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RESPONSE OF CO₂ AND CH₄ EMISSIONS FROM PEATLANDS TO WARMING AND WATER TABLE MANIPULATION

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Abstract. Projected changes in climate could shift northern peatlands from their current status as net C sinks toward that of being net C sources by changing soil temperatures and hydrology. We assessed the importance of water table and soil temperature as controls over ecosystem respiration in a bog and sedge fen in northern Minnesota, USA, by means of a manipulative mesocosm experiment. Fifty-four intact monoliths were removed from a bog and a fen and installed in insulated tanks that permitted control of the water table and were heated by overhead infrared heaters. The experimental design was a fully crossed factorial combination of two communities, three water tables, and three heat levels. Ecosystem respiration as indicated by emission of CO₂ and CH₄, dissolved nutrient fluxes, and productivity were measured and summarized for each growing season from 1995 to 1997.

Seasonal ecosystem respiration (ER) as indicated by CO₂ emissions responded almost exclusively to soil temperature and did not differ between community types (~630 g C/m²) or with water table level. These results suggest that community type, within certain limits, will not be an important factor in predicting temperature-driven increases in ER.

The response of CH₄ flux to soil temperature and water table setting became progressively stronger in each succeeding growing season. Seasonal CH₄ emissions were on average three times higher in the bog than in the fen mesocosms (21 vs. 7 g C/m²). Aboveground net primary productivity and dissolved N retention were also higher in the bog mesocosms. There were strong correlations between CH₄ flux and N retention, but generally weak correlations between CH₄ and plant primary production. The relatively lower CH₄ emissions from the fen mesocosms appear to result mainly from higher rates of methanotrophy in the aerated zone, possibly reinforced by the effects of higher porewater N concentrations and lower primary productivity compared to the bogs.

The results confirm the existence of strong environmental controls over ER and methanogenesis, which are modulated by complex interactions between plant community and soil nutrient dynamics. The differential responses of these ecosystem functions to climate change may complicate efforts to predict future changes in C dynamics in these important repositories of soil C.

Key words: C dynamics; CH₄; climate change; CO₂; dissolved N; Minnesota, USA; net primary productivity; peatlands; soil respiration; soil temperature; water table; wetlands.

INTRODUCTION

Approximately one-third of the world's soil carbon (C) is currently sequestered in boreal peatlands (Gorham 1991), although they occupy only ~2% of the earth's surface. Globally, peatlands account for as much as 9% of the methane (CH₄) released from natural sources (Bartlett and Harriss 1993). The potential impact of large shifts in peatland C dynamics on atmospheric chemistry is therefore considerable. Increases in atmospheric carbon dioxide (CO₂), methane, and other greenhouse gas concentrations are predicted to raise global mean temperatures up to 4.5°C by 2100 (Kattenberg et al. 1996). This increase is likely to be most pronounced in the boreal and arctic regions, re-

sulting in possible augmentation of both productivity (Chapin and Shaver 1996) and decomposition rates (Goulden et al. 1998). More rapid decomposition could result in a positive climatic feedback by accelerating the rate of increase in atmospheric CO₂ and CH₄ concentrations. Alternatively, increased productivity resulting from warmer mean temperatures and longer growing seasons would result in a negative feedback as more C was immobilized in biomass, although this might be offset by increased rates of decomposition. Whiting and Chanton (1993) demonstrated a strong correlation between primary productivity and CH₄ emissions across a range of wetland types. Peat accumulation rates may depend largely on the decomposition component of the production–decomposition mass balance (Clymo 1984). Therefore, predicting the contribution of peatlands to potential changes in the greenhouse gas composition of the atmosphere may

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depend partly on better elucidation of the dynamic balance between peatland productivity and decomposition (Tenhunen et al. 1995).

It has been suggested that, while boreal wetlands have historically accumulated C (Armentano and Menges 1986, Billings 1987, Gorham 1991, Alm et al. 1997), a warmer climate might convert them to net C sources by accelerating decomposition more than productivity. This may be particularly true if drier growing seasons (Manabe and Wetherald 1987) result in more rapid peat oxidation. However, forested fens in Finland were shown to store more C following drainage due to the increase in woody biomass, which offset peat oxidation (Laine and Vasander 1991, Laine and Minkinen 1996).

Studies of wetland ecosystem processes have often suffered from an inability either to control or measure key variables (such as groundwater fluxes). Most field studies that have examined trace gas fluxes have necessarily resorted to a correlative approach to link potential controlling variables and measured fluxes (Bubier et al. 1993, Whiting and Chanton 1993, Shannon and White 1994, Bridgham et al. 1995, Alm et al. 1997). While these studies have contributed valuable information, changes in many environmental variables are highly autocorrelated across wetland community gradients (Bridgham et al. 1996), and cause/effect relationships are difficult to verify. Moreover, correlative relationships across ecological gradients may not be good predictors of climatically induced changes within a particular wetland community. At the same time, there are logistical constraints on our ability to simulate the complex interactions between state factors in a controlled setting.

The limitations of both simulation modeling and correlative field approaches suggest the need for an experimental approach wherein climatic variables can be manipulated in a controlled manner. Such an approach would allow scope for the expression of autogenic controls (vegetation and nutrient dynamics) over the response of peatland ecosystems to changes in ambient temperature and hydrology. The response of ecosystem respiration (as CO₂ and CH₄) to climate change will reflect a combination of controlling factors, including plant community dynamics, net primary production (NPP), water table level, soil temperature, and nutrient availability.

There is substantial evidence that temperature and aeration status are the dominant controls over decomposition rates in peat soils (e.g., Svensson 1980, Benner et al. 1986, Johnsson and Damman 1991, Hogg 1993, Updegraff et al. 1995, Bridgham et al. 1998). Decomposition constitutes the largest source of respired CO₂ and CH₄ in soils. The main objectives of this paper are to evaluate the extent to which temperature and water table elevation control respiratory soil and plant C fluxes in peatland ecosystems and to explore the underlying mechanisms for the observed responses. By quantify-

ing these processes in intact ecosystems that allowed for natural interactions and feedbacks, we expected to improve our understanding of the extent of climate-related controls over boreal wetland C dynamics.

To this end we developed a mesocosm facility using 54 2.1-m² intact peatland monoliths contained in tanks that permit control of both soil temperature and water table. At the same time we quantified dissolved nutrient and C inputs and outputs, gaseous C emissions, and net primary productivity and plant community dynamics. These data were used to test the following hypotheses: (1) CO₂ respiratory flux within a given community would be primarily affected by soil temperature, with a secondary effect of water table level; (2) CH₄ flux within a given community would depend primarily on water table elevation, with a secondary effect of temperature; (3) both CH₄ and CO₂ fluxes would be greater in fens than in bogs because of higher soil C quality (substrate availability) in fens; (4) plant productivity would have a smaller effect than the physical variables (temperature, water table) on respiratory C flux. These hypotheses were evaluated based on data accumulated during three years of continuous manipulation of soil temperature and water table in bog and fen mesocosms.

METHODS

Experimental design

We designed a manipulative experiment as a 2 × 3 × 3 complete factorial, with two community types, three levels of infrared loading, and three water table elevations. The plots were set up in three rows, with alternating bog and fen mesocosms. Infrared and water table treatments were distributed randomly within each community type. Infrared input was controlled by regulating heater output, but soil temperature was actually a response variable. Water tables were initially set at +1, -10, and -20 cm relative to marked "datum hollows" (representative low spots), but as mosses grew in the bogs, the actual water tables dropped up to 11 cm relative to the datum locations. (This was not the case in the fens, where water tables remained roughly as set.) Therefore it was at times appropriate to treat water table as a continuous variable.

Sites

We selected two wetlands representing contrasting peat-forming communities: a patterned sedge (*Cyperaceae*) fen and a raised *Sphagnum* bog. Laboratory incubations of peat samples from these sites indicated that rates of both aerobic and anaerobic C turnover, measured as CO₂ and CH₄ emissions, were much higher in fen peat than in bog peat (Bridgham et al. 1998). These ecosystems are widely represented across the circumpolar boreal zone. Both sites are within 15 km of our experimental facility, in the glacial Lake Upham basin at 47° N, 92° W, ~65 km northwest of Duluth, Minnesota, USA.

The bog site forms the open center of the Toivola bog complex, where summer water tables routinely drop to -30 cm or lower, with somewhat attenuated hummock/hollow development. The dominant moss cover is a mix of *Sphagnum fuscum*, *S. capillifolium*, *S. magellanicum*, and *Polytricum strictum*.

Shrub cover is comprised largely of *Chamaedaphne calyculata*, *Ledum groenlandicum*, *Kalmia polifolia*, *Andromeda glaucophylla*, and *Vaccinium oxycoccus*. There is limited graminoid cover, including tussocks of *Eriophorum spissum* and scattered *Carex oligospermum*. Porewater pH at Toivola is generally <4 , with a mean H-corrected specific conductivity of ~ 1 $\mu\text{S}/\text{cm}$.

The fen site, near the township of Alborn, is part of an extensive patterned fen system. Water tables generally are above $+3$ – 4 cm in the flarks (pools). The flarks are dominated by wetland graminoid species such as *Carex lasiocarpa*, *C. livida*, *Scheuchzeria palustris*, *Rhynchospora* spp., and *Eriophorum* spp. The monolith source sites were located mainly in flarks in order to minimize within-plot variability and maximize vegetation contrast with the bog. Porewater pH is ~ 5 and mean conductivity is 9.3 $\mu\text{S}/\text{cm}$. Porewater cation concentrations (Mg, Ca, and Na) in samples of fen porewaters analyzed in 1995 were at least twice those seen in bog waters, although K was half as high as in the bog.

Mesocosm installation

A more complete description of the project setup is provided in Bridgman et al. (1999). A brief summary follows.

The mesocosm facility was constructed at the Fens Research Facility (FRF), a field station owned by the University of Minnesota, which was selected for its convenient access to a paved road, power, and communications, as well as its proximity to a wide variety of undisturbed wetland areas. Fifty-four 1.5 m diameter plastic stock tanks were insulated with urethane foam and installed in three 60-m trenches. Perforated polyvinyl chloride (PVC) pipes in the bottom of each tank ensured even drainage to the single outlet. Each outlet was connected via flexible tubing and PVC fittings to a 60-L sump bucket set level with the main tank. Within the sump bucket, the inlet fitting was connected to a vertical pipe which acted as a manostat to control the water table level within the main tank. The buckets had tight-fitting lids to prevent evaporation of overflow.

In late March of 1994 (while the ground was still frozen) a backhoe equipped with a large steel ring and a hydraulic clamshell device was used to excavate and remove 27 0.6 m deep, 1.5 m diameter peat monoliths from each source site. These were wrapped in polyethylene and protective aluminum flashing and transported to the FRF, where they were installed in the tanks. The surfaces of the frozen monoliths were largely undisturbed by removal and transfer.

Water tables were set by late May of 1994 and were maintained by weekly additions, as needed, of water pumped from a drainage channel near the bog source site. This water was similar to the bog porewater with respect to pH (4), although conductivity (9.6 $\mu\text{S}/\text{cm}$) was closer to that seen in the fen water. Nutrient (N and P) content, determined periodically, was comparable to that seen in bog porewater. The water was transported in a 1900-L tank and distributed via metered outlets to perforated standpipes in the center of each mesocosm, which allowed rapid diffusion of added water directly into the peat profile. This method circumvented a problem that commonly occurs when bog water is surface-applied to bryophytes: the mosses absorb and retain the dissolved humic material and become darkly stained, with unknown implications for surface albedo and plant function.

Because of our desire to maintain experimentally comparable conditions in both communities, we elected to set initial water tables at identical depths below a marked hollow (a representative low spot) in all the mesocosms. This decision has important implications for the interpretation of experimental data. At the fen source site the flarks typically have at least several centimeters of standing water, while standing water is seen in the bog hollows only under the wettest conditions. In the mesocosms, nominal water tables (nominal because water tables were reset weekly) ranged from 1 to -19 cm, depending on treatment. Therefore the fen mesocosms were much drier than the source site, especially in the low water table treatments. By contrast, nominal water tables in the bog mesocosms were quite similar to those seen at the bog source site, even though moss growth in the hollows resulted in an effective decline (by ~ 10 cm between 1995 and 1997) of bog mesocosm water tables.

Precipitation overflow collected in the sump buckets, where its depth was measured prior to pumping out. Rarely, large precipitation events resulted in such rapid overflow that the sump systems in some mesocosms were overwhelmed. On these occasions it was necessary to estimate actual amount of overflow by applying the average value for nonoverflowed replicates. Total outflow from both precipitation and excess additions of water was summed and subtracted from total inputs (rain + ditchwater) to obtain weekly, monthly, and seasonal water balances and also to estimate evapotranspiration (ET) losses (Bridgman et al. 1999). Water balances could not be calculated on an annual basis due to the necessity of disconnecting the tank plumbing to avoid ice damage in the winter. Therefore our "season" with respect to water budget calculations typically extended from early May to early October.

Soil heating was accomplished using overhead infrared heaters (Kalglo, Bethlehem, Pennsylvania, USA), which were installed during July 1994, ~ 130 cm above mean surface (moss or soil) level. Each 1500-W, 1.5 m long heater was sufficient to warm an entire

mesocosm. We estimated ground-level infrared (IR) inputs at a nominal 78 and 191 W/m² above background levels at half and full power, respectively, based on measurements with a THRDS-7 Total Hemispheric Radiometer (Radiation and Energy Balance Systems, Seattle, Washington, USA). Operationally, net IR inputs depended on many external factors, in particular wind-speed, and in practice was about half of our nominal values (J. Chen, *unpublished data*). Cover characteristics also influenced net IR inputs, with the result that the fen plots were, on average, 0.8°–1°C warmer than the bog plots. Overall increases in mean growing-season soil temperature ranged from 1.6° to 4.1°C (Bridgman et al. 1999). Many of the mechanical controllers of the infrared lamps failed, and by 1996 many of the “half-heat” treatments were in fact receiving full heat. All the controllers were replaced with digital models early in 1998, enabling the restoration of our original settings.

Soil temperatures were monitored using a single type-T glass-encased thermocouple, inserted to 15 cm, in each mesocosm. Thermocouples were calibrated using ice-water and ambient-temperature baths. Beginning in June 1995, a data acquisition system in an on-site shed recorded mean soil temperatures at hourly intervals. Prior to installing the data acquisition hardware, we used a hand-held meter connected directly to the thermocouples to measure soil temperature.

Gas fluxes

Ecosystem respiration (ER) was sampled at 2–3-wk intervals, throughout the growing seasons (May through September) of 1995–1997. The sampling days therefore represented the entire range of growing-season conditions, with soil temperatures ranging from 0° to 26°C. Because we were able to seal off each mesocosm under the chambers described below, the CO₂ and CH₄ fluxes represented the sum of both soil and plant (dark) respiration for the entire mesocosm.

We made portable static chambers that fit over the mesocosms on half-dome frames of steel conduit and fiberglass tent poles. These frames were covered variously with layers of FEP film (Norton Performance Plastics, Wayne, New Jersey, USA), metallized nylon-EVA (James River, Shreveport, Louisiana, USA) (for gas and light impermeability), and a white cross-laminated polyethylene vapor-barrier material for protection of the inner layers of teflon or nylon film. The plastic film “tent” was sealed to the sides of the tank using a ratchet-type load strap over closed-cell foam weatherstripping. The reflective white cover also served to keep the chambers cool, generally resulting in air temperature increases of <3°C during incubations. Soil temperature changes during the incubations were negligible. Small battery-operated fans were hung from the top of each dome to mix the chamber air. Approximate chamber volume was 1000 L, which was estimated as described below.

Using five chambers and total incubation times of ~40 min, we obtained flux measurements for all the mesocosms over a period of 2 d, usually between 0900 and 1600. Following at least a 10-min wait to allow for equilibration of chamber air, we withdrew a series of three duplicate samples at 15–20-min intervals from septum ports in the sides of the chambers. We used 10-mL nylon gas syringes with caps to collect and store our samples. Gas samples were usually run within 48 h, and flux rates were calculated based on the linear accumulation of CO₂ and CH₄. Linear estimates with *R*² values of <0.9 were not used (<5% of plots were unusable in any given sample period). Samples were analyzed for CO₂ on a Shimadzu GC 14-A (Shimadzu Scientific Instruments, Columbia, Maryland, USA) equipped with a 2-m Porapak Q column and thermal conductivity detector (TCD) and for CH₄ on a Hewlett Packard 5890 (Hewlett Packard, Palo Alto, California, USA) equipped with a 2-m Porapak Q column and flame ionization detector (FID).

For each sampled mesocosm we recorded the water table measured within the manostat pipe, as well as the air and soil temperatures. We obtained estimates of chamber volume by injecting known amounts of SF₆, an inert gas, prior to the last sample of the incubation. SF₆ is a convenient tracer, as it is detectable by TCD and may be analyzed simultaneously with CO₂.

Net ecosystem production

During the 1996 growing season we constructed an open chamber system modeled on that developed by Garcia et al. (1990), using a LI-COR 6400 Photosynthesis System (LI-COR, Lincoln, Nebraska, USA), that allowed rapid measurement of whole-mesocosm net ecosystem production (NEP). It consisted of a PVC frame ~1 m high that conformed to the shape of the mesocosm tank, covered with Propafilm CK (ICI Americas, Wilmington, Delaware, USA), a clear, PVDC-coated polypropylene film, and plates of rigid Plexiglas at either (flat) end. On these we installed 10 cm diameter PVC closet flanges for air intake and exhaust. The intake port fed into a perforated plastic baffle for even distribution of air. Two small fans mounted near the top of the chamber ensured mixing of the chamber air. The exhaust port was also baffled on the outside to prevent wind incursion. Air sampling inlets were installed in both the intake and exhaust flanges and connected to the paired infrared CO₂ analyzers on the LI-COR via Bev-a-line tubing and a 12-V double-headed diaphragm sampling pump (Brailsford, Rye, New York, USA). Type-E thermocouples installed in the intake and exhaust ducts allowed measurement of input and chamber air temperatures. The input air was pumped using a pair of 435 CFM two-speed blowers (Grainger, Plymouth, Minnesota, USA) that drew air through a 3-m vertical pipe into a large plywood box that served as a buffer volume. The height of the intake pipe and the buffer volume helped minimize variability

in the temperature and CO₂ concentrations of the air entering the chamber. The dual blowers provided a flow rate of ~2000 L/min, or two chamber volumes per minute, as measured by a flow-transducer (TSI, St. Paul, Minnesota, USA) in the intake pipe.

The chambers developed a slight positive pressure, which minimized the risk of contamination by inward leakage or diffusion. Garcia et al. (1990) noted that positive pressure tended to suppress soil respiration, as documented by Nakayama and Kimbal (1988), making this method unreliable for the estimation of absolute soil CO₂ fluxes. Therefore it is likely that our method slightly underestimated soil CO₂ fluxes. However, because this system was primarily intended to measure whole-ecosystem CO₂ fluxes—of which plants were the major components—we felt that the system was very sensitive to both temporal and spatial differences in NEP. For gross primary production (GPP) estimation, which required that the respiration component be added back in, we used respiration estimates derived from the regressions based on static-tent measurements.

We began regular measurements of whole-mesocosm NEP in mid-July of 1996, obtaining six measurements through September, and in 1997 we measured NEP at 3-wk intervals from early June to late September. At each date, we recorded 5 min of NEP data for each of the “corner treatment” mesocosms. The corner treatments represent the extremes of our 3 × 3 factorial treatment matrix, i.e., no heat or high heat at water table of +1 cm, no heat or high heat at water table of -20 cm. The regressions developed for estimating CO₂ and CH₄ flux were applied to the soil temperature and water table data collected during NEP measurements, and the resulting respiration estimates were added to the NEP values to generate estimates of instantaneous gross primary production. NEP data for the “corner” mesocosms were collected in weeks subsequent to static chamber measurements of ER.

Net primary productivity

Above- and belowground net primary productivity were measured beginning in 1994 and using a variety of methods, detailed in Weltzin et al. (2000), and summarized briefly below. In order to quantify shrub and graminoid productivity, four permanent 10 × 50-cm subplots were marked with stakes in each mesocosm and used for annual counts and measurements of the included vegetation. Aboveground net primary productivity (ANPP) was then estimated using a combination of allometric relationships and mean masses for shrub, forb, and graminoid species. Bryophyte ANPP was estimated by combining areal estimates of cover with monthly measurements of cranked wires (Clymo 1970), and allometric relationships between stem length and mass. Aboveground net primary productivity estimates were made annually from 1994 through 1997, by summing estimates by species and functional group (bryophytes, forbs, graminoids, and shrubs).

Belowground net primary productivity (BNPP) was estimated using root ingrowth cores, approximately five 27-cm cylinders sewn from polyethylene netting (0.5-cm mesh size) and filled with milled peat from the appropriate source site. These cores (three per mesocosm) were carefully cut out and removed each September, and immediately replaced with fresh cores, which then had the entire winter to equilibrate with their surroundings. The removed cores were emptied into polyethylene bags and refrigerated prior to processing. Each core was weighed, subsampled for moisture content, then homogenized by hand and divided roughly in half. The retained portion of the core was weighed, washed over a 0.6 mm screen, then sorted with forceps to locate live roots. We estimated areal root productivity values (BNPP) based on a rooting depth of 27 cm (the length of the core), root mass, and sample volume. Root mass below 27 cm was assumed to be negligible.

Water analyses

Porewater was collected monthly throughout each growing season by pumping samples through the manostat pipes in the sump buckets. This method ensured that we obtained an “integrated” water sample that represented the whole profile. Samples were collected at least 24 h after any additions of ditchwater and never during precipitation events. Water samples were refrigerated and analyzed for pH within 24 h, then filtered using glass-fiber syringe filters. Subsamples were subjected to persulfate digestion for total N (Owen and Axler 1991), and colorimetric analysis by autoanalyzer for NO₃-N and NH₄-N (Quickchem methods 12-107-04-1-A and 10-107-06-2-C, respectively, Lachat Instruments, Mequon, Wisconsin, USA).

Dissolved nitrogen (N) fluxes were estimated by the difference between N added (in rainwater and bogwater) and N leached (in porewater outflow). Concentrations of dissolved N were multiplied by monthly water budgets to obtain estimates of monthly mass balances (“net N”). Thus, higher values for net N imply greater N retention in the mesocosm. These balances were summed over the growing season, early May through early October.

STATISTICAL METHODS

Regressions.—The Systat (SPSS 1997) package was used for all statistical analyses. We derived seasonal estimates for gaseous C emissions either by interpolation between measurement dates or from regressions of instantaneous flux rates against measured soil temperature and water table (Table 1). Both CO₂ and CH₄ were exponentially distributed and were linearized using log transformations. These transformations provided better fits (*R*² and significance level) with respect to soil temperature and water table, although some resolution may have been lost in the back-transformed predicted values. Generally a single regression provid-

TABLE 1. Linear regression coefficients used to estimate daily emissions of CO₂ and CH₄ based on soil temperature and nominal water table in a bog and a sedge fen in northern Minnesota, USA.

Dependent variable	Site	Year	Constant			Soil temperature		
			Intercept	SE	P	Coefficient	SE	P
ln(CO ₂)	Fen	1995	3.49	0.10	0.000	0.120	0.006	0.000
		1996	3.67	0.10	0.000	0.138	0.006	0.000
		1997a	4.13	0.12	0.000	0.094	0.008	0.000
		1997b	2.99	0.24	0.000	0.153	0.016	0.000
	Bog	1995	3.88	0.11	0.000	0.095	0.006	0.000
		1996	4.67	0.10	0.000	0.088	0.006	0.000
		1997a†	5.33	0.11	0.000	0.033	0.008	0.000
ln(CH ₄)	Fen	1997b	3.74	0.01	0.000	0.124	0.012	0.000
		1995†	0.28	0.363	0.443	0.065	0.019	0.001
		1996	0.03	0.167	0.854	0.120	0.010	0.000
		1997a	-0.24	0.215	0.276	0.137	0.014	0.000
		1997b	0.53	0.352	0.149	0.083	0.023	0.002
	Bog	1995†	1.05	0.40	0.010	0.061	0.020	0.004
		1996	1.44	0.26	0.000	0.111	0.011	0.000
		1997a	0.68	0.33	0.051	0.129	0.018	0.000
		1997b	1.84	0.20	0.000	0.083	0.012	0.000

Notes: Resulting flux values are in millimoles per square meter per day. Coefficients for 1997 apply to two approximately equal periods.

† These regressions not used: estimates obtained by interpolation.

ed a satisfactory fit to the ER data over an entire growing season. However, in July 1997 our data acquisition system was struck by lightning and had to be replaced. An artifact of the repair process was that, due to the change in hardware offsets, we blocked the temperature data recorded before and after the replacement separately. Since we were unable to obtain an acceptable regression for CO₂ flux in the bog mesocosms during May–July of 1997, we interpolated between sample dates to estimate daily gas fluxes.

Methane flux was not strongly correlated with either (measured) temperature or water table for the 1995 growing season. Therefore we estimated daily flux rates based on linear interpolation between sample dates. In 1996 and 1997, however, the strong relationships between soil temperature and nominal water table (water table as set by the manostat) and CH₄ emission rates led us to estimate daily emissions based on these regressions.

Estimates of daily ER and CH₄ flux were based on recorded hourly soil temperature averages. This allowed diurnal fluctuations in temperature to be reflected in estimated flux rates. Daily rates were summed over the growing season, which was defined as the period between 15 May and 15 October, to provide estimates of total respired C.

Fixed-effects ANOVAs.—We used a repeated-measures ANOVA model with year as the within-subjects factor and community type, water table, and heating level as the between-subjects factors (Scheiner and Gurevitch 1993). The data were tested for normality using the Kolmogorov-Smirnov procedure, comparing to a standardized normal distribution (Lillifors test) (SPSS 1997). Data were log normalized where the transformation resulted in a significant improvement in overall distribution. The repeated-measures ANOVA

approach probably resulted in a fairly conservative assessment of heating effect, as the difference in soil temperature between the high and medium heat treatments was insignificant during at least one out of the three years. Season-total ecosystem respiration, dissolved N balances, and NPP were compared among ecosystems and treatments from 1995 to 1997. However, since soil temperature and water table were used to predict daily ER and CH₄ fluxes (Table 1), we did not include heat or water table level as main effects in the ANOVA analysis of seasonal values. Where appropriate, we also looked at treatment effects on within-season variables using a repeated measures analysis with month as the within-subjects factor. However, our focus with respect to the hypotheses stated above was on long-term cumulative effects, measured on an annual scale.

GPP estimation.—The periodic measurements of instantaneous NEP in 1996 and 1997 were combined with (regression-based) estimates of instantaneous CH₄ and CO₂ fluxes in order to generate point estimates of GPP. We compared the equality of slopes of the regressions between point estimates of CH₄ flux and GPP among the various treatments using the method outlined in Sokal and Rohlf (1995). While CH₄ flux was used to calculate GPP, it was a minor component of total ecosystem respiration, so the regression relationships do not reflect autocorrelation between these two variables. Regressions between CH₄ flux and NEP gave substantially similar relationships. In addition, we used a repeated-measures ANOVA framework to assess treatment effects on both NEP and GPP within the 1996 and 1997 growing seasons.

RESULTS

Community type was a more important influence on most response variables than were either water table

TABLE 1. Extended.

Nominal water table			R ²	P
Coefficient	SE	P		
			0.83	0.000
			0.84	0.000
			0.81	0.000
			0.79	0.000
			0.71	0.000
			0.69	0.000
			0.34	0.000
			0.80	0.000
0.076	0.010	0.000	0.40	0.000
0.097	0.085	0.000	0.82	0.000
0.096	0.006	0.000	0.92	0.000
0.110	0.007	0.002	0.91	0.000
0.025	0.011	0.026	0.13	0.001
0.036	0.010	0.000	0.59	0.000
0.021	0.012	0.091	0.64	0.000
0.038	0.005	0.000	0.86	0.000

or heating level (Table 2). Annual CH₄ flux, total net primary production (TNPP), net N flux (net N), and evapotranspiration were all significantly greater in the bogs than in the fens. An important exception to this trend was respiratory CO₂ flux (ER). Neither water table nor heating level affected TNPP in the bogs, but they significantly affected most other responses. There were few significant interactions among these main effects, and therefore interaction terms were omitted from the table, but are discussed individually. Because of

the preeminent importance of community type for all variables except BNPP and ER, all the analyses separated the fens and bogs a priori, even when the community effect was nonsignificant.

The significant interannual variation documented in Table 2 did not appear to represent a treatment-driven trend. Rather, it seemed to correspond to interannual climatic variation: the 1996 growing season was very wet and resulted in high productivity and respiration values, compared to the other years. This trend is illustrated by the relatively higher peaks in CO₂ (especially) and CH₄ daily flux rates in 1996, compared to the other years shown in Fig. 1. The exception to this pattern was BNPP, which increased each year from 1995 through 1997. In addition, the effects of heating and water table on CH₄ flux grew progressively stronger in 1996 and 1997 (Table 1), suggesting a cumulative treatment effect. On the whole, however, the lack of significant interaction terms between year and the main effects in Table 2 supports our initial assertion that interannual variation in the response variables was driven largely by weather.

Ecosystem respiration.—Instantaneous ecosystem respiration (ER) as CO₂ was strongly predicted by measured soil temperature alone, which explained up to 84% of variation in instantaneous CO₂ flux in the fens and up to 80% in the bogs (Table 1). It was not affected by water table. Mean daily CO₂ fluxes did not differ significantly between the bogs and fens over the course of the growing season (Fig. 1).

TABLE 2. Repeated-measures ANOVA significance statistics for annual cumulative totals.

Variable	Site	Mean	SD	P values for effects			
				Community	Water table	Heat	Year
ANPP†				<0.001			<0.001
	Bog	345	62		0.025 ↑	0.798	<0.001
	Fen	187	39		<0.001 ↑	0.003 ∩	<0.001
BNPP†				0.715			0.001
	Bog	145	65		0.004 ↓	0.058 ↑	<0.001
	Fen	125	44		0.537	0.007 ↑	0.047
NPP†				<0.001			<0.001
	Bog	517	96		0.537	0.291	0.031
	Fen	325	74		0.011 ↑	0.001 ∩	0.001
CO ₂ (ER)				0.346			0.000
	Bog	642	74		NA‡	NA‡	<0.001
	Fen	619	103		NA‡	NA‡	<0.001
CH ₄ †				<0.001			<0.001
	Bog	21	6		NA‡	NA‡	<0.001
	Fen	7	5.7		NA‡	NA‡	0.009
Net N				<0.001			<0.001
	Bog	0.31	0.12		0.001 ↑	0.001 ↑	<0.001
	Fen	-0.02	0.31		<0.001 ↑	<0.001 ∩	<0.001
ET				0.001			<0.001
	Bog	253	46		<0.001 ↑	<0.001 ↑	<0.001
	Fen	209	47		<0.001 ↑	<0.001 ↑	<0.001

Notes: ANPP = aboveground net primary productivity; BNPP = belowground net primary productivity; TNPP = total net primary productivity; ER = ecosystem respiration; ET = evapotranspiration. Means are for 1995–1997 except for ANPP, which was averaged from 1994 to 1997, and are expressed as biomass (NPP), C, or N in grams per square meter; ET is given in liters per square meter. The responses to increasing heat or higher water table are described by ↓ for a linear decrease, ↑ for a linear increase, and ∩ for a quadratic (nonlinear) trend.

† Variables were log-normalized prior to analysis.

‡ NA = Not applicable; not included in the ANOVA (see *Statistical Methods*).

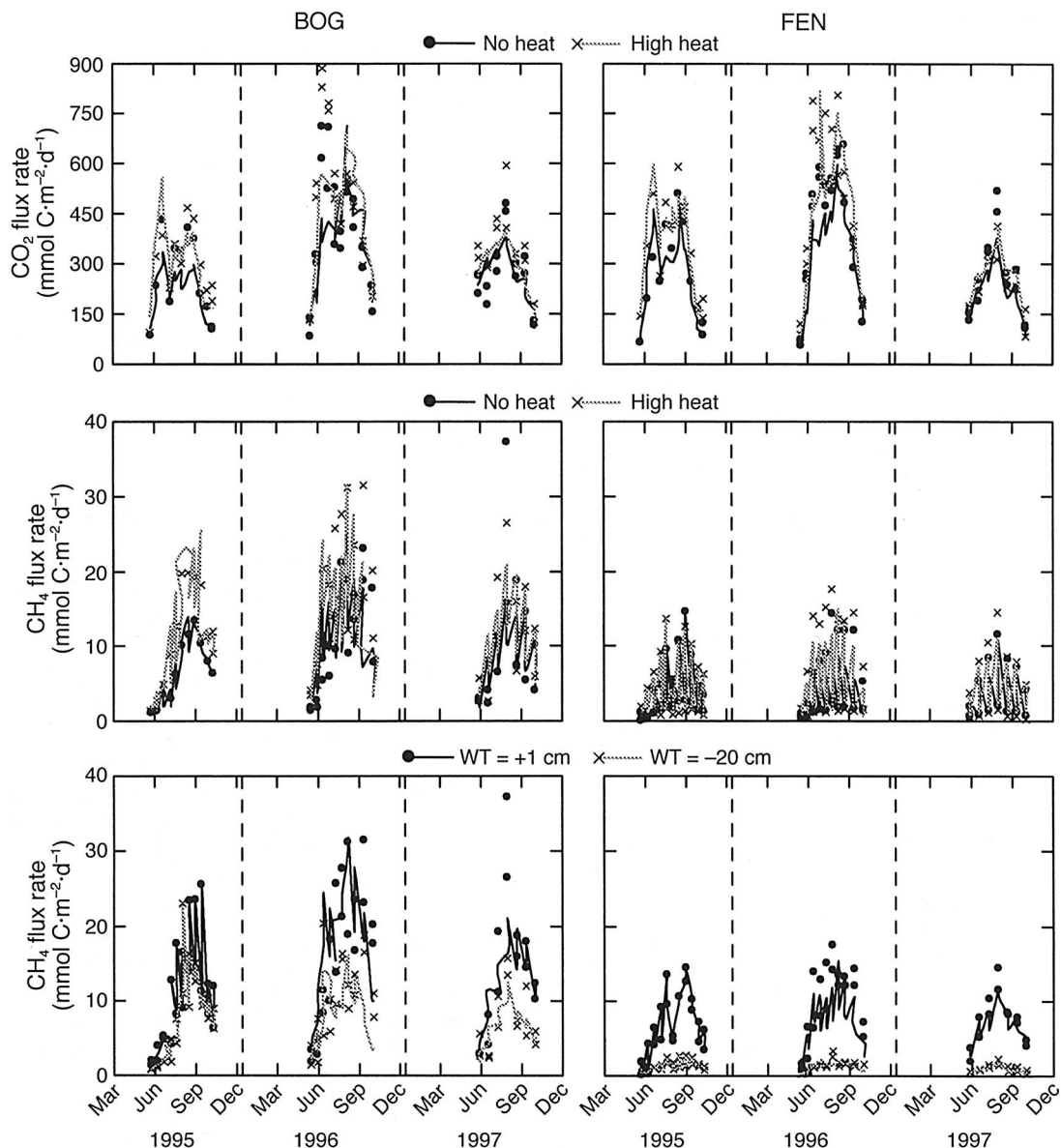


FIG. 1. Measured CO_2 and CH_4 flux rates for monoliths removed from a bog and a fen in northern Minnesota, USA, for the 1995, 1996, and 1997 growing seasons, averaged within the highest and lowest heating and water table (WT) treatments. CO_2 was not plotted by water table because that effect was not significant in the predictive regressions. The median treatment levels were omitted to simplify the plots. The lines trace the modeled rates for the measurement days, based on the regressions in Table 1.

Treatment effects on annual ER (CO_2 and CH_4) values could not be assessed in the repeated measures analysis documented in Table 2, since the annual values were the result of modeled instantaneous values and therefore dependent on water table and heating by definition. Seasonal (total) ER did not differ significantly between ecosystem types. Seasonal ER (as CO_2) was highest in 1996 in both communities, but in the bogs the lowest values were obtained in 1995, while in the fens the lowest values were in 1997. Fig. 2 provides a breakdown of 3-yr mean seasonal ER and CH_4 by com-

munity type and treatment. ER did not covary with any nutrient or productivity indicator (Table 3), although it was correlated with seasonal evapotranspiration. ET and ER were more strongly correlated in 1995 and 1996 than in 1997.

In contrast to CO_2 , instantaneous CH_4 emissions were not well-predicted by either soil temperature or water table in 1995. The regressions for estimation of CH_4 flux tended to grow progressively stronger from 1995 through 1997 (Table 1), suggesting that treatment effects become more important in determining anaer-

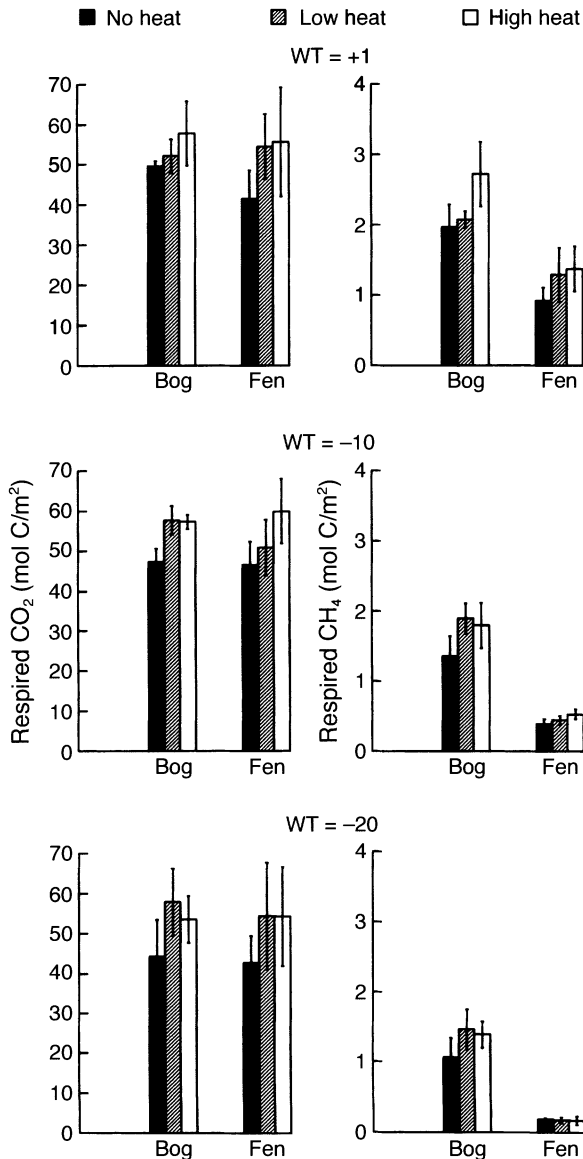


FIG. 2. Growing-season totals of respired CO₂ and CH₄ for 1995–1997, showing the effect of heating level within water table (WT) setting (mean ± 1 SE). See Table 2 for significance of effects.

obic respiration rates during that period. Therefore, in 1996 and 1997 measured soil temperature in combination with nominal water table depth explained up to 92% of variation in measured CH₄ in the fens and 86% in the bogs (Table 1). The use of nominal water table was necessary since we had no continuous measurements of water table depth, as we did for soil temperature. Therefore it was not possible to use instantaneous water table depth as a predictor variable. This compromise did not significantly weaken the regression relationships.

Season-total CH₄ was more strongly correlated with ET (Table 3) than was ER. Besides the dependence on

temperature and water table (Table 1) that allowed us to model instantaneous CH₄ flux, season-total CH₄ emissions were strongly correlated with net dissolved N flux and weakly correlated with ANPP ($P = 0.04$) in the fens (Table 3; Fig. 3). The effect of plant production on CH₄ was shown much more effectively by the correlation between estimated instantaneous CH₄ emissions and GPP (Fig. 4; $P < 0.001$ for all the regressions). However, the slope of this relationship varied significantly between community types ($P < 0.001$) and water table treatments ($P < 0.025$ for bog mesocosms, $P < 0.005$ for fen mesocosms). The average slope was four times steeper in the bog mesocosms (0.010) than in the fen mesocosms (0.0025), reflecting the consistently greater CH₄ emissions in the bogs (cf. Figs. 1 and 2). The slope was also steeper in the wetter water table treatment, with this effect being particularly pronounced in the fen mesocosms. There was a 400% increase in the slope between the high and low water table treatments in the fens, but only a 67% increase in the bogs. There was no effect heat level on the slope ($P > 0.10$).

To summarize: ER was most strongly related to soil temperature and ET, while respiration as CH₄ was strongly correlated with water table, soil temperature, ET, dissolved N flux, and GPP.

Moisture budgets and dissolved N.—We include discussion of these fluxes mainly to provide context for the examination of their possible relation to ecosystem respiration rates. The implications of higher ET in the bogs are discussed more fully in Bridgman et al. (1999). Both ET and net N (retention) were higher in the bogs than in the fens. While losing more water as evapotranspiration, the bogs were losing less water and less N in runoff (overflow) than the fens. Net N and ET both increased in response to higher heat and water table levels (Table 2). The significant interannual variation of both variables was also influenced by heating (year × heat for ET and net N in the bogs, $P < 0.006$) and water table (year × water table for net N and ET in the fens, $P < 0.001$).

Both net N and ET were significantly correlated with seasonal CH₄ emissions (Table 3). In the fens, but not the bogs, both net N and ET were correlated with ANPP and TNPP. Note that the correlation was positive, indicating that higher net N retention corresponded to higher productivity. Table 2 also shows that both net N and ANPP increased with higher water table and, to a lesser extent, with higher heat (the quadratic relationship reflects the large impact of heat compared to no heat, with a very small effect of increased heating), reinforcing the link between productivity and N flux. That this link was not significant in the bogs suggests a lower degree of either N, temperature, or moisture limitation in that environment.

NPP.—Total NPP (above- plus belowground NPP) was consistently greater in the bogs than in the fens. While TNPP was not significantly influenced either by

TABLE 3. Correlation matrix (Pearson's r^2) for three-year mean seasonal variables.

Variable	CH ₄	ER	ANPP	TNPP	Net N
Bog					
ER	0.281				
ANPP	0.063	0.007†			
TNPP	0.001	0.033	0.546*		
Net N	0.672***	0.149	0.001	0.005†	
ET	0.539***	0.353*	0.001	0.010	0.704*
Fen					
ER	0.017				
ANPP	0.303*	0.011			
TNPP	0.246	0.133	0.816***		
Net N	0.767***	0.056	0.534***	0.635***	
ET	0.512***	0.239	0.484***	0.638***	0.693***

Note: CH₄ = ln(CH₄ flux); ER = CO₂ flux; ANPP = aboveground net primary productivity; TNPP = total net primary productivity; net N = net dissolved N flux; ET = evapotranspiration.

* $P \leq 0.05$; *** $P \leq 0.001$.

† Negative correlation.

heating or water table in the bogs (Fig. 5), in the latter case this was likely due to the counteracting effects of (higher) water table, which increased aboveground and decreased belowground NPP (Table 2). In the fens, TNPP responded positively to heating and negatively to drying (Table 2). However, interannual variation in bog TNPP was somewhat influenced by heating (year \times heat, $P = 0.006$). Differing patterns of interannual variation resulted in a significant year \times type interaction for ANPP ($P < 0.0001$); this was also seen for BNPP, even though the main effect of community type was not significant in that instance. Aboveground productivity strongly correlated with net dissolved N flux in the fens (Table 3), but not in the bogs.

GPP.—Estimates of instantaneous GPP rates in the fens were below bog GPP at the beginning and end of the growing season. However, they peaked at rates similar to the those seen in the bogs. This was seen in both 1996 and 1997, although in 1996 we lacked early-sea-

son values. GPP was also more variable in the fens than in the bogs.

Repeated-measures ANOVA of the instantaneous GPP estimates for 1996 and 1997 showed no significant treatment (water table or heating) effect in the bog mesocosms in 1996, but a significant increase of GPP ($P = 0.017$) with heating in 1997. By contrast, GPP in the fens was significantly higher in the high water table treatment ($P = 0.008$) in 1997, though not in 1996 ($P = 0.095$). The reverse was true for heating treatments in the fens: for heating effect P was 0.074 in 1997, but 0.013 in 1996. The seasonal signal was also distinct for each ecosystem type, with a more pronounced peak, reflecting canopy development and senescence, in the fens.

DISCUSSION

ER as CO₂

ER as CO₂ manifested a strong response exclusively to soil temperature and was markedly insensitive to

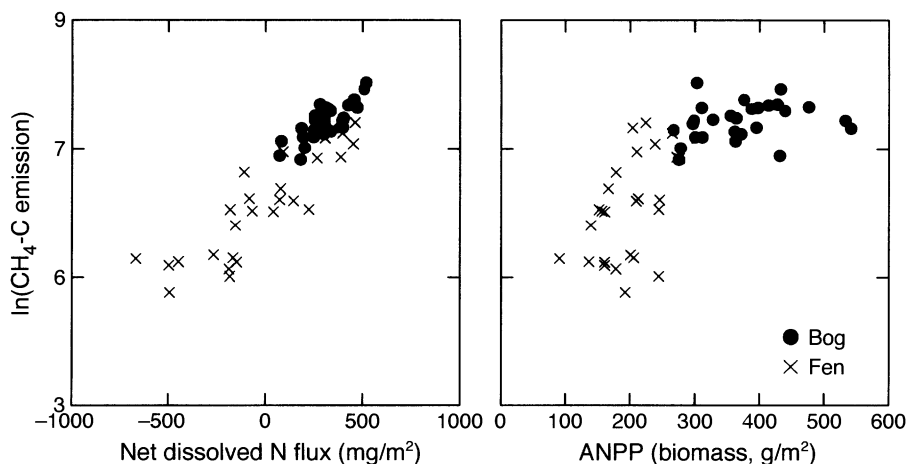


FIG. 3. Relationships between mean seasonal CH₄ emissions and mean net dissolved N flux and between mean seasonal CH₄ emissions and aboveground net primary productivity (ANPP), from bog and fen mesocosms for 1995–1997. Note that the horizontal scales are not the same.

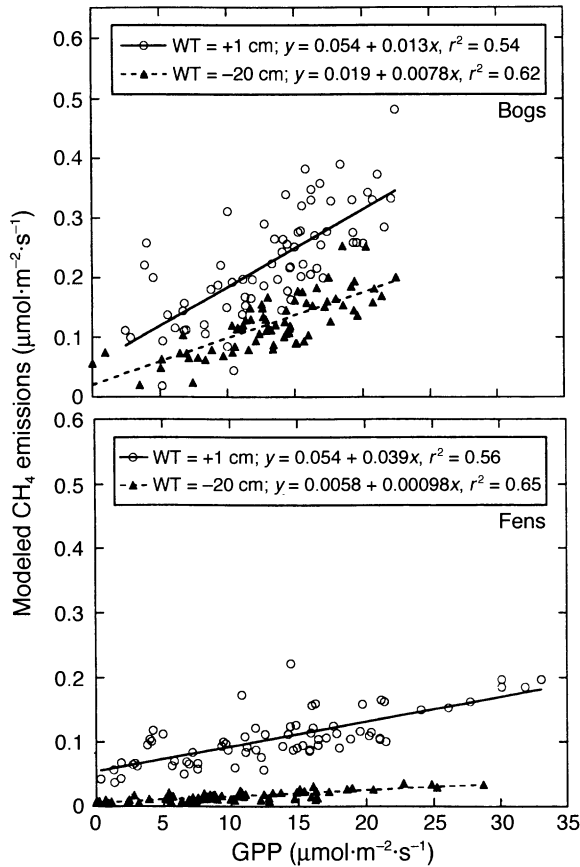


FIG. 4. Relationship between instantaneous CH₄ emissions (estimated based on soil temperature and water table) and gross primary production (GPP; calculated from net ecosystem production [NEP] plus estimated ecosystem respiration [ER]). The heat treatments had no significant effect on the slopes, so they were averaged across the water table treatments.

other ecosystem variables. That ER did not vary significantly across water tables contradicts the results of Tenhunen et al. (1995), who concluded that the depth of the aerated zone determined respiratory capacity of Alaskan tussock tundra ecosystems, while soil temperature profiles controlled diurnal CO₂ flux patterns. However, Bridgman et al. (1991) found little or no effect of water table on soil respiration in North Carolina peatlands. The lack of differences between communities with respect to ER was also surprising considering the differences in peat characteristics. In a laboratory incubation study of peat samples from a broad variety of Minnesota wetlands, both aerobic and anaerobic respiration of CO₂ were higher per volume of fen peat than in bog peat (Bridgman et al. 1998). However, when measuring whole-mesocosm ER our inability to isolate plant and soil sources of CO₂ apparently allowed differences in individual components to be smoothed out. The strong, and exclusive, effect of temperature suggests that ER will respond rapidly and positively to climate warming, and that this response will be similar among different types of peatlands despite variations in hydrology.

ER measured at the source sites in 1996 (P. Weisshampel, *unpublished data*) displayed dynamics similar to those observed in the mesocosms. Cumulative ER did not differ between the bog and fen source sites. Within individual sampling dates, ER was correlated with soil temperature ($r^2 = 0.21$ in the bogs and 0.58 in the fens), but not with measured water table. There is therefore no indication that the dry conditions of the fen mesocosms relative to the fen source site played an important role in determining mesocosm ER.

CH₄ fluxes

Despite the relatively minor role of CH₄ in the overall C budget (~3% in the bogs and 1% in the fens; Fig. 2), its importance as a greenhouse gas dictated particular attention to the differences in CH₄ emissions seen

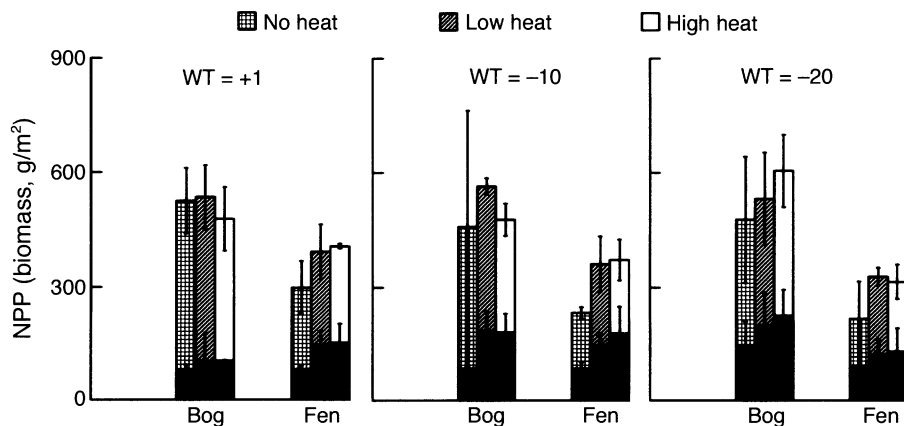


FIG. 5. Total net primary productivity (TNPP) partitioned into above- and belowground (solid black portion of bars) components for the 1995–1997 growing seasons, showing the effect of heating level within water table (WT) setting. Data are means \pm 1 SE.

in the mesocosms. In contrast to the lower CH₄ emissions seen in the fen mesocosms, past field and laboratory investigations conducted by us (Bridgman et al. 1995, 1998, Updegraff et al. 1995) and by others (e.g., Yavitt et al. 1990a, Valentine et al. 1992, Svensson and Sundh 1993, but cf. Roulet et al. 1992) have generally found that anaerobic sedge (fen) peat produces higher levels of CH₄ than *Sphagnum* peat. Our observations of fen CH₄ emissions that were less than half of those obtained from the bog mesocosms were therefore contrary to expectation.

Moreover, estimated cumulative CH₄ fluxes for the fen source site in 1996 (a wet year) were an order of magnitude higher than those estimated for the flooded fen mesocosms, while estimated fluxes at the bog source site were comparable to those seen in the bog mesocosms (P. Weishampel, *unpublished data*). The principal cause of the discrepancy between the fen source site and the mesocosms was probably the relatively drier conditions in the fen mesocosms compared to the source site, as mentioned in *Methods*. This “mesocosm” effect resulted from our initial decision to maintain similar water table elevations in both community types. This design was necessary to allow us to determine the relative importance of water table control over respiratory fluxes in the different peatland types; however, it eliminated the natural distinctions in water table between bogs and fens. Therefore, the bog mesocosms behaved quite similarly to the source site with respect to respiration, but this comparison could not be made for the fens.

Up to 95% of CH₄ produced may be oxidized in aerobic soil (Conrad and Rothfuss 1991, Cao et al. 1996). The majority of CH₄ oxidation (methanotrophy), and possibly most of the production, occurs at the oxic : anoxic interface or near the mean water table level (Rudd and Taylor 1980, Roulet et al. 1993, Bubier and Moore 1994). Many field studies have reported higher CH₄ fluxes for fens (compared to bogs) (e.g., Svensson and Rosswall 1984, Yavitt et al. 1990b, Dise et al. 1993, but cf. Roulet et al. 1992). The mesocosm results suggest that these higher measured emission rates in fens as compared to bogs reflect not only the greater production potential for CH₄ in fen peat, as indicated by laboratory experiments (Updegraff et al. 1995, Bridgman et al. 1998), but also a suppression of methanotrophy, due to the more consistently anoxic conditions. Yavitt et al. (1988) found that minerotrophic (fen-like) peatlands actually had higher methane oxidation potentials than ombrotrophic (bog-like) peatlands. Our lowering of water tables in the fen mesocosms allowed this oxidation potential to be realized. In the “low” water table treatments, there may also have been direct suppression of methanogenesis due to the establishment of aerobic conditions.

Methane flux in the bog mesocosms appeared to respond to different controls. Although moss growth in the bogs lowered effective water tables by ~11 cm

compared to the fens for any given treatment, net CH₄ flux was much higher in the bog mesocosms. This suggests that oxidation plays a less important role in moderating net CH₄ fluxes in bogs. These results demonstrate that substrate-dependent differences—those resulting from the differing origins of the peat, with attendant effects on C quality and nutrient availability—in CH₄ production potentials may be swamped by climatically induced changes in hydrology and that CH₄ fluxes in fens may be especially sensitive to water table fluctuations.

The suppression of net CH₄ emissions from the fens may also be related to soil N dynamics. Soil N availability has frequently been linked to increases in methanogenesis (Svensson and Sundh 1993, but cf. Bridgman and Richardson 1992) and suppression of methanotrophy (Bender and Conrad 1994, King and Schnell 1994). However, the nature of the control exerted by N is unclear. Field and laboratory studies have demonstrated inhibition of both CH₄ oxidation (Stuedler et al. 1989, Mosier et al. 1991) and production (Bollag and Czlonkowski 1973, Conrad and Rothfuss 1991) by added N compounds. In contrast, N fertilization was shown to stimulate the growth and activity of methanotrophic bacteria in the root zone of rice plants (Bodelier et al. 2000).

Schimel (2000) suggested three potential effects of increased N availability on CH₄ dynamics that may explain the often conflicting results of previous studies: (1) stimulation of plant productivity and C supply to methanogens, enhancing CH₄ fluxes, (2) stimulation of N-limited methanotrophic bacteria, decreasing CH₄ fluxes, and (3) competition of NH₄-N with CH₄ for methane monooxygenase, the enzyme responsible for CH₄ oxidation, increasing CH₄ fluxes. We suggest two other possible effects of increased N availability on CH₄ dynamics, (4) stimulation of denitrifying bacteria resulting in increased competition for C substrates with methanogens, decreasing CH₄ fluxes, and (5) a direct inhibitory effect of high N concentrations on methanogens, decreasing CH₄ fluxes. The sum of these five processes should determine the net effect of N availability on CH₄ fluxes. We examine below which of these hypotheses most effectively explains the strong and consistent correlations that we observed in our data between CH₄ emissions and net N flux (Fig. 3).

Porewater concentrations of total N and NH₄-N were significantly higher in the fens in all years of record. Since we had only one representative porewater sample for each month, we used monthly total estimates of CH₄ flux to run within-season correlation analyses with all our measures of dissolved N. There were consistent negative correlations in the fens between estimated monthly CH₄ emissions and porewater NH₄-N concentrations (both measures log normalized) in each year ($r^2 = 0.16$ – 0.5 , Bonferroni-adjusted $P = 0.001$ – 0.1). These correlations were not significant in the bogs ($r^2 < 0.4$; $P > 0.2$), possibly because ambient concentra-

tions of NH_4 were much lower in the bog porewater. No clear seasonal signals emerged from these analyses.

The notably negative relationship between porewater $\text{NH}_4\text{-N}$ and CH_4 flux in the fens suggests that the above mechanisms, (1) N enhancement of plant productivity and (3) competition between $\text{NH}_4\text{-N}$ and CH_4 for the enzyme methane monooxygenase, are not the dominant responses in the mesocosms, as they would yield a positive relationship. However, the other three mechanisms, (2) N stimulation of methanotrophic bacteria, (4) stimulation of denitrifying bacteria causing increased competition with methanogens, and (5) a direct inhibitory effect of high N concentrations on methanogens would all give the observed negative relationship between CH_4 fluxes and porewater $\text{NH}_4\text{-N}$ or net N retention. Our data do not allow us to separate out the relative importance of these mechanisms, and we are aware of no mechanistic studies that have directly examined N effects on methanogens or methanotrophs in peatland soils. However, the apparent overwhelming importance of CH_4 oxidation in the fen mesocosms, discussed previously, suggests that mechanism 2, N stimulation of methanotrophic bacteria, is a distinct possibility. Although we did not measure rates of denitrification in our plots, several studies do address the relative importance of denitrification in peatlands. This mechanism would require that the higher measured $\text{NH}_4\text{-N}$ in the porewater reflect higher rates of both nitrification and denitrification in the fens than in the bogs, which is plausible given the higher pH in the former. We have previously observed a very strong effect of pH on nitrification potential in peats (Bridgman et al. 1998). Measured porewater $\text{NO}_3\text{-N}$ was very low in both communities, which is the expected outcome if it is rapidly denitrified. However, the few studies that have measured denitrification in peatlands have indicated that low $\text{NO}_3\text{-N}$ concentrations in these systems are due more to low rates of nitrification than to denitrification, although recorded denitrification rates are higher in fens than in bogs (Urban et al. 1988, Verhoeven et al. 1994). Therefore, high rates of denitrification are unlikely in the bog mesocosms and probably in the fen mesocosms, too. Overall, our data suggest that mechanistic studies of the effects of N availability on CH_4 fluxes in wetland soils would be very helpful.

Numerous researchers have suggested a direct link between instantaneous primary production and CH_4 flux rates. Whiting and Chanton (1993) demonstrated a strong linear correlation between instantaneous NEP ($\text{GPP} - \text{ER}$) and CH_4 fluxes in a range of wetlands across a wide latitudinal gradient, suggesting "that net ecosystem production is a master variable, integrating many factors which control CH_4 emissions in vegetated wetlands" (Whiting and Chanton 1993:794). A study in two Canadian fens showing strong correlations between instantaneous CH_4 flux, NEP, and live plant bio-

mass supported that hypothesis at a more local scale (Whiting and Chanton 1992).

Instantaneous CH_4 emissions modeled from the water table and temperature regressions in Table 1 were highly correlated with the corresponding estimates of GPP (Fig. 4), reflecting a production-driven stimulation of methanogenesis by increased root exudation. However, this relationship was also strongly constrained by community type (i.e., bogs vs. fens) and water table elevation, but was not affected by the heating treatments. There was a greater proportional increase in CH_4 emissions with increased GPP in the bogs and in the high water table treatment. There was also a significant interaction between community type and water table elevation, with a much more pronounced response of CH_4 emissions to GPP in the high vs. low water table fen mesocosms. With a lower water table, a greater portion of the rooting zone will be aerobic, limiting methanogenesis, and much of the CH_4 that is produced will be oxidized by methanotrophs before it reaches the atmosphere.

The effects of plants are more complicated. Plants not only provide root exudates to fuel methanogenesis, but they can transport CH_4 to the atmosphere and/or O_2 to the rhizosphere through aerenchymous (i.e., air-filled) stem tissue (Chanton et al. 1988, Schimel 1995, Saarnio and Silvola 1999). It is the net effect of these processes that determines the overall effect of plants on CH_4 emissions. The positive effect of root exudates on methanogenesis in the fen mesocosms may have been partially offset by the transport of O_2 in aerenchyma of plant tissue to the rhizosphere, enhancing methane oxidation (in addition to the possible effects of N discussed above). Aerenchyma are much better developed in sedges than in the woody tissue of shrubs and are absent in mosses. Also, as mentioned previously, CH_4 oxidation appears to be particularly critical in limiting CH_4 emissions in the fen mesocosms.

It is interesting that we found much higher correlations between instantaneous CH_4 emissions and GPP than between seasonal CH_4 emissions and NPP. Over brief periods during the growing season, plant production would be mainly linked to methanogenesis through root exudates, whereas over an annual cycle there would be significant inputs of above- and belowground plant litter. Our data support a tight temporal coupling of plant production and methanogenesis that becomes much less clear over longer time frames.

A number of studies provide some basis for questioning the relationship between CH_4 production and plant productivity. Alm et al. (1997) found that although midsummer NEP was positively correlated with CH_4 flux, there was no relationship between annual C accretion and CH_4 flux in a Finnish fen. Waddington and Roulet (1996) found a negative relationship between NEP and CH_4 emissions in a Swedish peatland: topographic lows had greater CH_4 emissions and lower NEP, while the opposite was true for higher and drier

zones. Our data suggest a tight coupling between GPP and CH₄ flux, but this relationship is constrained by site-specific dynamics of community type and water table elevation.

To summarize, it appears that while the low water table was the most important reason for the anomalously low CH₄ emissions from the fen mesocosms, both N dynamics and productivity may be reinforcing this effect. The fen mesocosms had higher porewater N levels and tended to leach dissolved N, suggesting that N was mineralizing faster than it was immobilized. Several mechanisms could account for the observed decrease in CH₄ flux with increased N availability, including N stimulation of methanotrophic bacteria. On an instantaneous basis, GPP was highly correlated with CH₄ emissions, but this relationship was conditional on community type, water table elevation, and their interaction. The much lower correlation between NPP and seasonal CH₄ flux suggests that the relationship between plant production and CH₄ flux is much less direct and weaker on an annual time frame. Overall, our results illustrate a complex set of interacting factors regulating CH₄ fluxes in peatlands, including water table elevation, temperature, plant productivity, and N cycling. Such a complex system suggests that it will very difficult to accurately predict CH₄ fluxes in the future under altered climate scenarios.

Importance of community type

The autogenic nature of peat formation and ecology gives rise to a closely linked system of feedbacks between community type, nutrient availability, primary productivity, and decomposition. Productivity indices and seasonal phenology differ dramatically between the two communities (Weltzin et al., 2000). The bryophyte-dominated bog system remains green much longer than the graminoid fen, allowing a longer effective growing season. During all our years of record, NPP was significantly greater in the bog mesocosms (Table 2). The fact that the bogs maintained higher productivity than the fens but had similar rates of ER support a tentative conclusion that, within the range of conditions that obtain in the mesocosms, the bogs are accreting C while the fens are losing C. This conclusion is supported by data indicating losses in peat volume in the fens, compared to gains in the bogs (P. Weishampel, *unpublished data*). However, because ER in both bogs and fens is more sensitive to warming than is NPP, larger increases in soil temperature than were obtained in this experiment may result in increased C losses from both these ecosystems.

CONCLUSIONS

Respired CO₂ in peatland mesocosms was largely controlled by soil temperature and was unrelated to other measured variables, suggesting that, within the range of our experimental conditions, respiratory CO₂ fluxes from peatlands will increase exponentially in

response to predicted climate warming. Controls over CH₄ fluxes were more complex. Net methanogenesis seems to respond to environmental stimuli over much longer time frames than does aerobic respiration, as reflected in the increasing predictability of CH₄ flux by temperature and water table over time. The strong correlations with soil temperature and water table by the third year suggest that in the long run such direct climatic effects will dominate within peatlands, but these effects may be modulated across peatlands by differences in productivity and nutrient dynamics. Methane flux was negatively correlated with soil N availability and positively correlated with instantaneous GPP. However, the reduction in CH₄ fluxes from the fen mesocosms, relative to the source site, appears largely due to an increase in methanotrophy resulting from drying. By extension, CH₄ fluxes in contrasting peatland communities may respond very differently to climate-induced changes in hydrology due to differences in their resident microflora.

This study has afforded a unique opportunity to observe long-term ecosystem responses to direct manipulation of climate-related variables (infrared input and water table). During four years of sustained temperature and water table modification, *Sphagnum*-bog mesocosms have maintained higher net and gross primary productivity compared to intermediate fens, coupled with higher rates of respired CH₄, although ER as CO₂ emissions did not differ. To date, the effects of the treatments have remained largely linear with respect to individual ecosystem variables (above- and below-ground productivity, respiration, and dissolved nutrients), as demonstrated by the lack of interactions. However, our data suggest that biotic feedbacks may be exerting a dynamic control over mesocosm energy and moisture budgets, causing significant within-treatment temperature and ET differences between the two community types (Bridgman et al. 1999). There may therefore be important linkages between biotic and abiotic controls over trace gas fluxes. The continuing experiment will allow us to directly observe the evolving interactions of these controls.

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