THE EFFECTS OF LONG-TERM WATER TABLE MANIPULATIONS ON CARBON CYCLING IN A GREAT LAKES PEATLAND

By

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This report, "THE EFFECTS OF LONG-TERM WATER TABLE MANIPULATIONS ON CARBON CYCLING IN A GREAT LAKES PEATLAND," is hereby approved in partial fulfillment of the requirements for the Degree of MASTER OF FORESTRY.

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INTRODUCTION

Peatlands and Carbon

Peatlands are wetlands where long-term net primary productivity exceeds organic matter decomposition, leading to the accumulation of incompletely decomposed organic matter, or peat. The requirements of how much peat there must be for a wetland to be considered a peatland varies in different countries. In Canada, there must be at least 40 cm of peat, whereas in many countries 30 cm of peat are required (Joosten 2002). Peatlands are important ecosystems because their vast peat deposits store substantial amounts of carbon (C), particularly in the boreal regions and tropical regions (Wieder 2006). Peatlands cover approximately 4 x 106 km^2 globally, which is only 3 to 5% of the world's surface, yet they store roughly 20 to 30% of the earth's soil carbon (270-455 Pg) (Gorham 1991; Turunen and others 2002). Peatlands occupy ~3,460,000 km^2 in boreal & subarctic zones (Gorham 1991). The total area of peatland in North America is 1,735,000 km2, of which 3.5 percent or 60,000 km^2 are found in the Great Lake states, with most being found in boreal areas further north (Verry 1977).

Peatlands that receive their water mostly from precipitation are known as ombrotrophic peatlands or bogs, whereas peatlands that receive their water from groundwater are known as minerotrophic/geogenous peatlands or fens. The influx of groundwater causes the pH in fens to be higher but the differences vary depending on the bedrock composition (DuRietz 1954; Vitt 2000). Fens with a pH above 6.5 are known as rich fens. Fens that have a lower pH are known as poor fens, and they can support the growth of Sphagnum mosses which acidifies the wetland even further. The combination of higher nutrients and pH results in decomposition being more rapid in fens than bogs (Aerts and others 1999).

Carbon CO_2 emissions

Carbon accumulates in a peatland because the amount of organic matter entering the system exceeds that being decomposed. The amount of CO_2 peatlands emit during the year depends on physical, chemical, and biological conditions. Peatlands release carbon that they have stored by respiration, which depends mostly on temperature and water table levels (Updegraff and others 2001; Moore and others 2002; Chimner and Cooper 2003). Other important controls of the

carbon cycle in peatlands are the plant community, the hydrology of the peatland, and the chemistry of plant tissues and peat (Bubier 1995).

The many feedbacks with peatland carbon cycling make it difficult to predict if peatlands will act as sources or sinks of carbon in future climate scenarios. In northern latitudes, where temperature changes are expected to be greatest and plant species diversity is lower, there are likely to be extreme changes in species composition and abundance. With warmer temperatures, more CO_2 will likely be released, especially in southern boreal forest regions of the northern hemisphere due to more aerobic conditions. However, where there is permafrost, less CO_2 might be released, but it will be converted to methane (CH_4) due to more anaerobic conditions (Tarnocai 2009). With anaerobic conditions, more graminoids will likely grow given time, which could add to the flux of CH_4 to the atmosphere. Plants will have an earlier start to the growing season and more photosynthesis could occur during periods with high solar insolation and thus, there could be a higher uptake of CO_2 (Moore and others 1998).

During periods of lower water table levels, various types of vegetation could colonize (autogenic succession). If trees invade, the gross ecosystem production (GEP) of trees could counteract the increase from decomposition, actually increasing peatland carbon storage (Laine and others 1996; Hargreaves and others 2003; Wieder 2006). In Scotland, it has been reported that afforested peatlands after drainage accumulate more carbon in trees, litter, forest soil and products than is lost from the peat over a time period of 90-190 years (Hargreaves and others 2003). This calculation was derived with the assumption that trees accumulated carbon at rates commensurate with yield class 10 m3 ha-1 a-1, and that the peat beneath the trees after canopy closure was estimated to be decomposing at a rate of ~1 t C ha-1 a-1 or less (Hargreaves and others 2003). This can vary depending on other physical characteristics, such as different rates of fine root production, mineralization potential, bulk density of the peat, and changes in the carbon storage in biomass (type of trees or shrubs) (Laine and Minkkinen 1996). During the summer months, fires can also cause CO_2 to be released from peatlands and with more droughts; there may be more fires in the coming years (Turetsky and others 2004).

Only a few studies have been conducted in the Great Lakes region and they were mesocosm experiments (Chasar and others 2000; Updegraff and others 2001). The studies that have looked at long-term water table manipulations and their effects on carbon fluxes and vegetation patterns have mostly been conducted in drained forested mires in Finland (Laine and Minkkinen 1996; Laine and others 1996; Nykanen and others 1998). Drainage of peatland sites for forestry could be useful sampling sites to study the possible effects of climate change as they would simulate the lowering of the water table that could occur with greater evapotranspiration rates in the future (Faubert 2004).

Methane (CH_4) emissions

Peatlands not only store carbon dioxide, but also produce two other greenhouse gases, CH_4 and nitrous oxide. According to Bartlett and Harriss (1993), peatlands contribute up to 9% of the Earth's CH_4 from natural sources due to anoxic conditions often found in peatlands. CH_4 is 23 times better at absorbing ultraviolet radiation than carbon dioxide, but has a much shorter atmospheric residence time (Meehl and I.G. Watterson 2007). CH_4 is produced when there is organic matter present and when all electron acceptors (oxygen, nitrate, manganese and iron oxides, and sulfate), which all have higher reduction potentials than CO_2 are not present (Reddy 2008). The reduction potentials are determined from the Nernst equation (AG° = - n F AE°). The electron acceptors can be present in the same soil profile, but in a different layer, so methane could still get produced higher up in the soil profile (although typically it gets produced deeper in the soil where it is more anaerobic).

CH_4 is produced by the splitting of acetate (which comes from the fermentation of organic matter (Kelley 1992; Reddy 2008).

$$CH3COOH \rightarrow CO_2 + CH_4 \quad \text{(acetate fermentation)}$$

or by the reduction of CO_2 with hydrogen (H_2)

$$2CH_2O + 2H_2O \rightarrow 2CO_2 + 4H_2$$

$$CO_2 + 4H_2 \rightarrow CH_4 + 2H_2O \quad \text{(hydrogen pathway)}$$

This results an overall reaction for the CO2 reduction pathway:

$$2CH_2O \rightarrow CH_4 + CO_2$$

Temperature and substrate availability affect which pathway occurs (Ferguson and Mah 1983; Svensson 1984; Westermann 1993). At lower temperatures (between 10 and 15oC), the breakdown of organic matter is mainly by homoacetogenesis followed by acetotrophic methanogenesis, and this pathway (acetate) was found to contribute 85-90% of the methane produced (Wieder 2006). The production of methane via the hydrogen pathway, by syntrophic proton-reducing bacteria, plays a larger role when there is an increase in temperatures (Conrad 1996; Avery and others 1999; Fey and Conrad 2000). At higher temperatures, organic matter degradation is dominated by fermentation, followed by syntrophic H2 production and H2 dependent methanogenesis (Conrad 1996). In addition to temperature, pH and vegetation can affect the production pathway. In vegetated sites where fresh organic matter is available from plant productivity, the acetate pathway has been shown to dominate, while in non-vegetated areas the hydrogen pathway controls (Bellisario and others 1999; Popp and others 1999).

Methane is released from wetlands to the atmosphere in one of three ways. The first is through diffusion, however the diffusive transport in flooded soils is limited by the low solubility of methane, and most methane diffusing can be oxidized to carbon dioxide (Reddy 2008). The second way is through wetland plants that have aerenchyma tissue. Plants with aerenchyma tissue, however, can also reduce methane emissions by delivering oxygen to the rhizosphere that oxidizes methane. The third way is through ebullition, and since methane is insoluble in water, it forms bubbles of gases that are rapidly removed via ebullition. Causes of ebullition include a drop in atmospheric pressure (Tokida and others 2007a), a reduction of hydrostatic pressure (Strack and others 2005), and a rise in temperature (FechnerLevy and Hemond 1996). Ebullition may account for 30 to 85% of the total amount of methane emitted from wetlands depending on how much or deep of an oxic layer there may be near the surface (Tokida and others 2007b; Reddy 2008). When methane moves through diffusion or ebullition, it can move to where there

is oxygen and be rapidly consumed by methanotrophic bacteria. These bacteria convert methane gas to methanol, then formaldehyde, and finally CO_2:

$$CH_4 \rightarrow CH_3OH \rightarrow HCHO^- \rightarrow HCOOH \rightarrow CO_2$$

Unlike methanogens, methanotrophic bacteria are not very sensitive to changes in oxygen levels. They can oxidize methane within a few hours of re-exposure to oxygen (Walter and others 2001). Autotrophic nitrifier communities with NH_4^+ can carry out methane oxidation as well since it has a similar structure and size to methane.

Studies are showing that the higher the water table and/or soil temperature the higher the CH_4 efflux (Roulet and others 1993; Bubier 1995; Schlesinger 1997; Turetsky and others 2008). Where precipitation decreases in the future, more CO_2 could be released due to more oxic conditions deeper into the peat. Consequently if precipitation increases, less CO_2 is expected to be released, but more CH_4 will likely be produced. In a peatland mesocosm study, with three different water table levels and three different heat levels, seasonal methane emissions were three times higher (21 vs. 7 g C/m2) on average in bogs than fens (Updegraff and others 2001). This was because there was higher aboveground plant productivity and dissolved nitrogen retention in the bog mesocosms than the fens even though the fen monoliths consisted mostly of sedges (Updegraff and others 2001). There may have been higher amounts of methane from the bog monoliths than the fens because in a natural setting, the amount of methane from fens can likely be highly dependent on its landscape position, which affects the amount of nitrogen from the groundwater flowing through. In a study in Finnish peatlands that were drained 30-50 years prior to research done in 1991 and 1992, the data collected from various drained and undrained Finnish peatlands indicated that a 10 cm lowering of the water table reduced methane emissions by 70% in fens and 45% in bogs (Nykanen and others 1998). The peat type also affects methane production (Rydin 2006).

Plant composition has also been shown to have a large effect on the production of methane due to the amount of labile organic material, which includes fresh litter and root exudation that may reach the anoxic zone (Rydin 2006). For example, sedges produce more methane than

Sphagnum, because they have roots, which are a source of labile organic carbon (Strack and others 2006b). Sedge also have aerenchyma tissue which allows methane to escape by traveling up through the roots directly to the atmosphere. Sedges were found to have the strongest relationship between methane flux, water table, and temperature of any species composition (Treat and others 2007). Strack and others (2006b) found that CH_4 flux will likely decrease with a lowering of the water table even with new sedges invading except during seasonal wet periods. Gradual changes in water table levels from climate change may or may not have similar effects as spontaneous drainage to the vegetation community of peatlands. Changing water table levels are what form the zonation of vegetation communities, and these are very important in the carbon cycling of peatlands.

The amount of labile organic material, which includes fresh litter and root exudation that reaches the anoxic zone, is the main control on methane production (Rydin 2006). This means that plant productivity and depth to the water table are two important factors in methane production.

According to many studies with warming and water table manipulation studies, the conclusion seems to be that CO_2 fluxes from respiration will be affected mainly by soil temperature with a secondary effect of water table level. On the other hand, CH_4 fluxes will be dependent mainly on water table levels and plant productivity, with a secondary effect of soil temperature and peat chemistry.

Microtopography

When studying the carbon cycle, looking at both hummocks and lawns is very important because they are often prevalent in peatlands. Hummocks can range from 20 to 50 cm above the peat surface, and are often characterized by *Sphagnum*. However, during the summer and as the substrate becomes drier, more woody plants often grow on hummocks such as: *Picea mariana, Larix laricina, chamaedaphne calyculata,* and *Myrica gale*. Lawns are typically 5 to 20 cm above the water table (Rydin 2006). Lawns contain some species of *Sphagnum*, but often have more graminoids, because they have aerenchyma tissue to tolerate the wetter conditions. Such plants include *Carex exilis, C. oligosperma, C. pauciflora* and *S. angustifolium*. Species found on both hummocks and lawns include *Kalmia polifolia, Andromeda glaucophylla,* and *Vaccinium*

oxycoccus. Due to different plant communities and soil properties, hummocks and lawns will likely respond differently to changes in climate.

Since peatlands cover an expansive area in the northern hemisphere, it is important to study how carbon dioxide and methane fluxes will respond to climate change in different geographic areas across the northern hemisphere. In addition, many studies involve spontaneous drainage where plants may not respond the same way as if water table changes occur slowly over many years. More studies need to be done with long-term water table manipulations in southern boreal regions for modeling the affects of peatlands on the carbon cycle in the future. Therefore, the objectives of this study are: (1) how long-term changes in water table levels will alter carbon dioxide (CO_2) and methane (CH_4) fluxes, (2) how that differs between hummocks and lawns, and (3) how does increased tree growth alter carbon cycling?

LONG-TERM WATER TABLE MANIPULATIONS ON GREAT LAKES PEATLAND CARBON FLUXES

ABSTRACT

Peatlands cover 3 - 5% of the Earth's land surface, yet they store between 20% and 30% of the earth's soil carbon. However, climate change models are predicting altered precipitation patterns for the Great Lakes region, which strongly influences carbon cycling in peatlands. Therefore, the goal of this study was to quantify how changing long-term water table levels in peatlands altered carbon cycling. This study took place in a large peatland complex in Seney National Wildlife Refuge (SNWR) in the central Upper Peninsula (UP) of Michigan. Ecosystem respiration (ER), gross ecosystem production (GEP), net ecosystem exchange (NEE) and methane (CH_4) fluxes were measured roughly every two weeks during the snow free season during a two year period using chamber methods across a factorial design of different water table treatments and microtopography (hummocks vs. lawns). Historically these sites were one large poor fen complex, but a road and levee were built (~50 years ago) flooding one side and partially draining the other side. Our results indicate that raising long-term water table levels ~10 cm increased CH_4 fluxes by 65%, decreased ER by 15% GEP by 6% and increased NEE by 10% over the two years. Conversely, lowering the water table by roughly ~10 cm decreased CH_4 by 68%, increased ER by 23%, increased GEP by 10%, and decreased NEE by 12%. Our results indicate that long-term water table changes will have complex interactions on plant and gas fluxes. While there we some large differences in carbon fluxes between hummocks and lawns, we only found marginally significant differences with microtopography within treatments.

INTRODUCTION

Peatlands are important ecosystems because their vast peat deposits store substantial amounts of carbon (C), particularly in tropical and boreal regions (Wieder 2006). Peat accumulates when long-term net primary productivity has exceeded losses from decay and leaching, leading to the accumulation of incompletely decomposed organic matter, or peat. While peatlands cover only 3 to 5% of the world's surface, they store between 20 to 30% of the total earth's soil carbon (270-455 Pg) (Gorham 1991; Turunen and others 2002). The total area of peatland in North America is 1,735,000 km^2, of which 3.5 percent or 60,000 km^2 are found in the Great Lake states (Verry 1977). These large pools of carbon may be susceptible to changes in climate, especially in the Great Lakes region as they lie at the southern end of the northern peatlands region (Wieder 2006).

The exchange of CO_2 between peatlands and the atmosphere is the result of two major fluxes, carbon fixation associated with photosynthesis (GEP), and ecosystem respiration (ER), which is the summation of both heterotrophic and autotrophic respiration. The rate of heterotrophic respiration is controlled by soil temperature and pH, oxic peat layer volume, nutrients, and the quality and quantity of decomposable material while autotrophic respiration is modified by photosynthesis, temperature, and water and nutrient availability (Chapman and Thurlow 1998).

Ecosystem respiration responses to climate warming and precipitation changes are of particular concern today because carbon efflux to the atmosphere is a major positive feedback associated with global warming (Bond-Lamberty and Thomson 2010).

Peatlands have the capacity to limit global warming through carbon storage in soils, while at the same time, they emit methane, which has a global warming potential approximately 23 times greater than CO_2 over a time horizon of 100 years (Meehl and I.G. Watterson 2007).

Peatland carbon cycling is expected to be modified by changes in temperature and hydrologic conditions, both of which can affect rates of production and decomposition (Updegraff and others 2001; Chimner and Cooper 2003). Research has focused on how changing temperature will affect carbon cycling in peatlands (Dunfield and others 1993; Chen and others 2008; White

and others 2008), however, more recent research is indicating that changes in water table levels may be even more important in regulating carbon cycling (Dinsmore and others 2009; Strakova and others 2010). Recent IPCC predictions for the Great Lakes are predicting an increase in precipitation for the region (Meehl and I.G. Watterson 2007). They are also predicting warmer temperatures, which may alter the hydrologic budget even further by increasing evapotranspiration and perhaps by changing the form of precipitation from snow to rain.

There have been few studies conducted on how changing hydrology will alter carbon cycling in peatlands in the southern boreal forest regions of the northern hemisphere. Most studies have been short-term drainage studies (Strack and others 2006a); (Turetsky and others 2008) done in boreal regions and some as long-term studies in Finland (Laine and others 1995). The studies that have been researched in the Great Lakes region have been mesocosm studies (Updegraff and others 2001; Blodau and Moore 2003; Chen and others 2008; Knorr and others 2008; White and others 2008).

However, a problem with short-term water manipulation studies is that plant communities have not been allowed to change to reflect the new hydrologic conditions. It is possible that long-term drainage may show different responses than short-term drainage.

Therefore, the objective of this study was to test how long-term changes in water table levels alters ecosystem CO_2 fluxes (NEE, GEP and ER) and CH_4 fluxes in a peatland hydrologically altered ~50 years ago.

METHODS

Study site

We established a field experiment in Seney National Wildlife Refuge (SNWR), located in the east-central portion of Michigan's Upper Peninsula approximately halfway between Lake Michigan and Lake Superior (46oN & 86oW). The SNWR lies in the Manistique River watershed, which drains approximately 3,885 km^2 before emptying into the northeast corner of Lake Michigan. This area is within the southern-most area of widespread continental peatlands (Heinselman 1965). The Refuge is approximately 38,000 hectares, of which 2/3 is covered by

peat, with depths often exceeding 2 m (Kowalski and Wilcox 2003; Wilcox and others 2006). Mean annual precipitation is 390 cm (80% as snow), and mean average temperature is 5.1 oC. Most of the snowpack melts during April and May and combined with June being the wettest month of the year, often leads to a spike in water table levels.

In the late 1800s, the Refuge was heavily logged, burned, ditched, drained, and cultivated. Around 1908, a group called the Western Land Surety Company bought the land to convert it into farm land. However, the farming attempt failed and the land reverted back to the State of Michigan and eventually to the Federal government to form the Refuge. With the aid of The Civil Conservation Corps, a complex system of dikes, water control structures, ditches, and roads were built to convert peatland areas into more open water areas for waterfowl habitat.

Experimental Design

We established a field experiment to address peatland carbon cycling responses to changing water table levels. The sites were once all one large poor fen complex (Figure 1), but a service road was built in the early 1950s, flooding one side (Sites C & D) and partially draining the other side (Sites E & F). Two sites were picked in areas that appeared not to be altered to use as references (Sites A & B). All sites had 4 (2 x 1 meter) plots randomly placed for sampling and boardwalks were constructed to minimize disturbance while sampling. Plots were further divided into two hummock and two lawns with a 60 cm by 60 cm collar installed to put the chambers on for sampling.

The dominant vegetation at the sites included various plants, trees, graminoids, and shrubs (Table 1). The main species were *Chamaedaphne calyculata, Ledum groenlandicum, Andromeda glaucophylla, Vaccinium oxycoccos, Eriophorum vaginatum, Larix laricina, Picea mariana, Kalmia polifolia, Sphagnum sp. (fuscum, rubellum, magalanicum)* and *Carex Oligosperma*.

The vegetation was sampled in each plot from 14 August 2009 thru 1 September 2009 to capture the peak of the growing season. The vegetation was sampled using a grid intercept method (1 m2 quadrat) with 100 uniformly distributed points. The point grid sampling frame was constructed using an aluminum frame with a movable cross bar and was leveled above the plot. All plant

species the laser hit from the top of the canopy to the peat surface were recorded. Foliar cover of all species was calculated from the total number of laser hits divided by the total number of grid points.

CO_2 & CH_4 fluxes

Midday CO_2 exchange and CH_4 measurements were taken at least biweekly during the snow free periods (April-Oct) of 2009 and 2010 at each plot. All 24 plots were measured within four days of each other between 10:00 and 17:00 hours. We used chamber methods to measure CO_2 exchange (Vourlitis and others 1994); (Carroll and Crill 1997). An Infrared Gas Analyzer (PP-Systems, EGM-4, Amesbury, Massachusetts) was connected to a clear plexiglass chamber (60 cm x 60 cm x 60 cm) to quantify NEE, GEP, and ER. The chamber had two small fans to ensure mixing of the air and a removable lid to allow for air exchange between samples. During sampling, the chamber rested on square aluminum collars (10 cm deep x 60 cm on a side) that were installed in the center of each plot and left in place.

Flux rates were calculated by measuring the change in CO_2 concentrations within the chamber (Vourlitis and others 1993). After placement of the chamber, no measurements were taken until a steady mixing occurred. A steady mixing was assumed to occur when the CO_2 concentration in the chamber started increasing or decreasing at a constant rate (typically 20-30 seconds). After mixing occurred, measurement of net ecosystem exchange (NEE) commenced and lasted for roughly 2 minutes. The rapid measurements minimized temperature and water vapor increases inside the chamber (Vourlitis et al. 1993). In conjunction with CO_2 concentrations, we also measured relative humidity, photosynthetic active radiation (PAR), chamber temperature, and soil temperature inside the chamber using EGM-4 standard probes. After the NEE measurement, the top of the chamber was opened for 20-30 seconds for ventilation. The lid was then closed and an opaque cloth was put over the chamber, minimizing photosynthesis, to measure ecosystem respiration (ER) for the next two minutes. Gross ecosystem production (GEP) was calculated by subtracting ER from NEE (GEP = NEE - ER).

Methane fluxes was measured using the static chamber technique (Vourlitis and others 1994). The methane chambers (60 cm x 60 cm x 30 cm) were placed directly on the collars and samples

were collected every 10 minutes from 0 to 40 minutes (Tuittila and others 2000). Samples were collected using a syringe and injected into pre-evacuated vials. The samples were then analyzed within ten days using gas chromatography (Varian 3800). The CH_4 flux was calculated using the following equation (personal communication from Mike Dalva and Jill Bubier),

$$\frac{\text{ppmV min}^{-1}\text{ (slope) x 1 atm x Chamber Vol. (L) x 16 g CH}_4\text{ x 1000 mg x 60 min}}{\text{0.0821 L-atm K}^{-1}\text{ mole}^{-1}\text{ x 298 K}}$$

$$(1\text{x}10^6)\text{ x (Chamber Area in m}^2\text{)}$$

The final units were in mg CH_4 m^{-2} hr^{-1}. Due to ebullition events, which may have occurred when placing the chamber on the collars, high CH_4 fluxes in our first ten minutes of sampling were not included.

Methane isotopes

In addition to CH_4 flux rates, we also analyzed isotopes to quantify if the CH_4 was produced via acetate fermentation or carbonate reduction (Kelley 1992; Westermann 1993). Past research suggests that stable isotopic signatures of CH_4 relative to microbial respiratory production were as follows: acetate fermentation results in CH_4 relatively enriched in ^{13}C ($\Delta^{13}C$ of -65 to -50 $^o/_{oo}$), while CO_2 reduction results in CH_4 with a Δ^{13} of (-110 to -60 $^o/_{oo}$) (Whiticar MJ 1986).

CH_4 isotopic analysis was conducted in 2010 only. The first two rounds were conducted during May and June at sites B, C, and E. The last two rounds were collected from all sites in the middle of, and again at the end of July. All samples were collected at the end of 40 minutes from our CH_4 chambers and injected into evacuated 125 mL serum vials (Wheaton) fitted with butyl rubber stoppers. Gas samples were shipped to the UC- Davis Stable Isotope Facility for analysis of $\Delta^{13}C/^{12}C$ in methane and $\Delta D/H$ of methane.

Environmental Variables

Water table levels were monitored hourly at each site with pressure transducers (Levellogger Junior, Solinst, Georgetown, Ontario) and a barometric logger (Baralogger Gold, Solinst, Georgetown, Ontario) that was placed in 1.5 meter long, 10.16 cm diameter PVC well.

Soil temperature was measured in each plot (24 plots) using iButtons (I-Buttons, Maxim Integrated Products, Sunnyvale, CA) at three depths (5 cm, 22.7 cm, and 40.1 cm) below the peat surface. These measured soil temperature every hour during the snow free season and every three hours from November through April.

Statistical Analysis

A two-way, repeated measures analysis of variance was conducted using PROC MIXED to test for experimental differences in ecosystem CO_2 and CH_4 efflux (SAS 2009). Each plot was an experimental unit, so replicate measurements were averaged by plot for each year of analysis. Individual sites within each water table treatment were used as replications, water table treatments were treated as whole plots, and microtopography were treated as subplots. Water table treatment and microtopography and interactions were treated as fixed effects, plots were treated as random effects and sample years were treated as repeated measures. We used complex symmetry covariance structure for repeated measures analysis as determined by looking at the fit statistics and the Kenward and Roger's correction for degrees of freedom (Littell RC 2006). Differences between all treatments were conducted using Tukey's post-hoc test with differences at $P<0.05$ considered significant.

RESULTS

Environmental and Vegetative Parameters

Annual precipitation amounts were similar during 2009, and 2010, averaging 1.55 mm day-1 and 1.93 mm day-1, respectively (Figure 3). May and June was the wettest period in 2009, with a more even distribution in 2010. As expected, water table levels were highest in sites C and D, and lowest in sites E and F (Table 1).

Overall, total plant cover was lowest in the wettest site, and increased as conditions became drier. The wettest site D had the greatest graminoid cover and the lowest moss cover (Table 1). The shrub cover changed very little between the sites, and tree cover was greatest in the driest site. Moss cover also generally increased as conditions became drier.

Ecosystem carbon cycling (NEE, ER, and GEP)

Water table level was a significant factor explaining ER and GEP flux rates (Table 2). There was a significant difference in ER between the treatments (Figure 3). The dry treatments had significantly greater ER fluxes than both the wet ($p < 0.001$) and control ($p=0.01$) treatments. The fluxes from the dry treatment averaged (0.48 ± 0.05 µmol CO_2 m^{-2} s^{-1}), the control treatment (0.39 ± 0.05 µmol CO_2 m^{-2} s^{-1}), and the wet treatment (0.33 ± 0.04 µmol CO_2 m^{-2} s^{-1}) (Figure 3). The control and wet treatments were not significantly different from one another. ER was consistently greater in the lawns compared to the hummocks, but there were no significant ($p > 0.05$) differences found, or with year. We found that water table level was the best predictor of ER (Table 3).

GEP fluxes were also significantly different between the wet and dry treatments ($p=0.02$) and the control and dry treatments ($p=0.04$) (Figure 3). GEP was greatest in the dry treatment with an average flux of -0.79 ± 0.07 µmol CO_2 m^{-2} s^{-1}. The wet treatment (-0.68 ± 0.06µmol CO_2 m^{-2} s^{-1}) and control treatment (-0.72 ± 0.08 µmol CO_2 m^{-2} s^{-1}) were very similar. Microtopography did not have a significant effect on GEP for any of the treatments. We found that water table levels and plant cover, percent tree cover in particular, were the best predictors of GEP (Table 3).

Average NEE values were greatest in the wet treatments (-0.361 ± 0.04µmol CO_2 m^{-2} sec^{-1}), followed by the control (-0.328 ± 0.06 µmol CO_2 m^{-2} sec^{-1}) and least in the dry (-0.288 ± 0.05 µmol CO_2 m^{-2} sec^{-1}) (Figure 3). However, these differences were not significant. We did find a significant interaction of water table and microtopography with NEE significantly higher ($p = 0.05$) in the lawns than in the hummocks in the dry treatments (Table 2). Of all the predictors of NEE, percent tree cover and soil temperature at 40 cm below the peat surface showed the strongest correlations (Table 3).

CH_4 Flux

CH_4 fluxes were significantly different between the wet and dry treatments (p=0.03) (Table 2). The wet treatment had fluxes averaging 0.63 ± 0.27 mg CH_4 m-2 sec- 1, while the dry treatment had fluxes averaging 0.13 ± 0.07 mg CH_4 m-2 sec-1. The control site had fluxes averaging 0.38 ± 0.12 mg CH_4 m-2 sec-1.

We did not find a significant difference in CH_4 fluxes by year (0.44 mg CH_4 m^{-2} hr^{-1} vs. 0.31 mg CH_4 m^{-2} hr^{-1}). Methane emissions from hummocks and lawns decreased from wet to dry and were generally greater in the lawns (Figure 5). The sites with the largest differences in CH_4 emissions between the hummocks and lawns in order were C, A, B, D, E, and then F (Figure 6).

Our first set of isotope data from the non-treed sites suggests that the CH_4 was produced via acetate fermentation. When adding in the additional sites for our last collection, the values changed from an average of -50.55 $\Delta^{13}C/\Delta^{12}C$ to an average of - 41.92 $\Delta^{13}C/\Delta^{12}C$ (Table 4), we did a standard regression of CH_4 flux versus graminoids. Water table and percent cover of graminoids were the best predictors of CH_4 fluxes (Table 3). We found the higher the percentage of graminoid cover the greater the CH_4 flux (R2 = 0.26) (Figure 7).

DISCUSSION

Our results indicated that changes in long-term water table levels have the potential to influence peatland carbon cycling. Our study is unique because there are very few studies looking at the effects of long-term water table changes in peatlands, most are short-termed (Strack and others 2006a; Strack and others 2006b; Turetsky and others 2008) or mesocosm experiments (Aerts and Ludwig 1997; Updegraff and others 2001; Blodau and Moore 2003; Chen and others 2008; Breeuwer and others 2009; Dinsmore and others 2009).

Ecosystem respiration

With a ~10 cm lowering of the water table, ER rates increased by 23% in our study. Other studies support the importance of water table levels on ecosystem respiration. Strack and others (2006) reported in a study in Quebec, Canada that ER from hummocks, hollows, and lawns were

higher from the drained site which experienced a water table drawdown of ~20 cm 8 years prior to the study than the control site both in 2001 and 2002. In another long-term water table manipulation study, Faubert (2004) found that wetter conditions led to a decrease in ER and GEP.

In our study, ER increased slightly in the lawns, but increased more in the hummocks from the wet to control sites (Figure 3). This follows the pattern of other studies, as ecosystem respiration increases as the water table decreases until a certain threshold and then ER depends more upon temperature (Lafleur and others 2005) (Strack and others 2006a).

Gross ecosystem production

GEP was significantly different between both the wet and dry ($p=0.02$) and the control and dry treatments ($p=0.04$) (Figure 3). When looking further at site by site comparisons (Figure 4), GEP may have been lowest at Site C because it had the lowest percent cover of moss (Table 1). This goes along with Strack and others (2006a) who found a large reduction in the presence of mosses on drained hummocks despite a small increase in vascular plants resulted in lowered GEP values. Looking at GEP values and graminoids, we found that at our drained lawns GEP values were higher than there were at our wet lawns (Figure 4), even though the percent cover of graminoids was high at both some wet (B and C) and dry sites (E and F) (Table 1). We are not sure why exactly this maybe, but Strack and others (2006b) found a similar pattern where GEP was about twice as high from unclipped sedges at the drained site than that at the natural site.

While there were no significant differences between GEP*microtopography, GEP increased in the drained lawns and decreased in the drained hummocks compared to the control site (Figure 3). This follows the pattern that Strack and others (2006a) found in their study where GEP was significantly enhanced at the drained lawns and it declined at the drained hummocks. Less water may have been available for plant uptake from the hummocks in the dry treatment especially at site E, the site with the greatest changes in microtopography.

Net ecosystem exchange

We found NEE values to be greatest in the wet treatments (-0.361 µmol CO_2 m^{-2} sec^{-1}), followed by the control (-0.328 µmol CO_2 m^{-2} sec^{-1}) and least in the dry (-0.288 µmol CO_2 m^{-2} sec^{-1}) (Figure 3). NEE was lowest at Site F (Figure 4), a drained tree site, which is what would be expected because NEE is dependent on both ER and GEP. With more aerobic conditions and tree roots present, there is likely to be and was an increase in ER (Figure 3). However, as predicted, there was not as large of an increase in GEP because the trees were not all in the sample plots. However, we did not measure GEP of the trees, which would alter the amount of carbon stored.

We found a marginally significant interaction of water table and microtopography (Table 2) as NEE was higher in the lawns than in the hummocks in the dry treatments ($p = 0.057$). Since the lawns were saturated during parts of the growing seasons that could limit GEP, which affects the rates of NEE. NEE averaged -0.325 µmol CO_2 m^{-2} sec^{-1} in the lawns, and -0.251 µmol CO_2 m^{-2} sec^{-1} in the hummocks for the dry treatments. The hummocks at the dry sites might have had higher rates of NEE because hummocks have certain Sphagnum species of the section Acutifolia (e.g., *S. capillifolium, S. rubellum, S. fuscum*) that can grow very dense, and the total surface area exposed for evaporation is thus very small so they can withstand dry periods (Wieder 2006).

When looking further at the water table levels directly, our results indicate that a ~10 cm lowering of long-term water table levels at led to a 10% decrease in NEE. This does not follow the pattern of another long-term water table manipulations study in Finland that had been drained 55 years prior to the study. Faubert (2004) found that the drier region of the peatland had greater CO_2 sequestration (NEE).

CH_4 Fluxes

We found that CH_4 fluxes were significantly different between our wet and dry treatments. Our results indicated a rise in long-term water table levels by ~10 cm would increase CH4 emissions by 65% and consequently lowering by ~10 cm would decrease emissions by 68%. In Finland, 30 years after forested mires were drained; the effects on methane fluxes (Nykanen and others 1998) and vegetation composition (Laine and Minkkinen 1996; Laine and others 1996) were analyzed.

They found very similar results with methane fluxes reduced by 70% in fens when the water table was lowered by 10 cm (Nykanen and others 1998).

We did find significant differences between the CH_4 and the water table treatment (Table 2). Water table levels often affect plant communities, which then affect CH_4 emissions. In our study, even though sites B and D had similar water table levels (Table 1), site B had greater CH_4 emissions. When looking at the plant cover of different groups of plants, site B has 47% cover of graminoids, while site D has 19% cover of graminoids (Table 1). This agrees with past studies, in that greater sedge cover leads to greater CH_4 emissions (Treat and others 2007). Sedges have roots, unlike Sphagnum, which are a source of labile organic carbon that can be used by the microbial community for energy. Many graminoids also have aerenchyma tissue, which can allow CH_4 to travel more quickly to the atmosphere.

Methane emissions from hummocks and lawns followed the trend of going from higher to lower from wet to dry. There were higher emissions for the lawns than the hummocks in at each site, except F. Bubier and others (1993) found the same pattern in a peatland in northern Ontario. This is what would be expected because lawns are anaerobic for a longer time during the year and anaerobic conditions are necessary for the production of methane.

Many studies have reported that short-term changes in CH_4 emissions are primarily driven by microbial activity, while vegetation-mediated controls on CH_4 fluxes will become increasingly important over time when vegetation communities reach equilibrium with the manipulated water table levels (Bubier 1995). These include enhanced plant transport of CH_4, increased productivity, and changes in rooting zones. One drawback to our study was that we were not able to collect samples while there was snow and one type of ebullition is the release of CH_4 after spring-thaw events. More knowledge of ebullition induced events would be useful to design a better experiment and improve process-based models that can stimulate the CH_4 cycle under varying environmental factors (Tokida 2009).

Our isotope data indicated that the CH_4 being produced in our sites was produced via acetate fermentation. This agrees with past research indicating that the acetate pathway dominates in northern peatlands during the summer (Wieder 2006).

Conclusions

In conclusion, our research has shown that if water table levels increase in the long-term that more CH_4 will be produced, even though more CO_2 will be sequestered. Consequently if you lower the water table, less CH_4 will be produced, but more CO_2 will be released to the atmosphere. Lowering the water table also increases the likelihood of fires which can release large amounts of CO_2 to our atmosphere (Turetsky and others 2004) Water table height was one the most important drivers for all carbon fluxes. While we can expect more CO_2 if we have higher water table levels, we can also expect greater CH_4 emissions.

When peatlands are drained or the water table level is lowered, we can expect less CH_4 to be produced. Different results have been cited in the literature about CO_2 emissions following drainage. In the short-term some research suggests that when peatlands are drained, trees are able to move and counteract the amounts of carbon being lost, especially in northern peatlands where decomposition occurs very slowly (Hargreaves and others 2003; Laiho 2006). However, this may only hold true in boreal regions where decomposition occurs slowly. Conifers like black spruce and tamarack often grow in peatlands and their soils are typically acidic from the litterfall, which does hinder decomposition rates. However, increased oxygen due to drainage, might allow humic phenol compounds to be easier to degrade depending on pH (Williams and others 2000). After studying an afforested peatland in Scotland, Hargreaves and others (2003) suggested that afforested peatlands in Scotland accumulate more carbon in trees, litter, forest soil and products than is lost from the peat for 90-190 years.

In summary, we found that ecosystem carbon cycling and CH_4 rates in peatlands are influenced by changes in long-term water table levels. The long-term water table levels influenced directly the CO_2 and CH_4 flux rates by altering redox and oxygen levels in the soil, and indirectly by altering plant community composition. More research needs to be done on the different types of

peatlands and more long-term studies are necessary to get a better idea of what we can expect with changing climatic conditions.

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TABLES

Table 1. Water chemistry and percent cover of different groups of plants at all the sites.

Site	pH (SE)	Sp. Cond (µS cm-1) (SE)	WT (cm)	Plant cover (%) (SE)	Graminoid	Moss	Shrub	Tree
A	3.78 (0.02)	68.98 (1.60)	-12.1	252 (12.4)	26 (2.70)	101 (2.53)	119 (10.7)	11 (4.10)
B	3.77 (0.02)	57.05 (1.87)	-9.7	237 (12.3)	47 (6.70)	99 (5.8)	91 (10.3)	0
C	4.10 (0.06)	44.78 (1.70)	2.27	198 (15.3)	63 (11.1)	34 (10.2)	101 (5.80)	0
D	3.82 (0.01)	53.93 (1.70)	-7.6	277 (7.00)	19 (3.40)	111 (3.3)	97 (6.30)	1 (0.00)
E	3.69 (0.01)	79.45 (0.81)	-21.8	241 (7.70)	32 (10.0)	106 (2.9)	103 (5.90)	1 (0.00)
F	3.71 (0.02)	72 (3.95)	-20.0	254 (7.20)	48 (7.90)	109 (5.00)	96 (8.00)	4 1.70)

Table 2. Results of repeated measures ANOVA designed to test the singular and interactive effect of water table treatment and microtopography treatments on ecosystem C fluxes.

Net Ecosystem Exchange (NEE)	**Df (numerator, denominator)**	**F**	**P**
Water table treatment	2, 46.2	0.92	0.405
Microtopography	1, 56.6	0.02	0.903
Water table treatment x microtopography	2, 59.3	6.97	**0.002**

Ecosystem respiration (ER)	**Df (numerator, denominator)**	**F**	**P**
Water table treatment	2, 42.9	8.75	**0.001**
Microtopography	1, 53.2	0.01	0.921
Water table treatment x microtopography	2, 56.5	0.61	0.548

Gross ecosystem production (GEP)	**Df (numerator, denominator)**	**F**	**P**
Water table treatment	2, 47.9	4.89	**0.012**
Microtopography	1, 58.1	0.07	0.794
Water table treatment x microtopography	2, 61.1	2.19	0.121

Methane flux (CH_4)	**Df (numerator, denominator)**	**F**	**P**
Water table treatment	2, 18	3.83	**0.041**
Microtopography	1, 18	3.86	**0.065**
Water table treatment x microtopography	2, 18	0.60	0.559

Significant higher-level predictors are marked in bold ($P < 0.05$)

Table 3. Results of a backwards stepwise regression for CO_2 and CH_4 fluxes.

Net Ecosystem Exchange (NEE)	**Coefficient**	**Standard Error**	**t**	**P(2 Tail)**
Constant	-1.001	0.330	-3.029	0.014
Tree	-0.014	0.005	-2.573	0.030
Stemp40cm	0.071	0.030	2.360	0.043
Overall R^2 – 0.518				

Ecosystem respiration (ER)	**Coefficient**	**Standard Error**	**t**	**P(2 Tail)**
Constant	0.199	0.099	2.002	0.051
Water Table	-0.006	0.002	-2.655	0.011
Stemp5cm	0.007	0.005	1.385	0.173
Overall R^2 – 0.216				

Gross ecosystem production (GEP)	**Coefficient**	**Standard Error**	**t**	**P(2 Tail)**
Constant	3.733	1.880	1.986	0.082
Plant	-0.013	0.006	-1.959	0.086
Tree	0.081	0.018	4.523	0.002
Water Table	0.073	0.027	2.696	0.027
Overall R^2 – 0.518				

Methane flux (CH_4)	**Coefficient**	**Standard Error**	**t**	**P(2 Tail)**
Constant	0.366	0.125	2.926	0.005
Graminoid	0.006	0.002	2.851	0.007
Water Table	0.019	0.006	3.070	0.004
Overall R^2 – 0.518				

Table 4. Results of isotope data collected in the summer of 2010. The values under each month are for d13C vs. VPDB. Parenthesis indicate standard error.

Plot	**May**	**June**	**August**
Site A			-41.95 (0.20)
Site B	-50.02 (0.37)	-50.18 (0.68)	-42.58 (0.25)
Site C	-49.955 (0.61)	-52.02 (0.49)	-41.79 (0.28)
Site D			-41.82 (0.07)
Site E	-50.405 (0.50)	-50.715 (0.91)	-41.70 (0.18)
Site F			-41.79 (0.15)

FIGURES AND LEGENDS

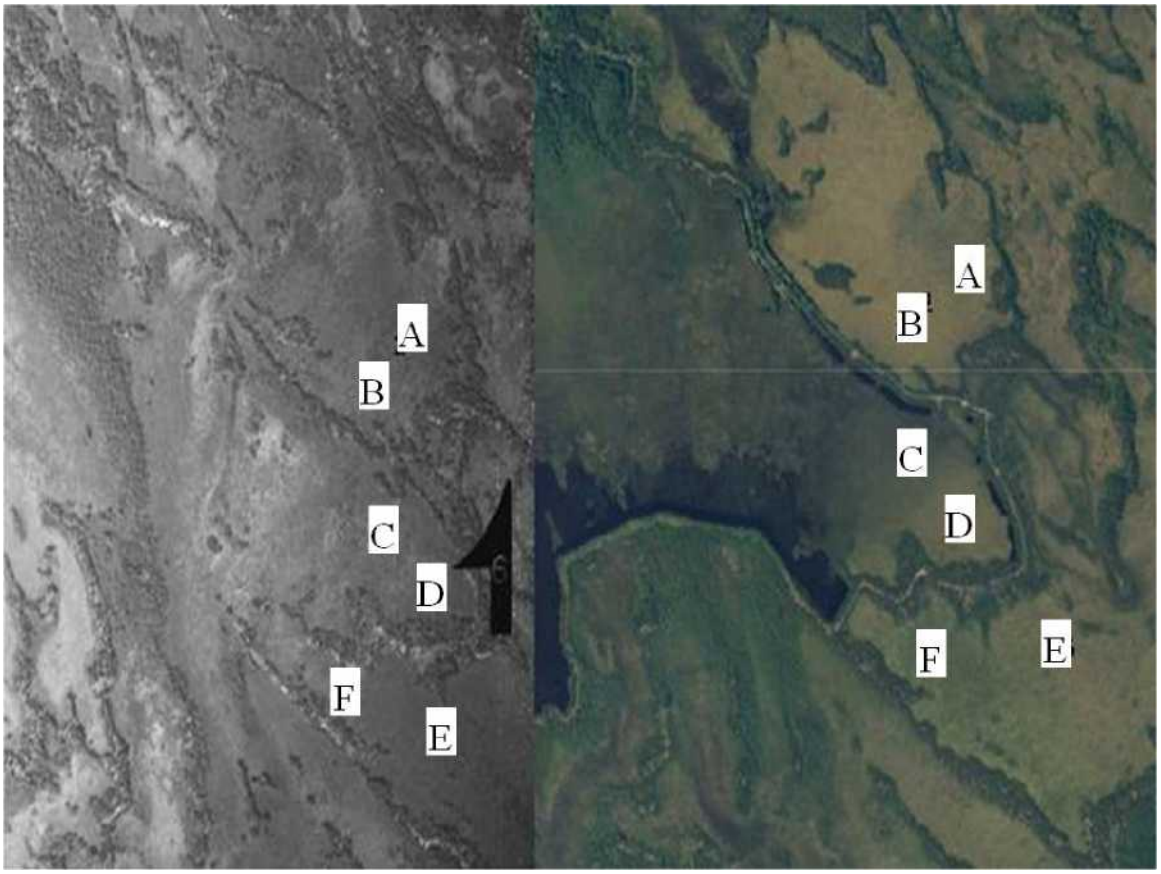

Figure 1. Locations of study sites in Seney NWR (C and D are in the wet treatment, A and B control, and E and F dry).

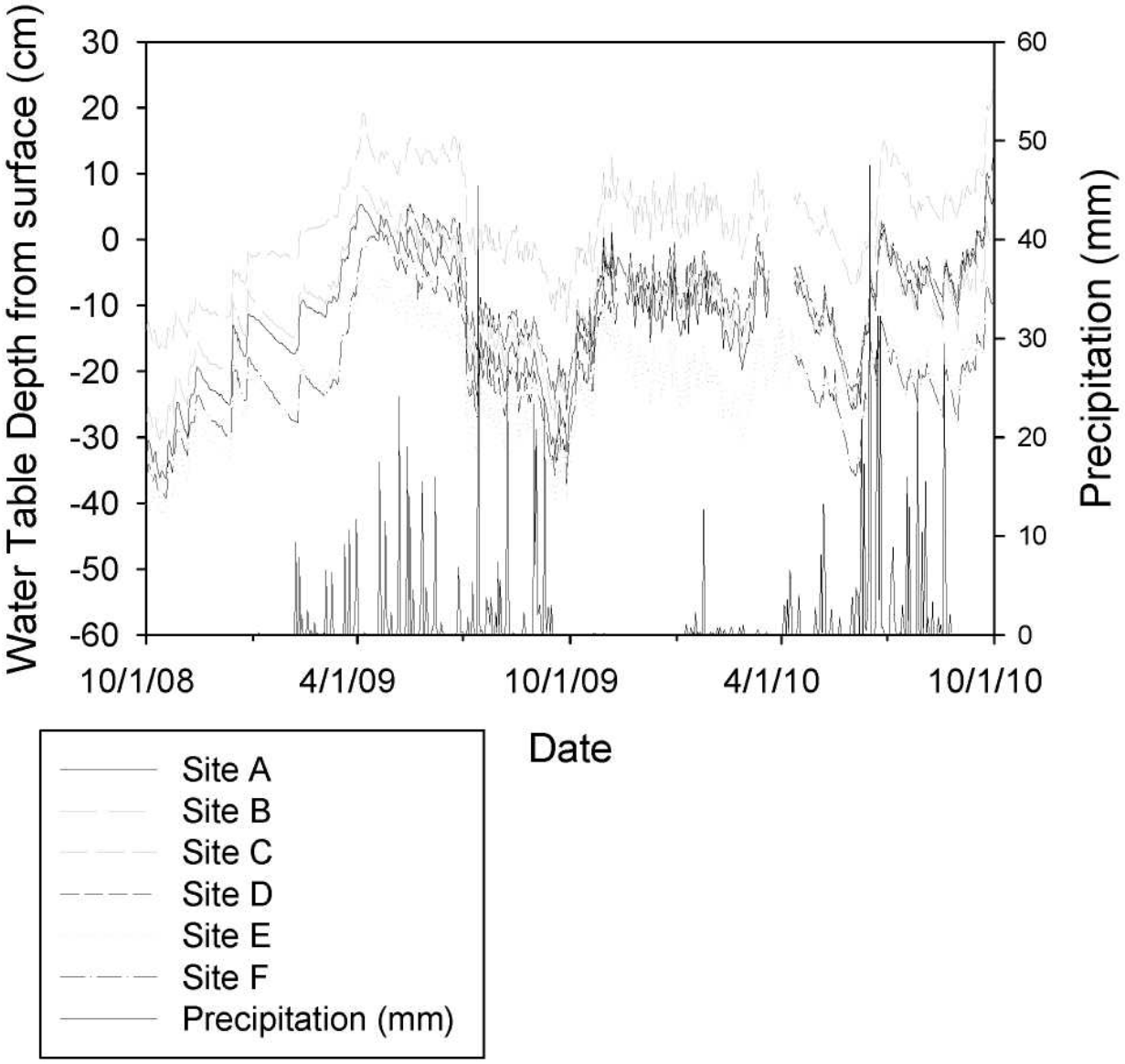

Figure 2. Water table levels at all the sites from May 2008 until October 2010.

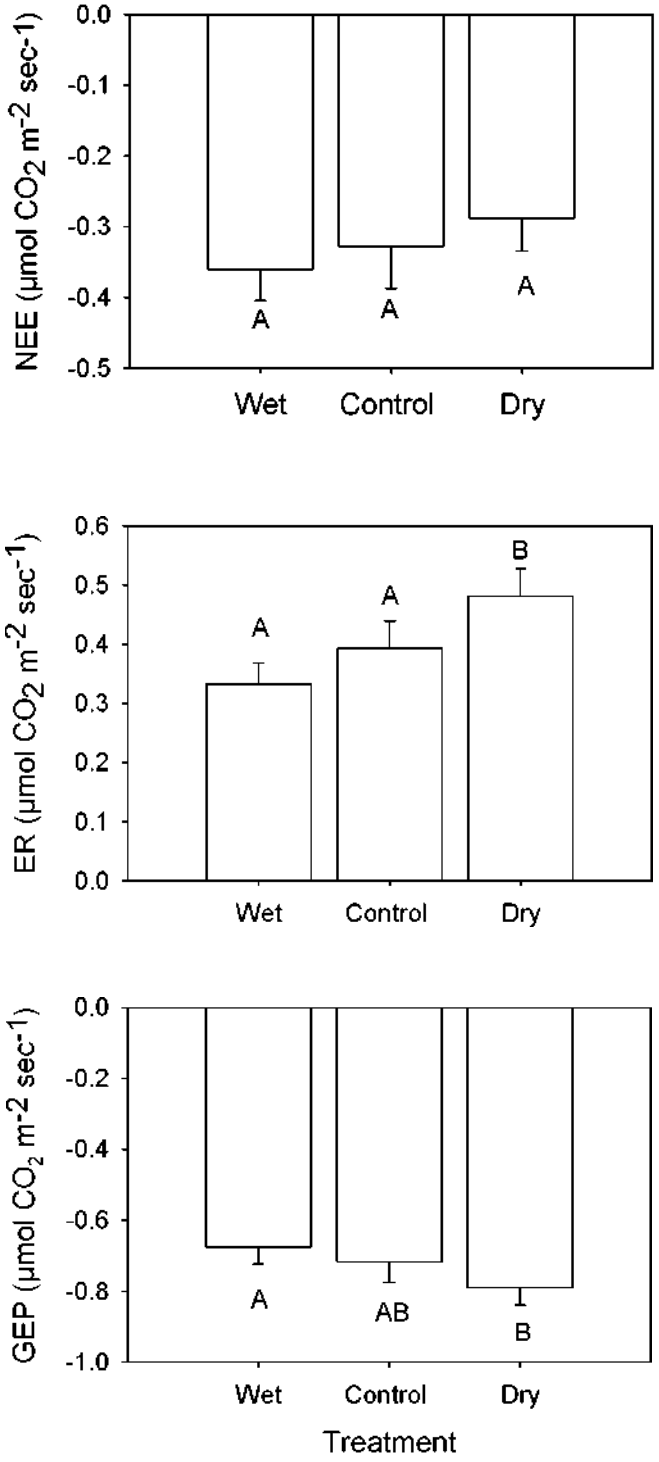

Figure 3. Two year averages of ecosystem respiration (ER), gross ecosystem production (GEP), and net ecosystem exchange (NEE) by water level treatment. Error bars indicate standard error.

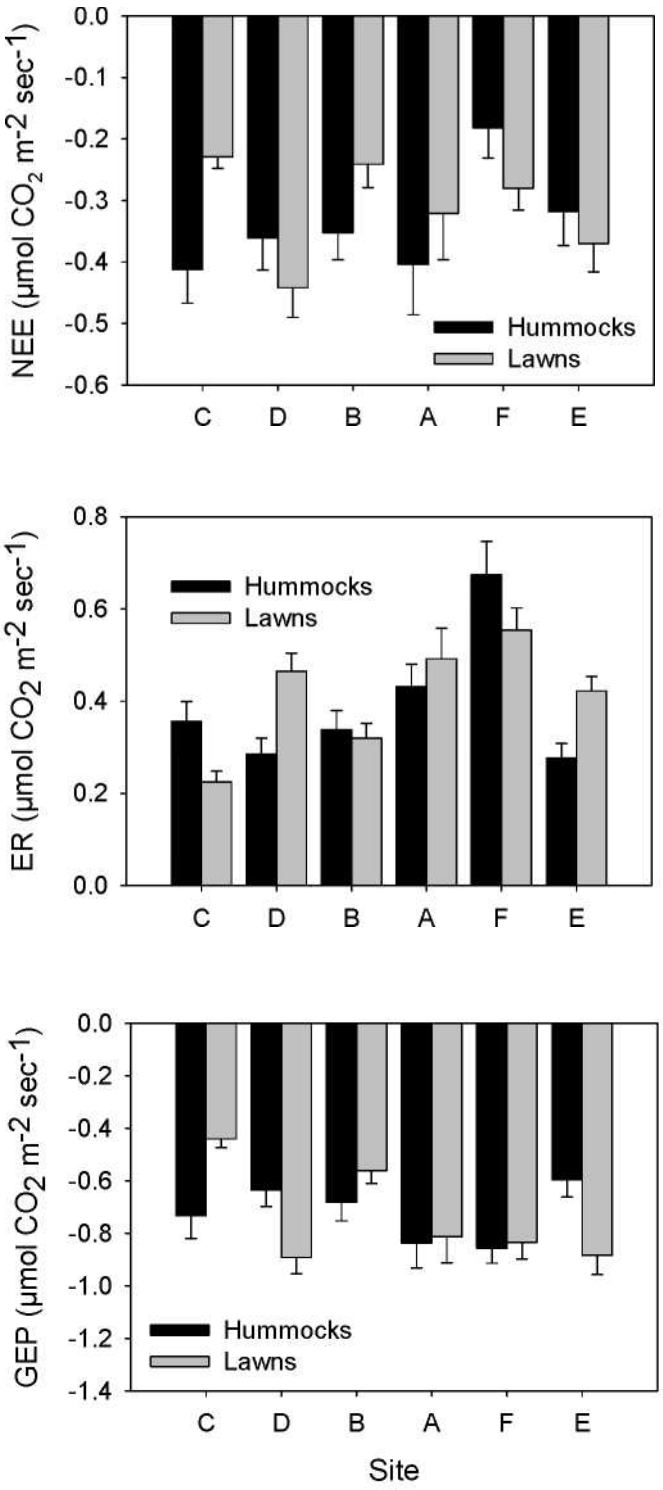

Figure 4. Two year averages of ecosystem respiration (ER), gross ecosystem production (GEP), and net ecosystem exchange (NEE) by site. Error bars indicate standard error. Sites are arranged from left to right by average water table depth.

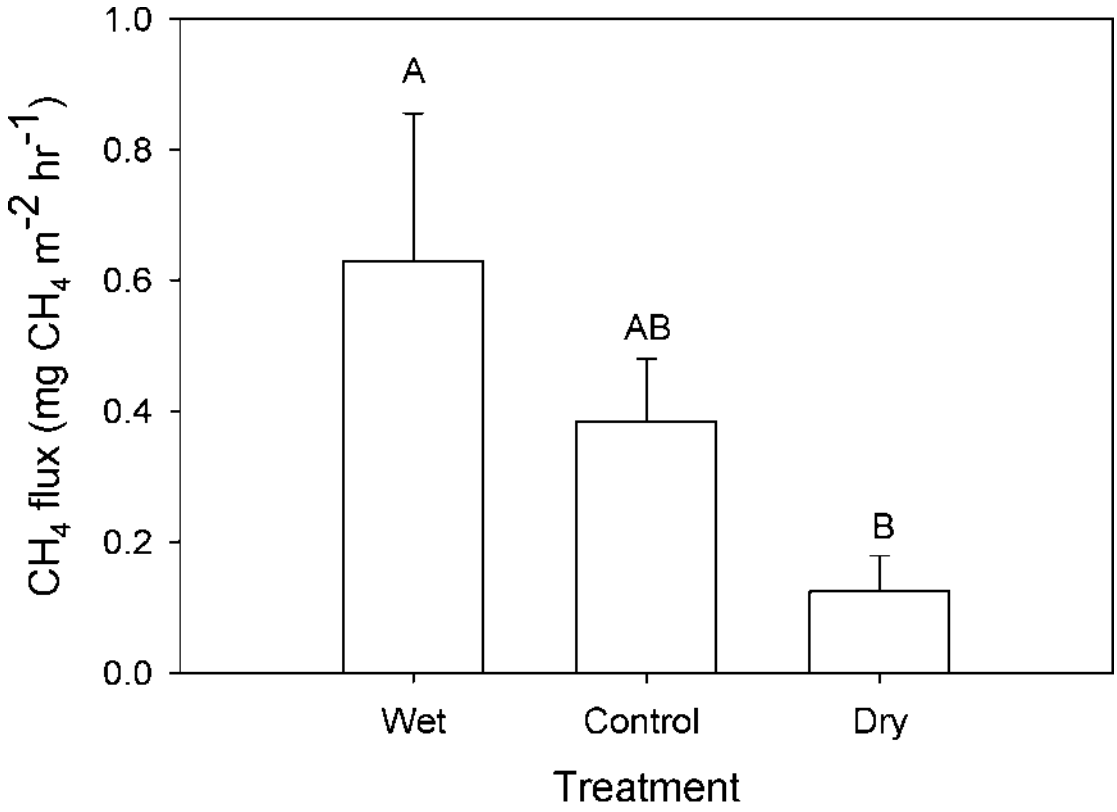

Figure 5. Two year average of Methane (CH_4) emissions in the hummocks and lawns by water table treatment. Error bars indicate standard error.

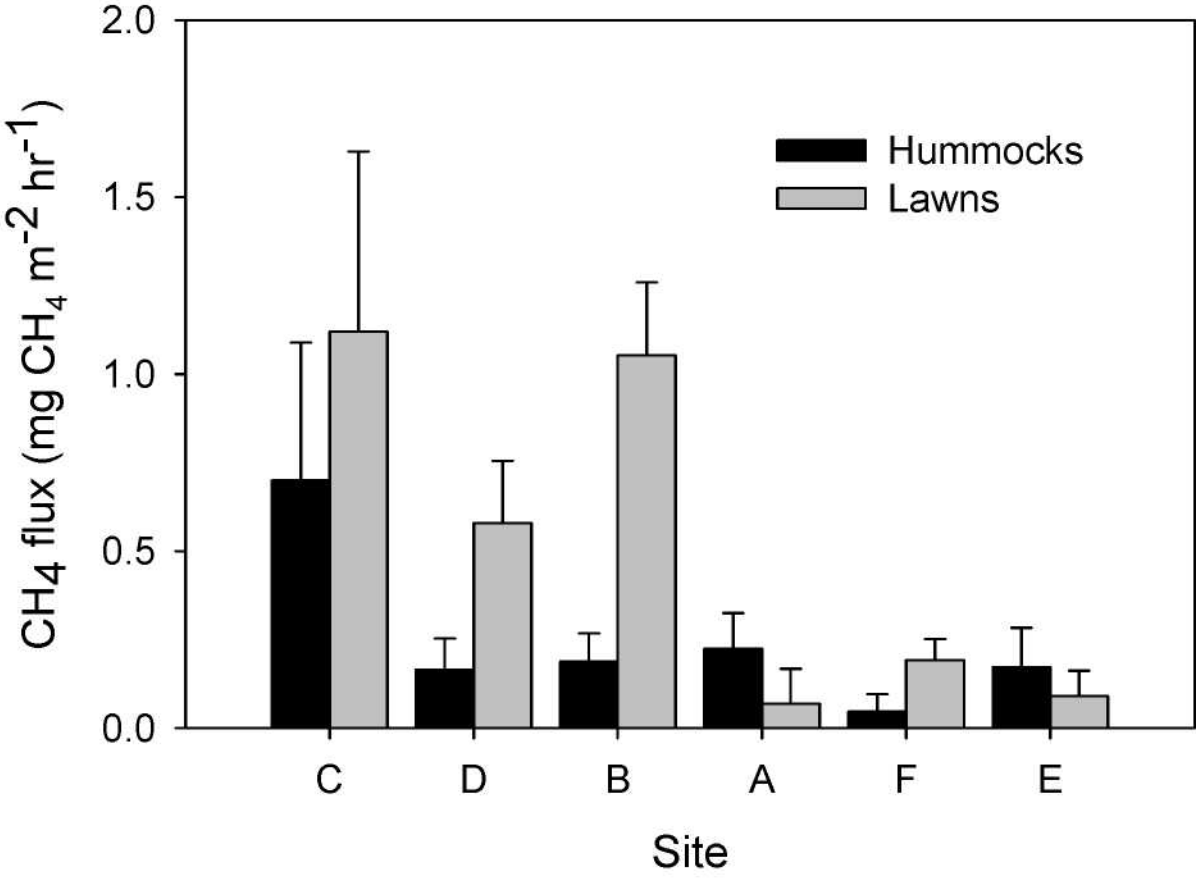

Figure 6. Two year average of Methane (CH_4) emissions in the hummocks and lawns by site. Error bars indicate standard error.

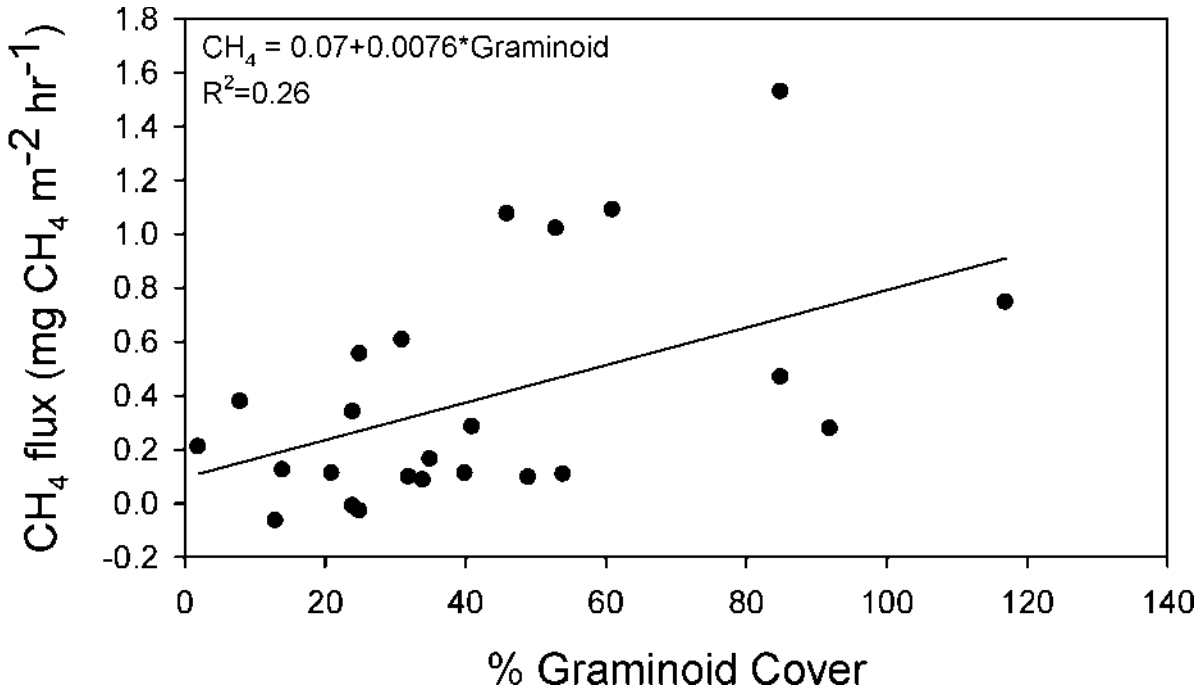

Figure 7. Correlation between Methane (CH_4) emission and percent graminoid cover.