

Decomposition in Extreme-Rich Fens of Boreal Alberta, Canada

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ABSTRACT

Rich fens (minerotrophic peatlands with surface water pH > 5.5) have greater alkalinity and species richness than other boreal peatlands. We used short-term laboratory incubations to quantify CO₂ and CH₄ production in peat from five extreme-rich fens in Alberta. Carbon dioxide production rates averaged 48.29 ± 1.36 μmol CO₂ g organic matter⁻¹ d⁻¹ across sites and sampling events. Peat from all sites produced CH₄ during anaerobic incubations, leading to average anaerobic CH₄ production rates of 359.53 ± 138.7 nmol CH₄ g organic matter⁻¹ d⁻¹. However, methane frequently was consumed (oxidized) during aerobic incubations, leading to aerobic CH₄ consumption rates averaging 75.2 ± 63.7 nmol CH₄ g organic matter⁻¹ d⁻¹ across sites. Calculated rates of dissolved H₂CO₃ + HCO₃⁻ production averaged 59.7 ± 13.4 μmol g organic matter⁻¹ d⁻¹, suggesting that dissolved inorganic C is important to the overall C fluxes in these rich fens. Our results suggest that changing hydrologic conditions will influence the balance between methanogenesis and methanotrophy in rich fens, but that surface water chemistry, likely influenced by marl precipitation, also is important to decomposition. Rich fens are estimated to represent the most common wetland type in Alberta, and these peatland ecosystems could play an important role in trace gas emissions across boreal regions.

PEATLANDS represent a variety of wetlands that are characterized by substantial accumulations of organic soils, but may differ in vegetation, hydrology, and chemistry. Ombrogenous bogs receive all water and nutrient inputs from the atmosphere alone, while geogenous fens are influenced by groundwater and/or surface waters. Bogs and poor fens are dominated by species in the genus *Sphagnum*, while rich fens tend to be dominated by brown mosses (Gorham and Janssens, 1992). Rich fens originally were distinguished as sites with high numbers of indicator species (Du Rietz, 1949), although they also tend to have higher species richness (Vitt and Chee, 1990), alkalinity (Slack et al., 1980; Vitt and Chee, 1990; Vitt et al., 1995), and surface water pH (5.5–7.0 in moderate rich fens; >7.0 in extreme rich fens) than other boreal peatlands.

Peatlands globally store more than 30% of the world's terrestrial C pool and represent a large natural source of CH₄ to the atmosphere (Wahlen, 1993; Matthews and Fung, 1987). Peat accumulates where net primary productivity (NPP) exceeds organic matter losses due to decomposition, disturbance losses (largely fire), and DOC export. Much of the work investigating C cycling

in northern peatlands has been conducted in bogs. However, across the western boreal forest of North America, fens represent about 65% of the total peatland area (Vitt et al., 2000). The continental climate and predominance of calcareous bedrock and groundwater in Alberta particularly favor the development of rich fens. Vitt et al. (1990) estimated that half of Alberta's wetlands are rich fens, equivalent to approximately 68 520 km² of peatland (National Wetlands Working Group, 1988).

Szumigalski and Bayley (1996) and Thormann and Bayley (1997) reported faster decomposition rates in rich fens relative to other peatland types in Alberta. Based on these data, Thormann et al. (1999) concluded that rich fens accumulate less peat than *Sphagnum*-dominated peatlands (bogs and poor fens) largely due to fast decomposition rather than slow NPP. These studies have quantified decomposition in rich fens through litter mass losses, which is useful for investigating decay processes in situ but does not provide information on the relative production of decomposition end-members such as CO₂ and CH₄. Methanogenesis is an anaerobic process that occurs in saturated peat layers; while CO₂ is produced during both aerobic and anaerobic microbial processes. Methane also can be oxidized to CO₂ by methanotrophic microorganisms in aerated surface peat.

Understanding the variation in CH₄ production from peat in various boreal wetland types is important since wetlands represent a large source of CH₄ to the atmosphere and since CH₄ is 23 times more effective per molecule in absorbing long-wave radiation than CO₂ on a 100-yr time scale (Ramaswamy et al., 2001). Here we quantify CO₂ and CH₄ production during short-term laboratory incubations of peat collected from five extreme rich fens in central Alberta. Our goals were to (i) quantify the production of CO₂ and CH₄ by rich fen peat and compare these results to other incubation studies in continental western Canada, (ii) relate gaseous C production rates to the surface water chemistry and moisture content of peat across sites, and (iii) estimate the importance of dissolved inorganic C to overall C fluxes in these sites. Due to high water tables and greater nutrient concentrations and alkalinity in rich fens compared with bogs or poor fens (Szumigalski and Bayley, 1996; Thormann and Bayley, 1997), our hypothesis is that rich fen peat will produce more gaseous C during incubations than other peat types, and that CH₄ production will be particularly high during rich fen decomposition. Given the high pH of rich fen systems, we also expected that decomposition could involve significant amounts of dissolved inorganic C production due to relationships between CO₂ speciation and pH.

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Abbreviations: C, carbon; CH₄, methane; CO₂, carbon dioxide; DOC, dissolved organic carbon; NPP, net primary productivity.

Table 1. Location, vegetation, and soil characteristics of five extreme-rich fen sites in Alberta, Canada. Mean annual temperature (MAT) and precipitation (MAP) at the closest weather station to the Calahoo and Wagner fens averaged 3.6°C and 461 mm, respectively (Environment Canada, 1998). At the station closest to the Hinton and Rock Lake fens, MAT and MAP averaged 3.1°C and 394 mm, respectively (Environment Canada, 1998). Soil water content was determined as the mass of water in each sample divided by the mass of oven-dry sample.

| Site | Location | Maximum peat depth in sampling areas | Soil water content | Dominant plant species |
|--------------|-----------------------|--------------------------------------|--------------------|---|
| | | cm | g g ⁻¹ | |
| Hinton | 55°05' N 113°17' W | 590 | 11.78 ± 0.13 | <i>Scorpidium scorpioides</i> , <i>Tomenthypnum nitens</i> , <i>Sphagnum warnstorffii</i> , <i>Larix laricina</i> |
| Rock Lake | 55°05' N 113°17' W | 520 | 11.74 ± 0.18 | <i>Scorpidium scorpioides</i> , <i>Tomenthypnum nitens</i> , <i>Sphagnum warnstorffii</i> , <i>Sphagnum fuscum</i> , <i>Larix laricina</i> |
| Wagner Road | 53°34' N 113°50' W | 30 | 5.47 ± 13 | <i>Scorpidium scorpioides</i> , <i>Hypnum lindbergii</i> , <i>Campylium stellatum</i> , <i>Bryum spp.</i> |
| Wagner South | 53°34' N 113°50' W | 25 | 5.64 ± 0.10 | <i>Scorpidium scorpioides</i> , <i>Drepanocladus spp.</i> , <i>Campylium stellatum</i> , <i>Tomenthypnum nitens</i> |
| Calahoo | 53°42' N 113°57' W | 40 | 5.91 ± 0.08 | <i>Scorpidium scorpioides</i> , <i>Hypnum lindbergii</i> , <i>Campylium stellatum</i> |

MATERIALS AND METHODS

We selected five extreme rich fens in central Alberta with similar vegetation and surface water pH (National Wetlands Working Group, 1988; Tables 1 and 2). Soils in all of our sites represent Typic Cryofibrists. Two of the sites were located in the Wagner Natural Area, about 30 km outside of Edmonton, AB. Both Wagner fens (referred to as the Wagner Road and Wagner South fens) and our site outside of Calahoo, AB (referred to as the Calahoo fen) had marl precipitates (highly calcareous deposits) in surface waters or pool bottoms. Peat depth in the areas we sampled at these three sites ranged from 10 to 40 cm above the mineral soil boundary (Table 1). The Hinton and Rock Lake fens are in the Rocky Mountain eastern foothills. Both sites have a sparse *Larix laricina* canopy and maximum peat depth exceeding 5 m.

We sampled all five sites every 2 wk from June to August 2000 (five sampling events, but only four events for the Rock Lake site). On each sampling date, all sites were sampled within 24 h. Surface waters were collected for pH and conductivity measurements, and Ca and Mg concentrations were measured on a subset of samples using a graphite furnace. Also, on each sampling date we collected replicate surface peat samples (5- to 10-cm depth interval beneath living vegetation) from five hummocks and five hollows from the Rock Lake, Hinton, and Calahoo fens. The Wagner fens had no distinct hummock-hollow topography, and in these two sites we collected a total of five replicate surface samples. The Calahoo, Rock Lake, and Hinton fens had *Scorpidium scorpioides* in pools, *Drepanocladus* and *Campylium spp.* mid-hummock, and *Tomenthypnum nitens* in hummocks. The Wagner fens had *Scorpidium scorpioides* and *Drepanocladus* species in large lawns interspersed with marl pools (Table 1).

Peat was placed in ziplock bags, with headspaces removed, and kept cold on ice during transportation. To preserve the original structure of organic matter and soil aggregates in our samples, we did not homogenize our samples. Coarse or medium sized roots were removed and were not included in the incubations. Gas production during these short-term incubations could include respiration of fine roots, which cannot be removed from peat without excessive damage to soil structure. We incubated 10 g of peat at field moisture in mason jars at room temperature with either aerobic (room air) or anaerobic (room air replaced with O₂-free N₂ five times with a vacuum pump) headspaces. Mason jars had lids fitted with rubber septa for headspace sampling. Headspaces were sampled 0, 4, 12, 24, and 48 h after sealing the jars. Gas samples were replaced with room air or N₂ to compensate for displacement and were shaken gently to promote headspace mixing.

Methane and CO₂ concentrations were quantified by gas chromatography using flame ionization and thermal conductivity detectors, respectively. The standard errors of injections of multiple external standards were <5% (Scott Specialty Gases, Plumbsteadville, PA). Methane and CO₂ production rates were calculated from the slopes of headspace gas concentration regressed with time. Nonlinear slopes ($p < 0.05$), due to possible disturbance effects, headspace leaking, or headspace saturation, were rejected (<15% of total slopes). Headspace volume was estimated by filling each jar to capacity with water and subsequently weighing jars. Samples then were oven dried to a constant mass for dry mass determination. Organic matter concentrations were determined on fresh subsamples by loss on ignition at 550°C for 5 h. We used Henry's Law and carbonate dissolution equilibria to calculate soluble H₂CO₃ + HCO₃⁻ production rates for each site × sampling event combination. Equations are outlined in Stumm and Morgan (1995), and include mean surface water pH, peat moisture content, organic matter concentrations, and CO₂ production rates.

Carbon dioxide and CH₄ production rates between hummock and hollow peat did not differ for the Calahoo, Rock Lake, and Hinton fens (1 df; $p > 0.05$ for each site). Thus, we combined hummock and hollow data at these sites. Because the Wagner fens lacked distinct microtopography, this allowed us to make comparisons across fens. Carbon dioxide (Shapiro-Wilk, $W = 0.673$, $p < 0.0001$) and CH₄ (Shapiro-Wilk, $W = 0.687$, $p < 0.0001$) production rates were not normally distributed. We analyzed production rates using nonparametric analysis of variance models, including date as a random factor, site and aeration status as fixed factors, interactions between site and aeration status, and least significant differences comparisons of means (SAS, 1998). Interactions between fixed factors and date were not included in our models given our unbalanced sampling design (four sampling events at Rock Lake fen). Due to our limited number of surface water samples, we used correlation tests based on Spearman's rank order correlation coefficients for preliminary analysis of relationships between surface water chemistry and gaseous C production (SAS, 1998).

RESULTS

The Calahoo and Wagner fens had lower organic matter concentrations, and greater surface water conductivity, Ca²⁺ concentrations, and Mg²⁺ concentrations than the other sites (Table 2). Average surface water pH was highest at the Wagner South fen and lowest at the Rock Lake fen (Table 2).

Table 2. Surface soil and water chemistry variables for five extreme-rich fens located in Alberta, Canada. Data are site means \pm one standard error. Rates of C production are expressed in units of μmol produced per gram organic matter per day. Gaseous production rates represent average CO_2 produced across all sampling dates in both aerobic and anaerobic incubations. Henry's Law and carbonate dissolution equilibria were used to estimate dissolved $\text{H}_2\text{CO}_3 + \text{HCO}_3^-$ production rates (Stumm and Morgan, 1995). Errors are compounded assuming Gaussian distributions.

| Sites | Organic matter | Surface water chemistry | | | | Rates of C production | | |
|-----------|-------------------|-------------------------|--------------------|------------------|------------------|-----------------------------|--|---|
| | | pH | Conductivity | Ca^{2+} | Mg^{2+} | Total gaseous CO_2 | Dissolved $\text{H}_2\text{CO}_3 + \text{HCO}_3^-$ | Total CO_2 (dissolved + gaseous) |
| | | | | | | | | |
| n | % | 15 | 15 | 3 | 3 | 50† | 10 | |
| Hinton | 83.08 \pm 9.61 | 7.67 \pm 0.04 | 245.09 \pm 6.71 | 34.29 \pm 4.34 | 9.02 \pm 0.70 | 51.23 \pm 2.54 | 68.39 \pm 5.32 | 119.63 \pm 11.04 |
| Rock Lake | 87.19 \pm 3.77 | 7.59 \pm 0.07 | 332.17 \pm 44.67 | 40.84 \pm 7.63 | 14.92 \pm 1.16 | 39.22 \pm 1.85 | 45.50 \pm 6.75 | 84.72 \pm 13.19 |
| Wagner Rd | 35.98 \pm 11.85 | 7.96 \pm 0.10 | 669.90 \pm 62.79 | 97.71 \pm 8.33 | 32.03 \pm 3.25 | 49.53 \pm 2.09 | 51.13 \pm 3.91 | 100.66 \pm 8.78 |
| Wagner S | 46.11 \pm 8.75 | 8.12 \pm 0.08 | 480.29 \pm 21.14 | 58.61 \pm 1.87 | 26.23 \pm 4.74 | 36.88 \pm 1.86 | 58.53 \pm 4.17 | 95.41 \pm 8.33 |
| Calahoo | 36.42 \pm 8.65 | 7.62 \pm 0.13 | 559.71 \pm 19.93 | 80.48 \pm 7.52 | 30.87 \pm 6.91 | 59.42 \pm 4.36 | 77.00 \pm 7.43 | 136.42 \pm 16.54 |

† n = 25 in the Wagner fen sites, which lacked distinct microtopography.

Carbon dioxide production ($\mu\text{mol CO}_2 \text{ g organic matter}^{-1} \text{ d}^{-1}$) varied by (i) site ($F = 10.21$, 4 df, $p = 0.0001$), (ii) date ($F = 4.97$, 4 df, $p = 0.0007$), and (iii) aeration status ($F = 34.64$, 1 df, $p = 0.0001$), with no significant aeration status \times site interaction ($p > 0.5$). On a dry mass basis, CO_2 production rates averaged 43.8 ± 1.9 , 44.9 ± 1.5 , 34.8 ± 2.9 , 27.8 ± 1.2 , $26.8 \pm 2.3 \mu\text{mol CO}_2 \text{ g dry mass}^{-1} \text{ d}^{-1}$ across the Hinton, Rock Lake, Calahoo, Wagner Road, and Wagner South sites, respectively. Thus, while Rock Lake and Hinton fen peat had higher CO_2 production rates on a dry mass basis, Calahoo peat generally produced more CO_2 per unit organic matter due to lower organic matter contents (Fig. 1; Table 2). Averaged across sites and aeration status, CO_2 production rates tended to increase during the growing season, but also were large during the first sampling event (not

sampled at the Rock Lake Fen; Fig. 1). Carbon dioxide production rates were faster during aerobic than anaerobic incubations, averaging 55.7 ± 2.3 and $40.6 \pm 1.3 \mu\text{mol CO}_2 \text{ g organic matter}^{-1} \text{ d}^{-1}$ in aerobic and anaerobic incubations, respectively.

Methane production varied by a site \times aerobic status interaction ($F = 2.53$; 5 df; $p = 0.0284$), with no other significant main effects. While rates of anaerobic CH_4 production were variable, peat from the two Wagner fens tended to produce more CH_4 under anaerobic conditions (Fig. 2). Methane production was reduced in peat from the Calahoo and Wagner fens during aerobic incubations relative to anaerobic production rates, while Hinton and Rock Lake fen peat consumed CH_4 under aerobic conditions (Fig. 2).

Surface water chemistry (pH, conductivity, Ca, Mg concentrations) and peat moisture content were not correlated with CO_2 production (Table 3). Peat moisture content was negatively correlated with CH_4 production/consumption in both aerobic and anaerobic incubations, while aerobic CH_4 production also was positively correlated to conductivity, Ca and Mg concentrations in surface waters (Table 3).

DISCUSSION

Due to the high water tables and rich mineral status typical of extreme-rich fens, we expected that peat in this study would decompose quickly, producing both

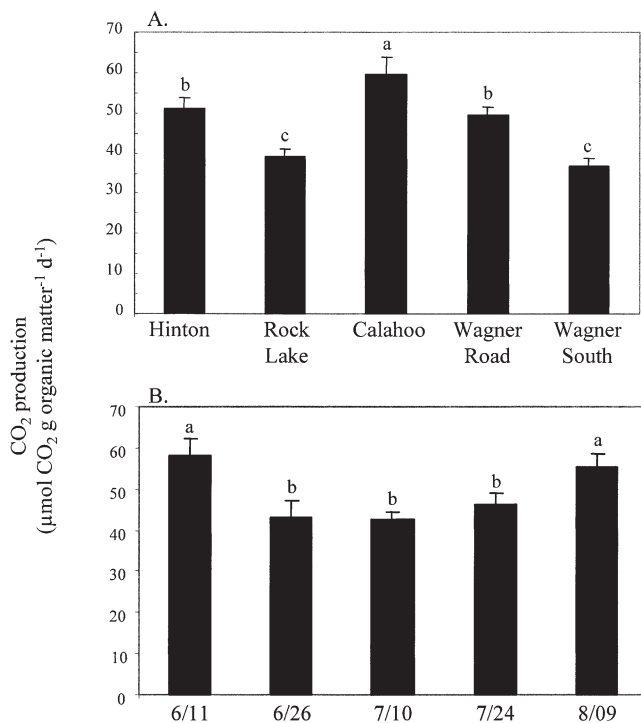


Fig. 1. Carbon dioxide production rates in surface peat from five extreme-rich fens varied by (A) site ($p = 0.0020$, $F = 4.33$, 4 df), and (B) date ($p = 0.0006$; $F = 5.06$, 4 df). Same-letter superscripts denote nonsignificant comparison of means. Data are means \pm one standard error.

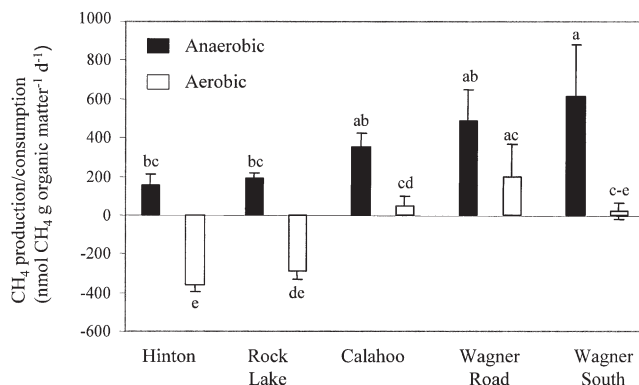


Fig. 2. Methane production rates in surface peat varied by a site \times aerobic status interaction ($p = 0.0035$, $F = 2.53$, 5 df). Same-letter superscripts denote nonsignificant comparison of means.

Table 3. Results of correlation tests exploring relationships between surface water chemistry and rates of C mineralization in rich fen peat. Correlations are based on Spearman's rank order correlation coefficients (SAS, 1998); *p* values are shown in parentheses. Because CH₄ production varied significantly by a site × aeration status interaction (Fig. 2), we show correlations separately for CH₄ production/consumption under aerobic and anaerobic incubations. Correlations between C mineralization variables are not shown here.

| | pH | Conductivity | Mg concentrations | Ca concentrations | Soil water content |
|--------------------------------------|---------------|---------------|-------------------|-------------------|--------------------|
| CO ₂ production | -0.4 (0.5046) | 0.1 (0.8729) | 0.3 (0.6238) | 0.1 (0.8729) | 0.3 (0.6238) |
| Aerobic CH ₄ production | 0.3 (0.6238) | 1 (<.0001) | 0.9 (0.0374) | 1 (<.0001) | -0.9 (0.0374) |
| Anaerobic CH ₄ production | 0.7 (0.1881) | 0.7 (0.1881) | 0.6 (0.2848) | 0.7 (0.1881) | -0.9 (0.0374) |
| pH | | 0.3 (0.6238) | 0.1 (0.8729) | 0.3 (0.6238) | -0.6 (0.2848) |
| Conductivity | 0.3 (0.6238) | | 0.9 (0.0374) | 1 (<.0001) | -0.9 (0.0374) |
| Magnesium concentrations | 0.1 (0.8729) | 0.9 (0.0374) | | 0.9 (0.0374) | -0.7 (0.1881) |
| Calcium concentrations | 0.3 (0.6238) | 1 (<.0001) | 0.9 (0.0374) | | -0.9 (0.0374) |
| Soil water content | -0.6 (0.2848) | -0.9 (0.0374) | -0.7 (0.1881) | -0.9 (0.0374) | |

CO₂ and CH₄. Mean CO₂ production rates from other incubation studies in Canada range from 0.1 to 113 μmol CO₂ g dry weight⁻¹ d⁻¹ (Moore and Dalva, 1997; Scanlon and Moore, 2000; Waddington et al., 2001; Turetsky, 2004). In this study, peat from the Hinton and Rock Lake fens produced more CO₂ on a dry mass basis than the other fens. However, there were large differences in peat organic matter content across sites (Table 1). Peat from the Wagner and Calahoo fens had lower organic matter contents than peat from the other sites, increasing rates of CO₂ production on an organic matter basis (Fig. 1). Across sites and sampling events, CO₂ production averaged 48.3 ± 1.4 μmol CO₂ g organic matter⁻¹ d⁻¹.

As CO₂ can dissolve readily with increasing pH, it is important to quantify soluble C production rates in rich fen waters, especially in extreme rich fens where surface water pH > 7. Averaged across sampling events, the Hinton and Calahoo fen peat had greater soluble H₂CO₃ + HCO₃⁻ production rates on an organic matter basis than the other sites (Table 2). Generally, soluble C production was large compared with gaseous C production in peat from these calcareous fens, and our results suggest that dissolved inorganic C is a significant component of total C fluxes in these extreme-rich fens.

Methane production in peatlands tends to vary tremendously both spatially and temporally (Waddington and Roulet, 1996; Kettunen et al., 2000). For example, CH₄ production rates in laboratory incubations ranged from approximately 0 to 4 nmol CH₄ g h⁻¹ in a New England bog (Krumholz et al., 1995); 2.5 to 17 nmol CH₄ g dry weight⁻¹ h⁻¹ in *Sphagnum* bog and sedge fen peat in Sweden (Bergman et al., 1998); and 0.1 to 2.4 μg CH₄ g dry weight⁻¹ h⁻¹ in a *Sphagnum* bog and pine fen in Finland (Kettunen et al., 1999). *Sphagnum* and vascular-derived peat also can be associated with significant rates of CH₄ consumption (Kettunen et al., 1999; Krumholz et al., 1995). Variation in peatland CH₄ fluxes, then, can be controlled by methanogenesis in anaerobic peat and/or methanotrophy in drier surface soils.

Previous studies have measured small CH₄ fluxes from *Sphagnum* dominated bogs and poor fens in Alberta (Vitt et al., 1990; Turetsky et al., 2002), likely due to methane oxidation in the thick acrotelms (surface peat above the permanent water table) of continental peatlands. However, acidic conditions also can inhibit methanogenesis in *Sphagnum* dominated peatlands, as optimal pH for methanogens tends to be neutral (O'Fla-

herty et al., 1998; Bergman et al., 1998; Duval and Goodwin, 2000). Our results show that microbial activity in brown moss dominated, rich fen peat can produce large amounts of CH₄ under anaerobic conditions, but frequently oxidizes CH₄ during aerobic incubations (Fig. 2). This suggests that periods of drought and lowered water tables are likely to reduce overall CH₄ fluxes from boreal rich fens to the atmosphere. Surprisingly, however, peat moisture contents were negatively correlated to CH₄ production/consumption rates (Table 3), as peat with the greatest moisture contents (from the Rock Lake and Hinton fens) had low CH₄ production rates and large CH₄ consumption rates (Table 1, Fig. 2). We feel this relationship is difficult to interpret, as surface water conductivity and concentrations of Ca and Mg were negatively correlated to peat moisture content and positively correlated to aerobic CH₄ production/consumption rates (Table 3). So while peat from the Calahoo and Wagner fens had lower moisture contents than peat from the other sites, these fens also had larger measurements of conductivity, Ca, and Mg in surface waters compared with the other sites and had the largest rates of CH₄ production.

Though preliminary, our results show that controls on CH₄ production and consumption in boreal rich fens can be complex. Numerous studies have shown generally that variability in moisture content and water table are primary controls on the processes contributing to CH₄ fluxes in peatlands. Our results suggest that variability in surface water chemistry and nutrient/cation availability also are important to microbial activity in extreme rich fens. Our sites included three rich fens (two Wagner fens, Calahoo fen) with visual and chemical (Table 2) evidence of marl precipitation. The influence of marl precipitates on nutrient availability and biological activity in peatlands certainly warrants further attention, but our results suggest that the presence of marl could stimulate methane production in peat, likely by increasing the availability of micronutrients such as calcium.

Rich fens are a common type of wetland in the boreal forest biome, where wetlands often store the majority of regional soil C pools. Our results show that decomposition in the surface peat of rich fens produces gaseous and dissolved CO₂, and can both produce and consume (oxidize) CH₄. Given their abundance in Canada's boreal forest region, rich fens likely play an important role in regional trace gas fluxes.

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REFERENCES

- Bergman, I., B.H. Svensson, and M. Nilsson. 1998. Regulation of methane production in a Swedish acid mire by pH, temperature and substrate. *Soil Biol. Biochem.* 30:729–741.
- Du Rietz, G.E. 1949. Huvudenheter och Huvudgranser I Svensk Myrvegetation. (In Swedish.) *Svensk Bot. Tidskr.* 43:274–309.
- Duval, B., and S. Goodwin. 2000. Methane production and release from two New England peatlands. *Inter. Microbiol.* 3:89–95.
- Environment Canada. 1998. Canadian climate normals 1960–1990. Ottawa, Ontario, Canada.
- Gorham, E., and J.A. Janssens. 1992. Concepts of fen and bog re-examined in relation to bryophyte cover and the acidity of surface waters. *Acta Soc. Bot. Pol.* 61:7–20.
- Kettunen, A., V. Kaitala, A. Lehtinen, A. Lohila, J. Alm, J. Silvola, and P. Martikainen. 1999. Methane production and oxidation potential in relation to water table fluctuations in two boreal mires. *Soil Biol. Biochem.* 31:1741–1749.
- Kettunen, A., V. Kaitala, J. Alm, J. Silvola, H. Nykänen, and P.J. Martikainen. 2000. Predicting variations in methane emissions from boreal peatlands through regression models. *Boreal Environ. Res.* 5:115–131.
- Krumholz, L.R., J.L. Hollenback, S.J. Roskes, and D.B. Ringelberg. 1995. Methanogenesis and methanotrophy within a *Sphagnum* peatland. *FEMS Microbiol. Ecol.* 18:215–224.
- Matthews, E., and I. Fung. 1987. Methane emissions from natural wetlands: Global distribution, area, and environmental characteristics of sources. *Global Biogeochem. Cycles* 1:61–86.
- Moore, T., and M. Dalva. 1997. Methane and carbon dioxide exchange potentials of peat soils in aerobic and anaerobic laboratory incubations. *Soil Biol. Biochem.* 29:1157–1164.
- National Wetlands Working Group. 1988. Wetlands of Canada. Ecological Land Classification Series, No. 24. Edited by Polyscience Publications, Inc., Montreal, Quebec, Canada.
- O'Flaherty, V., T. Mahony, R. O'Kennedy, and E. Colleran. 1998. Effect of pH on growth kinetics and sulphide toxicity thresholds of a range of methanogenic, syntrophic, and sulphate-reducing bacteria. *Proc Biochem.* 33:555–569.
- Ramaswamy, V., O. Boucher, J. Haigh, D. Hauglustaine, J.M. Haywood, G. Myhre, T. Nakajima, G.Y. Shi, and S. Solomon. 2001. Radiative forcing of climate change. *Climate change 2001: The scientific basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change.* Cambridge Univ. Press, New York.
- SAS. 1998. SAS, Release 8.02, Windows Version 4.10.1998. Edited by SAS Institute Inc., Cary, NC.
- Scanlon, D., and T. Moore. 2000. Carbon dioxide production from peatland soil profiles: The influence of temperature, oxic/anoxic conditions and substrate. *Soil Sci.* 165:153–160.
- Slack, N.G., D.H. Vitt, and D.G. Horton. 1980. Vegetation gradients of minerotrophically rich fens in western Alberta. *Can. J. Bot.* 58:330–350.
- Stumm, W., and J.J. Morgan. 1995. Aquatic chemistry: Chemical equilibria and rates in natural waters. 3rd ed. Edited by John Wiley & Sons, New York.
- Szumigalski, A.R., and S.E. Bayley. 1996. Decomposition along a bog to rich fen gradient in central Alberta. *Can. J. Bot.* 74:573–581.
- Thormann, M.N., and S.E. Bayley. 1997. Decomposition along a moderate-rich fen-marsh peatland gradient in boreal Alberta, Canada. *Wetlands* 17:123–137.
- Thormann, M.N., A.R. Szumigalski, and S.E. Bayley. 1999. Above-ground peat and carbon accumulation potentials along a bog-fen-marsh gradient in southern boreal Alberta, Canada. *Wetlands* 19:305–317.
- Turetsky, M.R., R.K. Wieder, and D.H. Vitt. 2002. Boreal peatland C fluxes under varying permafrost regimes. *Soil Biol. Biochem.* 34:907–912.
- Turetsky, M.R. 2004. Decomposition and organic matter quality in continental peatlands: The ghost of permafrost past. *Ecosystems* 7:740–750.
- Vitt, D.H., and W.-L. Chee. 1990. The relationships of vegetation to surface water chemistry and peat chemistry in fens of Alberta, Canada. *Vegetatio* 89:87–106.
- Vitt, D.S. Bayley, Jin T., L. Halsey, B. Parker, and R. Craik. 1990. Methane and carbon dioxide production from wetlands in boreal Alberta. 9820–106 St. Edmonton AB. Report on contract No. 90–0270 to Alberta Environment.
- Vitt, D.H., S.E. Bayley, and T.-L. Jin. 1995. Seasonal variation in water chemistry over a bog-rich fen gradient in continental western Canada. *Can. J. Fish. Aquat. Sci.* 52:587–606.
- Vitt, D.H., L.A. Halsey, I.E. Bauer, and C. Campbell. 2000. Spatial and temporal trends in carbon storage of peatlands of continental western Canada through the Holocene. *Can. J. Earth Sci.* 37:683–693.
- Waddington, J.M., and N.T. Roulet. 1996. Atmosphere-wetland carbon exchanges: Scale dependency of CO₂ and CH₄ exchange on the developmental topography of a peatland. *Global Biogeochem. Cycles* 10:233–245.
- Waddington, J.M., P.A. Rotenberg, and F.J. Warren. 2001. Peat CO₂ production in a natural and cutover peatland: Implications for restoration. *Biogeochemistry* 54:115–130.
- Whalen, M. 1993. The global methane cycle. *Annu. Rev. Earth Planet. Sci.* 21:407–426.