

ECOSYSTEM CONTROL OVER TEMPERATURE AND ENERGY FLUX IN NORTHERN PEATLANDS

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Abstract. Large-scale changes in climate may have many unexpected effects on ecosystems, given the importance of climate as a control over almost all ecosystem attributes and their many internal feedbacks. In particular, the interactions among energy flux, plant dynamics, and soil carbon and nutrient cycling are poorly known. In this study, we examined biotic controls over soil temperature and evapotranspiration (ET) in a climate change experiment in two peatlands, a bog and a fen. Bogs are isolated from groundwater inputs (i.e., ombrogenous) and are acidic, whereas fens receive groundwater inputs (i.e., minerogenous) and are more alkaline. They also have many associated differences in soil chemistry, nutrient availability, and plant communities.

We removed 27 intact peat monoliths each from a bog and a fen in northern Minnesota to construct a large mesocosm facility that allows for direct manipulation of climatic variables in a replicated experimental design. The treatment design was a fully crossed factorial with three infrared-loading treatments, three water table treatments, and two ecosystem types (bogs and fens), with three replicates of all treatment combinations. Heating was achieved with overhead infrared lamps, so soil temperature was a dependent variable.

Increased infrared loading caused mean monthly soil temperature to increase 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 the growing season than during the winter. Within the growing season, heating caused greater increases in soil temperature in May–June in the bog plots and in May–June and September–October in the fen plots. Occasionally during the winter, increased infrared loading cooled the soil by up to 5.1°C, probably due to melting of the insulating snow cover. Fen plots were on average 0.8–1.0°C warmer than bog plots during the growing season, although bog plots had a steeper soil temperature gradient with depth. Water level had no effect on soil temperature.

Annual ET was 12–23% greater in the bog plots than in the fen plots, at least partially explaining the cooler soil temperatures in the bog plots due to latent heat of evaporation. Additionally, warmer, wetter conditions increased ET. In the fen plots, ET was more sensitive to water table depth than in the bog plots. Differences in the composition and seasonality of the plant canopies accounted for much of the observed differences in ET between bog and fen mesocosms, and hence soil temperature. We present a conceptual model of how above- and belowground ecosystem processes control energy fluxes in northern peatlands and suggest that such controls represent a general phenomenon that should be incorporated into climate change models that include biotic feedbacks.

Key words: biogeophysical feedbacks; bog; climate change; evapotranspiration; fen; peatlands; soil temperature; soil warming; water table; wetlands.

INTRODUCTION

Wetlands only occupy ~4% of the global land surface (Matthews and Fung 1987, Aselmann and Crutzen 1989). However, their importance to climate change is much greater than indicated by their small area, because they are responsible for 17–28% of the global atmospheric methane flux, they contain a large fraction

of the world's soil organic pool, and they have many functional attributes that are given high value by society and that may be significantly impacted by climate change (Bridgham et al. 1995, Öquist and Svensson 1996).

Boreal peatlands are particularly important in this regard as they represent about half of the total wetland area (Matthews and Fung 1987, Aselmann and Crutzen 1989, Bridgham et al. 1999) and are responsible for about a third of the methane flux from wetlands (Bartlett and Harriss 1993). It has been estimated that 40–

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47% of all terrestrial organic carbon is stored in the above- and belowground pools of the boreal forest, with 57% of this sequestered in wetlands as peat (Sampson et al. 1993). Northern ecosystems may be particularly vulnerable to climate change due to large current temperature constraints on biological activity and greater than average predicted temperature increases at higher latitudes in most global climate change models (Apps et al. 1993, Bridgham et al. 1995). They may also serve as an important positive feedback mechanism to anthropogenic climate change, augmenting atmospheric concentrations of greenhouse gases, if a significant fraction of the soil organic pool is respired as methane and/or carbon dioxide.

Although there is widespread knowledge that natural ecosystems are globally important sinks and sources for greenhouse gases, most previous research has viewed ecosystems as passive recipients of increased infrared loading and the resultant temperature increases. However, ecosystems may have large biogeophysical feedbacks to climate change through ecosystem control over energy fluxes. Nonetheless, the magnitude of these feedbacks remains largely unexplored (Melillo et al. 1996).

In particular, although short- and long-wave energy inputs and temperature are related, they are not necessarily equal. The mechanism of global warming is increased atmospheric infrared loading (long-wave radiation) due to an accumulation of radiatively active gases. The partitioning of heat is the response of ecosystems to the increased loadings. The resultant soil temperature response depends on the distribution of thermal energy throughout the system, particularly to heat storage, evapotranspiration (i.e., latent heat), and canopy albedo (i.e., net radiation). All of these energy fluxes are under direct biological influence. Thus, it is critical to determine the biogeophysical dynamics of the temperature response of ecosystems to increased infrared loadings and how these dynamics differ among ecosystems.

Research that has compared micrometeorological data along either natural or human-made plant community gradients consistently shows significant changes in microclimate and energy fluxes over relatively short distances (e.g., Chen et al. 1993, 1995, 1999, Goodin et al. 1996, Brosofske et al. 1997, Walker et al. 1998). Moreover, land surface changes have a large effect on net radiation and its partitioning into latent and sensible heat fluxes (Bolle 1990). The few models that have coupled biogeophysical dynamics of ecosystems with global climate change models have suggested that biogeophysical feedbacks on climate may be of similar magnitude to the direct effects of radiative forcing (Melillo et al. 1996, Sellers et al. 1997).

Thus, there is abundant research that demonstrates that ecosystems have a large degree of internal (although not necessarily homeostatic) control over their

energy budgets. This knowledge leads to the hypothesis that a constant change in infrared flux will cause variable temperature responses in different natural ecosystems due to internal control over energy fluxes. Therefore, the transient responses of different ecosystems to a constant climate perturbation could be quite complex and varied, involving multiple biotic feedbacks and ultimately different equilibrium points. For example, Harte et al. (1995) found that increased atmospheric infrared loading caused differential soil temperature responses in various montane meadow communities.

The results reported in this paper are part of a large climate change experiment in northern Minnesota, where we are directly manipulating climate in a replicated experiment through the use of mesocosms in two peatland ecosystems, bogs and fens. The overall objective of the experiment is to examine interactions between plant communities, carbon and nutrient cycling, trace gas emissions, and the energy balance of these two ecosystems in response to climate change. This paper focuses on the energy balances of bogs and fens. More specifically, we compare how increased infrared loading and different water table levels affect soil temperature and evapotranspiration (ET) in bogs and fens.

Bogs and fens have fundamentally different plant community composition, hydrology, nutrient availability, and soil chemistry (Moore and Bellamy 1974, Gore 1983, Bridgham et al. 1996, 1998, 1999). 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 dominated by *Sphagnum* mosses, ericaceous shrubs, and black spruce (*Picea mariana* (Mill.) BSP). In contrast, fens are minerotrophic, i.e., they receive inputs of water and minerals from groundwater and/or overland runoff, which causes more alkaline, higher pH soils, more humified peat, and dominance by graminoids, nonericaceous shrubs, and trees such as northern white cedar (*Thuja occidentalis* L.) and tamarack (*Larix laricina* (Du Roi) K. Koch). Recent experimental evidence demonstrated higher phosphorus availability in bogs and higher nitrogen availability in fens (Bridgham et al. 1998, Chapin 1998).

We hypothesize that bogs and fens will differ in their thermal response to changing climate because of their fundamental physical, chemical, and biotic differences in ecosystem structure. Thus, a constant infrared input may affect the flux and storage of energy in these two ecosystems differently, resulting in different soil temperatures. In turn, different soil temperatures will cause varied biogeochemical responses. The end result is a series of biogeophysical feedbacks, such that local and transient, and even possibly equilibrium, responses to climate change may be ecosystem dependent. We conclude with a conceptual model of how energy, carbon, and nutrient fluxes interact with plant community dy-

namics in peatland ecosystems, and suggest that such interactions are common in other ecosystem types.

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 peat in the bog site is ~3.5 m deep with a basal date of 10 040 ± 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. The surface 0–25 cm of peat has a pH of 4.1, 42.2% carbon, 8.4% ash, and 73.7% rubbed fiber content on a dry mass basis (Bridgman et al. 1998). Current vegetation is dominated by stunted (<10 cm height) ericaceous shrubs (*Chamaedaphne calyculata* (L.) Moench., *Andromeda glaucophylla* Link., *Kalmia polifolia* Wang., *Vaccinium oxycoccus* L., *Ledum groenlandicum* Oeder.), mosses (*Sphagnum fuscum* (Schimp.) Klinggr., *S. capillifolium* (Ehrh.) Hedw., *S. magellanicum* Brid., *Polytrichum strictum* Brid.), and black spruce. We chose a large treeless area in the center of the bog that, based upon stratigraphic evidence, had burned ~100 yr ago.

The fen has ~4.4 m of sedge peat overlying ~2 m of unconsolidated aquatic (limnic) peat, with a basal age of 9730 ± 70 yr BP. The surface 0–25 cm of peat has a pH of 4.9, 38.6% carbon, 22.3% ash, and 29.2% rubbed fiber content on a dry mass basis (Bridgman et al. 1998). To maximize the contrast with the bog, we chose 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 by mosses.

Experimental design

We extracted intact peat monoliths from the two source sites and constructed a mesocosm facility to manipulate infrared inputs and water table levels in a replicated experimental framework. This design also allowed measurement of plant community response and carbon, nutrient, and energy fluxes. With closely monitored water budgets, the mesocosms serve as lysimeters from which evapotranspiration and latent heat can be calculated (Ingram 1983). Although we augment atmospheric infrared inputs into the experimental plots, we do not control soil temperatures at some set point above ambient conditions as is done in most other soil warming experiments (e.g., Van Cleve et al. 1990, Peterjohn et al. 1993, 1994). Therefore, in our experiment soil temperature is a dependent variable that can respond to internal ecosystem controls. To our knowledge, Harte and colleagues (Harte et al. 1995) have the only similar experiment to ours, where they are using overhead infrared lamps to warm montane meadows in Colorado. They too have emphasized the importance

of vegetation in controlling soil microclimate response to increased infrared loading.

The construction of the mesocosm facility was begun in autumn 1993 at the University of Minnesota Fens Research Facility (FRF), ~70 km north of Duluth, Minnesota. Twenty-seven intact cylindrical peat monoliths (2.1 m² 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 sunk into a large field. The peat monoliths were removed in late winter, while frozen, with no surface disturbance to vegetation. Infrared radiation was augmented with overhead lamps set at none (ambient), half, or full power (see *Infrared inputs and temperature response* for actual inputs). 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, –10, and –20 cm relative to its surface. Treatment combinations were replicated three times and randomly assigned within each ecosystem type, yielding a full-factorial experimental design (two ecosystem types × three water table treatments × three infrared-loading treatments × three replicates, $N = 54$).

A necessary trade-off in our experimental approach is that the monoliths for the mesocosms could only come from a single bog and fen. We realize that extrapolation to the larger universe of bogs and fens is limited by such a design (Hulbert 1984). However, the ecosystem characteristics of the Toivola bog and Alborn fen sites have been extensively compared to numerous peatlands from Florida to Alaska (Bridgman et al. 1998, 1999), and these sites are typical of other northern bogs and fens. Additionally, we suggest that although the absolute response of these two sites to the treatments may not be representative of all peatlands, the *qualitative interactions* between energy and carbon flow and plant community dynamics are representative of peatland response to future climate change.

Mesocosm construction

The plastic tanks were insulated with 8 cm of sprayed urethane foam, to reduce heat loss to the surrounding soil, and buried in the ground. Perforated, 1.25 cm diameter polyvinyl chloride (PVC) pipe was placed along the bottom of the mesocosms and connected to an adjacent small “sump” bucket with an L-shaped PVC standpipe, the height of which set the water table level in the adjoining mesocosm tank.

In the winter of 1993–1994, a local contractor constructed access roads built on frozen peat into the source sites for heavy equipment access. We used a backhoe, a steel ring approximately the same dimensions as the mesocosm tanks, and a hydraulic-powered “clamshell” apparatus to cut underneath the steel ring and extract the monolith. The peat monolith (weighing ~1.5 Mg, with intact vegetation and soil structure) was bundled and transported by trailer to the FRF. Straps

were slid under each monolith and it was carefully lowered with a forklift into its recipient tank.

Infrared inputs and temperature response

Heating began on 27 July 1994 with infrared heat lamps (Kalgro Electronics Company, Bethlehem, Pennsylvania) that are identical to those used by Harte et al. (1995). A 1.2 m long lamp was mounted ~130 cm above the mean surface height of each plot and left on continuously. Reflectors on the lamps distributed the infrared radiation evenly over the entire surface of the plot.

To determine the infrared input for each heating treatment, we used a THRDS-7 Total Hemispheric Radiometer (Radiation and Energy Balance Systems, Seattle, Washington) connected to a Li-Cor LI-1000 datalogger (Li-Cor Incorporated, Lincoln, Nebraska). The radiometer and infrared output of the lamps are both highly sensitive to wind speed, so we determined maximum lamp output at 130 cm height from numerous lamps in an enclosed garage. The half-power heat treatment was estimated to augment ambient infrared input at the surface by 78 W/m², whereas the full-power treatment was estimated to augment input by 191 W/m². These increased infrared loads are considerably greater than those predicted to occur at the end of the 21st century by climate change models (Kattenberg et al. 1996), but were necessary to achieve the predicted degree of soil warming because of heat loss to the atmosphere and surrounding soil. Presumably, infrared inputs distributed over the globe would result in lower heat losses and an infrared radiation:temperature response ratio more similar to that predicted by the climate change models. Our measured values are maximum infrared inputs, and the actual infrared inputs into the plots were lower because of the cooling effect of the wind in the open field on the lamps. The project did not have the resources to put radiometers in every plot, so we could not determine the actual infrared load each plot received. Instead, we began continuous soil temperature measurements in all plots on 19 June 1995.

A T-type thermocouple was inserted 15 cm into the soil at ~30 cm from the edge of each plot, and a single air temperature thermocouple (added in the spring of 1996) was housed in a weather shelter. Data were recorded onto a computer in an adjoining shed via a multiplexor board (CIO-EXP32) and an A-D data acquisition board (CIO-DAS08, ComputerBoard, Incorporated, Middleboro, Massachusetts). During the growing season, temperature was recorded every 5–60 min, depending on our needs for biological data, based on the mean of a scan interval of 5–30 s. During the winter, temperature was scanned at 30-s intervals and recorded every 2 h.

Thermocouples were calibrated against a hand-held temperature probe (YSI Incorporated, Yellow Springs, Ohio) using ice water and ambient temperature. Vertical temperature profiles were also obtained with the

hand-held temperature probe. Profiles were measured on 28 July (one day after the lamps were turned on), 3 and 8 August and 10 October in 1994, and on 11 May, 13 June, 8 August, and 18 October in 1995. Typical vertical profile intervals were at 5, 10, 20, 30, and 40 cm (or some subset thereof).

Water table control and evapotranspiration calculations

Water levels in each plot were maintained relative to a marked datum hollow in each plot using a PVC pipe manostat. They were initially set to +1, –10, and –20 cm. As the surface grew upward due to vigorous moss growth in some of the bog plots, it became difficult to maintain the flooded (+1 cm) condition without overflowing the tanks. We also viewed this increase in elevation as a biotic feedback to our infrared and hydrology manipulations, and have let the surface of the plots rise relative to the water table 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 fen plots remained relatively close to their original set values with treatment means of 0, –10, and –19 cm.

Water table control of the mesocosms was maintained only during the growing season to prevent ice damage to the PVC manostat assemblies. Water tables were set from 14 July–1 November in 1994, 11 May–31 October in 1995, and 13 May–14 October in 1996. All mesocosms were allowed to fill and freeze during the remainder of the year. During the growing season, water was replenished by natural rainfall and, during dry periods, by measured 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. The water tables were topped off at approximately weekly intervals, using a flow meter (Omega Engineering Incorporated, Stamford, Connecticut) to quantify water inputs into each plot. Excess water from the mesocosm tanks due to precipitation events was collected in the accompanying sump buckets, where its volume was determined before pumping out. Rainfall was measured with a recording rain gauge.

Therefore, we have a complete input–output water budget for two and a half growing seasons in all mesocosms, with an approximately weekly time step. Evapotranspiration was estimated as

$$ET = P + W_i - W_o$$

where P equals precipitation inputs, W_i equals water put into the mesocosms to maintain water table levels, and W_o equals water collected in the sump buckets after rain events.

There were six times over the 2.5-yr measurement period when heavy rainfall caused overflow from the mesocosms, artificially inflating calculated ET. Therefore, we excluded these six periods and used the average of the two adjoining weeks. Evapotranspiration losses from November to April were considered to be negligible, as soil temperatures were near or below freezing during this period and potential evapotranspiration was zero.

Potential evapotranspiration (PET) was estimated with the Thornthwaite equation (Dunne and Leopold 1978). Monthly air temperature values were taken from the weather station at the Hibbing-Chisholm airport, ~25 km from the site, from January 1994 to May 1996. From June to December 1996, we were able to use monthly mean air temperature measured on site to estimate PET.

Statistics

To test the hypothesis that soil temperature response to a changing climate depends on ecosystem type, we did three-way repeated-measure ANOVAs with mean monthly soil temperature as the dependent variable and water table level, infrared loading, and ecosystem type as the independent variables. Additionally, two-way (water table level, infrared loading) repeated-measures ANOVAs were used to examine temperature effects separately for bog plots and fen plots. Because of the dominant effect of season on temperature response, we also did three-way (water table level, infrared loading, ecosystem type) ANOVAs or two-way ANOVAs (water table level, infrared loading, by ecosystem type) on data from individual months.

The continuous temperature data for the above ANOVAs were recorded at 15 cm soil depth. However, temperature often varied greatly across soil depth profiles. Therefore, we compared our results from the continuous temperature data with our more limited data set of vertical temperature profiles with four-way ANOVAs (water table level, infrared loading, ecosystem type, and depth), and three-way ANOVAs (water table level, infrared loading, depth) for bog plots and fen plots separately.

The infrared heaters have mechanical switches that control their output. These switches began failing in the winter of 1995–1996, causing the half-heat treatments to become full-heat treatments. Because there may have been time-lag effects of heating, we continued to assume that we had three infrared-loading treatments in 1996 in all statistical analyses. The effect of this is to reduce the statistical sensitivity of detecting significant responses of soil temperature and ET to the infrared-loading treatments and their interactions.

We also examined the effect of ecosystem type on annual ET (summed over the growing season) with three-way (water table level, infrared loading, ecosystem type) and two-way (water table level, infrared load-

ing, by ecosystem type) repeated-measures ANOVAs with 1995 and 1996 data. Data from 1994 were not included in the repeated measures analysis because they were only taken for half of the growing season. Nonrepeated ANOVAs were also run on annual ET values for each year from 1994 to 1996. Seasonal effects on ET were examined with ANOVAs run on data from separate months. Data distributions of all variables were examined, and data were log transformed when appropriate to ensure a normal distribution. All ANOVAs used fixed-effects models.

RESULTS

Soil temperature

Soil temperature measured at 15 cm depth from June 1995 to December 1996 displayed the sharp seasonal changes expected for northern Minnesota (Fig. 1). Both infrared loading ($P < 0.001$) and ecosystem type (i.e., bog or fen, $P = 0.02$) were significant in explaining soil temperature in 1995, whereas only infrared loading was significant in 1996 ($P = 0.004$, repeated-measures ANOVA). However, there were strong seasonal interactions with both infrared loading and ecosystem type, with much greater effects during the growing season than during the winter in both years (Fig. 2). Increased infrared loading significantly increased soil temperature only from June through November in 1995 ($P \leq 0.06$) and from April through November in 1996 ($P \leq 0.06$), but had no effect on soil temperature during the winter months. During the growing season (May–October), monthly mean temperature in the high-heat treatment was on average 3.0°C warmer than ambient in 1995 and 2.2°C warmer in 1996 ($P < 0.001$ for main effect of heat in every month).

Within growing seasons, there was also a significant monthly effect on soil temperature response to infrared inputs (Fig. 2). Heating caused greater soil temperature increases in May and June than from July to October in the bog plots ($P < 0.001$, repeated measures ANOVA). A different temporal effect was found in the fen plots ($P < 0.001$), with heating causing greater soil temperature increases in May–June and September–October than in midsummer (July–August). This difference among bog plots and fen plots was reflected in a significant ($P < 0.001$) ecosystem type \times month interaction in the repeated-measure ANOVA.

Although increased infrared loading had no significant effects on monthly mean temperature over the winter months, we were surprised to find six dates in the bog plots and nine dates in fen plots during the winter of 1995–1996 when soil in the heated treatments was actually cooler by up to 5.1°C than the ambient treatments (i.e., the downward spikes in Fig. 2, $0.001 \leq P \leq 0.08$ on individual dates).

The effect of ecosystem type on soil temperature was significant from June through August, October, and December in 1995 and from May through July in 1996

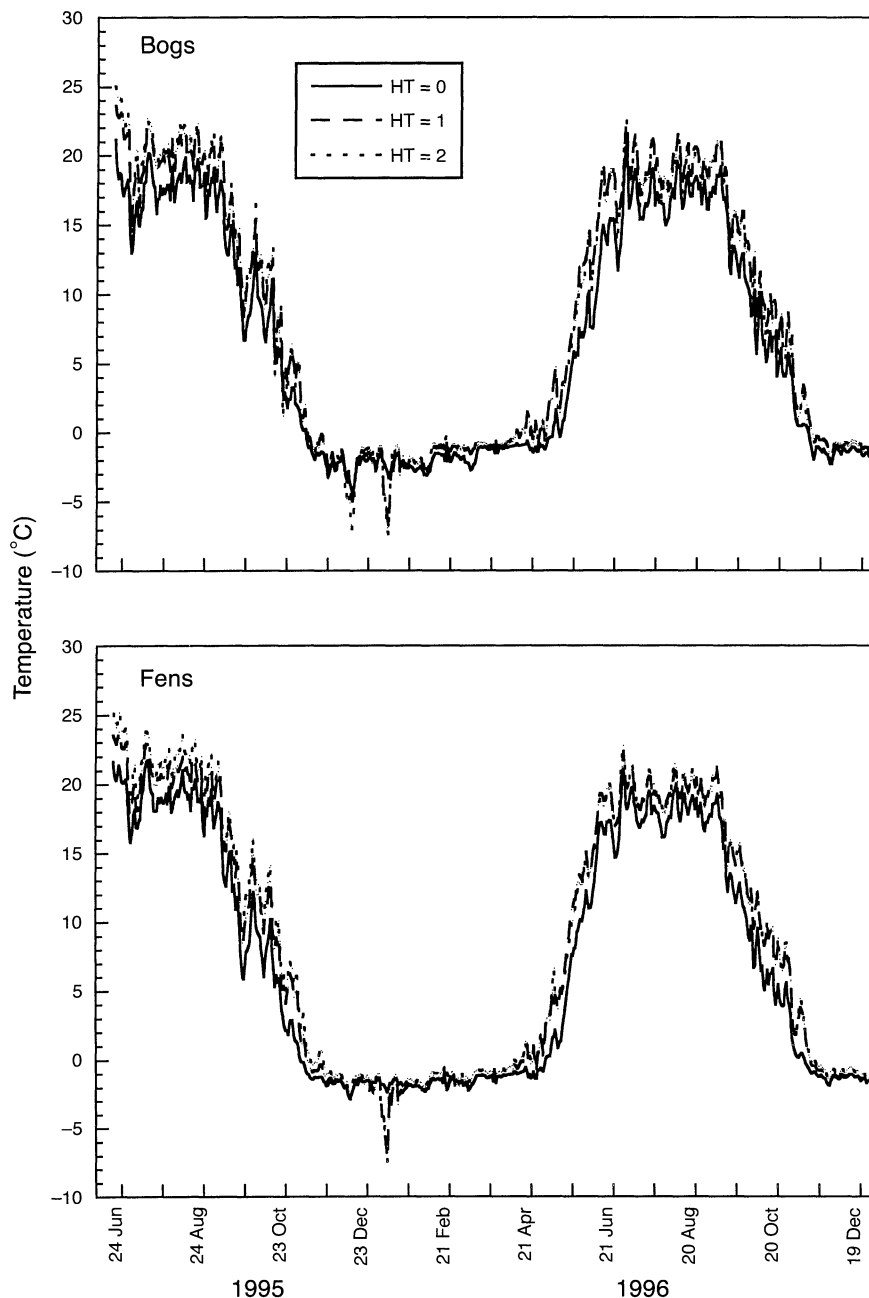


FIG. 1. Soil temperature measured at 15 cm depth from June 1995 to December 1996 for bog and fen plots averaged over water table treatments. HT = 0 refers to ambient, HT = 1 to half-heat, and HT = 2 to full-heat treatments.

($P \leq 0.05$). During these months, monthly mean temperatures in the fen plots were 0.8° – 1.6°C warmer than the bog plots. Over the entire growing season, the fen plots were on average warmer than the bog plots by 1.0°C in 1995 ($P = 0.02$) and 0.8°C in 1996 ($P = 0.05$).

Water table level and the interactions between infrared loading, ecosystem type, and water table level never significantly affected soil temperature ($P > 0.05$).

Vertical temperature profiles

The fen mesocosms were warmer by 0.3° – 1.9°C than the bog mesocosms when temperatures were averaged across all plots and depths ($P < 0.02$) on six of the eight dates that vertical temperature profiles were measured. The two ecosystems had similar soil temperatures on 10 October 1994 ($P = 0.13$ for ecosystem type effect), and on 3 August 1994 the bog plots were warmer by 0.4°C ($P = 0.02$). Thus, we conclude that our

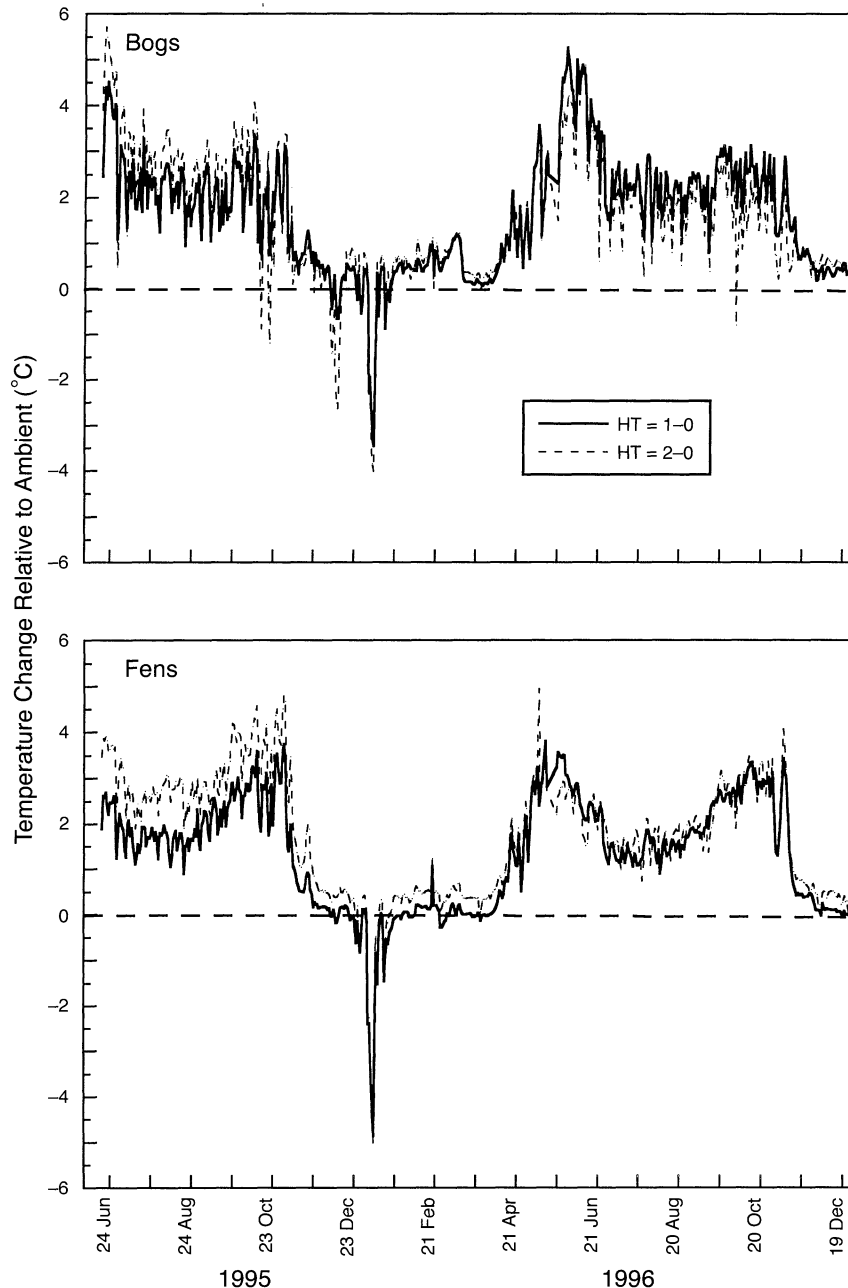


FIG. 2. Soil temperature response relative to ambient conditions at 15 cm depth from June 1995 to December 1996 for bog and fen plots averaged over water table treatments. HT = 0 refers to ambient, HT = 1 to half-heat, and HT = 2 to full-heat treatments.

results for ecosystem effects on soil temperature were not an artifact of only measuring temperature at a single depth.

There were significant soil depth and infrared loading effects on soil temperature on most dates. Water table depth and the interaction terms generally had no significant effect on soil temperature in 1994, but significant water table effects and water table \times infrared-loading treatment effects were commonly observed in

1995. This could have been due to either real differences between 1994 and 1995 in water table effects on soil temperature, or due to the greater number of soil depths typically measured in 1995.

Although the fen plots were overall generally warmer, on six of the eight dates the bog plots had a greater vertical temperature gradient ($P < 0.04$), with a temperature decrease of 0.4° to 5.0°C (averaged over all heat and water table treatments) from 10 to 30 cm depth

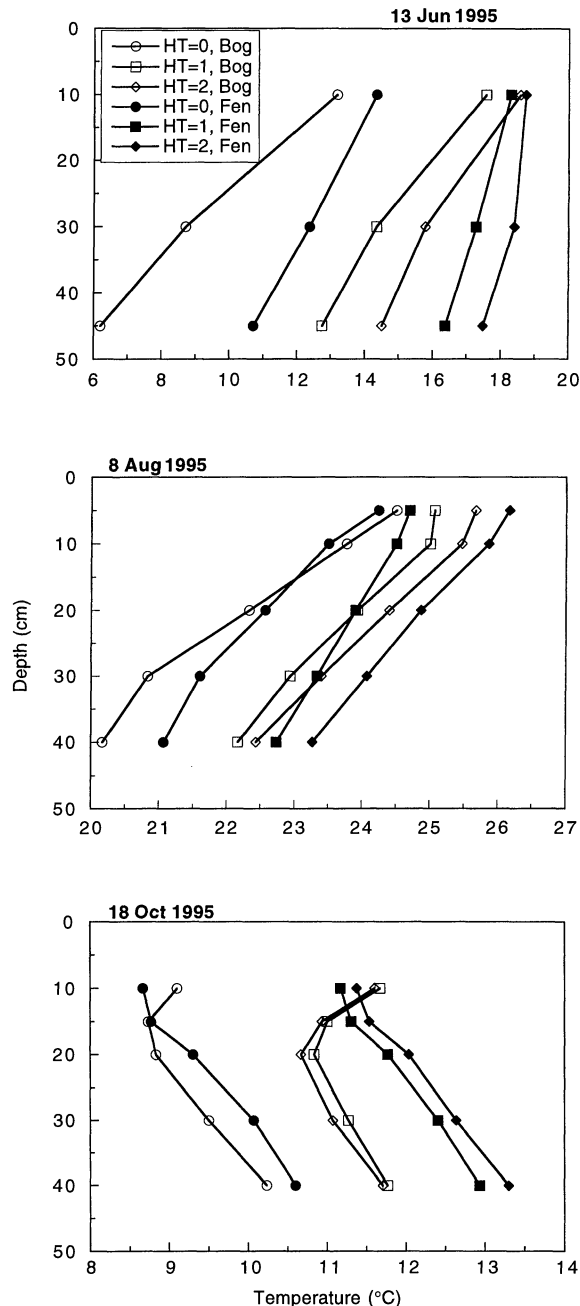


FIG. 3. Soil temperature averaged over water table treatments relative to soil depth (0 = surface) on three dates in 1995. HT = 0 refers to ambient, HT = 1 to half-heat, and HT = 2 to full-heat treatments.

in the bog plots, compared to a more muted temperature decrease of 0.1° to 2.8°C in the fen plots (Fig. 3). The peat was often frozen into late May or early June in the bog plots, whereas the fen peat typically thawed several weeks earlier. Autumn temperature profiles were quite different from those observed in the summer. For example, on 18 October 1995 the coolest temperature was at intermediate depth in the bog plots,

whereas temperature increased with depth in the fen plots—the inverse of the typical summer depth profile (Fig. 3, $P < 0.001$ for ecosystem type effect).

In summary, we consistently found significant effects of ecosystem type, season, and infrared loading on vertical temperature profiles.

Evapotranspiration

Ecosystem type, infrared loading, and water table level had significant effects on cumulative ET over the growing season ($P \leq 0.001$, Fig. 4) in all three years (1994–1996). In 1994 and 1995, there was a significant ecosystem type \times water table interaction ($P \leq 0.05$). The bog mesocosms had 12–23% greater cumulative ET than the fen mesocosms in each of the three years. Daily ET averaged over the growing season in the bog plots was 0.30 and 0.36 cm/d in 1995 and 1996, respectively, and in the fen plots was 0.27 and 0.29 cm/d, respectively (Fig. 5).

Warmer, wetter conditions enhanced ET. The significant ecosystem type \times water table interaction in 1994 and 1995 reflected a greater sensitivity of ET to water table depth in the fen plots than in the bog plots (Fig. 4). For example, an increase in the nominal water table level from –20 cm to +1 cm caused an increase in cumulative ET in 1994 of 27% in the fen plots, compared to an increase of only 5% in the bog plots. Similarly, in 1995 this water table difference caused a 45% increase in ET in the fen plots compared to a 14% increase in the bog plots. This trend continued in 1996 (a 25% increase in the fen plots compared to a 12% increase in the bog plots), although the interaction term was not statistically significant ($P = 0.35$).

The seasonal dynamics of potential evapotranspiration (PET) paralleled actual evapotranspiration in the unheated plots (Fig. 5). Measured evapotranspiration in the ambient plots from 1994 to 1996 ranged from 70 to 91% of PET in the bog plots and from 62 to 69% of PET in the fen plots.

DISCUSSION

Soil temperature

The infrared lamps increased mean monthly soil temperature by 1.6°–4.1°C at 15 cm depth, which is within the range of predicted mean global temperature increases with a doubling of current atmospheric carbon dioxide levels (Kattenberg et al. 1996). Even greater temperature increases are predicted to occur at high latitudes (Kattenberg et al. 1996).

Corresponding to these increases, we confirmed our hypothesis that soil temperature response in peatlands is ecosystem dependent because of biogeophysical feedbacks. The fen plots were consistently warmer than the bog plots during the growing season by ~1.0°–1.5°C at 15 cm soil depth. Additionally, temporal effects of heating on soil temperature response within the growing season were expressed differently in the bog

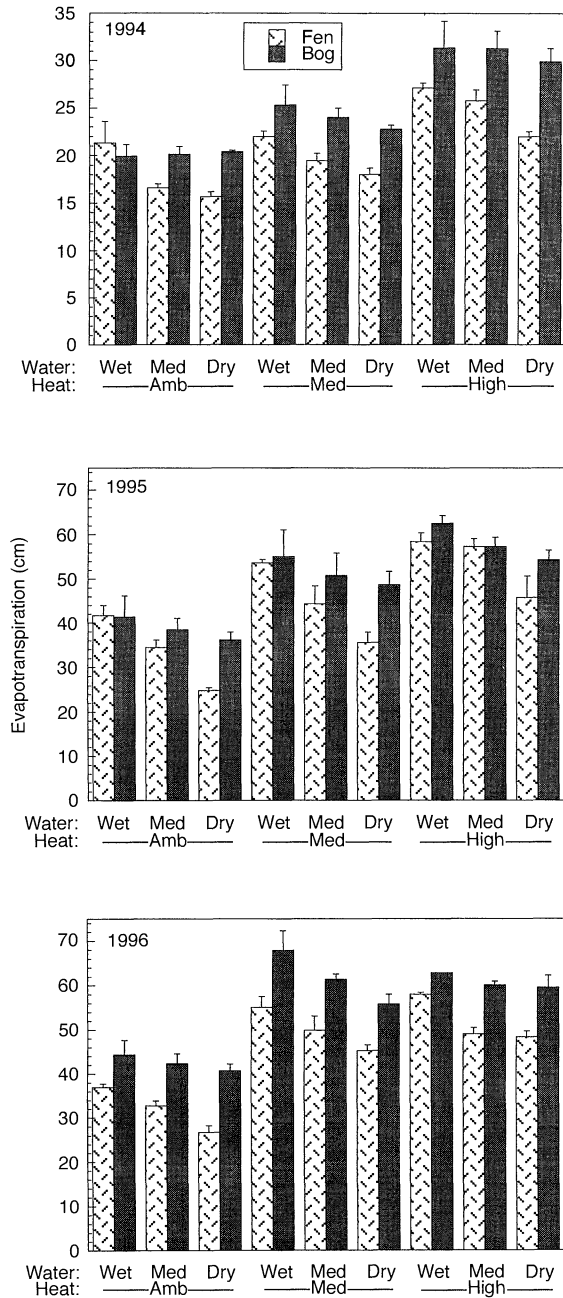


FIG. 4. Cumulative evapotranspiration for all nine treatment combinations for bog and fen plots from 14 July to 1 November in 1994, from 11 May to 31 October in 1995, and from 13 May to 14 October in 1996. Data are means + 1 SE.

and fen plots. The bog plots showed the greatest heating effects in May–June, whereas the fen plots showed the greatest heating effects in both May–June and September–October. Moreover, the bog plots experienced a much steeper vertical temperature gradient in the soil during much of the summer, and the peat remained frozen longer in the bog plots during the beginning of the growing season. The physical characteristics of peat

that could affect their energy budgets (e.g., density, water-holding capacity) are a direct reflection of biotic processes (plant species composition, net primary production, and decomposition dynamics). Thus, we have demonstrated that significant biotic control over internal thermal conditions is at least a short-term response of peatlands to climate change.

The seasonality of the temperature response was a dominant factor in explaining all other treatment responses. Although we added infrared radiation year-round, soil temperature only increased during the growing season. Such a strong seasonal soil temperature signal is probably due to high heat loss from the mesocosms to the surrounding cold soils and air during the winter. This result emphasizes the importance of considering heat flow to groundwater, the atmosphere, and surrounding ecosystems in determining ecosystem temperature response to climate change. The seasonal temperature effect is likely exaggerated in the mesocosms, but similar qualitative effects would be expected to occur in natural ecosystems.

Soils in the plots receiving enhanced infrared radiative inputs actually cooled by up to 5.1°C on several dates during the 1995–1996 winter (Fig. 2). We suggest that these temperature anomalies were due to infrared treatment effects on snow cover. We quantified depth and cover of snow in the plots on several occasions during this winter, and enhanced infrared loading reduced snow cover by >50%, whereas ambient plots were always snow covered. The temperature anomalies did not begin until after there was deep snow cover in the ambient plots and very cold air temperatures. We suggest that during such periods enhanced infrared loading may paradoxically cool the soil due to melting of the insulating blanket of snow.

Evapotranspiration

Evapotranspiration is a central component of the energy and water fluxes within an ecosystem. As expected, greater infrared inputs and a water table closer to the surface enhanced ET. Moreover, there were important ecosystem differences in evapotranspiration rates, with the bog plots having from 12 to 23% greater cumulative ET than the fen plots. Additionally, ET in the fen plots was more sensitive to changes in water table level.

In contrast to our results, Ingram (1983) concluded that ET was lower in bogs dominated by mosses than in fens dominated by vascular plants. In another study, a higher maximum and daily amplitude of air temperature, yielding higher ET, was found in open *Sphagnum* areas compared to areas with trees or dwarf shrubs in Czechoslovakian peatlands (Neuhäusl 1975, as cited in Ingram 1983). Others have measured similar ET rates in bogs and fens (Tinbergen 1940, Nichols and Brown 1980, Lafleur and Rouse 1988).

The greater sensitivity of ET in the fen plots to changes in water table level is somewhat surprising,

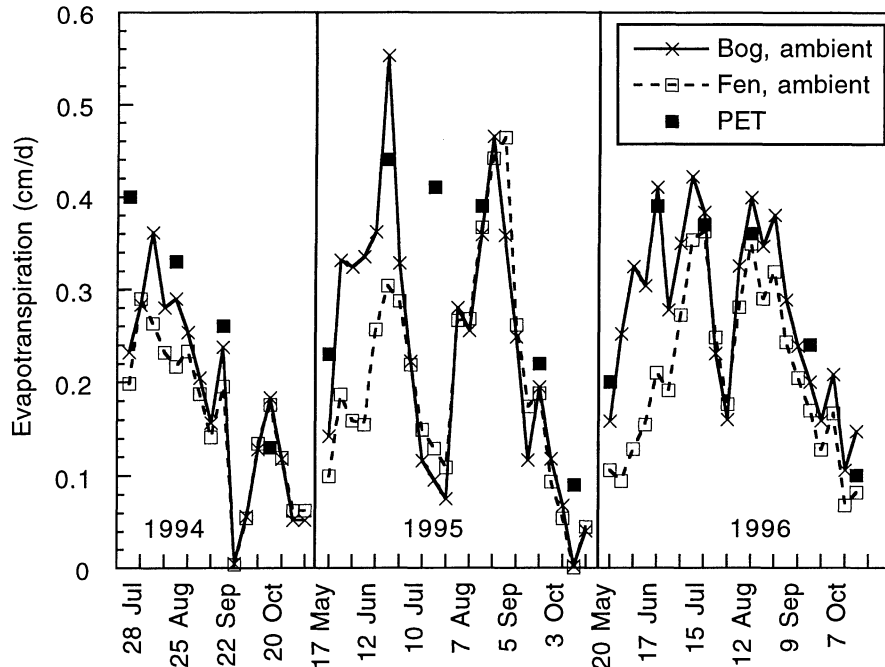


FIG. 5. Evapotranspiration determined over approximately weekly intervals for ambient bog and fen plots averaged over water table treatments from 1994 to 1996. PET refers to potential evapotranspiration estimated by the Thornthwaite equation.

because the fen plots are dominated by vascular plants that can access water within the rooting zone, whereas the bog plots are dominated by nonvascular mosses. However, hummock-forming *Sphagnum* species, which dominate our bog plots, have pendent branches that are tightly appressed to their stems, forming a “wick” that effectively transports water by capillary action to the surface (Rydin 1985). Moreover, *Sphagnum* leaves have very large surface area and are composed of numerous porous, dead hyaline cells that can store large amounts of water (Clymo and Hayward 1982).

The seasonal dynamics of the canopies of the two plant communities may explain many of their seasonal differences in ET. The bog plots have >95% cover by *Sphagnum* mosses, which stay green underneath the snow and start photosynthesizing as soon as the snow melts. In contrast, the fen plots are dominated by graminoids, which do not have a fully developed green canopy until midsummer and experience dieback in the autumn. This seasonality in the canopies is translated into the observed differences in ET (Fig. 5), with ET in the bog plots much greater until about the beginning of July, when differences are either small or nonsignificant. Large differences in ET also occurred in autumn, particularly in 1996, when the fen vegetation had begun to senesce.

The seasonal dynamics of ET, driven by the canopy dynamics of the two communities, also likely explain our observed temporal effects of heating on soil temperature during the growing season (Fig. 2). The mid-summer depression of the effect of heating on soil tem-

perature response is likely due to higher ET during this period (Fig. 5). This effect appears to dissipate in the fall in the fen plots with the senescence of their canopy, but not in the bog plots with their evergreen canopies.

We estimated the latent heat of ET from each plot, assuming the peat to be 90% moisture by volume, with a latent heat of 2.46 MJ/L. Relative to ambient (i.e., unheated) conditions, the full-heat plots lost an additional 3.5–6.9 MJ/d averaged over the growing season from 1994 to 1996. This corresponds to a cooling of 0.7°–1.3°C, indicating that higher ET significantly ameliorated the heating effects of increased infrared loading. Over this 3-yr period, latent heat loss in the bog plots averaged over all heating treatments was 1.7–3.7 MJ/d greater than in the fen plots, accounting for 0.3–0.7°C of the cooler temperature found in the bog plots (about a third to a half of the actual temperature differential). Other factors such as soil moisture, atmospheric humidity in the canopy layer, and the amount of green vegetation also govern the partitioning of available radiative energy into latent and sensible heat fluxes (Bolle 1990).

Overall, ET was a dominant component of the energy budget in these ecosystems. The latent heat of evaporation in our ambient plots ranged from 8.9 to 15.0 MJ·m⁻²·d⁻¹. We did not measure net radiation in our plots, but we can compare them to Nebraska Sandhills wetlands, where net radiation was ~16 MJ·m⁻²·d⁻¹ over two growing seasons (Goodin et al. 1996). If we assume similar values in our plots, ET was the dominant pathway of net energy loss in the ambient plots,

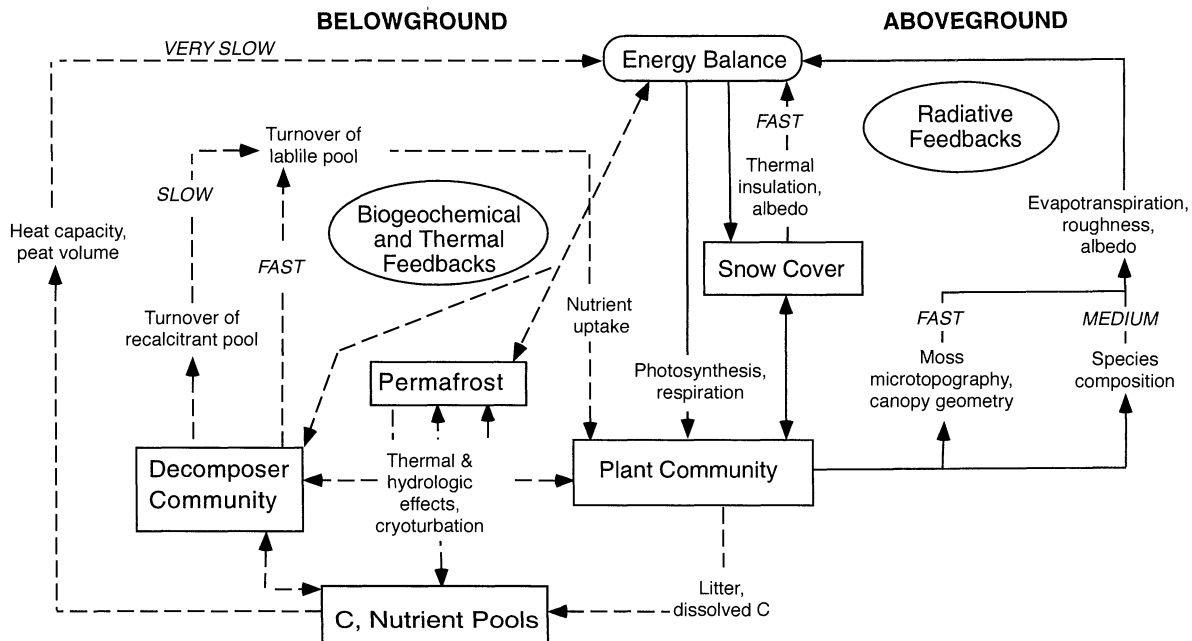


FIG. 6. A conceptual model of feedbacks among ecosystem energy balance, plant community composition, snow cover, and carbon and nutrient pools in peatlands.

and would have considerably reduced sensible heat and temperature response. Similar calculations cannot be made for the heated plots, as we did not continuously measure the actual amount of infrared radiation entering the plots from the heat lamps, which varied considerably, particularly in relation to wind speed. However, we would expect a similar importance of latent heat flux in the heated plots.

A conceptual framework for biogeophysical feedbacks in peatlands

Biotic processes in northern ecosystems are constrained by low temperatures and short growing seasons (e.g., Van Cleve et al. 1991), and predicted warmer temperatures under climate change will likely have a direct impact on these ecosystems by reducing temperature constraints (Apps et al. 1993, Bridgham et al. 1995). However, our results suggest that the effects of climate change may be much more complicated than predicted by direct temperature effects. In particular, we have demonstrated that northern peatlands have a significant degree of internal control over their energy budgets that is likely mediated through a variety of ecosystem and community feedback loops.

We have developed a conceptual model of potential biogeophysical feedbacks that may be operating in these peatlands (Fig. 6). The energy balance (including both long- and short-wave radiation) directly mediates processes such as photosynthesis and respiration of both the autotrophic and heterotrophic communities. On the right side of the figure are aboveground radiative feedbacks that are the result of changes in plant com-

munity composition, canopy characteristics, and snow cover. In our mesocosm experiment, we have observed significant changes in plant species composition, microtopography due to differential moss growth in various microhabitats, and the canopy geometry of shrubs after only 1 or 2 yr under our various climate treatments (S. D. Bridgham et al., unpublished data). Also, we have observed large changes in snow cover that we suggest are important in controlling winter soil temperatures and depth and duration of soil freezing. Thus, aboveground changes in plant community composition, canopy characteristics, and snow cover have a moderate to fast response time to climatic perturbations. Longer lived vegetation, such as black spruce, would have a slower response time. In turn, these variables control evapotranspiration rates, surface roughness, albedo, and the thermal insulation of the soil, which are important controls over the energy balance of the ecosystem.

Belowground biogeochemical processes also affect energy flow and storage, mediated by temperature-regulated changes in microbial respiration rates and plant inputs of organic matter (Fig. 6). Biogeochemical feedbacks involve changes in the rate of cycling of carbon and nutrients, which in turn provide the nutrients for plant growth and can have significant control over plant community composition and canopy characteristics (Pastor et al. 1984, Van Cleve et al. 1991). In our experiment, we observed significant changes in net ecosystem respiration (measured as CH₄ and CO₂ flux), nutrient availability, and nutrient and carbon flux in porewater after only 1 yr of treatment (S. D. Bridgham

et al., unpublished data). Thus, changes in nutrient and carbon cycling due to climate change appear to have a relatively fast response time, likely due to the turnover of a relatively labile carbon pool (cf. Bridgham et al. 1998).

Through the vast amounts of soil organic matter stored as peat and accompanying water storage, these wetlands also serve as very large heat sinks. As the net carbon balance (i.e., production minus decomposition) of these systems shifts with climate change, then peat volume, and hence its heat capacity, will also change, adding another internal ecosystem thermal feedback (Fig. 6). We expect this feedback to have a very long response time due to the size of the soil carbon pool. However, studies of peatlands drained for agriculture and forestry practices indicate that much drier climatic conditions could result in rapid oxidation of the peat stores in these wetlands and serve as an additional, potentially very large, source of atmospheric carbon dioxide (Armentano and Menges 1986, Gorham 1991, Bridgham et al. 1995).

Minnesota peatlands are at the southern edge of the boreal zone and do not have permafrost. However, a substantial fraction of peatlands are in the zones of continuous or discontinuous permafrost (Gorham 1991, Bridgham et al. 1999). Studies of peatlands in these zones have shown important ecosystem feedbacks on the formation and stability of permafrost (Fig. 6). For example, succession in Alaskan taiga forests leads to *Picea mariana* with a thick understory carpet of feather mosses that have low thermal conductance. This results in a dramatic reduction in soil temperature, which in turn causes a reduction in decomposition rates, a build-up of peat, and eventually the formation of permafrost (Van Cleve et al. 1991). Similarly, local processes, particularly *Sphagnum fuscum* cover, were found to be more important than regional temperature gradients in controlling permafrost dynamics in Canadian peatlands (Camill and Clark 1998). The mixing of permafrost-affected soils by cryoturbation (i.e., freeze-thaw processes) has a large impact on their soil structure, soil carbon pool size and bioavailability, and hydrologic characteristics (Michaelson et al. 1996). Additionally, the formation and development of several major peatland types are the direct result of permafrost action (Moore and Bellamy 1974, National Wetlands Working Group 1988).

Ecologically significant feedbacks between biotic processes and energy flux at multiple spatial scales are a generalizable attribute of most ecosystems. Net radiation was found to vary significantly in different parts of Nebraska Sandhill wetlands, primarily due to albedo differences reflecting canopy height or open-water coverage (Goodin et al. 1996). Similarly, significant microclimatic differences occur among forests, forest edges, clearcuts, and streams (Chen et al. 1993, 1995, Brosofske et al. 1997), and dynamic variation exists in many climatic variables at various spatial and temporal

scales (Chen et al. 1996, 1999). Fertilization of arctic tundra increased net primary production and soil litter accumulation, decreasing soil temperatures and subsequently causing an inhibition of methanogenesis (Moosavi and Crill 1998). Arctic moist acidic and non-acidic tundra communities had large differences in energy and carbon fluxes, despite close proximity, because of biogeophysical feedbacks within each community (Walker et al. 1998). Energy budgets were more strongly correlated with community type than with climate. McFadden et al. (1998) found large differences in heat and energy fluxes among various arctic ecosystems along a climatic gradient. They caution that shifts in dominant vegetation types with climate change could be an important regional climate-forcing function. Moreover, models predict that changes in the boundary between boreal forest and tundra can have dramatic impacts on climate at hemispheric to global scales (Bonan et al. 1992, Foley et al. 1994). Camill and Clark (1998) suggested that transient responses to climate change of peatlands in the discontinuous permafrost zone could be quite complex and be driven locally by small-scale vegetation and ecosystem processes.

All these examples suggest that shifts in vegetation caused by anthropogenic, global-scale climate change may cause unexpected, but potentially dramatic, changes in local and regional climate through internal ecosystem control of energy fluxes. Additionally, our research has demonstrated that these feedbacks can occur within 1 yr under an altered climatic regime. Most previous research on potential terrestrial ecosystem feedbacks to climate change has focused on the effects of carbon storage and trace gas emissions. Our study and those cited above suggest that the biogeophysical dynamics of ecosystems may be as important as their biogeochemistry in determining their response to climate change (cf. Melillo et al. 1996). Regional and global climate models need to include ecosystem effects on energy fluxes if they are to effectively capture climatic responses to the greenhouse effect.

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