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Response of anaerobic carbon cycling to water table manipulation in an Alaskan rich fen

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ABSTRACT

To test the effects of altered hydrology on organic soil decomposition, we investigated CO_2 and CH_4 production potential of rich-fen peat (mean surface pH = 6.3) collected from a field water table manipulation experiment including control, raised and lowered water table treatments. Mean anaerobic CO_2 production potential at 10 cm depth (14.1 ± 0.9 μmol C g^{-1} d^{-1}) was as high as aerobic CO_2 production potential (10.6 ± 1.5 μmol C g^{-1} d^{-1}), while CH_4 production was low (mean of 7.8 ± 1.5 nmol C g^{-1} d^{-1}). Denitrification enzyme activity indicated a very high denitrification potential (197 ± 23 μg N g^{-1} d^{-1}), but net NO_3^- reduction suggested this was a relatively minor pathway for anaerobic CO_2 production. Abundances of denitrifier genes (*nirK* and *nosZ*) did not change across water table treatments. SO_4^{2-} reduction also did not appear to be an important pathway for anaerobic CO_2 production. The net accumulation of acetate and formate as decomposition end products in the raised water table treatment suggested that fermentation was a significant pathway for carbon mineralization, even in the presence of NO_3^-. Dissolved organic carbon (DOC) concentrations were the strongest predictors of potential anaerobic and aerobic CO_2 production. Across all water table treatments, the CO_2:CH_4 ratio increased with initial DOC leachate concentrations. While the field water table treatment did not have a significant effect on mean CO_2 or CH_4 production potential, the CO_2:CH_4 ratio was highest in shallow peat incubations from the drained treatment. These data suggest that with continued drying or with a more variable water table, anaerobic CO_2 production may be favored over CH_4 production in this rich fen. Future research examining the potential for dissolved organic substances to facilitate anaerobic respiration, or alternative redox processes that limit the effectiveness of organic acids as substrates in anaerobic metabolism, would help explain additional uncertainty concerning carbon mineralization in this system.

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1. Introduction

About 12% of the global wetland area occurs in boreal and arctic regions of Alaska (Bridgham et al., 2006). While the aerial extent of wetlands in Alaska is nearly twice that of wetlands in the continental United States (Ford and Bedford, 1987), there are relatively large gaps in our understanding of soil processes in this region (Bridgham et al., 2006; Johnson et al., 2011). High latitude wetlands and peatlands in particular are important in the global C cycle because they store a large component (>30%) of the world's soil C stocks (Gorham, 1991; Tarnocai et al., 2009). Peat accumulation generally depends on anoxic conditions that impede rates of decomposition. The formation and maintenance of boreal wetlands

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is influenced by relatively low rates of evaporation and impediments to site drainage (such as the presence of perennially and seasonally frozen ground, and relatively high water table position; Dingman and Koutz, 1974; Roulet and Woo, 1986). Overall, the fate of northern wetland C stocks will depend in part on the response of site drainage and other hydrological aspects to changing climate regimes (Woo et al., 1992; Tarnocai, 2009; Avis et al., 2011).

During anaerobic decomposition, carbon dioxide (CO_2) is derived from fermentation reactions and terminal metabolism with alternative (to O_2) terminal electron acceptors (TEAs). In anaerobic conditions, microbes preferentially reduce several alternative TEAs for respiration, with thermodynamic yield declining in the order: nitrate (NO_3^-) reduction, manganese (Mn[IV]), ferric iron (Fe[III]), sulfate (SO_4^{2-}), and ultimately CO_2 reduction. Reduction of inorganic TEAs other than CO_2 competitively suppresses CH_4 production. Once these TEAs have been depleted, methanogens produce CH_4 either by acetoclastic methanogenesis (splitting acetate to CO_2 and CH_4) or hydrogenotrophic methanogenesis (reducing CO_2 in a reaction coupled to H_2 oxidation).

The supply of alternative electron acceptors is generally low in peatlands, owing to permanently waterlogged conditions (low mineralization rates) and the tight cycling of inorganic nutrients (Reddy and DeLaune, 2008). However, drying of peat soils, which occurs with peat harvesting, periodic drought, or the recession of permafrost, also increases aeration and can replenish the supply of TEAs. In turn, these electron acceptors facilitate anaerobic decomposition upon saturation (rise in water table), or within anaerobic microsites in peat (Heitmann et al., 2007; Knorr et al., 2009; Deppe et al., 2010). For example, water table drawdown can stimulate sulfate reduction and suppress methanogenesis by increasing SO_4^{2-} pools through remineralization of organic sulfate and/or reoxidation of iron sulfides (cf. Blodau and Moore, 2003). The degree of hydrologic connectivity with groundwater also plays a strong role in solute chemistry, with higher variation in porewater TEA concentrations occurring in fens compared with more ombrotrophic systems (Vitt et al., 1995). In addition to water table drawdown, changes in active layer depths can change surface water runoff and/or groundwater connectivity in northern wetlands (McKenzie et al., 2009), thereby altering TEA concentrations.

Ratios of CO_2:CH_4 production in wetland soils have been used to develop a more detailed understanding of anaerobic soil processes. Under conditions that support methanogenesis, CO_2 and CH_4 are produced in equal amounts resulting in a 1:1 ratio of CO_2:CH_4, barring the reduction of CO_2 to CH_4 (Conrad, 1999). However, studies that incubate peat under anaerobic conditions often report CO_2:CH_4 exceeding 1 (cf. Bridgham et al., 1998). While these data indicate that TEA reduction is important for anaerobic decomposition, responses of potential CO_2 and CH_4 production vary across studies. For example, NO_3^- and SO_4^{2-} additions resulted in both reduced and enhanced CH_4 production in different fen types (Dettling et al., 2006). Several studies have quantified high CO_2 fluxes resulting from anaerobic decomposition that cannot be completely explained by measured pathways of microbial respiration (Vile et al., 2003; Dettling et al., 2006; Keller and Bridgham, 2007; Wüst et al., 2009; Knorr and Blodau, 2009; Deppe et al., 2010), and collectively these studies reveal large uncertainties in our understanding of TEA reduction in fen peat.

Mechanisms explaining why anaerobic decomposition does not necessarily follow the sequential reduction of TEAs in all cases are not well understood. For example, fermentation pathways are important for the anaerobic mineralization of organic matter in acidic fen ecosystems, however to date most information regarding the critical intermediate processes involved in fermentation, and their consequences for organic acid production and consumption, are largely conceptual (Drake et al., 2009). Adding to this complexity, recent studies have hypothesized that humic substances contained in dissolved organic matter (DOM) support anaerobic microbial respiration by acting as organic electron acceptors (Heitmann et al., 2007; Keller et al., 2009; see also Alewell et al., 2008). In general, any mechanism that diverts anaerobic electron flow from methanogenesis has implications for the ratio of CO_2:CH_4 production in wetland soils, and ultimately the amounts of CO_2 and CH_4 released from wetlands to the atmosphere.

Here we investigated CO_2 and CH_4 production and net changes in pools of electron acceptors in peat from an experimental rich fen in which we raised and lowered water table position for two years prior to peat collection. By examining potential rates of CO_2 and CH_4 production under controlled laboratory conditions, we were able to test whether the field manipulation affected peat chemistry and thus TEA reduction. We hypothesized that the lowered water table treatment would have greater availability of TEAs to support CO_2 production. However, an alternative hypothesis is that because the raised water table treatment increased plant productivity (Chivers et al., 2009), more labile DOM quality could lead to higher rates of both aerobic and anaerobic CO_2 production relative to the control treatment. In terms of the importance of individual TEAs, we hypothesized that NO_3^- reduction would contribute significantly to anaerobic CO_2 production given that porewater NO_3^- concentrations increased with fluctuations in water table position across all treatment plots (Kane et al., 2010). We did not expect the reduction of Fe[III] to be a significant component of anaerobic CO_2 fluxes in this rich fen, because Fe[III] exists predominantly in the solid phase at circumneutral pH (e.g., Drever, 1997). To provide insight into denitrification dynamics, we quantified the abundances of *nirK* and *nosZ* genes in peat extracts, as these functional genes code for the essential enzymes that are active in the sequential reduction of NO_3^- by the microbial community (NO_2^- and N_2O, respectively; Ye et al., 1994; Zumft, 1997). We also incubated peat with and without molybdate additions, which inhibits sulfate reducing bacteria, to better understand the importance of sulfate reduction to anaerobic CO_2 production in our peat soils.

2. Materials and methods

2.1. Study site and experimental design

The peat soil used for this incubation experiment was collected from the Alaska Peatland Experiment (APEX), which has previously been described in detail (Turetsky et al., 2008). Briefly, the APEX site is located just outside the Bonanza Creek Experimental Forest, in the interior region of Alaska, USA (www.lter.uaf.edu). The rich fen study site is located within a narrow alluvial plain <2 km north of the Tanana River, in the Middle Tanana Valley region (Hopkins et al., 1955). This site lacks trees and is dominated by brown moss, *Sphagnum*, and emergent vascular genera (*Equisetum*, *Carex*, and *Potentilla*). The APEX site is representative of extensive boreal peatland complexes, as rich fens are one of the most common peatland types in western boreal North America (Vitt, 2006).

During early spring of 2005, we established three plots (approximately 20 × 20 m) and assigned each to one of three water table treatments (raised, lowered, and a control reference plot, each approximately 25 m apart), as previously described (Turetsky et al., 2008). While soils were still frozen, an excavator and chainsaws were used to dig channels facilitating water drainage from the lowered water table plot to a small holding trench downslope from the plot. Throughout the growing seasons of 2005–2010, solar powered bilge pumps moved water into the raised water table treatment from a surface well located about 20 m downslope of the treatment (rate of approximately 10 cm d^{-1}). The mean (±standard error) growing season water table position from 2005 to 2008 for

the control and drained plots was 7.2 ± 3.2 and 10.0 ± 3.8 cm beneath the surface of the peat, respectively, whereas the water table was flush with the moss surface (0.1 ± 2.2 cm) at the raised water table treatment (Kane et al., 2010).

2.2. Soil sampling and preparation for laboratory incubation

In September 2007 (approximately 2.5 years after initiation of the field manipulations), we obtained 8 peat soil cores (7 cm diameter, 25 cm long) from each water table plot (24 cores total). The coring occurred at approximately 4 m spacing along two transects, approximately 4 m in from the sides of each treatment plot. In the field, the cores were cut into 5 cm increments, and peat from depths of 5–10 (the surface-most increment with no green moss) and 20–25 cm were used in this study. Each 5 cm section was sealed in a ziploc bag with as little headspace as possible, and immediately transferred in a cooler to the University of Alaska Fairbanks where they were frozen. Any artifacts of freezing on microbial activity are likely to be small as the timing of soil collection was coordinated approximately with natural freezing occurring late in the fall in this system (Henry, 2007). Frozen cores were placed in ice chests and shipped overnight to Michigan State University.

While frozen, each depth increment was subdivided into quarters using a band saw. To minimize any effects of thawing on microbial respiration, peat from one quarter was thawed at 2 °C over a 24 h period (see Schimel and Clein, 1996). Large roots (greater than 0.5 cm) were removed by hand, and the peat was homogenized gently by hand. Ten grams of wet soil (at field capacity) from each depth increment were placed into 250 mL incubation jars (Chromatographic Specialties, Inc.; Ontario, Canada). Jars assigned to the aerobic headspace treatment were flushed with ambient room air (~400 ppm CO_2) and sealed with lids fitted with septa. Jars assigned to the anaerobic headspace were flushed continuously with dinitrogen gas (N_2) in an anaerobic glove box for 10 min during processing and homogenization. In the anaerobic glove box, the jars were sealed with lids fitted with septa. They were then purged with 60 mL of N gas followed by the removal of 60 mL of headspace; this process was repeated three times to ensure an anaerobic headspace. To create similar soil moisture conditions and to ensure moisture was not a limiting factor for mineralization across all incubation samples, each incubation sample was brought to 50% moisture content by adding distilled water, given its bulk density and moisture content. All jars (96 total; 2 depths × 2 headspace treatments × 3 water table treatments × 8 replicates) were then equilibrated for 9 days at 2 °C to allow for the C mineralization pulse from dying roots to pass. All jars were incubated in the dark at constant room temperature conditions (approximately 22 °C) for the 38 day incubation experiment.

Bulk density and field volumetric moisture content were determined on a separate quarter (i.e. subsample) of peat. The subsample was dried at 55 °C for 72 h to obtain bulk density. Dry subsamples were ground using a cyclone sample mill (UDY Corporation; Fort Collins, CO) and analyzed for C and N percent with an elemental combustion system (Costech ECS 4010, Valencia, CA).

2.3. Carbon dioxide and methane production

Rates of CO_2 and CH_4 production were estimated during five 24-h periods over the 38 day experiment. The five 24-h periods began on days 1, 2, 9, 23, and 38 of the incubation. During each period, a 10 mL headspace gas sample was taken from each jar using syringes equipped with three way stopcocks immediately after jars were sealed (time = 0), and then every 12 h over the 24 h period (3 headspace samples/24 h). Prior to sampling, each jar was gently shaken by hand to mix the gases within peat pore spaces and to release trapped gas bubbles. Because high headspace CO_2 and CH_4 concentrations can become toxic to microbes, we purged jars with either a gentle stream of room air (aerobic treatment) or with N_2 in an anaerobic glove box (anaerobic treatment) prior to and after each 24 h sampling period. After headspace samples were collected, all jars were backfilled with 10 mL of N_2 gas to ensure constant air volume/pressure. After each 24 h sampling period, lids of jars in the aerobic treatment were removed, and jars were covered with plastic wrap to prevent moisture loss.

Five mL of each sample was analyzed for CH_4 concentrations using a Varian 3800 gas chromatograph (GC) equipped with a Haysep Q column (GC; Varian Inc., Palo Alto, California). The GC was calibrated using four CH_4 standard gases (0, 10.2, 100, 1000 μL L^{-1}) on a daily basis. Standards also were run as "unknowns" every 10 samples as internal checks for drift. The remaining 5 mL of each sample was analyzed for CO_2 concentrations via direct injection into a PP-system EGM-4 infrared gas analyzer (IRGA; PP Systems, Haverhill, MA, USA), which was calibrated daily. CO_2 standard gases were also run after every 10 samples.

Before assessing production rates, the measured concentrations were corrected for headspace dilution caused by backfilling with N gas, corrected for standard pressure and temperature using the ideal gas law, and multiplied by the corrected headspace volume. Overall gas production rates were calculated from the slope of the linear relationship between gas concentration and incubation time, and then were divided by the dry peat weight (g) to report data on a mass basis (nmol CH_4 g^{-1} day^{-1}, μmol CO_2 g^{-1} day^{-1}). Slopes with r^2 values less than 0.75 were examined and typically discarded (representing < 2% of the CO_2 data and <5% of the CH_4 data).

We conducted an additional incubation experiment to better quantify CO_2 production via sulfate reduction using a molybdate addition (Na_2MoO_4), which inhibits sulfate reducing bacteria (Wieder and Lang, 1988; Blodau et al., 2007). We added 10 g of peat from each water table treatment to each of 24 jars (8 sample cores × 3 water table treatments) within an anaerobic glove box with an N_2 headspace. To 12 of these jars (4 randomly selected from each of the 3 water table treatments), we added 500 μL of 20 mM Na_2MoO_4. The other 12 jars received an equivalent amount of distilled deionized water. We incubated the molybdate amended and control samples anaerobically for 36 h and measured CH_4 and CO_2 concentrations every 6 h beginning at 24 h, using the methods previously described.

2.4. Leachate chemistry

To quantify concentrations of TEAs of peat at the start of the incubation experiment, we leached a quarter (subsample) of each peat sample that had not been incubated. We also leached all incubation samples following the last sampling period to quantify concentrations of TEAs after the 38 day incubation period. 10 g soil samples were mixed with 50 mL of deionized water, gently shaken by hand and then equilibrated for an hour, and then filtered through a Whatman 0.45 μm nylon membrane filter following Huang and Schoenau (1996) and Kane et al. (2006). Filtered leachates were split, and half was acidified (pH 2) and refrigerated prior to dissolved organic carbon (DOC) and total dissolved nitrogen (TDN) analysis and the remaining leachate was frozen prior to anion and cation analysis. Blanks of deionized water (with and without acidification) were run with all analyses (approximately one for every nine samples). DOC and TDN were analyzed using a TOCV Analyzer with TDN module (Shimadzu Scientific

Instruments, Columbia, MD, USA). Ammonium (NH_4^+), nitrate (NO_3^-), nitrite (NO_2^-), sulfate (SO_4^{2-}), chloride (Cl^-), acetate, formate, lactate, and propionate concentrations were determined with an ICS 2000 ion chromatograph (IC, Dionex Corporation, Bannockburn, IL, USA). For the IC data, 0.02 mg L^{-1} was our detection limit. All concentration data are reported per dry mass of soil, accounting for dilution (Robertson et al., 1999).

2.5. Microbial characterization and activity

We quantified total bacterial abundance and two groups of denitrifiers using quantitative PCR (qPCR). Five complementary soil cores were taken to a depth of 15 cm at each water table treatment plot using a 10.2 cm diameter sharpened steel core barrel attached to a cordless drill. All samples were refrigerated and shipped overnight to U.C. Berkeley, California, USA. Throughout this paper, the abundance of genes is used instead of the abundance of organisms because such a calculation is based on a theoretical average number of functional gene copies per microorganism. All gene abundances are reported per dry mass of soil.

Soil community DNA was extracted from 0.25 g of soil using the MoBio PowerSoil kit. The manufacturers guidelines were followed, except that bead beating was used for cell lysis (30 s at 5.5 m s^{-1}) (BIO-101 bead beater, Savant), and extracted DNA was eluted with 50 μl dilution buffer. The total amount of DNA was quantified spectrophotometrically using a NanoDrop® ND-1000 spectrophotometer (NanoDrop Technologies).

Quantitative PCR was performed to assess the abundance of the following genes: the 16S rRNA gene (total bacteria), *nirK* (nitrate reducers carrying a NO_2^- reductase gene) and *nosZ* (denitrifiers carrying the N_2O reductase gene). All qPCR reactions were conducted on an iCycler thermal cycler equipped with an optical module (Bio-rad, USA). All samples were run in triplicate, and specific primer combinations and qPCR conditions were as previously described (Henry et al., 2004, 2006; Fierer et al., 2005). Single qPCR reactions were prepared in a total volume of 20 μl including 10 μl of iQ SYBR Green super mix (Bio-Rad), 4 μl of forward and reverse primers (3 μM) (Sigma–Aldrich), 1 μl PCR grade MQ-water (MP Biomedicals) and 1 μl of template DNA (2 ng μl^{-1}). At the end of each qPCR run, a melting curve was conducted from 55 to 99 °C with an increase of 0.5 °C every 10 s, and purity of the amplified fragment was checked by the observation of a single melting peak. Also an agarose gel (1%) with the qPCR products were run to check for correct sized amplicon.

A separate suite of soil cores was obtained in August of 2008 to examine changes in denitrification potential. A denitrification enzyme assay (DEA) was performed on five soil cores from the control plot, following Petersen et al. (2012). Thirty mL of DEA solution (1 mM glucose and 1 mM KNO_3, Fisher Scientific) was added to 20 g of moist soil in 225 mL jars and shaken by hand (end over end five times). The headspace was flushed with N_2 three times and afterward equilibrated with atmospheric pressure using a glass syringe. 20 mL of headspace was removed and replaced by 20 mL of acetylene, after which initial samples were taken and analyzed immediately by pulsed-discharge detection (Valco Instruments Co, Inc, Houston, TX, USA) on a 6890 gas chromatograph (Agilent Technologies, Santa Clara, CA, USA). The soils were incubated for 45 min at 22 °C on a rotary shaker (100 rpm), after which final samples were taken and analyzed. A control jar with 30 mL of DEA solution but no soil was included in the analysis.

2.6. Statistical analysis

Potential rates of CO_2 and CH_4 production on day 0 (i.e., the first round of measurements) are excluded from all analyses due to possible artifacts of disturbance. However, our qualitative results do not change if these data are included. We used a general linear model (Proc GLM, SAS v 9.2) to explore the effects of bulk density, peat C and N, headspace concentration, changes in the concentrations of various electron acceptors (DOC, TDN, NO_3^-, and organic acids) in peat leachates, and interactions among these effects on CO_2 production. Data were blocked by peat core number because splits of peat material for aerobic and anaerobic incubations came from the same sample. A similar GLM was used to examine controls on CH_4 production, minus the headspace treatment effect as we did not quantify CH_4 production in aerobic conditions. For all significant higher order effects, we used protected Fisher least significant differences tests for post hoc comparison of means ($\alpha = 0.05$); post-hoc analyses were used to determine differences in peat properties, leachate concentrations, and microbial activity. Throughout the paper, data are presented as means ± standard error.

3. Results

3.1. Peat properties and potential rates of CO_2 and CH_4 production

Peat bulk density at the 10 cm ($F_{2,47} = 1.68$, $p = 0.20$) and 25 cm ($F_{2,47} = 0.50$, $p = 0.61$) depths did not vary across the water table treatments (Table 1). Peat C concentrations in cores taken from the raised water table treatment were higher than those obtained from the control and lowered water table treatments at both 10 and 25 cm depths (Table 1). However, peat N concentrations were variable across all treatments and depths, and C:N differences across treatments were marginal ($F_{5,47} = 2.32$, $p = 0.06$; Table 1). Peat C:N ratios were higher at 10 cm (18.3 ± 0.7) than at 25 cm (15.2 ± 0.6; $t = 4.15$, $p < 0.001$) across all water table treatment plots.

Rates of aerobic CO_2 production in peat at 10 cm depth collected at the control, lowered, and raised plots averaged 11.0 ± 1.2, 9.7 ± 0.9, and 11.1 ± 1.1 μmol g^{-1} day^{-1}, respectively. Mean rates of anaerobic CO_2 production at the control, lowered, and raised plots were 15.1 ± 1.4, 14.2 ± 2.3, and 12.9 ± 1.0 μmol g^{-1} day^{-1}, respectively (Fig. 1). More CO_2 was produced from peat from 10 cm depth than from 25 cm depth in aerobic and anaerobic incubations, but at 10 cm depth, the mean CO_2 production rate in anaerobic incubations (14.5 ± 1.2 μmol C g^{-1} day^{-1}) did not differ from the mean CO_2

Table 1
Mean general physical and chemical properties of peat collected within each water table (WT) manipulation treatment. Different letters denote significant differences according to post hoc comparison of means.

WT treatment	Depth (cm)	Bulk density (g cm^{-3})	(SE)	C (%)	(SE)	N (%)	(SE)	C:N	(SE)
Control	5–10	0.088a	0.005	40.35ab	0.41	2.49ab	0.07	16.29	0.51
Control	20–25	0.138b	0.014	39.96a	0.52	2.96c	0.04	13.50	0.19
Lowered	5–10	0.097a	0.012	41.76bc	0.44	2.41ab	0.16	18.14	1.85
Lowered	20–25	0.126b	0.012	39.46a	0.75	2.55ab	0.24	17.16	2.51
Raised	5–10	0.082a	0.006	44.11d	0.39	2.28a	0.16	20.44	2.30
Raised	20–25	0.130b	0.014	42.38c	0.86	2.85bc	0.04	14.92	0.39

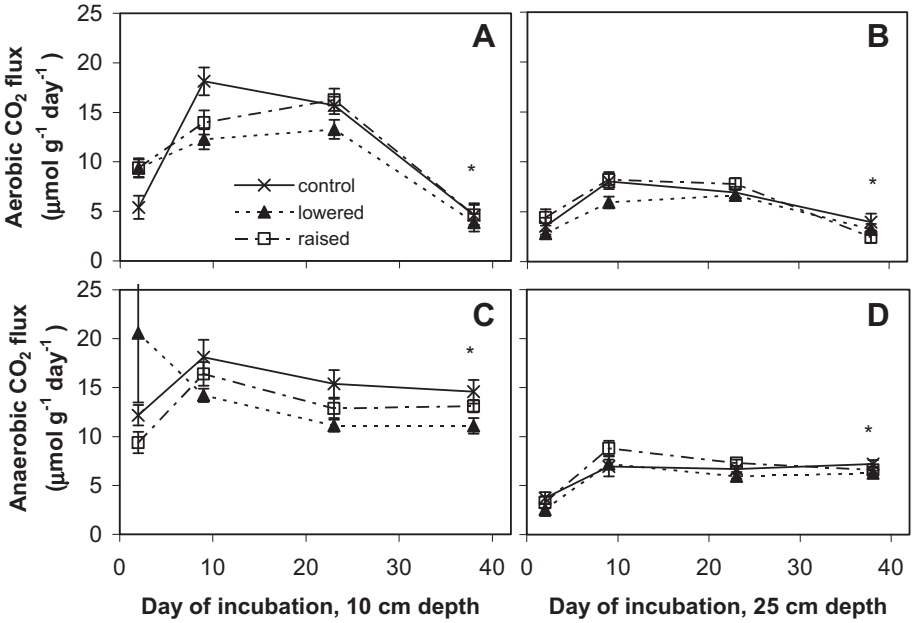

Fig. 1. Potential rates of aerobic and anaerobic CO_2 and CH_4 production during a 38 day incubation of peat from field water table treatments at an experimental rich fen. The three water table treatments were control, lowered (drained) and raised. Error bars represent standard errors of the mean values. Asterisks denote significant differences in mean values (all treatments) for a given day (t-test, $\alpha = 0.05$).

production rate in aerobic incubations (12.6 ± 1.3 μmol C g^{-1} day^{-1}) after 23 days. The mean anaerobic CO_2 production exceeded that of aerobic CO_2 production on day 38 of the incubation (Fig. 1; $t = 8.20$, $p = 0.001$). Anaerobic CO_2 production rates on average also were higher than aerobic CO_2 production for samples measured after 38 days at the 25 cm depths (Fig. 1; $t = 6.67$, $p = 0.003$). The mean difference between headspace treatments across all days was only marginally significant at 10 cm ($t = 2.03$, $p = 0.055$), and was not significant at 25 cm ($t = 0.87$, $p = 0.39$).

Mean rates of anaerobic CH_4 production (10 cm) at the control, lowered, and raised plots ranged from 9.8 ± 2.6, 8.2 ± 3.1, and 11.4 ± 4.4 nmol g^{-1} day^{-1}, respectively (Fig. 2). The ratio of the two terminal products of anaerobic respiration, CO_2:CH_4, was higher in incubated peat (10 cm) from the lowered water table treatment (4077 ± 1234; mol:mol) than the control (2219 ± 247) or raised (2446 ± 392) water table treatments (Fig. 3). The mean rates of CO_2 and CH_4 production from anaerobic incubations amended with molybdate to inhibit sulfate reducing bacteria were not significantly different from unamended anaerobic incubations ($F_{1,23} = 2.55$, $p = 0.12$ and $F_{1,23} = 0.24$, $p = 0.63$, respectively).

3.2. Leachate chemistry and mineralization pathways

The leachate chemistry of peat (10 cm depth) incubated aerobically and anaerobically changed by drainage treatment (Fig. 4). As expected, net DON and DOC mineralization (initial − final concentration) was greater with aerobic incubation (decline of approximately 84% and 55% from pre-incubation samples, respectively) than with anaerobic incubation (decline of approximately 63% and 31% from pre-incubation samples, respectively; Fig. 4A and B). There were no water table treatment effects on net DON and DOC mineralization, and SO_4^{2-} concentrations were not significantly different by water table treatment or incubation conditions (Fig. 4C). NO_3^- increased following incubations, relative to pre-incubation leachates (only traces of NO_3-N was measured in pre-incubation samples, mean of 0.003 ± 0.0009 mg g $soil^{-1}$). The lowered water table treatment had significantly higher concentrations of NO_3^- than the control plot in anaerobically incubated samples (Fig. 4D). NH_4^+ concentrations were very low and variable at the beginning of the experiment (mean of 0.015 ± 0.004 mg g $soil^{-1}$), and there was net NH_4^+ consumption following aerobic and anaerobic incubations (means of 0.012 ± 0.005 and 0.006 ± 0.003 mg g $soil^{-1}$ at the end of the 38 day experiment, respectively). NO_2^- was not detected.

Averaged across water table treatments, there was net production of acetate in aerobic incubations (Fig. 5A). There was net production of the sums of two typical end products of fermentation pathways, acetate and formate, in anaerobic incubations from the raised water table treatment whereas lactate was consumed following the aerobic and anaerobic incubations on average across all treatments (Fig. 5). Propionate was not detected.

In general, changes in peat leachate concentrations following aerobic and anaerobic incubation were greater in the 10 cm cores than in the 25 cm cores. Of all the analytes, depth was only a significant factor in explaining changes in peat leachates following aerobic and anaerobic incubations for NO_3^- ($F_{1,29} = 63.80$, $p < 0.001$ and $F_{1,29} = 20.39$, $p < 0.001$, respectively across all treatments) and DON ($F_{1,29} = 52.54$, $p < 0.001$ and $F_{1,29} = 33.77$, $p < 0.001$, respectively across all treatments). While there was a net loss of DON and net nitrification occurred in the 10 cm samples (Fig. 4), there were no significant net changes in DON and NO_3^- following incubation of the 25 cm depth samples. Leachates of peat from 25 cm contained only traces of NO_3-N following aerobic and anaerobic incubations (0.006 ± 0.001 and 0.003 ± 0.0006 mg g $soil^{-1}$, respectively). There was a water table treatment × depth interaction in explaining post-incubation leachate concentrations of DOC ($F_{2,29} = 2.85$, $p = 0.077$ and $F_{2,29} = 3.86$, $p = 0.035$, for aerobic and anaerobic incubations, respectively) and lactate ($F_{2,29} = 4.24$, $p = 0.027$ and $F_{2,29} = 4.34$, $p = 0.025$, respectively). The changes in DOC and lactate concentrations following incubations (pre-incubation − post incubation) were the smallest in leachates extracted from peat originating from the raised water table treatments plots, and from the deepest (25 cm) sampling depths. The mean reduction in DOC concentrations following aerobic incubation was 70% lower in the 25 cm samples than in the 10 cm samples. The mean reduction in lactate

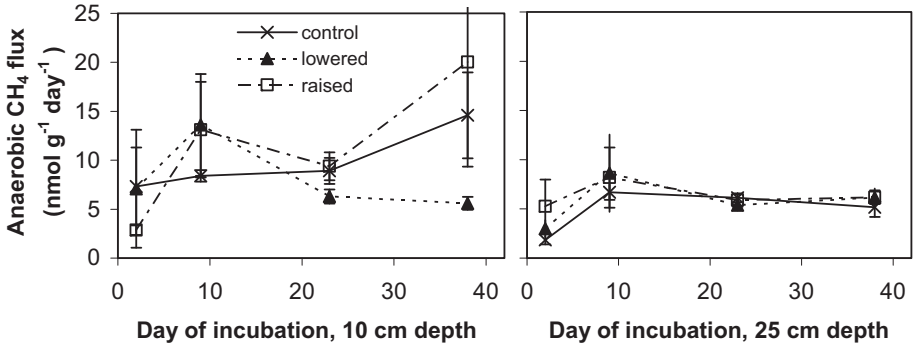

Fig. 2. Potential rates of anaerobic CH_4 production during a 38 day incubation of peat from field water table treatments at an experimental rich fen. Error bars represent standard errors of the mean values.

concentrations following aerobic incubation was 55% lower in the 25 cm samples than in the 10 cm samples.

CO_2 production varied significantly with peat depth, headspace treatment, DOC concentration, and the DOC:TDN ratio measured from peat subsamples leached at the beginning of the incubation (Table 2A). There was an interaction between headspace treatment and initial DOC concentrations in explaining variation in CO_2 production (Table 2A). In fact, initial DOC, the change in DOC over the 38 day incubation, and initial DOC:TDN were the strongest predictors of anaerobic and aerobic CO_2 production (Fig. 6). There were significant differences in the relationships between mean CO_2 production and initial DOC concentrations as a function of headspace treatment (analysis of covariance; $F_{1,59} = 5.31$, $p = 0.025$; Fig. 6A), and the relationship between CO_2 production and the change in DOC concentrations over the 38 day incubation was marginally affected by headspace treatment ($F_{1,59} = 3.76$, $p = 0.058$; Fig. 6B). There was no significant difference in the relationship between mean CO_2 production and initial leachate DOC:TDN as a function of headspace treatment (analysis of covariance; $F_{1,57} = 1.56$, $p = 0.217$; Fig. 6C). On the other hand, none of these variables, in addition to C%, N%, C:N ratio, bulk density, depth and drainage treatment, explained significant variation in mean CH_4 production over the 38 day incubation (Table 2B). Anaerobic CO_2 production relative to CH_4 production (CO_2:CH_4 ratio) was positively correlated with initial leachate DOC concentrations ($R^2 = 0.17$, $F_{1,29} = 5.72$, $p = 0.024$), the net increase in leachate NO_3^- concentrations ($R^2 = 0.48$, $F_{1,29} = 25.35$, $p < 0.001$), and with the change (pre-incubation − post incubation) in leachate DOC concentrations ($R^2 = 0.37$, $F_{1,29} = 16.47$, $p < 0001$) measured over the 38 day incubation period across water table treatments and sampling depths.

DEA assays indicated a very high denitrification potential (197 ± 23 μg N g^{-1} d^{-1}). There were marginal differences in bacterial 16S rRNA gene abundances across the three water table treatments ($F_{2,7} = 3.87$, $p = 0.096$), with the highest abundance occurring at the lowered treatment plot (Fig. 7A). The abundances of genes coding for the sequential reduction of NO_3^-, *nirK* and *nosZ*, were highest in the lowered water table treatment plot (Fig. 7B), though variability was high and differences were not statistically significant ($F_{5,14} = 2.44$, $p = 0.116$).

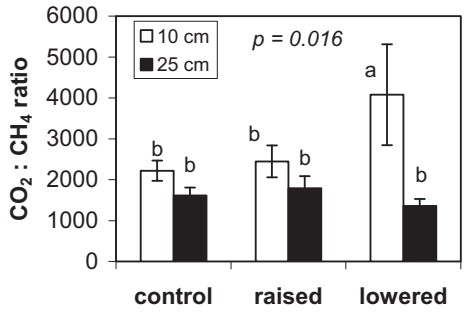

Fig. 3. Ratios of CO_2 to CH_4 production under anaerobic conditions averaged across all sampling periods. Error bars represent standard errors of the mean values. Different letters denote significant differences according to post hoc comparison of means.

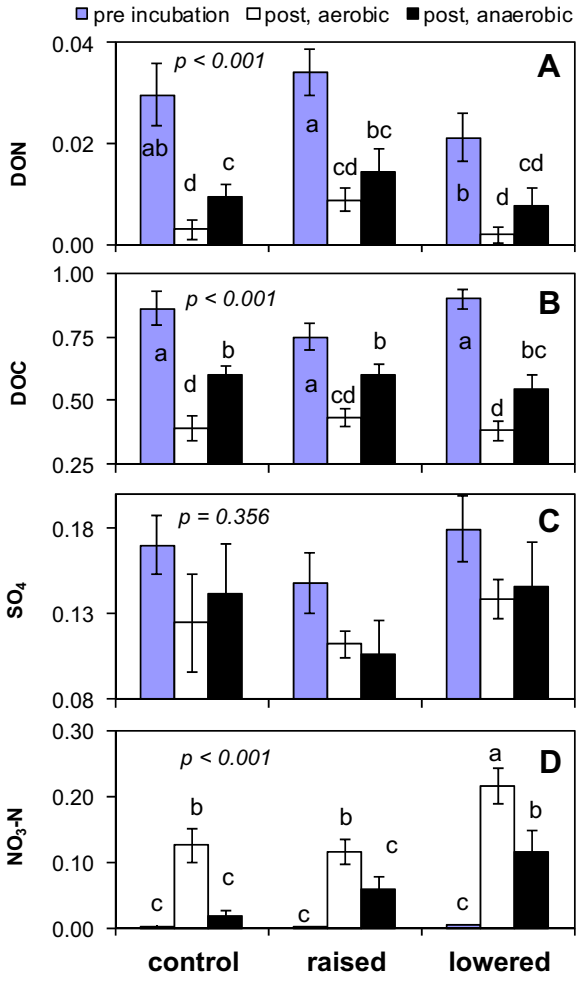

Fig. 4. Changes in leachate chemistry for 10 cm depths during the 38 day incubation study. Data are in mg g $soil^{-1}$. Error bars represent standard errors of the mean values. Different letters denote significant differences according to post hoc comparison of means.

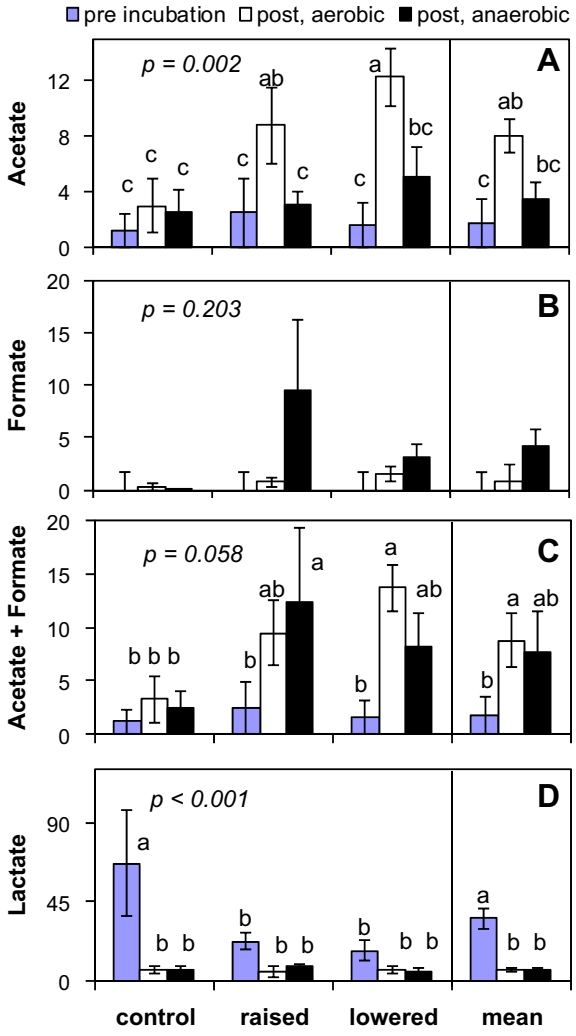

Fig. 5. Changes in leachate organic acids (10 cm depth) from before and after 38 day incubation treatments (all units are in μg g soil^{-1}). Error bars represent standard errors of the mean values. Different letters denote significant differences according to post hoc comparison of means.

Table 2
Results of a general linear model examining (A) controls on potential rates of CO_2 production (mean daily CO_2 μmol g soil^{-1} day^{-1} over the 38 day incubation) and (B) potential rates of anaerobic CH_4 production (mean daily CH_4 nmol g soil^{-1} day^{-1}) in peat soils from the experimental rich fen. Values in bold font are significant at $\alpha = 0.05$.

Source	DF	SS	MS	*F*	*p*
(A)					
WT treatment	2	1.55	0.77	0.45	0.643
Core	7	38.01	5.43	3.14	**0.010**
Headspace	1	8.74	8.74	5.06	**0.031**
Depth	1	10.30	10.30	5.96	**0.020**
Bulk density	1	0.64	0.64	0.37	0.548
C:N ratio (peat)	1	1.59	1.59	0.92	0.344
DOC:TDN (initial)	1	7.51	7.51	4.35	**0.044**
Initial DOC	1	19.42	19.42	11.25	**0.002**
Initial NO_3	1	3.36	3.36	1.94	0.172
Change in Acetate	1	0.17	0.17	0.10	0.753
Initial DOC × WT treatment	2	7.13	3.57	2.06	0.141
Initial DOC × headspace	1	30.06	30.06	17.41	<**0.0001**
Model	20, 57	861.10	43.06	24.93	<**0.0001**
(B)					
WT treatment	2	27.96	13.98	0.15	0.866
Core	7	214.05	30.58	0.32	0.930
Depth	1	14.05	14.05	0.15	0.709
Bulk density	1	19.25	19.25	0.20	0.663
C:N ratio (peat)	1	39.75	39.75	0.41	0.533
DOC:TDN (initial)	1	63.34	63.34	0.66	0.434
Initial DOC	1	96.41	96.41	1.00	0.338
Initial NO_3	1	157.05	157.05	1.64	0.227
Change in acetate	1	15.95	15.95	0.17	0.691
Change in formate	1	16.94	16.94	0.18	0.682
Model	17, 28	1205.94	70.94	0.74	0.721

4. Discussion

4.1. C mineralization potential in an Alaskan rich fen

We observed no significant water table treatment effects on CO_2 or CH_4 production potential (Table 2), which might suggest that peat quality has not changed appreciably in the first 2.5 years of water table manipulation. Additionally, the peat bulk density did not differ between field treatments after 2.5 years, indicating that the physical peat structure remained unchanged by drainage and flooding. *In situ* CO_2 and CH_4 flux differences (c.f. Turetsky et al., 2008; Chivers et al., 2009) can be attributed to effects of the altered soil climate such as a regeneration of TEAs (Deppe et al., 2010) and/or the adaptation of microbial communities to novel conditions. However, the similar rates of CO_2 and CH_4 production potential across field treatments during the 38-day incubation indicates that microbial communities remained functionally similar across all field treatments. In agreement with previous studies (Yavitt et al., 1987; Bridgham and Richardson, 1992; McKenzie et al., 1998; Waddington et al., 1998; Glatzel et al., 2004), CH_4 and CO_2 production rates decreased with depth in this study, which likely is because older soils found in deeper peat layers contain higher proportions of recalcitrant C than younger soils at the surface (Nadelhoffer et al., 1991; Hogg et al., 1992). Aerobic CO_2 production changed much less with depth (mean decline of 5.3 μmol g^{-1} day^{-1} from 10 to 25 cm) than did anaerobic respiration (mean decline of 8.1 μmol g^{-1} day^{-1} from 10 to 25 cm); this likely reflects declines in substrate quality as well as declines in favorable terminal electron acceptors occurring in the anaerobically incubated deeper peat.

Generally, rates of aerobic CO_2 production from this study fall within the range of other bog and fen incubation studies that have considered a range of depths (range of 0.37–48.29 μmol g^{-1} day^{-1} reported; Magnusson, 1993; Moore and Dalva, 1997; Waddington et al., 2001; Glatzel et al., 2004; Turetsky and Ripley, 2005). Mean anaerobic CO_2 production rates in this study were higher than most reports (range of 0.2–16.5 μmol g^{-1} day^{-1} reported; Yavitt et al., 1987; Magnusson, 1993; Moore and Dalva, 1997; Waddington et al., 2001; Glatzel et al., 2004; Dettling et al., 2006), but were not unprecedented (Wüst et al., 2009; Drake et al., 2009; Lipson et al., 2012). Surprisingly, anaerobic CO_2 production was only marginally different from aerobic production across all water table manipulation treatments (Fig. 1). While most studies reviewed reported mean aerobic:anaerobic CO_2 production ratios within the range of 1:1 to 6:1 (Bridgham and Richardson, 1992; Johnson et al., 1990; Updegraff et al., 1995; Segers, 1998; Bergman et al., 1999; Waddington et al., 2001; Glatzel et al., 2004; Lee et al., 2011), we measured mean daily aerobic:anaerobic CO_2 ratios of 0.31:1–1.26:1 in this study (Fig. 1). These data suggest that aerobic respiration was often secondary to anaerobic processes involving alternative (to O_2) electron acceptors and fermentation in mineralization of the fen peat.

4.2. Alternative electron acceptors

Results from the leaching experiment provide insights into the dominant controls over anaerobic CO_2 production in this system. The net mineralization of DON following anaerobic incubations was only 21% less than that measured in the aerobic incubations (not

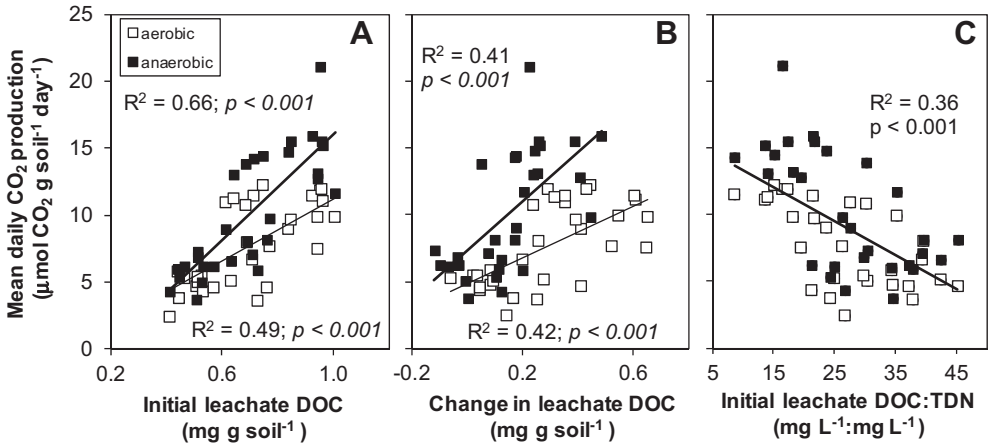

Fig. 6. Mean daily CO_2 production changes with the initial DOC concentrations measured in leachates from subsamples of peat obtained at the beginning of the incubation (A), the change in DOC concentrations over the 38 day incubation (initial − final concentration, B), and the initial DOC:TDN ratio of leachates from peat subsamples (C).

significantly different, Fig. 4A), which implies that the inorganic pool of N did not vary dramatically between the aerobic and anaerobic incubations. However, NO_3^- leached from peat following anaerobic incubations was significantly less than NO_3^- leached from aerobic incubations (Fig. 4D). If it is assumed that denitrification explains the difference in NO_3^- concentrations between the aerobic and anaerobic incubations, the potential amount of NO_3-N denitrified in the anaerobic incubation leachates would be 0.09 mg g soil^{-1} on average across the water table treatments. This would indicate a maximum potential denitrification loss of 6.25 µmol NO_3 L^{-1} g soil^{-1}, which would yield 7.81 µmol CO_2 g soil^{-1} over the course of the 38 day incubation given the molar ratio of NO_3:CO_2 in the oxidation of organic matter via denitrification is 24:30 (Reddy and DeLaune, 2008). Therefore, the mean amount of CO_2 that could be produced anaerobically by denitrification in this case (0.21 µmol CO_2 g soil^{-1} day^{-1}) would only account for ~2% of the mean daily CO_2 produced anaerobically (Fig. 1). This can only be used as a coarse estimate of the potential for NO_3^- reduction, as it does not account for mineralization of the peat material and assumes all net NO_3^- reduction was attributed to denitrification; it also assumes that no denitrification occurred in the aerobic incubation. It should be noted that the anaerobic incubations likely had some O_2 present within the peat porespace (or dissolved), as evidenced by the net production of NO_3^-. Notwithstanding, this exercise suggests NO_3^- respiration is a minor component of anaerobic CO_2 production in this system.

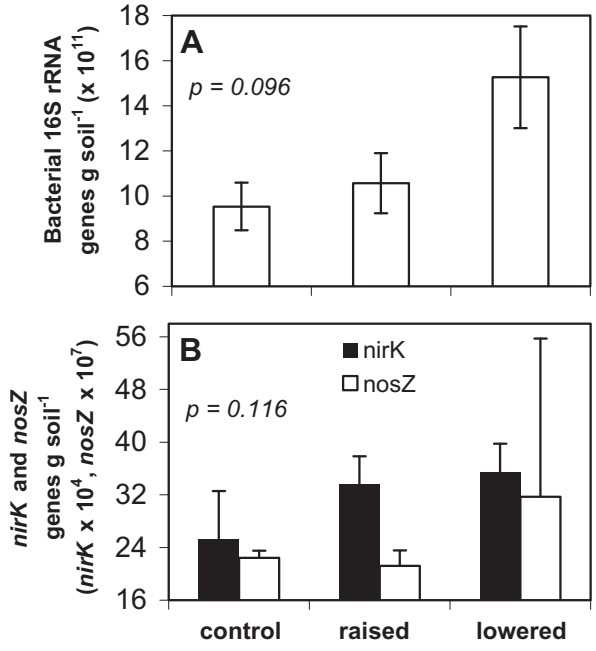

Fig. 7. Total bacterial gene abundance (A) and the abundances of genes describing denitrifier communities (B) for surface peat across the three water table treatments. *nirK* and *nosZ* code for the reduction of nitrite and nitrous oxide, respectively. Error bars represent standard errors of the mean values.

While we did not expect Fe^{3+} reduction to be a dominant process in the mineralization of organic matter owing to the relatively high pH of this system, recent research has demonstrated that certain biologically produced organic molecules (siderophores) have a high capability of solubilizing Fe^{3+}, and that there can be an interaction between flooding and the accumulation of dissolved Fe^{3+} in an Alaskan arctic thaw lake basin (Lipson et al., 2012). In turn, the dissolution and reduction of Fe^{3+} was thought to divert anaerobic electron flow from methanogenesis to CO_2 production, resulting in high CO_2:CH_4 ratios. While the surface porewater of the arctic study presented by Lipson et al. (2012) was substantially more acidic (seasonal mean pH of 4.7 of flooded area) than this study (mean pH of 6.3), there is evidence that Fe^{3+} can also act as an e-acceptor in temperate, brackish systems with circumneutral pH (e.g., Neubauer et al., 2005). Analyses of siderophore concentrations or Fe^{3+} interactions with humic substances were outside the scope of this paper, but certainly future research exploring mechanisms of Fe^{3+} solubility in boreal ecosystems with relatively high pH is necessary to fully realize the potential for Fe^{3+} reduction, in the context of altered hydrology in rich fens.

The lack of a significant change in SO_4^{2-} leached from aerobic or anaerobically incubated peat, as well as no change in CO_2 or CH_4 evolution following molybdate treatments also suggests that SO_4^{2-} reduction was not a major contributor to anaerobic CO_2 production. In addition, the CO_2:CH_4 ratio was very high across all water table treatments (cf. Segers, 1998; van Hulzen et al., 1999), suggesting some inhibition mechanism for methane production in this system. Future studies exploring the presence of more favorable electron acceptors (e.g., thermodynamic inhibition mechanism; see also Knorr and Blodau, 2009), particularly dissolved humic substances (Keller et al., 2009; Minderlein and Blodau, 2010), are needed to understand the high CO_2:CH_4 ratios observed.

The strongest predictors of anaerobic and aerobic CO_2 production in this study were initial DOC concentration of leached peat, the change in DOC over time, and the DOC:TDN ratio (Fig. 6). These findings could suggest that DOC was acting as a carbon source for

mineralization (an electron donor) in this system, because when there was more DOC, or a greater rate of DOC consumption, anaerobic CO_2 production increased. Notwithstanding, when we consider the ratio of two terminal products of anaerobic metabolism, we found a significant positive correlation between mean CO_2:CH_4 production and initial DOC concentrations, and a significant positive correlation between mean CO_2:CH_4 production and the change in leachate DOC over the 38 day incubation. While largely descriptive, these relationships support previous research demonstrating that DOM extracted from wetland soils can act as TEAs, increasing CO_2 production in anaerobic incubation experiments and diverting electron flow from methanogenesis (Heitmann et al., 2007; Keller et al., 2009; cf. Drake et al., 2009). However, DOM controls over anaerobic decomposition are not straightforward. Other studies in natural, disturbed, and restored northern peatlands have observed mixed relationships between anaerobic CO_2 production and leachate chemistry, with negative trends occurring with humic fraction DOC and positive trends occurring with water-extractable DOC and NH_4^+ generally observed across all sites (Basiliko et al., 2007). Adding to this complexity, Minderlein and Blodau (2010) have shown that the addition of DOM generally diminished anaerobic CO_2 production in incubation experiments of peat soils. Because the authors previously observed substantial anaerobic CO_2 production at similar DOC concentrations, they concluded that DOM quality (in particular, extracts rich in humic substances) plays a significant role in anaerobic decomposition. While biomolecular characterization of DOM was outside the scope of this study, the decline in mean daily CO_2 production as DOC:TDN increased (Fig. 6C) supports the importance of DOM quality in anaerobic and aerobic decomposition. In fact, there was an initial DOC:TDN $\times$ NO_3^- interaction in explaining variation in CO_2 production in this study ($F_{10,57} = 4.25$, $p = 0.04$; after core, headspace, and DOC:TDN were accounted for), which might suggest that anaerobic decomposition in sites with limited DOC lability would be more closely coupled with the availability of alternative TEAs (see Alewell et al., 2008); this might also be supported, for example, by the positive correlation exhibited between mean incubation CO_2:CH_4 and the net increase in leachate NO_3^- concentrations measured over the 38 day incubation period ($r = 0.69$, $F_{1,29} = 25.35$, $p < 0.001$). Understanding how changes in DOM compound classes affect anaerobic CO_2 production, such as the concentrations of proteins or aminosugars (relatively high nitrogen and more oxidized) relative to lipids or condensed hydrocarbons (relatively low nitrogen and more reduced) (cf. Hedges, 1990) is likely to clarify the role of humic materials in the cycling of carbon in this system.

4.3. Fermentation and methane precursors

The summed accumulation of acetate and formate as decomposition end products indicated that fermentation was a significant process involved in anaerobic CO_2 production. Fermentation has previously been shown to be the dominant pathway for anaerobic CO_2 production in ombrotrophic Alaskan bogs (Hines et al., 2001), and while acetate was the dominant end product of fermentation it was not metabolized to CH_4 (Duddleston et al., 2002). Anaerobically incubated German fen peat (10 cm) also accumulated acetate while yielding high levels of CO_2 production (10 μmol g dry soil^{-1} day^{-1}) in the first 20 days (Wüst et al., 2009; see also Deppe et al., 2010). Previous research has suggested that peat taken from cold environments can foster fermentation and the accumulation of acetate as an end product over CH_4 production (Nozhevnikova, 2000), which is an effect that has been shown to persist even when incubated at warmer temperatures (Duddleston et al., 2002). We observed very slow rates of CH_4 production as well as the accumulation of methanogenic precursors (acetate and formate) in the raised water table treatment (Fig. 5C), though responses by water table treatment were variable and it is difficult to ascertain exactly what the direct effect of the field water table manipulation was on the accumulation of these two organic acids. Notwithstanding, the net accumulation of acetate and formate could suggest that H_2/CO_2 was the primary precursor for methanogenesis, not the acetoclastic pathway (see Megonigal et al., 2004). While this is corroborated by the low field fluxes of CH_4 previously measured from the peat surface across the water table treatment plots (mean of 3.6 ± 0.9 g CH_4 m^{-2} growing season^{-1}, Turetsky et al., 2008; compare with 0.6–129.0 g CH_4 m^{-2} year^{-1} for other peatlands, Vitt and Chee, 1990; Whalen and Reeburgh, 1990; Roulet et al., 1994), we were only able to examine net changes in methanogenic precursors in this study. Future work examining complex intermediate processes involved in the production of these organic acids could help explain the lack of a consistent response in acetate and formate in the aerobic and anaerobic incubations.

Net acetate accumulation in the aerobic incubations was higher than in the anaerobic incubations (Fig. 5A). Previous research has suggested that both obligate anaerobes and facultative aerobes are involved in the formation of methanogenic substrates (such as acetate) during the decomposition of fen organic matter (Drake et al., 2009; and references therein), and that acetogenic bacteria exhibit a high tolerance to O_2 and can utilize a broad range of electron acceptors (Drake et al., 2008). While there is still much uncertainty as to the functionality of different communities of acetogenic bacteria in the conversion of simple sugars to acetate (Wüst et al., 2009), these data suggest facultative aerobes may play a significant role in the production of acetate in this rich fen ecosystem.

4.4. Effects of altered hydrology on microbial communities

Changes in leachates and trace gas effluxes across the water table treatments could reflect alterations to the microbial consortia, owing to the experimental changes in hydroclimate in the field. For example, Turetsky et al. (2008) measured lower field fluxes of CH_4 in the lowered water table plot, and showed a tight coupling between field fluxes and methanogen abundance in the peat. Not only was the water table consistently lower at the lowered treatment plot in this study, but the water table was more variable than the other plots (Kane et al., 2010). In the field we observed a sharp increase in porewater [NO_3^-] at 25 cm as the water table fluctuated approximately 5–10 cm beneath the peat surface, but relatively low concentrations at otherwise high or low water table heights; this might suggest high nitrification potential when the water table fluctuates in shallow peat. In this study the lowered water table treatment had the highest concentrations of NO_3^- following incubations (Fig. 4D), the highest anaerobic CO_2:CH_4 ratio (Fig. 3), and total bacterial and archaeal abundance (as reflected by the abundance of 16S rRNA genes) was marginally higher at the lowered plot (Fig. 6A). Taken together, these factors could indicate a higher potential for denitrification (cf. Drury et al., 1991) at the lowered water table plot; however, DEA was only measured in the control plot in this study. Longer term changes in environmental conditions could affect the tolerances of different denitrifier communities ("distal controls on community structure", as discussed by Wallenstein et al., 2006). However, the lack of differences in the abundances of genes describing different denitrifier communities across the water table treatments (Fig. 6B) suggests that distal controls over community composition were not manifested in the 2.5 years of variation in microclimate. Alternatively, the denitrifiers could be plastic in their response to microclimatic variation, and changes in gene abundances may not become apparent until physical characteristics change more dramatically in response to

microclimate (for example, with changes in dominant vegetation cover and peat character with increased depth to water table; Petersen et al., 2012; Waldrop et al., 2012).

Potential denitrification rates estimated with DEA were comparable to potential rates found in an urban riparian zone in Baltimore, USA (Groffman and Crawford, 2003), but exceeded potential rates from other studies with water- logged soils by one or two orders of magnitude, including a poorly drained peat soil from Scotland (Wheatley and Williams, 1989), and riparian fens in New Zealand (Schipper et al., 1993). The DEA approach uses excess nitrate and a carbon source, and therefore DEA activity could be artificially high in systems that are otherwise highly limited by nitrate or a labile carbon source. In order to better understand such hot-spots for denitrification we need to measure *in situ* rates of both nitrification and denitrification, but such measurements are challenging (Groffman et al., 2006). Sophisticated stable isotope techniques, which would allow us to monitor each process in nitrogen cycling separately under *in situ* conditions (Nielsen, 1992), are necessary to elucidate the role of denitrification in the carbon balance of these rich-fen ecosystems.

5. Conclusions

Our measurements of potential anaerobic and aerobic mineralization of peat did not differ across water table treatments, even after two years of differences in water table position maintained in the field. The peat in this study exhibited a very high denitrification potential (cf. D'Angelo and Reddy, 1999) in the control water table treatment, and while NO_3^- was present, potential net NO_3^- reduction could only account for a relatively small amount (<5%) of the CO_2 produced anaerobically. Moreover, SO_4^{2-} reduction could not be implicated as a dominant source of CO_2. Initial DOC concentrations, the change in DOC over the course of the incubation, and the initial ratio of DOC to TDN from peat leachates were the strongest predictors of CO_2 production potential, all of which suggest strong controls of DOM quantity and quality on metabolic processes in the peat, particularly in anaerobic conditions. These data suggest that with continued drying or with a more variable water table in rich-fen peatlands, anaerobic CO_2 production will likely be favored over CH_4 production. While patterns of net acetate production were variable among the headspace and water table treatments, these data suggest that acetate production in aerobic conditions can be as significant as anaerobic production. Future research examining alternative redox processes that limit the effectiveness of organic acids as substrates in anaerobic metabolism may help explain additional uncertainty concerning mineralization in this rich fen ecosystem.

Contributions

All authors contributed to the writing of the manuscript. MT, JH, and ADM designed the field manipulation; MT, MC, and CT designed the soil incubations; EK and MT designed the leaching study; and DP and MW conducted microbial analyses. EK led the overall data analyses and writing.

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