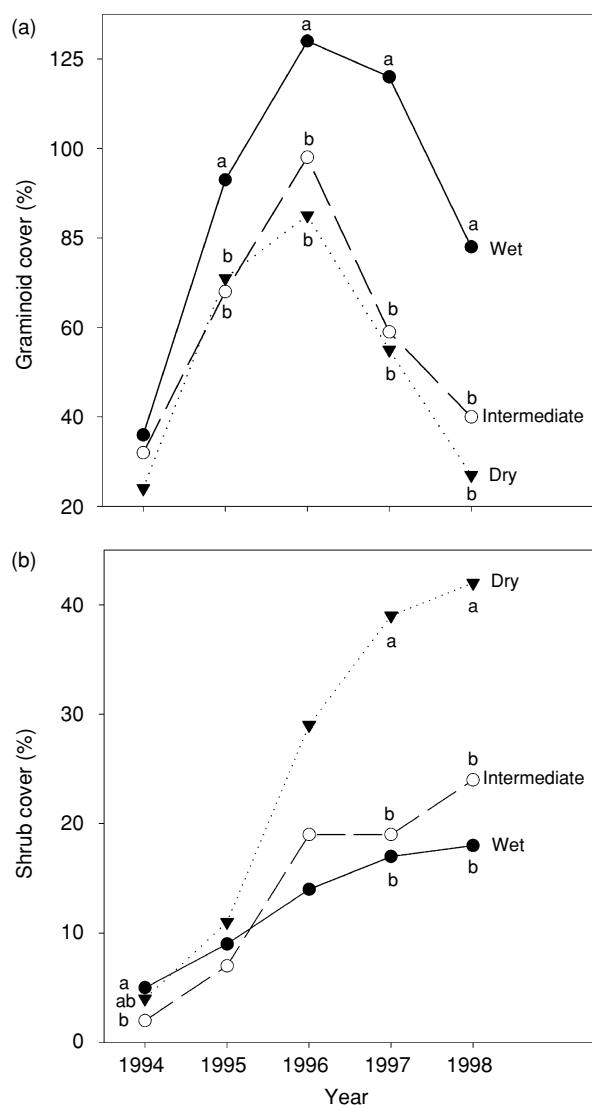
Cover of mosses in the fen mesocosms was about two- and four-fold greater in the wet treatment ( $16 \pm 2\%$ ) than

in the intermediate ( $7 \pm 1\%$ ) and dry ( $4 \pm 1\%$ ) treatments, respectively (Table 1). Moss cover was greater in the ambient ( $10 \pm 2\%$ ) and medium ( $11 \pm 2\%$ ) heat treatments than in the high ( $6 \pm 1\%$ ) heat treatment. Averaged across treatments, moss cover increased from  $4 \pm 1\%$  in 1994 to  $13 \pm 2\%$  in 1997, but declined in 1998 to  $6 \pm 1\%$ .

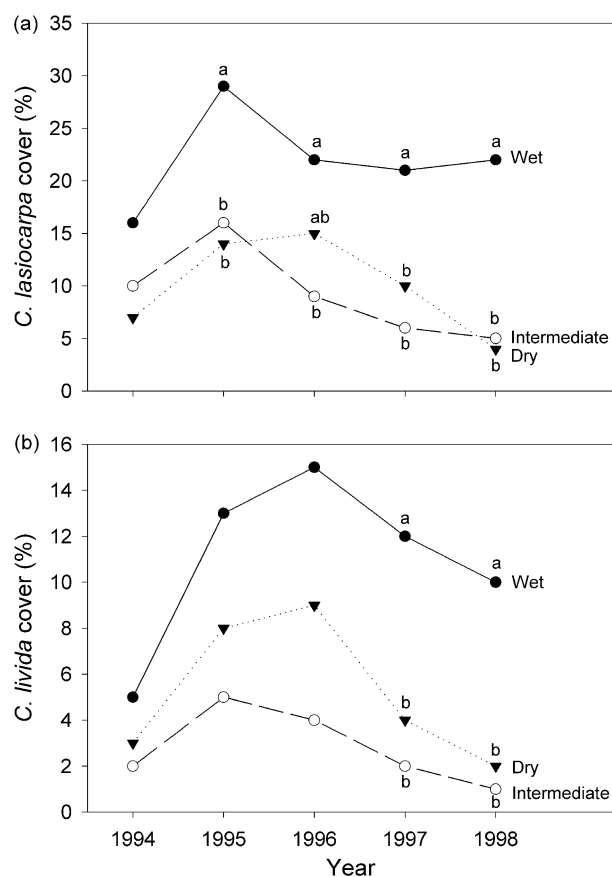
Cover of forbs in the fens was greatest in medium heat plots ( $23 \pm 2\%$ ), least in high heat plots ( $12 \pm 1\%$ ), and intermediate in ambient heat plots ( $18 \pm 2\%$ ). Forb cover in fen mesocosms increased from  $9 \pm 1\%$  in 1994 to  $26 \pm 3\%$  in 1998.

#### Fen community taxa

Cover of *C. lasiocarpa* did not differ between water-table settings in 1994, but thereafter was generally 2–4 times greater in the wet than intermediate or dry treatments (Table 4, Fig. 3a). Cover of *C. lasiocarpa* in the wet treatment stabilized at about 20% after 1995, whereas in the drier treatments it declined through 1998. Similarly, cover of *C. livida* was at least three times greater in the wet than intermediate or dry plots in 1997 and 1998 (Fig. 3b). *C. livida* cover peaked in 1995 and 1996, and declined thereafter in all treatments. Cover of *Rhynchospora spp.*, the dominant graminoid in the fen mesocosms, differed between water-table settings only in 1997, when its cover was greater in wet ( $63 \pm 7\%$ ) than either intermediate ( $31 \pm 3\%$ ) or dry ( $31 \pm 3\%$ ) water-tables (data not shown). Averaged across time,



**Fig. 2** Cover (%) of graminoids (a) and shrubs (b) in mesocosm fen communities between 1994 and 1998 as affected by water-table setting (dry, intermediate, wet) ( $n = 9$ ). Within year, means with different lowercase letters were different ( $P < 0.05$ ).



**Fig. 3** Cover (%) of *Carex lasiocarpa* (a) and *Carex livida* (b) in mesocosm fen communities between 1994 and 1998 as affected by water-table setting (dry, intermediate, wet) ( $n = 9$ ). Within year, means with different lower-case letters were different ( $P < 0.05$ ).

**Table 4** MANOVA  $P$ -values for cover (%) of dominant shrub (S) and graminoid (G) species within fen plots for effects of water-table setting (dry, intermediate, wet), infrared warming (ambient, medium, high), and year (1994–1998). Species codes are described in the legend of Table 2

Source	Taxon/Lifeform						
	Andrglau S	Chamcaly S	Vaccmacr S	Carelasi G	Carelivi G	Rhyn spp. G	Schepalu G
Water	0.01	0.03	0.74	0.006	0.05	0.12	0.13
Infrared	0.57	0.51	0.58	0.32	0.37	0.71	0.03
Water × Infrared	0.26	0.79	0.87	0.59	0.77	0.77	0.20
Year	<0.0001	0.002	0.006	<0.0001	0.001	<0.0001	<0.0001
Year × Water	0.18	0.19	0.81	0.07	0.06	0.004	0.14
Year × Infrared	0.54	0.81	0.57	0.50	0.01	0.48	0.13
Year × Water × Infrared	0.52	0.96	0.43	0.07	0.16	0.93	0.29

cover of *Scheuchzeria palustris* was greater in high ( $14 \pm 2\%$ ) than medium or ambient heat treatments (both  $8 \pm 1\%$ ). In 1998, *S. palustris* cover was about three times greater in wet than intermediate or dry water-tables (Table 3).

Through time, covers of the two dominant shrubs in the fen mesocosms, *A. glaucophylla* and *C. calyculata*, were on average at least three times greater in the dry than in either intermediate or wet water-table treatments (Tables 3 and 4). Covers of *A. glaucophylla*, *C. calyculata* and *Vaccinium macrocarpon* in the fen mesocosms increased from about 1% in 1994 to about 7% in 1998.

Ordination of species and quadrat scores for the fen plots did not exhibit any patterns relative to the treatments. Quadrat scores for 1994 ordinated positively along Axes I and II, and were clustered relative to data from other years (data not shown). With each successive year (i.e. 1995, 1996, etc.), the breadth of quadrat scores along the first two axes expanded, until quadrat scores from 1998 practically defined the limits of Axes I and II. Thus, the fen plots were relatively homogeneous at experiment initiation, and diverged in composition throughout the experiment. However, ordination of species and quadrat scores for 1998 did not indicate any particular response of the fen community, *sensu stricto*, to the experimental treatments.

## Discussion

Within and between the bog and fen communities, different lifeforms and species responded differently to manipulations in water-table elevation and infrared warming designed to simulate potential climate change. These results suggest that bog and fen plant communities will respond differently to warming and/or changes in water-table elevation.

### *Bog community and taxa*

Results suggest that warming may lead to an increase in abundance and production (Weltzin *et al.*, 2000) of woody plants in this and similar bog communities. In addition, lowered water-table elevations that are predicted to occur in mid-continental areas as a result of changes in rates of ET (Roulet *et al.*, 1992; Rouse, 1998) are also likely to favour woody plants (Gorham, 1991).

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 impact these ecosystems by alleviating temperature constraints (Gorham, 1991; Apps *et al.*, 1993; Bridgham *et al.*, 1995). In the bog community, increases in soil temperature commensurate with model

predictions of global warming increased cover of shrubs by 50% and decreased cover of graminoids by 50% in only four years. However, the different shrub species responded quite differently to the heat treatments. Increases in shrub cover were caused primarily by the response of *A. glaucophylla*. In contrast, heating did not affect cover of the other dominant shrub *C. calyculata*, or the subdominant shrubs *L. groenlandicum* and *V. oxycoccus*. Finally, cover of the subdominant shrub *K. polifolia* in the heated plots decreased by about 66% relative to the unheated plots.

Although the response of shrubs to changes in water-tables was somewhat muted relative to changes in heat loading, total cover of shrubs was inversely correlated with water-tables. This response is consistent with observations of the response of shrubs to gradients of water-table elevation in this and other systems (Backéus, 1990; Gorham, 1991; Szumigalski & Bayley, 1996; Thormann & Bayley, 1997a, b; Weltzin *et al.*, 2000).

In contrast with observed changes in total cover of shrubs along the drying gradient, changes in the cover of individual dominant shrub species was not statistically discernable. This suggests that changes in the shrub community may be subtle – even after four years of treatment – and better expressed as the sum of relatively small shifts in the cover of individual species than consistent and large responses across taxa. This interpretation coupled with the species-specific and sometimes opposite response of individual shrub taxa to the warming gradient, illustrates the complexity of predicting the response of the bog plant community as a whole to gradients of warming and drying.

Moreover, changes in cover or abundance of shrubs or other taxa ignore the critical component of below-ground production or biomass, which may equal or exceed the above-ground response. For example, Weltzin *et al.* (2000) quantified above- and below-ground production of shrubs in these same mesocosms. They found that although above-ground production was 30% greater in dry plots than wet plots, below-ground production was 100% greater in dry plots than wet plots. These differences in compartmental production may be further complicated by species-specific responses to changes in environmental conditions.

### *Fen community and taxa*

In contrast to the bogs, manipulation of water-table elevations was the most important driver of cover of species and lifeforms in the fens. Increases in water-table elevation increased cover of graminoids – in particular *C. lasiocarpa* and *C. livida* – as well as mosses. In contrast, decreases in water-table elevation increased cover of shrubs, in particular *A. glaucophylla* and *C. calyculata*.

Similarly, other research has demonstrated the importance of water-table elevation and available soil moisture to the species and lifeform composition of fen plant communities (Szumigalski & Bayley, 1996; Thormann & Bayley, 1997a,b; Weltzin *et al.*, 2000).

The response of graminoids and shrubs to the water-table treatments illustrate apparently different thresholds of response to water-table elevation for these lifeforms. After five growing seasons, total cover of graminoids in the wet treatment was roughly twice that of the intermediate and dry treatments. In contrast, cover of shrubs in the dry plots was almost twice that of the intermediate or wet plots. These results suggest that water-table depths greater than 10 cm are most conducive to shrubs, but that water-tables shallower than 10 cm are conducive to most graminoids. However, because individual shrub and graminoid species responded individualistically to variations in water-table elevation, such generalizations are not necessarily appropriate at the species level.

Large temporal variations in fen graminoid cover, as seen here between 1994 and 1998, seem characteristic of fen peatlands (Thormann & Bayley, 1997a,b; Chapin, 1998). In our experiment, graminoid cover and production peaked in 1996, likely the result of relatively high growing season precipitation in 1995 and 1996. The buildup of senescent litter or thatch may have caused the subsequent declines in cover of graminoids, because of changes in light or temperature regimes at the soil surface. This interpretation is consistent with modelled and empirical observations that ecosystems may have biogeophysical feedbacks to climate change through ecosystem control over energy fluxes equivalent in magnitude to the direct effects of radiative forcing (Melillo *et al.*, 1996; Chapin *et al.*, 1997; Sellers *et al.*, 1997; Walker *et al.*, 1998; Bridgham *et al.*, 1999; Weltzin *et al.*, 2000).

#### *Peatland response to warming and drying*

The differential and even opposite response of species and lifeforms to our experimental gradients of warming and water-table is consistent with the widely supported observation that species respond individualistically to changes in environmental conditions (Gleason, 1926). This conclusion has been supported by experimental research, which further indicates that component lifeforms and species within a community may respond differently, or even oppositely, to environmental change, and that these changes in lifeform or species composition may cancel out at higher levels of organization (Chapin *et al.*, 1995; Harte *et al.*, 1995; Weltzin *et al.*, 2000). Nonetheless, changes in the abundance, production, or distribution of

species are often sufficient to alter both structure and function of the ecosystem (Chapin *et al.*, 1995).

Changes in the abundance or production of lifeforms and species within peatland plant communities are likely to have dramatic effects on peatland water and energy fluxes and budgets (van Cleve *et al.*, 1991; Bridgham *et al.*, 1999; Chen *et al.*, in review). For example, differences in species and lifeform composition between the bog and fen plant communities are likely responsible for the observation that fen plots are on average 0.8–1.0 °C warmer than bog plots during the growing season, even with the same infrared inputs (Bridgham *et al.*, 1999). Similarly, although ET increased with warming and height of the water-table, annual ET was 12–13% greater in bog mesocosms than in fen mesocosms (Bridgham *et al.*, 1999). Consequent losses of energy to the latent heat of ET may partially explain the cooler soil temperatures observed in the bog plots. Thus, the differential response of the plant communities that characterize bogs and fens have the clear potential to affect energy flux, and could thus serve as negative or positive feedbacks on ecosystem response to climate forcing.

Clearly, investigations of interactions and feedbacks between the plant canopy and ecosystem energy budgets as well as other environmental variables (e.g. temperature, vapour density, and soil moisture) in both bog and fen peatlands are warranted. Future research should focus on the relative importance of different terms in the energy budgets *vis-a-vis* responses of different components of the plant community to directional shifts in environmental variables.

In summary, the compositions of bog and fen plant communities will likely change – in different directions and at different magnitudes – in response to warming and/or changes in water-table elevation commensurate with predicted changes in regional or global climates. Further, these changes in community composition may be translated to the level of the ecosystem (e.g. Bridgham *et al.*, 1999; Weltzin *et al.*, 2000), depending on the initial structure and composition of the plant community, and the strength and nature of the environmental driving variables.

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