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# Effect of *Carex rostrata* removal on methane emissions from a temperate peatland

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EFFECT OF *CAREX ROSTRATA* REMOVAL ON CH<sub>4</sub> EMISSIONS  
FROM A TEMPERATE PEATLAND

BY

GENEVIEVE L. NOYCE  
BA, Mount Holyoke College, 2009

THESIS

Submitted to the University of New Hampshire  
in Partial Fulfillment of  
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in  
Earth Sciences

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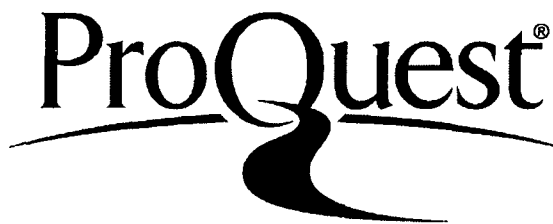
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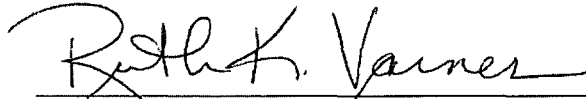
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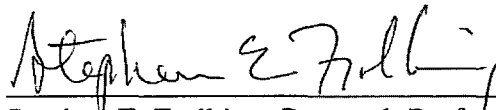
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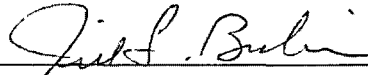
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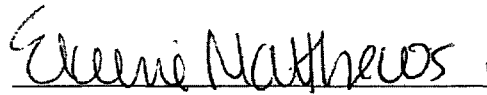
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12 August 2011

Date

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## ABSTRACT

### EFFECT OF *CAREX ROSTRATA* REMOVAL ON CH<sub>4</sub> EMISSIONS FROM A TEMPERATE PEATLAND

by

Genevieve L. Noyce

University of New Hampshire, September, 2011

Peatlands are a large natural source of atmospheric methane (CH<sub>4</sub>). *Carex rostrata*, a sedge species, has a critical role in the production, oxidation, and emission of CH<sub>4</sub> from these systems. This study examined the changes in CH<sub>4</sub> emissions from a temperate peatland after removing all aboveground *C. rostrata* biomass. Methane flux, dissolved CH<sub>4</sub> concentration at various depths, *C. rostrata* green leaf area, temperature, and water table depth were measured from June 2008 to November 2010.

There is a strong positive correlation between *C. rostrata* green area and CH<sub>4</sub> flux and the mean summer CH<sub>4</sub> flux from the control plots was always higher than from the plots without *C. rostrata*. Model results indicate that 35-74% of total summer CH<sub>4</sub> emissions may come from transport through *C. rostrata*, though *C. rostrata* green area, water-table depth, and temperature only explain around 35% of the observed CH<sub>4</sub> flux variability, perhaps because of inter-annual variability.

# 1. INTRODUCTION

## 1.1 Peatlands and the carbon cycle

Peatlands are terrestrial waterlogged or flooded ecosystems where the overall rate of net primary production is greater than the rate of decomposition, resulting in an accumulation of partly decomposed organic matter, more commonly known as peat [Vitt, 2006]. Peat can be composed of woody material, leaves, rhizomes, roots, or bryophytes, though it generally originates from belowground substances [Rydin and Jeglum, 2006]. Peatlands vary in their hydrological, climatic, chemical, substrate, and vegetation characteristics [Vitt, 2006] and there are extensive classification systems that seek to distinguish the subtleties among peatland types. In North America, peatlands are generally divided into bogs and fens. Fens are minerotrophic and soligenous, i.e. fed by mineral-rich ground or surface water [Crum, 1992]. These sites are generally characterized by grassy plants such as sedges [Crum, 1992], but can also have a diverse collection of shrubs, graminoids, and herbs [Roulet *et al.*, 1992b]. Fens are further classified as mineral-poor or mineral-rich [Rydin and Jeglum, 2006]. In contrast, bogs are ombrotrophic, receiving minerals only through precipitation, and are thus mineral-poor and often support slightly different vegetation species [Crum, 1992].

Peatlands cover about 4 million km<sup>2</sup> [Frolking *et al.*, in press] or less than three percent of the world's land area [Gorham, 1991]. Nevertheless, because of their slow rates of decomposition, peatlands have 50 to over 500 kg carbon (C) m<sup>-2</sup> [Frolking *et al.*, in press]. This means that peatlands contain a large portion of the world's soil C

pool [Gorham, 1991] and thus the C stored in peatlands is estimated to be more than half the amount of C currently in the atmosphere [Rydin and Jeglum, 2006]. Annual peat accumulation is 1-20% of annual gross primary production [Vasander and Kettunen, 2006]. Approximately one-third of all the C taken up through photosynthesis is released back to the atmosphere as carbon dioxide (CO<sub>2</sub>) through autotrophic respiration, which is controlled by many variables, including temperature, water and nutrient availability, pH, and substrate quality [Vasander and Kettunen, 2006]. The remaining C from photosynthesis is used by plants and then subsequently deposited as litter. In the aerobic acrotelm, the thin upper layer of peat with a high rate of decay [Kuhry and Turunen, 2006], this litter is decomposed by aerobic bacteria and again released as CO<sub>2</sub> [Vasander and Kettunen, 2006]. Up to 90% of the new growth may be lost as CO<sub>2</sub> through this aerobic decay [Rydin and Jeglum, 2006]. The biomass that decays more slowly causes the buildup of peat that is characteristic of these ecosystems. As the litter migrates to the water-saturated catotelm, part of the mineralized C is released as methane (CH<sub>4</sub>). Because of the many environmental controls, peatlands can change from net sources of C to net sinks from year to year [e.g. Carroll and Crill, 1997; Bubier et al., 2003, Roulet et al., 2007]. This means that an increase in C fluxes from peatlands could not only increase the rate at which C is added to the atmosphere, but at the same time mean the loss of a C sink, resulting in a positive climate feedback.

## **1.2 Importance of methane**

Annually, 503-610 Tg of CH<sub>4</sub> are estimated to be emitted from natural and anthropogenic sources [IPCC, 2001]. Of these, wetlands are the single largest CH<sub>4</sub>

source, emitting 100-231 Tg CH<sub>4</sub> year<sup>-1</sup> or up 75% of all natural CH<sub>4</sub> [IPCC, 2007; Beerling *et al.*, 2009]. The majority of wetland CH<sub>4</sub> emissions are from the tropics [Frolking *et al.*, in press], but northern wetlands, which are mostly peatlands, are responsible between a third and a half of the CH<sub>4</sub> emissions from all wetlands [Matthews, 2000; Christensen *et al.*, 2003; Vasander and Kettunen, 2006]. Currently, peatlands are estimated to contribute 40 Pg CH<sub>4</sub> year<sup>-1</sup> [Frolking *et al.*, in press]. Like CO<sub>2</sub>, CH<sub>4</sub> interacts with long-wave radiation, contributing to the greenhouse effect [Dlugokencky *et al.*, 1994]. After CO<sub>2</sub>, CH<sub>4</sub> has the next largest radiative forcing potential of any greenhouse gas [IPCC, 2007], which means it has a strong ability to trap radiation in the atmosphere. Global warming potential (GWP) takes into account the atmospheric life span of a greenhouse gas and its radiative forcing [Ramaswamy *et al.*, 2001] and on a 100 year time horizon, CH<sub>4</sub> has a GWP of 25 times that of CO<sub>2</sub> [IPCC, 2007].

In 2009, the global mean CH<sub>4</sub> concentration based on NOAA measurements was 1,794 ppb [Duglokencky *et al.*, 2011]. In comparison, ice core data indicate that the atmospheric concentration of CH<sub>4</sub> ranged from 350-750 ppb up until 300 years ago [Rasmussen and Khalil, 1984]. The end of the Younger Dryas period (around 11,600 years ago) has also been attributed to a substantial increase in atmospheric CH<sub>4</sub>, most of which probably came from wetlands [Petrenko *et al.*, 2009].

The growth rate of atmospheric CH<sub>4</sub> has a great deal of inter-annual variability, but overall it slowed since 1990 [Duglokencky *et al.*, 2009]. The decrease is presumably due to unidentified changes in sources and sinks [Simpson *et al.* 2002]. Duglokencky *et al.* [2003] proposed that the CH<sub>4</sub> budget was approaching steady state, i.e. that the sources and sinks cancelled each other out, and between 1999 and 2006 the mean

atmospheric CH<sub>4</sub> concentration did remain approximately constant [Duglokencky *et al.*, 2011]. However, from 2007 to 2009 the CH<sub>4</sub> growth rate increased again, perhaps due to climate feedbacks [Duglokencky *et al.*, 2011]. In particular, the increase in CH<sub>4</sub> concentration observed in 2007 was probably resultant of warmer temperatures in northern wetlands and more precipitation in tropical wetlands [Dlugokencky *et al.*, 2009].

The main sink of CH<sub>4</sub> is through reaction with the hydroxyl free radical ( $\cdot\text{OH}$ ) in the atmosphere to create  $\cdot\text{CH}_3$ :  $\text{CH}_4 + \text{OH} \rightarrow \cdot\text{CH}_3 + \text{H}_2\text{O}$  [Mayer, 1982; Ramanathan, 1988]. Along with similar oxidation in the stratosphere, these  $\cdot\text{OH}$  reactions make up 90% of the CH<sub>4</sub> sinks [IPCC, 2001]. Increased atmospheric CH<sub>4</sub>, and other atmospheric constituents, can decrease  $\cdot\text{OH}$  concentrations and consequently increase concentrations of ozone (O<sub>3</sub>), another greenhouse gas, leading to an indirect positive feedback on the greenhouse effect [Ramanathan, 1988]. Atmospheric CH<sub>4</sub> can also be biologically oxidized to CO<sub>2</sub> in dry soils [IPCC, 2007], however the importance of this terrestrial CH<sub>4</sub> sink may be overestimated [Bastviken *et al.*, 2011]. Another lesser sink is the reaction of CH<sub>4</sub> with free chlorine in the marine boundary layer to form HCl and CH<sub>3</sub> [Wang and Keyser, 1999; Allan *et al.*, 2005].

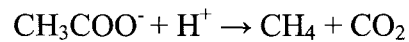
### 1.3 Methanogenesis

Methane is formed as the final product of anaerobic degradation of organic matter [Vasander and Kettunen, 2006]. Methane is produced by five orders of Archaea, known as methanogens, whose activity is mainly controlled by the availability of substrate in the anoxic zones of the peat and thus shifts with the rise and fall of the water table [Juottonen *et al.*, 2005; Krüger *et al.*, 2005; Rydin and Jeglum, 2006; Rooney-Varga *et al.*, 2007].

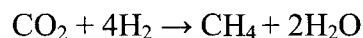
There are three main pathways through which CH<sub>4</sub> production occurs, but only two of these occur in peatlands: acetoclastic methanogenesis (acetate fermentation) and hydrogenotrophic methanogenesis (CO<sub>2</sub> reduction) [Deppenmeier, 2002]. Through fermentation reactions, organic matter is decomposed into acetate, hydrogen, and carbon dioxide [Vasander and Kettunen, 2006]:



Acetoclastic methanogens then split the acetate into CH<sub>4</sub> and CO<sub>2</sub> through the process of acetate fermentation [Schlesinger, 1997]:



In most anaerobic environments, about two-thirds of the biogenic CH<sub>4</sub> originates from acetate [Hines *et al.*, 2001; Krüger *et al.*, 2005; Rooney-Varga *et al.*, 2007] and sites with higher CH<sub>4</sub> emissions tend to have acetate fermentation as the dominant pathway [Bellisario *et al.*, 1999; Ström *et al.*, 2005]. High dissolved CH<sub>4</sub> concentrations are also often correlated with isotopic signatures unique to CH<sub>4</sub> formed through acetate fermentation [Itoh *et al.*, 2008]. Alternatively, hydrogenotrophic methanogens can use CO<sub>2</sub> as the terminal electron acceptor and produce CH<sub>4</sub> through CO<sub>2</sub> reduction [Schlesinger, 1997]:



Because both these reactions are energetically unfavorable, CH<sub>4</sub> is only produced in anoxic environments in which alternative electron acceptors are unavailable, which often means flooded systems [Hedin *et al.*, 1998].

The relative dominance of CH<sub>4</sub> production pathways is generally determined by temperature and substrate quality and availability, as well as by the present methanogen

community. At 5°C, acetate accumulates in peatland soils [Rooney-Varga *et al.*, 2007]. Between 10-15°C, acetate fermentation is responsible for 85-90% of the produced CH<sub>4</sub>, but at higher temperatures CO<sub>2</sub> reduction becomes more important [Vasander and Kettunen, 2006]. High CH<sub>4</sub> emissions have been observed in the spring, probably because of the increased mineralization of organic matter accumulated over the winter [Wilson *et al.*, 1989; Sachs *et al.*, 2008]. During the summer months in northern peatlands, the acetate pathway tends to dominate, as shown by isotopic analysis [e.g. Bellisario *et al.*, 1999; Popp *et al.*, 1999]. However, temperature is not the only control on shifting methanogenic pathways [Hines *et al.*, 2001]. Vegetation provides substrates for methanogens in the form of litter and root exudates [Whiting and Chanton, 1992; Thomas *et al.*, 1996; Bellisario *et al.*, 1999; Popp *et al.*, 1999]. This fresh organic carbon allows the acetate fermentation pathway to dominate over CO<sub>2</sub> reduction when sites have high plant productivity [Bellisario *et al.*, 1999; Popp *et al.*, 1999], while the hydrogen pathway contributes more in sites with few vascular plants [Vasander and Kettunen, 2006]. Acetate fermentation is also generally dominant in shallow depths, where there is a consistent supply of fresh carbon, while CO<sub>2</sub> reduction is dominant at depths where the peat is older and less reactive but oxygen concentrations are lower [Hornibrook *et al.*, 1997; Popp *et al.*, 1999; Hornibrook *et al.*, 2000; Vasander and Kettunen, 2006].

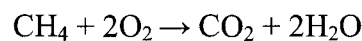
Sites with varying methanogenic pathways have microbial communities with multiple species of methanogens [Hines *et al.*, 2001; Rooney-Varga *et al.*, 2007]. The families of *Methanomicrobiaceae* and *Methanobacteriaceae* are nonacetoclastic, whereas the families of *Methanosarcinaceae* and *Methanosaetaceae* use acetate as a substrate [Rooney-Varga, 2007]. In Alaskan peatlands, the presence of *Sphagnum* or *Carex*



species significantly explains most of the variability in archaeal community composition, with temperature significantly improving predictions [Rooney-Varga *et al.*, 2007]. Sedge-dominated fens also have higher methanogen diversity than ombrotrophic *Sphagnum* bogs, which may result from differences in ecohydrology [Juottonen *et al.*, 2005]. In a Finnish fen, an *Eriophorum*-dominated site had a high abundance of *Methanosarcinaceae* and higher CH<sub>4</sub> emissions than a nearby *Methanomicrobiaceae*-dominated site [Galand *et al.*, 2003]. Although there was no difference in potential CH<sub>4</sub> production in that particular study, Juottonen *et al.* [2005] found changes in potential CH<sub>4</sub> production that correlated with changes in the community structure of methanogens. Different depths in the peat also tend to support different methanogenic species, potentially depending on the main available substrate [Juottonen *et al.*, 2005].

#### 1.4 Methanotrophy

Methane emissions from the peat to the air above reflect the difference between the amount of CH<sub>4</sub> produced in the saturated peat and the CH<sub>4</sub> oxidized when it diffuses through the upper zone of the peat with higher redox potential [Schlesinger, 1997]. In peatlands, CH<sub>4</sub> oxidation has been experimentally determined to be aerobic, rather than anaerobic [Yavitt *et al.*, 1988]. In aerobic environments, i.e. above the water table, populations of methanotrophic bacteria flourish and CH<sub>4</sub> is consumed by these methanotrophs in the process of CH<sub>4</sub> oxidation or methanotrophy [Vasander and Kettunen, 2006]:



Oxidation rates are affected by both the community of methanotrophs and the availability of CH<sub>4</sub> [Urmann *et al.*, 2007].

It is generally thought that up to 90% of produced CH<sub>4</sub> may be oxidized to CO<sub>2</sub> before it can be released into the atmosphere [Yavitt *et al.*, 1988; Bubier and Moore, 1994], though other estimates range up to 100% [Vasander and Kettunen, 2006]. In peat column experiments, around 50% of the produced CH<sub>4</sub> was oxidized in the first 3 cm of the oxic zone, while by 15 cm above the production zone that increased to 97% [Urmann *et al.*, 2007]. In these columns, oxidation was the main control on the CH<sub>4</sub> emissions, but oxidation rates were also one to two orders of magnitude higher than those reported for field measurements [Urmann *et al.*, 2007]. Oxidation in the field may reduce seasonal emissions by 20% [Popp *et al.*, 2000] or from 20 to 90% on a daily basis [Frenzel and Karofeld, 2000].

### **1.5 Methane transport**

Methane is released from peatlands through three known processes: diffusion through water- and gas-filled pores in the peat, ebullition (or bubbling), and plant-mediated transport. Of these three, diffusion, i.e. movement of molecules down a concentration gradient, accounts for the smallest proportion of emitted CH<sub>4</sub> [Schlesinger, 1997], though diffusion rates depend on various factors such as the gradient of CH<sub>4</sub>, peat porosity, tortuosity, and peat porewater content. Porous soils and soils with high water content have high rates of diffusion [Arah and Stephen, 1998], though the diffusion coefficient and the concentration gradient also control the diffusive rate [Chanton, 2005]. Methane is sparingly soluble in water [Chanton, 2005], so when the concentration of

dissolved CH<sub>4</sub> in the saturated layer builds up, bubbles with a high concentration of CH<sub>4</sub> form and are released in the process of ebullition [Schlesinger, 1997]. The same conditions that control redox potential can affect ebullition rates; ebullition has its highest contribution to CH<sub>4</sub> emission in wet, warm soils where there are substantial amounts of trapped CH<sub>4</sub> due to high production and low solubility [Kellner *et al.*, 2006]. Bubbling is also triggered by belowground pressure changes, sometimes as a result of a dropping water table [Glaser *et al.*, 2004; Chanton, 2005; Goodrich *et al.*, 2011]. Ebullition is difficult to quantify, but causes the highest individual CH<sub>4</sub> fluxes [Schlesinger, 1997] and is thus often an important, albeit sporadic, component of a wetlands' CH<sub>4</sub> budget [Chanton, 2005].

The third transport method is through plants with aerenchymous or hollow stems, such as rice or sedge species [Schlesinger, 1997]. Because peatlands are waterlogged, and thus anoxic, vascular plants do not reliably have oxygen available in the rhizosphere [Thomas *et al.*, 1996; Rydin and Jeglum, 2006]. Plants adapted by developing channels through which oxygen could be transported downward [Thomas *et al.*, 1996]. Aerenchyma are widened intercellular spaces that extend from the leaves and down through the stem and bring oxygen to the roots and rhizomes [Rydin and Jeglum, 2006]. This lacunar system also allows CH<sub>4</sub> to be transported from belowground to the atmosphere [Thomas *et al.*, 1996]. This transport can be either through molecular diffusion (passive transport) or by convective/pressurized ventilation (active transport) [Dacey and Klug, 1982; Bubier and Moore, 1994]. Plant-mediated transport is presumed to be responsible for over 90 percent of CH<sub>4</sub> emissions from peatlands with aerenchymous plants [Whiting and Chanton, 1992], because this pathway bypasses the

main aerobic oxidation zone in the peat, unlike diffusion or ebullition. Accordingly, sedge-dominated sites can have up to 10 times the CH<sub>4</sub> emissions of neighboring areas lacking aerenchymous vegetation [Chanton, 2005]. Plant-associated transport can also lower porewater CH<sub>4</sub> concentrations by 50%, which causes a decrease in the CH<sub>4</sub> concentration gradient, reducing both the amount of CH<sub>4</sub> released through diffusion and the rate at which bubbles form [Chanton, 2005]. As such, plant-associated transport is presumed to be the foremost method of CH<sub>4</sub> release in sedge-dominated wetlands.

### **1.6 *Carex rostrata***

*C. rostrata* is a wetland sedge species found in both North America and Europe that reproduces clonally [Hultgen, 1989a] and by seed [Budelsky and Galatowitch, 2002]. Shoots can emerge from the horizontally growing rhizomes or from the bases of old shoots [Hultgen, 1989a]. Newly-emerged shoots do not have roots [Hultgen, 1989a] and even though many shoots emerge in late spring or early summer, growth of new roots and rhizomes may not begin until early July [Bernard, 1974]. Estimates of total root and rhizome biomass vary from less than half of the total plant biomass [Bernard, 1974; Hultgen, 1989a] to over 75% of total biomass [Saarinen, 1996]. *C. rostrata* has the ability to produce aerenchymous roots that allow it to thrive in waterlogged environments. These highly aerenchymous roots are mostly composed of cells that are not physiologically active [Moog and Brüggemann, 1998].

Individual *C. rostrata* plants generally live for more than one growing season. They emerge as green shoots in spring or summer and even though the leaves senesce over the winter, the overwintering shoots below the moss remain alive [Hultgen, 1989b].

These stems produce green leaves again the next spring, flower during the summer, and then die [Gorham and Somers, 1973; Anderson, 2008]. The maximum height of the shoot depends on its place in the life cycle, with fertile shoots reaching their maximum leaf biomass early in the summer [Hultgen, 1989a]. Though most shoots emerge at the beginning of the growing season, there is a second peak in new shoots in late summer when many shoots are senescing [Gorham and Somers, 1973; Bernard, 1974]. This new growth partly slows the overall decline of *C. rostrata* biomass during the fall, but the maximum senescence rate of green leaves is greater than the late summer and early fall maximum growth rate [Gorham and Somers, 1973]. Lifespan estimates for *C. rostrata* range from 18 months for shoots that emerge in spring [Gorham and Somers, 1973] to a maximum of 24 months for late summer shoots in temperate zones [Gorham and Somers, 1973; Anderson, 2008], though some studies claim that shoots may be photosynthetically active for as many as four growing seasons [Hultgen, 1989b].

### **1.7 Controls on methane emissions**

Methane emissions are not only a function of belowground CH<sub>4</sub> production [Schimel, 1995; King *et al.*, 1998; Bellisario *et al.*, 1999]. High variability in the magnitude of CH<sub>4</sub> fluxes has been observed both between and within sites [e.g. Moore and Knowles, 1990; Roulet *et al.*, 1992; Dise *et al.*, 1993; Bubier, 1995] as well as under laboratory conditions [Moore and Knowles, 1989]. Moore and Knowles [1990], in particular, measured CH<sub>4</sub> fluxes at a single site that differed by up to two orders of magnitude. Bubier *et al.* [2005] and Treat *et al.* [2007] both observed high levels of inter-annual variability within a single peatland site. Emissions of CH<sub>4</sub> are controlled by

near-surface variability in vegetation composition, moisture content, and temperature and it has been observed that CH<sub>4</sub> concentrations at depth are not proportional to the observed fluxes [Crill *et al.*, 1988]. Near-surface CH<sub>4</sub> concentrations (i.e. within 20 cm of the peat surface) are more variable than deeper concentrations [Wilson *et al.*, 1989], presumably due to their lack of insulation from changing temperature and moisture as well as proximity to vegetation. As such, extensive research has focused on the differences in CH<sub>4</sub> emissions from peatlands varying in surface qualities, including nutrients, hydrology, and vegetation.

Methane fluxes are controlled by complex interactions among the numerous factors controlling methanogenesis, methanotrophy, and transport and can include vegetation and methanogen communities, water-table level, water content in the unsaturated zone, and air or peat temperatures [Dise *et al.*, 1993]. According to Roulet *et al.* [1992a], no single environmental variable is a good predictor for CH<sub>4</sub> emissions from an individual wetland. Even within a single site, spatial variability in water-table depth, vegetation composition, substrate sources, methanogen communities, and factors controlling lags between production, transport, and emission can result in wide-ranging CH<sub>4</sub> fluxes [Moore and Knowles, 1990].

### ***1.7.1 Vegetation controls on methane emissions***

Many studies have reported a positive correlation between the presence of aerenchymous vegetation and high CH<sub>4</sub> emissions. In Canadian peatlands, [Bubier *et al.*, 1995] and [Bubier, 1995] found correlations between large CH<sub>4</sub> fluxes and sedge-dominated sites, in contrast to those sites dominated by shrubs. Shannon and White [1994] compared sedge (*Carex oligosperma*) plots with shrub (*Chamaedaphne*

*calyculata*) plots and found CH<sub>4</sub> fluxes ranging from 11.5 to 209 mg CH<sub>4</sub> m<sup>-2</sup> day<sup>-1</sup> at the sedge sites versus 0.6 to 68.4 mg CH<sub>4</sub> m<sup>-2</sup> day<sup>-1</sup> at the shrub-dominated sites. *Dise et al.* [1993] observed significant CH<sub>4</sub> emissions only after the emergence of *Calla palustris* in the spring and the fluxes decreased in the fall when these plants senesced. Similarly, *Wilson et al.* [1989] saw an increase in CH<sub>4</sub> flux when *Peltandra*, an aerenchymous plant species, emerged. In a wet tundra in Greenland, *Eriophorum scheuchzeri* and *Carex subspathacea* biomass was correlated with high CH<sub>4</sub> emissions, most likely due to the sedges' ability to transport CH<sub>4</sub> [*Joabsson and Christensen, 2001*].

Vegetation can influence CH<sub>4</sub> fluxes by affecting production as well as transport. All vegetation provides substrate for methanogens and such that belowground productivity increases CH<sub>4</sub> production [*Turetsky et al., 2008*]. However, the root biomass of sedges is a particularly important source of high-quality carbon [*Thomas et al., 1996*]. In contrast, shrubs add a higher amount of acid-insoluble carbon to the peat, which is a less-labile substrate for acetate reduction than is the labile carbon input by sedges, and is thus harder for methanogens to use [*Shannon and White, 1994*]. Consequently, sites dominated by the sedge species *Carex* show a greater percentage of acetate fermentation than do *Sphagnum*-dominated sites [*Bellisario et al., 1999; Popp et al., 1999; Prater et al., 2007; Rooney-Varga et al., 2007*] which may lead to more CH<sub>4</sub> production and higher CH<sub>4</sub> emissions. Studies looking at other sedge species, such as *Eriophorum*, have found that potential CH<sub>4</sub> production is strongly correlated with acetate input from sedges [*Ström et al., 2003; Ström et al., 2005*]. The dominant rooting zone is generally coincident with high CH<sub>4</sub> concentration and thus seasonal changes in CH<sub>4</sub> flux may be related to vascular plants [*Wilson et al., 1989*]. High CH<sub>4</sub> emissions are correlated with periods of active

plant growth and with autumnal litter fall, both of which are inputs of carbon [Wilson *et al.*, 1989]. High CH<sub>4</sub> production is also generally correlated with photosynthesis even on hourly timescales [Thomas *et al.*, 1996], because that is when root exudates are produced [Joabsson and Christensen, 2001].

*Carex* species in particular are intriguing both because of their role in CH<sub>4</sub> transport and because their root exudates enhance CH<sub>4</sub> production, so they have been the focus of several studies. Most *Carex* roots are in the top 15-20 cm of the peat, but *C. rostrata* also has extremely long tap roots, which have been shown to transport gas from 230 cm below the surface of the peat [Rydin and Jeglum, 2006]. Bellisario *et al.* [1999] discovered a strong positive correlation between *Carex* biomass and the measured CH<sub>4</sub> flux. In clipping experiments, CH<sub>4</sub> emissions were highest from sites with intact sedges [Whiting and Chanton, 1992; King *et al.*, 1998]. Sites with clipped sedges tend to have CH<sub>4</sub> emissions that are only 3-40% of those from nearby unclipped sites [King *et al.*, 1998; Verville *et al.*, 1998; Strack *et al.*, 2006]. In particular, Waddington *et al.* [2006] saw CH<sub>4</sub> fluxes decrease by 30 percent at clipped sites. Ström *et al.* [2005] observed higher CH<sub>4</sub> emissions from *Carex*-dominated sites than those containing *Juncus* or *Eriophorum*. All of these studies suggest that there is an important correlation between high CH<sub>4</sub> emissions and the presence of *Carex* species. King *et al.* [1998] also found that adding straw-like tubing to clipped plots at about 87% of the average sedge density increased CH<sub>4</sub> emissions by 379%, to about half the magnitude of the CH<sub>4</sub> fluxes from the unclipped plots. Because the tubing only affected transport and not substrate input and production, this argues for the importance of vegetation-mediated transport in controlling CH<sub>4</sub> emissions from sedge-dominated systems.



### 1.7.2 Temperature controls on methane emissions

*Dise et al.* [1993] found that the seasonal patterns of CH<sub>4</sub> flux in a Minnesota peatland corresponded with the temperature variations of the peat. Overall, 38% of the observed variation in CH<sub>4</sub> emissions could be accounted for by temperature, meaning that over a daily to weekly timescale, peat temperature is the dominant control on CH<sub>4</sub> flux from that site [*Dise et al.*, 1993]. *Crill et al.* [1988] found that the temperature 10 cm below the peat surface is the most important control of CH<sub>4</sub> emissions in another Minnesota peatland. This means that increases in summer maximum temperatures have the potential to trigger a positive feedback in CH<sub>4</sub> emissions from northern peatland sites, presuming all other variables are constant, [*Nisbet and Chappellaz*, 2009]. Modeling scenarios show that a 0.8°C increase at 10 cm depth can increase CH<sub>4</sub> emissions by 5% [*Roulet et al.*, 1992b]. An average summer warming of 2°C could thus lead to a 45% increase in mean CH<sub>4</sub> emissions, if the water-table depth remains constant [*Christensen et al.*, 2003]. In some studies, once soil temperature is included as a predictor of CH<sub>4</sub> flux, water-table depth has no significant predictive power, except in the driest sites [e.g. *Wilson et al.*, 1989; *Dise et al.*, 1993].

*Treat et al.* [2007] found that air temperature is the most consistent predictor of CH<sub>4</sub> fluxes for a variety of time scales at Sallie's Fen, a temperate peatland. *Moore and Knowles* [1990] also found air temperature to be the strongest control on CH<sub>4</sub> flux on a seasonal scale and *Crill et al.* [1988] found that daily and monthly mean air temperature is strongly correlated with CH<sub>4</sub> flux, as well.

Observed correlations between high CH<sub>4</sub> emissions and warm air or peat temperatures are presumably due to the effect of temperature on the metabolic rate of the

methanogens [Dise *et al.*, 1993], though warmer temperatures may also increase ebullition and solubility, which in turn affects the rate of diffusion [Kellner *et al.*, 2006]. Porewater CH<sub>4</sub> concentrations increase throughout the spring and summer, which corresponds to warming temperatures [Crill *et al.*, 1988], and Yavitt *et al.* [1988] found that sub-surface CH<sub>4</sub> production increased with temperature. With more production the size of the belowground CH<sub>4</sub> pool, and thus the peat-surface CH<sub>4</sub> gradient, increases which in turn increases the rate of diffusion through both the peat and vegetation aerenchyma [Dise *et al.*, 1993]. There appears to be a relatively-consistent relationship between temperature and CH<sub>4</sub> sources and sinks [Christensen *et al.*, 2003], though temperature has a stronger effect on CH<sub>4</sub> production than it does on CH<sub>4</sub> oxidation.

However, not all studies have found this correlation between temperature and CH<sub>4</sub> flux [Roulet *et al.*, 1992a]. Dise *et al.*, 1993 found that sites with plant-associated CH<sub>4</sub> transport had the smallest correlation between temperature and CH<sub>4</sub> emissions. Yavitt *et al.* [1988] saw no effect on CH<sub>4</sub> production when temperature was increased at 30-95 cm below the peat surface, though that may be due to substrate limitation at depth. In addition, even when relationships are found, they are rarely linear. Instead, the best relationship between soil temperature and CH<sub>4</sub> flux may be logarithmic, exponential [Christensen *et al.*, 2003], or a step function [Wilson *et al.*, 1989].

### ***1.7.3 Water-table controls on methane emissions***

The depth of the water table affects CH<sub>4</sub> emissions from peatlands because it controls the size and location of oxic and anoxic zones [Moore and Knowles, 1990; Bubier *et al.*, 1993, Dise *et al.*, 1993; Shannon and White, 1994; Bubier *et al.*, 1995; Waddington *et al.*, 1996; Bellisario *et al.*, 1999; Strack *et al.*, 2004; Treat *et al.*, 2007;

*Strack and Waddington, 2007; Turetsky et al., 2008; Leppälä, 2011*]. In column experiments, the highest oxidation rates occur just above the water table [*Urmann et al., 2007*]. In Finnish sites, the highest rates of CH<sub>4</sub> production were observed at or just below the water table [*Juottonen et al., 2005*] and the most active CH<sub>4</sub>-production zone is often just below the water table [*Rydin and Jeglum, 2006*]. Water-table depth may affect CH<sub>4</sub> fluxes on longer time scales than temperature does [*Dise et al., 1993*] and surface saturation is also an important control on CH<sub>4</sub> emissions [*Roulet et al., 1992a*].

Water-table fluctuations cause variability in CH<sub>4</sub> fluxes through both direct and indirect effects, such as shifting the distribution of the anoxic and oxic zones and increasing substrate availability [*Crill et al., 1988; Turetsky et al., 2008*]. *Turetsky et al. [2008]* found that water-table depth explains 48% of the observed CH<sub>4</sub> flux variability and surface peat temperature and water table together explain 70%. *Roulet et al. [1992a]* proposed that 43% of CH<sub>4</sub> variability is due to water-table level, versus only 6% from temperature changes. However, variation in water-table depth may mask correlations between CH<sub>4</sub> flux and other variables, including temperature [*Moore and Knowles, 1989*].

*Waddington et al. [1996]* and *Christensen et al. [2003]*, among others, have proposed that water-table level can act as a switch. If the water table drops below the rhizosphere, the effect of vegetation on CH<sub>4</sub> emissions may be minimized. *Leppälä et al. [2011]* found that temperature and vegetation only had a significant effect on CH<sub>4</sub> emissions if the water table was at a critical depth (which varied among sites). Other studies have observed that lowering the water table results in smaller CH<sub>4</sub> fluxes [*Moore and Knowles, 1989; Strack et al., 2004; Strack and Waddington, 2007*] and similar results

have been seen in dissolved CH<sub>4</sub> concentrations [Strack *et al.*, 2004]. Model summaries of field data estimate that dropping the water table by 14 cm can reduce CH<sub>4</sub> emissions by 74-81% [Roulet *et al.*, 1992b]. However, a recent field experiment only found a 55% reduction in CH<sub>4</sub> flux in response to draining [Strack *et al.*, 2004].

Rises in water table may be more influential than water-table drawdown, though this is dependent on initial and final water levels [Dise *et al.*, 1993; Moore and Dalva, 1993; Turetsky *et al.*, 2008]. Though significantly higher CH<sub>4</sub> fluxes have been observed in sites with high water tables, there is not always a correlation between daily water-table position and CH<sub>4</sub> flux, implying that the direction in which the water table is moving may be important [Strack *et al.*, 2004]. When the water table is close to the surface, CH<sub>4</sub> production increases because the freshest carbon is then in the anoxic zone [Rydin and Jeglum, 2006]. Water-table depth may also control heat transfer to soil depths through thermal conductivity [Roulet *et al.*, 1992a; Turetsky *et al.*, 2008] and water fluxes may increase input of nutrients and substrates into otherwise-limited systems [Yavitt *et al.*, 1988].

## 1.8 Methane and stable isotopes

Each CH<sub>4</sub> process (production, oxidation, and transport) influences the isotopic signature, due to the fractionation of <sup>12</sup>CH<sub>4</sub> and <sup>13</sup>CH<sub>4</sub>. Consequently, stable isotope analysis can be a useful tool for understanding the roles of the underlying processes. Methane from acetate fermentation is <sup>13</sup>CH<sub>4</sub>-enriched ( $\delta^{13}\text{CH}_4 = -65$  to  $-50$  ‰) relative to CH<sub>4</sub> from CO<sub>2</sub> reduction ( $\delta^{13}\text{CH}_4 = -110$  to  $-60$ ) [Popp *et al.*, 1999]. Diffusive CH<sub>4</sub> transport through plants also results in mass-dependent fractionation, which is signified

either by more  $^{13}\text{CH}_4$  in the plant lacunae than in emissions or belowground or by isotopic fractionation between the  $\text{CH}_4$  produced belowground and the emitted  $\text{CH}_4$  [Popp *et al.*, 1999].

In general, sites with higher sedge cover have enriched  $\delta^{13}\text{CH}_4$  signatures in porewater  $\text{CH}_4$ , ranging from -65 to -47.5‰ [Bellisario *et al.*, 1999; Prater *et al.*, 2007]. Enriched  $\text{CH}_4$  is strongly correlated with large  $\text{CH}_4$  fluxes [Bellisario *et al.*, 1999; Prater *et al.*, 2007]. Sites in the same systems with less than 15% sedge cover had  $\delta^{13}\text{CH}_4$  values ranging from -95 to -55‰ [Bellisario *et al.*, 1999; Prater *et al.*, 2007]. A similar effect is apparent in the fractionation (i.e. difference in  $\delta^{13}\text{C}$ ) between  $\text{CH}_4$  and  $\text{CO}_2$  in these systems, where more than 50% sedge cover resulted in fractionation factors ( $\alpha$ ) between 1.07 and 1.04 [Prater *et al.*, 2007]. Isotope analysis is also a useful tool for determining oxidation rates. Methanotrophs preferentially use  $^{12}\text{CH}_4$ , meaning that  $^{13}\text{C}$ -enriched  $\text{CH}_4$  in the unsaturated zone relative to the dissolved  $\text{CH}_4$  in the saturated zones indicate a substantial effect of  $\text{CH}_4$  oxidation [Happell and Chanton, 1993].

## 1.9 Purpose of this study

Sallie's Fen is a temperate peatland that can act as either a source or sink of carbon to the atmosphere, depending on environmental factors [Carroll and Crill, 1997]. Historical records and recent studies imply that predicted climate change could cause a strong positive feedback on  $\text{CH}_4$  emissions from northern wetlands, which includes peatlands [Nisbet and Chappellaz, 2009]. Though the global budget of  $\text{CH}_4$  sources and sinks is relatively well quantified, it requires improvement [Duglokencky *et al.*, 2011]. In the case of natural sources, such as from wetlands, this means determining the

distribution and seasonality of CH<sub>4</sub> emissions on local and regional scales [Duglokencky *et al.*, 2011].

Consequently, better understanding of the controls on CH<sub>4</sub> emissions from peatlands is vital for predicting potential feedbacks that could enhance or reduce greenhouse gas emissions. Two decades of CH<sub>4</sub>-flux data from Sallie's Fen show that fluxes tend to be higher from sedge-dominated plots than from shrub-dominated plots [Varner *et al.*, 2008], but it is currently not known exactly what processes are responsible for this observation. This study was designed to understand the extent to which *C. rostrata* influences the timing, magnitude, and source of CH<sub>4</sub> emissions from a temperate peatland and increase understanding of the contributions of CH<sub>4</sub> production, oxidation, and transport to the net CH<sub>4</sub> emissions at *C. rostrata*-dominated sites through a vegetation clipping experiment. This is crucial for better predicting responses of CH<sub>4</sub> emissions to precipitation and temperature changes, and subsequent vegetation shifts, forecasted for the future.

The following are the hypotheses that this study tests:

Hypothesis 1: Methane emissions will be highest from *C. rostrata*-dominated plots. *C. rostrata* green area will be strongly positively correlated with the magnitude of CH<sub>4</sub> flux, both prior to implementing the clipping experiment in all plots and in the control plots throughout the experiment. In addition, the control plots will have larger CH<sub>4</sub> fluxes than the experimental plots. The largest treatment effect will occur during summer, when the *C. rostrata* plants are at their peak biomass.

Hypothesis 2: When *C. rostrata* are present, vegetation-assisted transport is the main pathway for CH<sub>4</sub> migration from belowground to the atmosphere. The

experimental plots will have more dissolved CH<sub>4</sub> around the sedge rooting zone than the control plots, despite a presumed smaller input of labile carbon and lower rates of CH<sub>4</sub> production, due to the disruption of plant-associated transport. These differences should be largest when the water table is at or above the *C. rostrata* rooting zone. If the water table drops, treatment differences in CH<sub>4</sub> will be minimized, due to a decoupling of the *C. rostrata* roots from the anoxic methanogenesis zone.

Hypothesis 3: When *C. rostrata* are present, more CH<sub>4</sub> is produced and oxidized in the rhizosphere. Peat cores from the control plots will have higher potential CH<sub>4</sub> oxidation and higher potential CH<sub>4</sub> production at the 10-20 cm depth than the cores from the experimental areas.

Hypothesis 4: Temperature and water-table depth affect CH<sub>4</sub> emissions from *C. rostrata* dominated plots. Methane flux will be positively correlated with both air temperature and peat temperature on a daily time scale. Higher water table will result in higher CH<sub>4</sub> fluxes; both these relationships will be stronger in the control plots than in the experimental plots.

## 2. METHODS AND MATERIALS

### 2.1 Site description

Sallie's Fen is a temperate poor fen located in Barrington, New Hampshire (43°12.5' N, 71°03.5' W). The minerotrophic peatland is approximately 1.7 ha and receives water from runoff, rainfall, and a small ephemeral stream that runs along the north edge. The pH ranges from 4.1 to 5.7 [Treat *et al.*, 2007]. The 30-year mean annual temperature (1971-2000; measured in Durham, NH) is 8.0°C and the 30-year mean summer temperature (June-August) is 19.7°C [CARA, 2006]. Mean annual precipitation is 1100 mm [Frolking and Crill, 1994]. The biologically-active season runs from late April to October, with senescence of most species beginning in late August [Treat *et al.*, 2007]. The fen is dominated by *Sphagnum* species (e.g. *Sphagnum fallax* and *S. magellanicum*). Dominant vascular plants include ericaceous shrubs such as leatherleaf (*Chamaedaphne calyculata*), sheep laurel (*Kalmia angustifolia*), and cranberry (*Vaccinium oxycoccus* and *V. macrocarpon*) and deciduous shrubs such as speckled alder (*Alnus incana ssp. rugosa*) and highbush blueberry (*Vaccinium corymbosum*), as well as sedges (*Carex rostrata* and *C. aquatilis*) and three-leaved Solomon's-plume (*Maianthemum trifolium*). Red maple (*Acer rubrum*) is the dominant tree and lines the edges of the fen.



## 2.2 Experimental design

In April 2008, we inserted six 60 cm by 60 cm aluminum collars into the northeast part of the fen, where *C. rostrata* is the dominant vascular species (Fig. 1). Each plot had near 100 percent *Sphagnum* cover. Other species in these plots included *C. calyculata*, *V. oxycoccus*, *M. trifolium*, and *A. rubrum*. The collars were distributed in pairs such that each was in close proximity to a partner with comparable temperature and water-table conditions. June 2008 served as a calibration period to determine the similarity of the plots prior to clipping. Data were collected weekly to sub-weekly in the summer and intermittently in the spring and fall from June 2008 to December 2010.

On July 2, 2008, around the peak of the *C. rostrata* growing season, we removed all the aboveground *C. rostrata* from the collar in each pair that had the highest sedge cover. Though this was not random, we wanted the clipping to have the strongest effect possible. *C. rostrata* plants were clipped to just below the *Sphagnum* surface. The remaining aerenchymous stems were covered with plastic bags full of petroleum jelly and sealed at their base, to prevent CH<sub>4</sub> and oxygen transport through the aerenchyma. The three control plots were left undisturbed. Prior to CH<sub>4</sub> flux measurements, *C. rostrata* stubble in the experimental plots was re-clipped and re-sealed as needed. By 2010, *C. rostrata* growth in the clipped plots was minimal and re-clipping was rarely necessary.

## 2.3 Methane flux measurements

Methane fluxes were measured once or twice per week during summer (June, July, and August) and biweekly or monthly in fall (September, October, November) in 2008, 2009, and 2010. In 2010, CH<sub>4</sub> fluxes were also measured weekly or biweekly in

spring (March, April, and May), just after the emergence of green *C. rostrata* growth, and continued through December, when almost all of the summer's *C. rostrata* growth had senesced. Fluxes were measured using a static chamber technique [e.g. *Frolking and Crill, 1994*]. A clear Teflon chamber measuring 60 by 60 by 90 cm (see *Carroll and Crill [1997]* for description) was placed in the grooved aluminum collars. The chambers contained fans to circulate the internal air and a climate control system to keep relative humidity and temperature close to ambient conditions. After placement, the chamber was left open for 5-10 minutes to minimize disturbance effects and allow the air inside the chamber to return to ambient conditions. To measure the CH<sub>4</sub> fluxes, the chamber was closed and covered with a shroud designed to block out all light and thus minimize changes in temperature and relative humidity. Five 60 mL headspace samples were taken from inside the chamber every two minutes for a 10 minute period using polypropylene syringes (BD, Franklin Lakes, New Jersey) equipped with 3-way stopcocks. Ambient air outside the chambers was also sampled.

The air samples were analyzed on a gas chromatograph equipped with a flame ionization detector (GC-FID, Shimadzu GA-14A) within 6 hours. The GC-FID was calibrated using a standard of 1.8612 ppm CH<sub>4</sub> (2008-2010) or 3.266 ppm CH<sub>4</sub> (2010). Standards are cylinders of compressed ambient air calibrated against NOAA's Environmental Systems Research Laboratory in the Global Monitoring Division's Carbon Cycle Greenhouse Gasses Group that maintains the World Meteorological Organization (WMO) mole fraction scales for CO<sub>2</sub>, CH<sub>4</sub>, N<sub>2</sub>O, and CO. Twelve standards were run on each day samples were analyzed and the highest and lowest areas were dropped. The mean of the ten remaining standards was used to calculate the

response factor in ppmv/area count. Each sample was run twice and the average concentration was used for the final calculations. Fluxes were calculated as the slope of the linear regression of CH<sub>4</sub> concentration versus time. Non-linear regressions, most likely due to chamber leakage or disturbance, were discarded from subsequent analyses (approximately 10% of data). Non-linearity was determined as data falling outside the 95% confidence level for linear regressions, which is dependent on the sample size. Fluxes were discarded when they had an R<sup>2</sup> of less than 0.75 for five samples, 0.87 for four samples, or 0.95 for three samples. Other discarded data included any measurements where the initial CH<sub>4</sub> concentration in the chamber was substantially above ambient concentrations and any negative fluxes because these were presumed to be due to disturbance from placing the chamber, as well as any fluxes with large jumps in CH<sub>4</sub> concentration that many have come from episodic ebullition.

#### **2.4 Porewater methane measurements**

Two small, perforated metal sippers were inserted inside each collar in June 2008, adjacent to a *C. rostrata* plant, to sample porewater at 18 and 60 cm below the peat surface. 18 cm was determined to be the dominant rooting zone for *C. rostrata*, while 60 cm is presumably below the bulk of the *C. rostrata* roots and always below the water table. During late summer and early fall of 2010, the water table was too low to collect 18 cm porewater for analysis. In May 2010 an additional set of six metal sippers was installed in one pair of collars to collect porewater samples at 10, 20, 30, 40, 50, and 60 cm below the peat surface. Plastic tubing was attached to the top of each sipper and sealed with a three-way stopcock. After flux measurements, any water sitting in the

sippers was drawn up and discarded after which a 30 mL sample was drawn and stored in a plastic syringe.

In the laboratory, each syringe was filled with 30 mL of ambient air and shaken vigorously for two minutes to allow the dissolved CH<sub>4</sub> to equilibrate with the air. Two 10 mL replicates of the headspace air were then immediately analyzed on a GC-FID that had been calibrated using 1000.6 ppm CH<sub>4</sub> (Scott Specialty Gases, Plumsteadville, Pennsylvania). The average of these replicates was used as the sample concentration. Occasionally, water samples were stored in a refrigerator overnight, instead of being analyzed on the same day as collection. In these cases, the samples were returned to room temperature before being analyzed.

## **2.5 Isotopic analysis**

In 2010, 32 porewater samples collected on five days between July and October from depths between 20 and 60 cm below the peat surface were analyzed for <sup>13</sup>CH<sub>4</sub>. The 30 mL samples were equilibrated with 30 mL of helium, using the above technique. The 30 mL headspace air was then transferred into a 25 mL evacuated vial and stored until analysis. <sup>13</sup>CH<sub>4</sub> was analyzed using a preconcentration continuous flow method [see *Rice et al.*, 2001] on a GC IsoLink with a PoraPlot fused silica column (25 m x 0.32 mm).

## **2.6 *Carex rostrata* measurements**

Every other week throughout summer 2008 and 2009 and spring through fall 2010, *C. rostrata* Green Area Index (GAI) was measured in each plot using a technique similar to that used by *Wilson et al.* [2007]. Each *C. rostrata* leaf in the plots was

measured and assigned to an approximate height class (0-20 cm, 21-40 cm, 41-60 cm, 61-80 cm, and 81+ cm). Outside of the plots, widths of five *C. rostrata* leaves from each height class were measured. These widths were averaged together and multiplied by the midpoint of each height class and the number of leaves in that class to approximate *C. rostrata* GAI in each plot in  $\text{m}^2 \text{C. rostrata per m}^2 \text{ ground}$ . *C. rostrata* GAI was linearly interpolated between measurement days. In addition, the maximum and minimum heights of *C. rostrata* green-leaf area were measured for ten *C. rostrata* plants in three sections of the fen biweekly during the growing season for all years.

Following the initial clipping in 2008, the clipped *C. rostrata* leaves were dried and weighed for a biomass estimate. These weights were plotted with corresponding GAI measurements to give an equation for calculating biomass from GAI: *C. rostrata* dry biomass ( $\text{g/m}^2$ ) =  $107.03 * \text{C. rostrata GAI (m}^2/\text{m}^2) + 14.04$  ( $R^2 = 0.98$ ). This equation was then used to approximate *C. rostrata* biomass in the unclipped collars.

## 2.7 Incubations

Two plots for destructive sampling (approximately  $0.5 \text{ m}^2$  apiece) were established adjacent to the long-term plots in May 2010. All aboveground *C. rostrata* biomass was clipped and removed from the experimental plot and the stubble was sealed using the same process as for the  $\text{CH}_4$  flux collars. Six 30-cm cores (10 cm in diameter) were collected on June 28, 2010 and July 27, 2010 using a metal peat corer--three from the clipped area and three from the control area. In the control plot, these cores were centered around a *C. rostrata* plant. The cores were then divided into three 10-cm segments.  $30\text{-}60 \text{ cm}^3$  of each segment was placed in a one-quart jar with a septum in the

lid, sealed, and flushed with helium for 10 minutes to ensure anoxic conditions. Efforts were made to minimize exposure of the core to oxygen prior to its incubation. An additional 30-60 cm<sup>3</sup> of the core was sealed in a one-quart jar and spiked with 10 mL of 1000 ppm CH<sub>4</sub>. One set of anoxic and spiked “blank” jars was also created, containing approximately 40 mL of water instead of a peat sample. All the jars were incubated in the dark at 15°C for and sampled shortly after sealing and approximately every 24 hours for the next four days. Sampling consisted of injecting 20 mL of helium (for the anaerobic jars) or ambient air (for the aerobic jars), pulling headspace into a syringe and releasing it back into the jar several times to ensure it was fully mixed, and finally withdrawing a 20-mL sample of the headspace. These samples were analyzed in duplicate on the same GC-FID used for CH<sub>4</sub> flux analysis.

Rates of potential CH<sub>4</sub> production or oxidation were calculated as the linear increase or decrease in headspace CH<sub>4</sub> concentrations over the incubation period, using the same rejection criteria as for the chamber CH<sub>4</sub> fluxes.

## **2.8 Abiotic variables**

Meteorological data were collected continuously at Sallie's Fen using an automated meteorological station located in the approximate center of the fen (Fig. 1). Daily mean water-table depth and air temperature from the met station were used in analysis. When continuous temperature data were not available, we interpolated using a linear relationship with data from a secondary temperature probe ( $R^2 = 0.91$ ).

Perforated PVC wells were inserted next to each collar for water-table measurements. Water-table depth was measured manually relative to the peat surface on

the same days as flux measurements were taken. The average difference in water-table depth at each collar relative to the continuous data was used to calculate collar water-table depth at each collar between measurement days. Air and peat temperature, at the surface and 10 cm below the peat surface, were manually measured at the same time as the CH<sub>4</sub> fluxes.

## 2.9 Data analysis

Data were divided into seasons based on *C. rostrata* growth. Spring (March 1 to May 31) is when *C. rostrata* begins to produce green leaves, summer (June 1 to August 31) is when *C. rostrata* is at its maximum biomass, and fall (September 1 to November 30) is when *C. rostrata* is senescing.

R 2.10.1 and IBM SPSS Statistics 19.0 were used for all statistical analysis. For correlations and regressions, a natural-log transformation was used on the CH<sub>4</sub> flux data to more closely approximate a normal distribution. Relationships between ln CH<sub>4</sub> flux, 18 cm dissolved CH<sub>4</sub>, 60 cm dissolved CH<sub>4</sub>, *C. rostrata* GAI, water-table depth, air temperature, and temperature 10 cm below the peat surface were examined using a correlation matrix at  $\alpha = 0.05$ . Correlations were calculated using all the data, using only data from control plots, and using only data from clipped plots, but always including all three years. Multiple linear regressions were conducted at  $\alpha = 0.05$  using all daily data. The final models were determined using the stepwise method ( $F \leq 0.05$  to enter,  $F \geq 0.10$  to remove) so not all possible predictors were included in the best models. Regressions were run for the natural log of CH<sub>4</sub> flux, 18 cm dissolved CH<sub>4</sub>, and 60 cm dissolved CH<sub>4</sub> using *C. rostrata* GAI, water-table depth, air temperature, and 10 cm temperature as

possible predictors and for *C. rostrata* GAI using water-table depth, air temperature, and 10 cm temperature as possible predictors.

To determine the effect of treatment on CH<sub>4</sub> flux and dissolved CH<sub>4</sub> concentration, treatment averages before clipping and for the subsequent years were calculated. Because the data are not evenly distributed, means were calculated for each collar and then averaged within each treatment. T-tests were conducted using a sample size (*n*) of 3 for both treatments. This kept the averages from being skewed towards collars with more data points. T-tests were also conducted in the same manner for *C. rostrata* GAI, water-table depth, and 10 cm temperature.

To estimate how much CH<sub>4</sub> was transported through *C. rostrata*, estimates of the diffusive flux were calculated using the following equation:

$$F_{diff} = K * \frac{\Delta CH_4}{z} \quad \text{Eq. 1}$$

where  $F_{diff}$  is the diffusive flux of CH<sub>4</sub>,  $\Delta CH_4$  is the change in CH<sub>4</sub> concentration from depth to surface,  $z$  is the depth of the layer, and  $K$  is a coefficient that incorporates the rates of oxidation and diffusion. In the clipped plots, CH<sub>4</sub> was only released through diffusion and ebullition and any flux measurements that contained ebullition events were discarded from the analysis. Consequently,  $F_{diff}$  was assumed to equal the measured CH<sub>4</sub> flux for these plots and  $K$  was calculated per plot per day. Oxidation rates were assumed to be the same for a pair of control and clipped plots, and thus  $F_{diff}$  for the control plots was calculated using the daily  $K$  from their paired clipped plot. The CH<sub>4</sub> flux from *C.*



*rostrata* transport was then calculated as the total flux from the collar minus the calculated diffusive flux.

### 3. RESULTS

#### 3.1 Hydrological and temperature conditions

Depth to water table varied by year, but was generally lowest from mid-summer to early fall (Fig. 2). 2010 was a much drier summer overall than 2008 or 2009 (Fig. 2). On average, the 2010 water table was almost 33 cm below the peat surface, compared to mean water-table depths of 14.5 and 14.0 cm in 2008 and 2009, respectively (Table 1). The lowest water table in 2010 was 48.5 cm on August 3, which was much lower than the maximum water-table depths in the previous two summers (about 22 cm on July 9, 2008 and August 28, 2009) (Table 1). Water-table depth was not significantly different between treatments for any of the three years (Table 2).

Air temperature varied across the three years, but followed the same general seasonal trend (Fig. 2). The most inter-annual variability occurred during spring and fall, whereas the mean seasonal temperature and the minimum and maximum daily temperatures for all three summers were very similar (Fig. 2). Air temperature from the meteorological station is measured at 25 cm above the peat surface and the sensor is thus sometimes in the snow pack. This was the case in early spring 2008, which is why the air temperature remained at 0°C (Fig. 2). The temperature measured at 10 cm below the peat surface varied slightly between plots, but the mean 10 cm temperature was not significantly different between treatments for any of the three years (Table 2).

### 3.2 Comparison of plots prior to experiment implementation

Plots were set up as spatially-correlated pairs to ensure similar environmental conditions within a pair and reduce variability in fluxes, and thus highlight the treatment effect. Throughout the calibration month in 2008, the water table ranged from 10.5 to 21 cm below the peat surface in the experimental collars and from 12 to 21.5 cm below the peat surface in the control collars (Fig. 2). The temperature at 10 cm below the peat surface ranged from 12.0 to 24.1 °C in the experimental collars and from 13.0 to 25.3 °C in the control collars (Fig. 2c). Average monthly water-table depth and peat temperature were not significantly different between treatments. The control plots tended to be slightly wetter in 2008 and slightly drier in 2009 and 2010, but these differences were negligible and thus most likely had little to no effect on overall methane dynamics.

Prior to clipping, CH<sub>4</sub> fluxes ranged from 19.3 to 563.6 mg CH<sub>4</sub> m<sup>-2</sup> day<sup>-1</sup> in the experimental collars and from 9.7 to 580.0 mg CH<sub>4</sub> m<sup>-2</sup> day<sup>-1</sup> in the control collars (Fig. 3a). On average, CH<sub>4</sub> fluxes from the experimental collars were almost 40 mg CH<sub>4</sub> m<sup>-2</sup> day<sup>-1</sup> higher than CH<sub>4</sub> fluxes from the control collars before clipping, but the means were not significantly different ( $p = 0.974$ ) (Fig. 4). During the same time period, dissolved CH<sub>4</sub> at 18 cm below the peat surface ranged from 481 to 4767 ppm CH<sub>4</sub> in the control collars and from 802 to 4955 ppm CH<sub>4</sub> in the experimental collars (Fig. 5a). Dissolved CH<sub>4</sub> at 60 cm below the peat surface ranged from 1495 to 7252 ppm CH<sub>4</sub> in the experimental collars and from 3089 to 5266 ppm CH<sub>4</sub> in the control collars (Fig. 6a). Despite the observable differences in CH<sub>4</sub> flux magnitude, there were no significant differences in mean dissolved CH<sub>4</sub> concentrations between the two sets of plots at either 18 or 60 cm below the peat surface during the pre-clipping period ( $p = 0.320$ ).

### 3.3 *Carex rostrata* growth

In each year, *C. rostrata* began to produce green leaf area in March or April and continued to grow through the summer. In 2008 and 2009, even though *C. rostrata* started senescing in mid- to late-July, overall green leaf area increased (Figs. 7,8). In 2010, however, *C. rostrata* biomass in the control plots peaked in the beginning of July and tailed off through the summer and fall (Figs. 7,8). The maximum height of *C. rostrata* was similar across all three summers (around 90 cm), but total *C. rostrata* biomass in the control collars (as approximated by GAI) was much higher in 2009 and 2010 than in 2008. Peak *C. rostrata* biomass during the growing season was 96 g m<sup>-2</sup> in 2008, compared to 172 g m<sup>-2</sup> and 185 g m<sup>-2</sup> in 2009 and 2010, respectively (Table 3).

Across all three years, *C. rostrata* GAI was significantly correlated at  $\alpha = 0.05$  with water-table depth ( $r = 0.192$ ), air temperature ( $r = 0.208$ ) and 10 cm peat temperature ( $r = 0.175$ ).

### 3.4 Methane fluxes

Over three years, CH<sub>4</sub> fluxes after clipping ranged from 6.6 to 686.7 mg CH<sub>4</sub> m<sup>-2</sup> day<sup>-1</sup> in the control collars with a mean flux of 131.6 mg CH<sub>4</sub> m<sup>-2</sup> day<sup>-1</sup> and from 1.8 to 389.7 mg CH<sub>4</sub> m<sup>-2</sup> day<sup>-1</sup> in the experimental collars with a mean flux of 79.9 mg CH<sub>4</sub> m<sup>-2</sup> day<sup>-1</sup> (Fig. 3). Methane fluxes from the control collars were almost always higher than the fluxes from their paired experimental collar. The treatment difference in CH<sub>4</sub> flux magnitude increased throughout the experiment. During the summer growing season, the average difference in CH<sub>4</sub> flux between a pair of collars was 42.8 mg CH<sub>4</sub> m<sup>-2</sup> day<sup>-1</sup> in 2008, 58.5 mg CH<sub>4</sub> m<sup>-2</sup> day<sup>-1</sup> in 2009, and 67.9 mg CH<sub>4</sub> m<sup>-2</sup> day<sup>-1</sup> in 2010 (Fig. 4).

After clipping in 2008, the mean CH<sub>4</sub> flux over the remainder of the summer increased by 30% in the control plots and decreased by 22% in the experimental plots, though these responses were not significantly different from each other (Fig. 10). Throughout the rest of the experiment, CH<sub>4</sub> fluxes from experimental plots were equal to 87% of the fluxes from the control plots in 2008, 70% in 2009, and 63% in 2010. In 2008, there was no significant difference in mean CH<sub>4</sub> flux between treatments (Table 2). In 2009 and 2010 treatment effects on mean CH<sub>4</sub> flux were significant at the 95 and 90% confidence levels, respectively (Table 2). Mean seasonal CH<sub>4</sub> fluxes were significantly different between the control and experimental plots in June-August 2009, September-November 2009, and September-November 2010 (Table 4).

Overall, the natural log of CH<sub>4</sub> flux was significantly correlated at  $\alpha = 0.05$  with *C. rostrata* GAI ( $r = 0.360$ ), daily air temperature ( $r = 0.569$ ), 10 cm peat temperature ( $r = 0.465$ ), 18 cm dissolved CH<sub>4</sub> ( $r = 0.353$ ) and 60 cm dissolved CH<sub>4</sub> ( $r = -0.156$ ) (Table 5). In the control plots, the natural log of CH<sub>4</sub> flux had slightly stronger significant correlations with all the above variables, as well as with water-table depth ( $r = -0.166$ ) (Table 5). The relationship between ln CH<sub>4</sub> flux and *C. rostrata* GAI was relatively weak in 2008 and 2009, but exceptionally strong in 2010 ( $r = 0.94$ ) (Fig. 11). In the experimental plots, the natural log of CH<sub>4</sub> flux was significantly correlated only with air temperature ( $r = 0.684$ ), 10 cm peat temperature ( $r = 0.520$ ), and 18 cm dissolved CH<sub>4</sub> ( $r = 0.423$ ) (Table 5).

The best predictive model for the natural log of CH<sub>4</sub> flux across all three years of the experiment used *C. rostrata* GAI, water-table depth, air temperature, and 10 cm peat temperature as significant predictors ( $R^2 = 0.423$ ,  $F_{4,257} = 47.12$ ,  $p < 0.001$ ; Table 6).

Air temperature was the best predictor of CH<sub>4</sub> flux, followed by *C. rostrata* GAI, but adding water-table depth and peat temperature significantly improved the model.

### 3.5 Porewater methane

Over the three years, the concentration of dissolved CH<sub>4</sub> at 18 cm below the peat surface ranged from 199 ppm to 10,625 ppm in the control collars with a mean concentration of 3188 ppm and from 107 ppm to 10,710 ppm in the experimental collars with a mean concentration of 4168 ppm (Fig. 5). In the spring the dissolved CH<sub>4</sub> concentrations were very similar between treatments, but in the summer concentrations at 18 cm were generally higher in the experimental collars than in their paired control collars (Fig. 5). In 2008, the mean CH<sub>4</sub> concentrations were significantly different between collars, but treatment differences were not significant in 2009 or 2010 (Table 2).

Over the three years, the concentration of dissolved CH<sub>4</sub> at 60 cm below the peat surface ranged from 93 to 38,245 ppm in the control collars with a mean of 6876 ppm and from 21 to 51,921 ppm in the experimental collars, with a mean of 7395 ppm (Fig. 6). In 2010, there was a spike in dissolved CH<sub>4</sub> concentrations at the end of April (Fig. 6c). The mean CH<sub>4</sub> concentrations were not significantly different between treatments in any of the three years of measurement (Table 2).

In 2008, the mean dissolved CH<sub>4</sub> concentration at 18 cm below the peat surface increased by 105% from June (before clipping) to July and August (after clipping) in the experimental plots while the mean concentration in the control plots only increased by 35%. These responses were significantly different. At the same time, the ratio of the belowground CH<sub>4</sub> storage pool (measured as the concentration of dissolved CH<sub>4</sub> at 18

cm) relative to the measured CH<sub>4</sub> fluxes increased 147% in the experimental plots while decreasing by 44% in the control plots.

In 2010, dissolved CH<sub>4</sub> was measured at closer intervals along a depth profile of 10 to 60 cm in one pair of plots. All 10 cm CH<sub>4</sub> concentrations, half the 20 cm concentrations, and some of the 30 and 40 cm CH<sub>4</sub> concentrations were measured in the unsaturated peat above the water table, meaning they were gas, rather than dissolved CH<sub>4</sub>. These concentrations were always one to three orders of magnitude smaller than the CH<sub>4</sub> concentrations measured below the water table. In general, CH<sub>4</sub> concentrations were higher at depth, even when compared only among saturated depths (Fig. 12). Between 10 and 30 cm, no treatment effect on CH<sub>4</sub> concentration was apparent. Between 40 and 60 cm, mean summer CH<sub>4</sub> concentrations were significantly higher (for  $\alpha = 0.10$ ) in the experimental plots than in the control plots. The differences between treatments remained relatively constant across the measurement period.

### **3.6 Potential methane production and oxidation**

In June 2010, potential CH<sub>4</sub> production rates were an order of magnitude higher than potential CH<sub>4</sub> oxidation rates. Mean potential production across all depths and treatments was 38  $\mu\text{mol CH}_4 \text{ cm}^{-3} \text{ sec}^{-1}$ , compared to a mean oxidation rate of 4.2  $\mu\text{mol CH}_4 \text{ cm}^{-3} \text{ sec}^{-1}$  (Fig. 13). In July, the production and oxidation rates were much more similar with a mean production rate of 0.22  $\mu\text{mol CH}_4 \text{ cm}^{-3} \text{ sec}^{-1}$  and a mean oxidation rate of 0.28  $\mu\text{mol CH}_4 \text{ cm}^{-3} \text{ sec}^{-1}$  (Fig. 14). Correspondingly, July 2010 rates of both production and oxidation were much lower than June rates. The maximum potential production measured in the July cores was 1.9  $\mu\text{mol CH}_4 \text{ cm}^{-3} \text{ sec}^{-1}$  compared to 176.5

$\mu\text{mol CH}_4 \text{ cm}^{-3} \text{ sec}^{-1}$  in June and the maximum potential oxidation in July was  $0.4 \mu\text{mol CH}_4 \text{ cm}^{-3} \text{ sec}^{-1}$  compared to  $7.8 \mu\text{mol CH}_4 \text{ cm}^{-3} \text{ sec}^{-1}$  in June.

In June, the potential  $\text{CH}_4$  production rate was higher in the control plots than in the experimental plots only in the top 10 cm of the peat core. Between 10 and 30 cm, the experimental plots had substantially higher rates of potential  $\text{CH}_4$  production, though the treatment averages were not significantly different (Fig. 13b). In July, potential  $\text{CH}_4$  production rates were very similar for both treatments in the top 10 cm, but were also much larger in the experimental plots between 10 and 30 cm, though not significantly so. In all cores, potential production increased with depth (Fig. 14b). In contrast, average potential  $\text{CH}_4$  oxidation rates showed little to no trend with respect to depth or treatment (Figs. 13a,14a).

### **3.7 Methane transport modeling**

In 2008,  $\text{CH}_4$  emission attributed to *C. rostrata* transport made up a larger percentage of the total summer  $\text{CH}_4$  fluxes than  $\text{CH}_4$  from diffusion, 74% vs. 26% (Fig. 15). In 2009, however, *C. rostrata* transport was only responsible for about a third of the summer  $\text{CH}_4$  emissions and in 2010 *C. rostrata* transport and diffusion contributed about equally to the total flux (Fig. 15). Methane flux from *C. rostrata* transport was slightly higher at mid-summer (i.e. at peak *C. rostrata* growth) in all years (Fig. 16), but showed no correlation with *C. rostrata* GAI in 2008 and only a weak relationship in 2009 (Fig. 17). There is a significant correlation between summer *C. rostrata*  $\text{CH}_4$  emissions and *C. rostrata* GAI in 2010 (Fig. 17). Depth to water table was not correlated with  $\text{CH}_4$  from *C. rostrata* transport, but it was significantly correlated with air temperature (Fig. 17)



### **3.8 Isotopes**

In both the control and experimental plots, all the  $^{13}\text{C}$  signatures of the dissolved  $\text{CH}_4$  samples are within the range expected for  $\text{CH}_4$  formed through acetate formation, rather than through  $\text{CO}_2$  reduction (Fig. 18). At 40, 50, and 60 cm below the peat surface there is little to no difference in isotopic signatures between  $\text{CH}_4$  from the control and experimental treatments. In general, the dissolved  $\text{CH}_4$  is more  $^{13}\text{C}$ -enriched closer to the peat surface.

## 4. DISCUSSION

### 4.1 Effect of *Carex rostrata* on methane emissions

Confirming hypothesis 1, *C. rostrata* green area (GAI) is significantly positively correlated with instantaneous CH<sub>4</sub> flux across all seasons and all years (Table 5), indicating that *C. rostrata* plays a significant role in CH<sub>4</sub> emissions across a variety of water-table depths and temperatures. This is similar to relationships of seasonal sedge biomass and CH<sub>4</sub> flux observed in a number of other studies [e.g. *Whiting and Chanton*, 1992; *Bubier et al.*, 1995, *King et al.*, 1998; *Bellisario et al.*, 1999].

However, the exact relationship between CH<sub>4</sub> flux and sedge biomass varies between this and other studies. In this experiment in a poor fen, the slope of the regression line is 0.006, whereas *Whiting and Chanton* [1992] observed a slope of 0.34 in a different fen and *Bellisario et al.* [1999] found 0.007 in a peatland gradient spanning a bog to a rich fen. This variability may be due to climatic differences between various study sites or to the classification of the peatland (e.g. ombrotrophic bog, poor fen, or rich fen). *Bubier* [1995] found that chemical and moisture gradients control vascular species distribution in Canadian peatlands and these same geochemical gradients are the basis of peatland classifications [*Rydin and Jeglum*, 2006]. Bogs often have different vegetation than fens [*Crum*, 1992], so even if two sites have aerenchymous sedges, their relationship with CH<sub>4</sub> emissions is expected to vary because each species has different effects on the amount of oxygen and acetate it releases into the rhizosphere. For example, less

oxidation occurs around the roots of *Carex rostrata*, than around those of *Juncus effusus* or *Eriophorum vaginatum* [Ström *et al.*, 2005].

The presence of aerenchymous species can also increase CH<sub>4</sub> emissions from other types of wetland ecosystems. In prairie wetlands, temporal patterns in CH<sub>4</sub> flux are controlled by the release of CH<sub>4</sub> through *Phragmites spp.*, another aerenchymous plant [Arkebauer *et al.*, 2001]. In lake environments, vegetation can enhance CH<sub>4</sub> emissions at lake fringes. Bartlett *et al.* [1992] measured an average flux of 89 mg CH<sub>4</sub> m<sup>-2</sup> day<sup>-1</sup> when aquatic vegetation was present, compared to 77 mg CH<sub>4</sub> m<sup>-2</sup> day<sup>-1</sup> from open water. In a Finnish lake, Juutinen *et al.* [2004] observed high seasonal CH<sub>4</sub> emissions correlated with increases in aboveground biomass and Kankaala *et al.* [2004] also found a significant correlation between CH<sub>4</sub> emission and *Phragmites australis* biomass in a boreal lake. Methane emission was also positively correlated with *Typha domingensis* and *Cladium jamaicense* biomass in the Florida Everglades [Chanton *et al.*, 1993]. On the other hand, Koelbener *et al.* [2010] saw no significant relationship between CH<sub>4</sub> emissions from wetland sites and corresponding measures of shoot or root biomass.

Before the implementation of the clipping experiment, the major difference between the two sets of plots was that the experimental plots had, on average, about 50% higher *C. rostrata* biomass than that of the control plots. Some variability is unavoidable because the plots were chosen in mid-April 2008 when the *C. rostrata* growing season was just beginning and it was not possible to predict the exact distribution of the summer's growth. Also, the plot in each pair with the highest *C. rostrata* biomass in July 2008 was chosen as the experimental plot. Though this means the experimental design was not entirely randomized, clipping the plots with more *C. rostrata* plants should lead

to a stronger treatment response and increase the ability to understand the role that these plants play in CH<sub>4</sub> cycling at Sallie's Fen.

Methane fluxes from the experimental plots were 25% higher than fluxes from the control plots during the pre-clipping period (Fig. 3), though the mean CH<sub>4</sub> fluxes were not significantly different between the two sets of plots (Fig. 4). The difference is probably due to the higher *C. rostrata* biomass in the experimental plots, given the significant correlation between CH<sub>4</sub> flux and *C. rostrata* GAI found in this study (Table 5). However, again confirming hypothesis 1, the mean summer CH<sub>4</sub> fluxes were higher from the control plots than from the experimental plots in all three years, with average summer fluxes from the clipped plots ranging from 53% (2010) to 75% (2008) of average summer fluxes from the control plots (Fig. 10). In particular, a large effect was observed in summer 2008, directly after the initial clipping. Even though plots in both treatments experienced similar temperatures and water-table levels (Table 2), CH<sub>4</sub> fluxes increased by 30% in the control plots from June (pre-clipping) to July and August (post-clipping) but decreased by 22% in the experimental plots. The difference between mean summer CH<sub>4</sub> fluxes for each treatment is only significant in 2009, but this may be partly an artifact of the conservative manner in which the statistics were conducted (using an n of 3) or an unavoidable result of the large day-to-day variability in CH<sub>4</sub> flux due to environmental controls. However, there is still a clear tendency for larger fluxes to occur from the control collars, despite the experimental collars having higher fluxes prior to the clipping experimental implementation, implying that removing *C. rostrata* reduces overall CH<sub>4</sub> emissions from this peatland.

These results are consistent with those found in other sedge-removal experiments. For example *Kelker and Chanton* [1997] and *Waddington et al.* [1996] both saw similar responses in CH<sub>4</sub> flux when *Carex* species were removed from Canadian fens. Other studies observed a more pronounced response, with CH<sub>4</sub> emissions from clipped plots totaling only 3 to 40% of those from nearby control plots [*Whiting and Chanton*, 1992; *King et al.*, 1998; *Verville et al.*, 1998; *Frenzel and Karofeld*, 2000; *Strack et al.*, 2006]. *Frenzel and Karofeld* [2000], in particular, saw a 97% decrease in CH<sub>4</sub> flux after clipping *Scheuchzeria palustris* and *Eriophorum vaginatum*. This variability may be related to the amount of sedge biomass removed in these experiments or to the particular sedge species [*Ström et al.*, 2005].

The mean difference in summer CH<sub>4</sub> flux between the treatments (i.e. the average effect of removing *C. rostrata* plants) increased from 2008 to 2010 (Fig. 9). This could indicate that the system is approaching steady-state as residual effects of the clipped *C. rostrata* are no longer affecting the experimental collars. In a similar vegetation-removal experiment in Finland, the first two years of CH<sub>4</sub> data were inconclusive, presumably due to residual disturbance effects, but year 3 showed statistically-significant differences [*Riutta*, 2008]. In a clipping experiment of *E. angustifolium* and *C. rostrata* in a wet-sedge meadow in Alaska, CH<sub>4</sub> fluxes from the clipped plots were 40% of the fluxes from the control plots in the first year, but only 25% after three years [*Verville et al.*, 1998].

In this experiment, the treatment difference may have been limited in the first year after clipping due to an increase in available substrate from decomposing *C. rostrata* belowground. Sedges break down faster than shrubs do (*C. rostrata* roots have a decay constant between 0.077 and 0.214 year<sup>-1</sup>) [*Moore et al.*, 2007], making them a ready

carbon source for methanogens. Rhizomes start to decompose after only four days under anoxic conditions [Barclay and Crawford, 1982] and 10-45% of the total mass of *C. rostrata* roots and rhizomes decomposes during the first 12 months after separation from the aboveground shoots [Scheffer and Aerts, 2000]. Increased substrate availability is consistent with the high concentrations of dissolved CH<sub>4</sub> around the *C. rostrata* rooting area in the experimental plots after clipping, especially because this trend is less apparent in the second and third years of the experiment (Fig. 5).

These data also show a strong effect of *C. rostrata* on fall (September through November) CH<sub>4</sub> emissions. In both 2009 and 2010, the fall mean CH<sub>4</sub> emissions were significantly higher in the control plots than in the experimental plots (Fig. 10). In 2009 in particular, CH<sub>4</sub> fluxes from the experimental plots decreased from mid-summer through fall, while the fluxes from the control plots stayed high (Fig. 3). *C. rostrata* green area was not measured during that time period, but the plants were presumably starting to senesce. This may imply that *C. rostrata* can affect CH<sub>4</sub> emissions outside the peak growing season. On the other hand, the single year of spring measurements (2010) shows no significant difference in CH<sub>4</sub> emissions between control and experimental plots (Fig. 10). Instead, the CH<sub>4</sub> fluxes are very similar in the beginning of the *C. rostrata* growing season (Fig. 3). An additional set of spring-through-fall CH<sub>4</sub> flux measurements, in conjunction with *C. rostrata* cover estimates, is necessary to draw conclusions, but it is possible that the effect of *C. rostrata* on CH<sub>4</sub> emissions is different in spring and fall months, even though both seasons have similar amounts of *C. rostrata* green area.

## 4.2 Inter-annual variability in *Carex rostrata* growth

In 2009 and 2010, peak *C. rostrata* biomass was nearly twice that in 2008 (Fig. 7). There are two controls on total aboveground green *C. rostrata* biomass: the number, or density, of *C. rostrata* shoots and the maximum height to which shoots grow. In 2008, maximum *C. rostrata* density in the control collars was 336 green shoots per m<sup>2</sup>, compared to 656 shoots per m<sup>2</sup> the following year. In addition, the green *C. rostrata* shoots reached a taller maximum height in 2009 and 2010 than in 2008.

The difference in shoot density may be a consequence of inserting CH<sub>4</sub> flux collars in April 2008. In order to insert the collars, a 10 to 20 cm deep slit was cut into the peat, through fine and coarse roots. Previous studies have observed a loss of both fine-root density [Wang *et al.*, 2005; Heinemeyer *et al.*, 2011] and vascular-plant density [Heijmans *et al.*, 2004] as a result of collar insertion. A significant decline in CO<sub>2</sub> flux has been observed after collars are cut in, presumably from a loss of root respiration [Wang *et al.*, 2005; Heinemeyer *et al.*, 2011]. Heinemeyer *et al.* [2011] suggest that total soil CO<sub>2</sub> efflux rates from peatlands may be underestimated by 10-20%, from the residual effects of collar insertion.

Given that inserting flux collars disrupts roots enough to cause an observable effect on respiration, enough roots may have been cut while inserting the collars in April 2008 to limit aboveground *C. rostrata* biomass for the rest of the growing season. Because one of the sources of new *C. rostrata* shoots is horizontally-growing rhizomes [Hultgren, 1989a], cutting through these structures may have a large effect on the emergence of new shoots during the immediately-following growing season. In addition, the largest peak in new *C. rostrata* shoots generally occurs in the beginning of the

growing season [Gorham and Somers, 1973; Hultgren, 1989a; Saarinen, 1998], which was shortly after the collars were installed.

Inter-annual variability in peat temperature and saturation can affect the growth rate and maximum biomass of emergent *C. rostrata*. If the spring thaw of the peat is delayed, *C. rostrata* shoot growth is also delayed [Hultgren, 1989b] and shoots that emerge later in the summer do not grow as tall as those that emerge at the beginning of the season [Gorham and Somers, 1973; Hultgren, 1989b]. 2008 had a cold spring and the temperature at 10 cm below the peat surface did not get above 0°C until 12 April in 2008, compared to 20 March in 2009 and 9 March in 2010, so the delayed onset of spring may also have contributed to the lower overall *C. rostrata* biomass in 2008. Sallie's Fen also had snow cover into April in 2008, causing the typical spring flooding to occur later than usual (Fig 8a). In lake environments, high water levels in early summer reduce the number of emergent *C. rostrata* shoots [Hultgren, 1989a], so delayed flooding in the fen may also have limited early shoot growth. Finally, the insulating effect of snow resulted in relatively stable peat temperature through early spring. This may have affected *C. rostrata* growth from seeds, because germination of *C. rostrata* seeds occurs best when ambient temperatures fluctuate diurnally, rather than remaining static [Budelsky and Galatowitch, 2002].

The other aspect of *C. rostrata* growth that differed among the three years was the early onset of senescence in 2010, compared to 2008 and 2009. This may be a result of the low water-table level throughout most of 2010 (Fig. 8c). Lab manipulations show water level to have a significant effect on *C. rostrata* height, leaf biomass, and root biomass [Kennedy *et al.*, 2003]. Field observations also indicate that large inter-annual



variations in water table can affect shoot length and density, with the shortest shoots observed in low water years and the tallest observed in high water years [Hultgen, 1989b].

### 4.3 *Carex rostrata* as methane transport mechanism

Over the six weeks immediately after clipping, the rhizospheric dissolved CH<sub>4</sub> concentration in the experimental plots more than doubled, while control-plot concentrations increased by only 35% (Fig. 5). These responses were significantly different ( $F_{1,4} = 7.713$ ,  $p = 0.050$ ). An increase in dissolved CH<sub>4</sub> is expected because late summer conditions are more favorable for methanogenesis [Treat *et al.*, 2007], but the magnitude of the difference indicates that clipping and sealing the *C. rostrata* plants had an effect on the dissolved CH<sub>4</sub>. These dissolved-CH<sub>4</sub> concentrations at 18 cm below the peat surface continued in 2009 and 2010, though not to the same extent (Fig. 5), most likely because of the increased substrate availability after the initial clipping in 2008, from decomposing roots and rhizomes. The dissolved CH<sub>4</sub> at 60 cm below the peat surface shows no effect of clipping, presumably because it is below the dominant rooting zone of *C. rostrata* (Fig. 6).

These results are consistent with those of other clipping experiments. King *et al.* [1998] observed 10 cm dissolved CH<sub>4</sub> concentrations that were 70% higher in the clipped plots than in the control plots. Verville *et al.* [1998] also found higher rooting zone dissolved CH<sub>4</sub> concentrations in clipped plots than in control plots. In those experiments, which were in an Alaskan wet sedge meadow dominated by *Eriophorum* and *Carex* species, the differences in dissolved CH<sub>4</sub> between the treatments were similar to those in

this study, even after multiple years of the clipping experiment [King *et al.*, 1998; Verville *et al.*, 1998]. Waddington *et al.* [1996] saw higher dissolved CH<sub>4</sub> concentrations in clipped plots in a Canadian fen, but the magnitude of difference was considerably larger than that observed in this study, even though the dominant species was also *C. rostrata*. This may be a result of the amount of sedge biomass removed from the clipped plots, which was not reported for that study but has the potential to affect the treatment response.

The differing porewater concentrations of CH<sub>4</sub> most likely indicates a disruption in transport mechanisms, as predicted, especially because the size of the 18 cm CH<sub>4</sub> pool is significantly correlated with CH<sub>4</sub> flux in both the control and experimental plots (Table 5). When King *et al.* [1998] added gas-permeable tubing to clipped plots to mimic the transport effect of aerenchymous sedge stems, CH<sub>4</sub> concentrations at 25 cm below the peat surface were 20% lower than those in the original clipped plots, though still slightly higher than those in the vegetated sites, because CH<sub>4</sub> was released to the atmosphere by diffusing through the straws. Given the higher dissolved-CH<sub>4</sub> concentration in the experimental plots, especially in 2008, those plots should have emitted more CH<sub>4</sub>, if CH<sub>4</sub>-transport mechanisms were equal between the two treatments and all emitted CH<sub>4</sub> diffused up through the peat column instead of also via *C. rostrata* shoots. Instead, daily CH<sub>4</sub> fluxes from the control plots were consistently higher across all three years (Fig. 3), implying that CH<sub>4</sub> is transported from belowground to the atmosphere at a faster rate in the control plots than in the experimental plots. Waddington *et al.* [1996] also observed lower concentrations of dissolved CH<sub>4</sub> at sites with high CH<sub>4</sub> emissions and concluded it was the result of the transport effect of aerenchymous vegetation. Alternatively,

oxidation rates in the experimental plots could be much higher, but there is no reason to expect that would be the case and the incubations show no treatment effect on potential oxidation rates (Figs. 13,14).

To quantify this presumed transport effect, one can calculate how much CH<sub>4</sub> would be emitted from the control plots if their transport rates are identical to those of the experimental plots. The size of the CH<sub>4</sub> flux from the anoxic zone of the peat to the air above depends on three things: CH<sub>4</sub> diffusion rates in water and air, rate of oxidation, and gradient of dissolved CH<sub>4</sub> [Lerman, 1979]. The diffusion rate of CH<sub>4</sub> is a function of peat density, which is presumed to be the same for the control and experimental collars in a given pair. Water-table depth can also affect diffusion and oxidation rates, but it is also consistent between the two treatments (Table 2). Consequently, the diffusion coefficient can be assumed to be equivalent for both types of plots. Some CH<sub>4</sub> may be removed from the plots via horizontal flow [Waddington and Roulet, 1997; Billett and Moore, 2007], but because the control and experimental collars are located near each other, these rates should not differ and thus would be incorporated into our calculated coefficient along with diffusion and oxidation rates. Thus, the only control on diffusive flux rates that differs between the control and experimental plots is the measured CH<sub>4</sub> gradient, which relies on the concentration of dissolved CH<sub>4</sub> at 18 cm below the peat surface.

These calculations remove the effect of *C. rostrata* on increasing CH<sub>4</sub> production because they merely look at the gradient between the CH<sub>4</sub> concentration measured at 18 or 20 cm below the peat surface (i.e. the CH<sub>4</sub> already produced, regardless of its origin) and the atmospheric CH<sub>4</sub> concentration measured just above the peat surface. Similarly, if oxidation rates are higher in the control plots, using the same coefficient for the

experimental and control plots only underestimates the amount of CH<sub>4</sub> transported through *C. rostrata*. Consequently, these results may actually be a conservative estimate of the role of CH<sub>4</sub> transport.

In almost all cases, the calculated diffusive flux for the control collars was substantially lower than the measured flux (Fig. 16), implying that transport through the aerenchyma of *C. rostrata* is responsible for 35-74 % of the emitted CH<sub>4</sub> from the control plots, confirming hypothesis 2 (Fig. 15). This range is comparable to that of *Kutzbach et al.* [2004], who estimated plant-mediated CH<sub>4</sub> flux to account for  $66 \pm 20\%$  of total CH<sub>4</sub> emissions. The total amount of CH<sub>4</sub> flux attributed to *C. rostrata* transport is significantly correlated with both air temperature and 18 cm CH<sub>4</sub> (Table 5, Fig. 17), which is reasonable. The concentration of CH<sub>4</sub> at 18 cm is one of the inputs to the calculation and thus the correlation is a calculation artifact. Total emitted CH<sub>4</sub> is strongly correlated with air temperature, so it is a proxy for the seasonal effect of *C. rostrata*. Though not significantly correlated with water-table depth, the largest contribution from *C. rostrata* transport occurred during periods with high water tables (Fig. 17).

The total *C. rostrata* flux was significantly correlated with *Carex* GAI only in 2010 (Fig. 17). What is more interesting is the percent of the total flux attributable to vegetation-assisted transport as opposed to diffusion. This percentage is significantly correlated with *C. rostrata* green area, but not with any other variables (Table 5). Given that this is presumed to be an estimate of CH<sub>4</sub> transport by *C. rostrata*, the lack of correlation with either temperature or water table is reasonable. Temperature exerts control on CH<sub>4</sub> production and oxidation rates, rather than on transport. Similarly, the greatest effect of *C. rostrata* on CH<sub>4</sub> production is when the majority of sedge roots are in

the anoxic zone of the peat and thus water table is a significant control on rates of methanogenesis [Waddington *et al.*, 1996; Strack *et al.*, 2006; Leppälä *et al.*, 2011]. However, *C. rostrata* also has long tap roots that can reach to deeper pools of CH<sub>4</sub>, even when the water table is low, as in summer 2010 [Hultgen, 1989a]. The main control on how much CH<sub>4</sub> is transported through *C. rostrata* aerenchyma is the diffusion resistance between the rhizosphere and the root aerenchyma [Kutzbach *et al.*, 2004]. Thus, as long as some roots are in a zone of high CH<sub>4</sub> concentration, CH<sub>4</sub> will be transported to the atmosphere through the plants and water table will be a less important control on transport.

*Kelker and Chanton* [1997] suggest that *Carex* species emit CH<sub>4</sub> from the plant base where leaves bundle together and thus vegetation height (i.e. the green area measurement in this study) is not a factor in the ability of *C. rostrata* to transport CH<sub>4</sub>. Studies have found that clipping aerenchymous plants, such as *C. rostrata*, above the peat surface does not decrease CH<sub>4</sub> flux. In Siberia, *Kutzbach et al.* [2004] clipped *C. aquatilis* 5 cm above the tundra surface and did not see any decrease in CH<sub>4</sub> flux relative to the control sites. Similarly, *Kelker and Chanton* [1997] clipped *C. rostrata* at 15 and 20 cm above the surface of the peat and did not see a decrease in CH<sub>4</sub> emissions, even when they sealed the cut top of the sedges. On the other hand, adding gas-permeable tubing to clipped plots to mimic the aerenchymous sedge stems, increased CH<sub>4</sub> emissions by 379% relative to clipped plots without tubing and by [King *et al.*, 1998]. Instead of vegetation height, it is the root structure that determines the ability of *C. rostrata* to transport CH<sub>4</sub> [Kelker and Chanton, 1997]. However, vegetation height is a good predictor of the size of the belowground root system [von Fischer *et al.*, 2010], which

explains the significant correlation found in this study between aboveground biomass and the percentage of CH<sub>4</sub> transported through *C. rostrata* aerenchyma.

#### 4.4 Effect of *Carex rostrata* on methane oxidation and production rates

Contrary to hypothesis 3, cores taken from the control plots did not show higher rates of potential CH<sub>4</sub> oxidation around the *C. rostrata* rhizosphere in lab incubations (Figs. 13,14). Instead, potential oxidation rates for the experimental plots were significantly larger at 10 to 20 cm below the peat surface. These results are inconsistent with field studies in which oxidation was found to be an important control on overall methane emissions from sedge-dominated systems. *Frenzel and Karofeld* [2000] found that CH<sub>4</sub> emission is mainly controlled by the rate of CH<sub>4</sub> oxidation, and consequently aerenchymous vegetation has an important role. In an Alaskan wet sedge tundra, oxidation rates can be as high as 88.7 mg CH<sub>4</sub> m<sup>-2</sup> day<sup>-1</sup>, which is nearly 80% of the rate of potential CH<sub>4</sub> production [*Moosavi and Crill*, 1998]. At a *Sphagnum* mire, oxidation rates were 19.2 to 52.8 µg CH<sub>4</sub> g<sup>-1</sup> wet peat hour<sup>-1</sup> in a minerotrophic area dominated by *C. rostrata*, but considerably lower in other portions of the site. *Carex*-specific rhizospheric oxidation has also been estimated in a mesocosm study as 20 to 40% of produced CH<sub>4</sub> [*Ström et al.*, 2005].

Our results may be an artifact of the experimental procedure. Potential aerobic CH<sub>4</sub> oxidation and potential anaerobic CH<sub>4</sub> production are estimates of the viable biomass of CH<sub>4</sub>-oxidizing and CH<sub>4</sub>-producing microbes, respectively [*King*, 1990; *Sundh et al.*, 1995]. Rather than an accurate measure of the rate or total amount of methanotrophy or methanogenesis occurring in the field, they represent maximum

possible rates with the current microbial communities. Given this, the incubation measures would only differ between treatments if the methanotrophs and methanogens had time to adjust to the new post-clipping environment.

Root-associated CH<sub>4</sub> consumption has been observed for a variety of plants and ecosystems, implying that methanotrophs thrive in the rhizosphere of aerenchymous plants [e.g. King, 1994; Gilbert and Frenzel, 1995; Bosse and Frenzel, 1997; Calhoun and King, 1997; Popp *et al.*, 2000; Fritz *et al.*, 2011]. Measured oxidation rates have been observed to follow the same distribution with depth as *Carex* roots, again implying that methanotrophic communities are greatest around these roots [Popp *et al.*, 2000]. Oxygen concentration has been shown to be significantly higher under *C. rostrata* plants than in a nearby control plot (ranging from 5.3 to 93.3% and 0 to 80.2 %, respectively) [Mainiero and Kazda, 2004]. Prior to clipping, the areas from which the cores were taken were dominated by *C. rostrata* plants and thus presumably had thriving communities of CH<sub>4</sub>-oxidizing microbes in the rhizosphere. The designated experimental plot was clipped on 7 May 2010, only seven weeks before the first set of cores were collected, so it is possible that the microbial community did not undergo significant changes during this time period. Though factors such as vegetation removal can affect methanotrophic communities [Chen *et al.*, 2008], aerobic methanotrophs can persist under less-than-ideal environmental conditions. Though the microbes are not found at depths that are always saturated, they can thrive at depths that fluctuate between being aerobic and being anaerobic [Shannon and White, 1994]. Their distribution is often set by the availability of oxygen (i.e. depth of the water table) and CH<sub>4</sub> [Sundh *et al.*, 1995], but methanotrophs are able to persist in anoxia and without an available carbon source for

long periods of time [Popp *et al.*, 2000]. Consequently, even if the removal and sealing of the aboveground *C. rostrata* biomass reduced the availability of oxygen in the experimental plots, the methanotrophic community may not have adjusted to this change and thus might have been reactivated during the incubation process when supplied with a high concentration of CH<sub>4</sub>.

Again contrary to hypothesis 3, peat cores taken from the control plots did not show higher rates of potential CH<sub>4</sub> production, compared to the experimental plots (Figs. 13,14). 2010 was a particularly dry summer and cores for incubations were collected when the water was below the sedge rooting zone, which may limit the effect of *C. rostrata* on production rates. Also, methanogens exposed to oxygen have failed to produce CH<sub>4</sub> in subsequent incubations [Whalen and Reeburgh, 2000]. Although the <sup>13</sup>CH<sub>4</sub> data from summer 2010 are limited, we were able to collect and analyze samples of dissolved CH<sub>4</sub> from below the water table on five dates between July and October 2010. All values are within the range expected for CH<sub>4</sub> formed from acetate fermentation rather than CO<sub>2</sub> reduction (Fig. 18), implying that the presence or absence of *C. rostrata* may not be affecting the mechanism of methanogenesis or the composition of the methanogen communities in Sallie's Fen, which could also explain the limited treatment effect observed.

Data from 2008 show a build-up of dissolved CH<sub>4</sub> around the *C. rostrata* roots in the experimental plots (Fig. 5a). This may partially be a residual effect of increased CH<sub>4</sub> production due to greater substrate availability as the *C. rostrata* roots and rhizomes decompose after the clipping treatment. Presuming the area clipped in spring 2010 for coring responded in a similar manner, the observed high production rates at lower depths



of the experimental cores may be an artifact of the clipping, rather than an accurate assessment of CH<sub>4</sub>-production rates when *C. rostrata* is removed from the system. Collecting and incubating cores for an additional growing season may provide clearer results; measurements of dissolved CH<sub>4</sub> in the original plots show that the dissolved CH<sub>4</sub> concentrations in each treatment became more similar in the second and third years after the initial clipping (Fig. 5b,c).

#### **4.5 Abiotic controls on methane emissions from *Carex rostrata*-dominated plots**

Because the control plots remained undisturbed throughout the study, they can be used as an exploration of how sedge-dominated peatland systems respond to changes in environmental variables. Fluxes from 2008 to 2010 ranged from 6.6 to 686.7 mg CH<sub>4</sub> m<sup>-2</sup> day<sup>-1</sup> across all seasons. These are within the range of summer fluxes reported by both *Frolking and Crill* [1994] and *Treat et al.* [2007] from the same peatland. Similar ranges of summer fluxes have also been observed by *Bellisario et al.* [1999] in a Canadian peat complex, by *Turetsky et al.* [2008] in an Alaska peatland, and by *Ström and Christensen* [2007] in a Swedish sub-arctic wetland, most of which are sedge-dominated. This suggests that the CH<sub>4</sub> emissions observed in this study, and thus the driving controls, are probably typical of a sedge-dominated peatland. Despite a smaller amount of *C. rostrata* biomass in 2008 than 2009 or 2010, mean summer CH<sub>4</sub> fluxes were largest in 2008 (Fig. 4). Similarly, 2010 has the smallest summer CH<sub>4</sub> emissions of the three years (Fig. 4) but the largest *C. rostrata* green area, implying that *C. rostrata* is not the only control on CH<sub>4</sub> emissions at this site.

Porewater CH<sub>4</sub> concentrations in 2008 to 2010 ranged from 199 to 10,625 ppm CH<sub>4</sub> at 18 cm below the peat surface and 93 to 38,245 ppm CH<sub>4</sub> at 60 cm depth. In 2008, 18 cm CH<sub>4</sub> concentrations peaked in late summer, but in 2009 and 2010 the seasonal trend was more muted (Fig. 5). Previous observations at Sallie's Fen showed relatively constant 10 cm porewater CH<sub>4</sub> concentrations throughout the summer [Treat *et al.*, 2007] which is more consistent with our 2009 and 2010 data than with 2008. However, summer 2008 experienced rather drastic fluctuations in water-table depth (Fig. 2), which probably shifted the zones of methanogenesis and methanotrophy and may thus have affected belowground CH<sub>4</sub> storage. In addition, high levels of precipitation can create dilution of CH<sub>4</sub>-rich porewater with surface water, as well as increase rates of lateral transport [Billett and Moore, 2007]. Groundwater flow can be a significant control on dissolved CH<sub>4</sub> concentrations in peatlands [Waddington and Roulet, 1997].

The deeper CH<sub>4</sub> showed similar trends in summer and fall for all three years in that there was minimal observable seasonal variation in 60 cm dissolved CH<sub>4</sub> concentrations (Fig. 6). However, the concentration of CH<sub>4</sub> at 60 cm did spike considerably in late April 2010 (Fig. 6c). This spike may be due to a buildup of acetate during the early spring that then became available for methanogenesis, as has been observed in other peatlands [Shannon and White, 1996]. Methane formed deeper in the peat is generally presumed to come from carbonate reduction as opposed to acetate formation because the substrates available are older and more thus recalcitrant forms of carbon [Hornibrook *et al.*, 1997]. However, the isotopic signatures of dissolved CH<sub>4</sub> at this site imply that acetate fermentation is the dominate pathway of methanogenesis even at 60 cm below the peat surface (Fig. 18; Shoemaker *et al.*, unpublished). Given the rapid

increase of dissolved CH<sub>4</sub>, the buildup may have triggered ebullition events [Fechner-Levy and Hemond, 1996; Chanton, 2005; Kellner et al., 2006; Goodrich et al., 2011], which would explain the subsequent return to a relatively consistent CH<sub>4</sub> concentration for the rest of the year. This pattern may have occurred in 2008 and 2009 as well, but the measurement periods for those years do not include spring.

Average daily air temperature increased considerably in late spring, peaked in late July through August, and cooled off rapidly from fall into winter, though there was considerable day-to-day variation in all years (Fig. 2). Water-table depth fluctuated considerably, both within and between years, but the higher water table in the 2008 and 2009 summers probably contributed to the high fluxes from the control plots, compared to those of summer 2010 (Fig. 3). Warm, wet climates are ideal for methanogenesis, given substrate availability, and in 2008 and 2009 the water table remained at or above the sedge rooting zone during the peak summer temperatures. A combination of temperature and water table has been found to control both CH<sub>4</sub> flux and dissolved-CH<sub>4</sub> concentrations in many sedge peatlands [e.g. Whiting and Chanton, 1992; Frohling and Crill, 1994; Waddington et al., 1996; Treat et al., 2007; Turetsky et al., 2008].

Air temperature and 10 cm peat temperature were both significantly correlated with CH<sub>4</sub> flux as predicted in hypothesis 4 while air temperature was also significantly correlated with 18 cm dissolved CH<sub>4</sub>, though not with 60 cm dissolved CH<sub>4</sub> (Table 5). This was expected because temperature affects microbial activity and because temperature and *C. rostrata* biomass follow similar seasonal patterns [Crill et al., 1988; Moore and Knowles, 1990; Dise et al., 1993; Frohling and Crill, 1994; Treat et al., 2007]. In addition, regression analysis shows that peat temperature and air temperature

are both significant predictors in the final model of CH<sub>4</sub> flux (Table 6). These results are consistent with many studies that have found significant correlations between CH<sub>4</sub> emissions and peat temperature across a variety of wetlands: poor fens and open and forested bogs in Minnesota [Crill *et al.*, 1988; Dise *et al.*, 1993], wet meadow tundra in Alaska [Bartlett *et al.*, 1992], Canadian fen and bog sites [Moore and Knowles, 1990; Bubier *et al.*, 1995], peatlands in northwestern Europe and Greenland [Christensen *et al.*, 2003], and Michigan bogs [Shannon and White, 1994]. A previous study at Sallie's Fen also concluded that air temperature is the most consistent predictor of CH<sub>4</sub> fluxes across a variety of time scales [Treat *et al.*, 2007]. However, Roulet *et al.* [1992a] suggest that there is no single predictor of methane emissions that will be consistently accurate, which is why the best regression model includes air temperature, peat temperature, water-table depth, and *C. rostrata* biomass as predictors (Table 6). Even so, the model only explains just over a third of the observed intra- and inter-annual variability in CH<sub>4</sub> emissions from the *C. rostrata*-dominated plots.

Nevertheless, the significant correlation between CH<sub>4</sub> flux and temperature across all three years implies that production rates probably have a large effect on the magnitude of CH<sub>4</sub> emissions from *C. rostrata* plots. Methane oxidation is also temperature-dependent, but oxidation rates are far less sensitive to temperature fluctuations than are production rates [Dunfield *et al.*, 1993; Dinsmore *et al.*, 2009]. Literature Q<sub>10</sub> values for methanotrophy range from 1.2 to 2.1, while Q<sub>10</sub> values for methanogenesis range from 2.7 to 20.5 [Moosavi and Crill, 1998]. This means that with a 10°C temperature increase, methanogenesis rates will generally increase 1.3 to 17.1 times as much as oxidation rates.

Instantaneous CH<sub>4</sub> flux is also negatively correlated with water-table depth, meaning that CH<sub>4</sub> fluxes are higher when the water table is closer to the surface (Table 5). Again, this confirms hypothesis 4 and is consistent with the many studies concluding that increases in both water table and temperature increase CH<sub>4</sub> emissions [e.g. *Moore and Knowles*, 1990; *Dise et al.*, 1993; *Bubier*, 1995; *Treat et al.*, 2007]. *Turetsky et al.* [2008] found that variability in water-table depth explained 40% of the variability in CH<sub>4</sub> flux, though, in our study, water table in combination with the other factors explained only 35% of observed CH<sub>4</sub> flux variability. This correlation may be complicated because wetter soils are also generally warmer [*von Fischer et al.*, 2010], so when the water table is low, soil temperature has a reduced effect on CH<sub>4</sub> emissions [*Kutzbach et al.*, 2004]. Water table may be a weaker control on CH<sub>4</sub> emissions in our study because the data only included the depth of the water table, not if it was rising or falling. Methane emissions may be slower to respond to a rising water table because of a lag in the re-establishment of the anoxic zone and subsequent methanogenesis [*Moore and Roulet*, 1993]. Essentially, the water table can be at the same level on two different occasions, but the CH<sub>4</sub> flux may still vary depending on whether the water table rose or fell in the preceding days. If such hysteresis occurs in this site, it could explain the limited predictive power of water-table depth on CH<sub>4</sub> emissions from the control plots. However, *Moore and Roulet* [1993] based their conclusions on a lab experiment in which they manipulated the water table to rise or fall by 2 cm per day. In the field, the water table rarely changes that quickly.

The water-table depth varied significantly across the three years, mainly because 2010 was very dry (Table 1). This wide range of water-table levels could also lead to

conflicting controls on CH<sub>4</sub> emissions and explain the low correlation we observed. In addition, the pressure gradient in peat soils shifts when the water table drops sharply, which can lead to the release of large pulses of stored CH<sub>4</sub> [Treat *et al.*, 2007; Goodrich *et al.*, 2011] and mask other relationships between water-table depth and CH<sub>4</sub> flux. On several days when the water table recently dropped, we observed unusually high CH<sub>4</sub> fluxes (e.g. 18 July 2008, 10 June 2009, 3 August 2010) (Fig. 3). *Frolking and Crill* [1994] also found a weak relationship between water-table depth and CH<sub>4</sub> flux at Sallie's Fen, which they attributed to the suppression of CH<sub>4</sub> emissions due to precipitation events, mainly because of inputs of oxygenated water, loss of substrate and dissolved CH<sub>4</sub> through runoff, and changes in porewater hydrostatic pressure. On the other hand, *Crill et al.* [1988], *Roulet et al.* [1992], *Shannon and White* [1994], *Bubier* [1995], *Bubier et al.* [1995], and *Verville et al.* [1998] observed the opposite relationship, on both daily and seasonal scales. *Strack et al.* [2006] and *Dise et al.* [1993] found highest CH<sub>4</sub> fluxes from sites with high water tables, either artificially flooded areas or in comparison to nearby drained sites.

Water-table depth is not significantly correlated with CH<sub>4</sub> flux from the experimental collars, implying that the presence of *C. rostrata* increases the importance of water-table depth as a control on CH<sub>4</sub> emissions. Many studies have found that the effect of aerenchymous vegetation on CH<sub>4</sub> emissions is strongly mitigated by water-table depth [e.g. *Waddington et al.*, 1996; *Kutzbach et al.*, 2004]. This is partly because water-table depth can be a significant control on aboveground and belowground biomass in *C. rostrata* [*Kennedy et al.*, 2003], but also because vegetation can only affect CH<sub>4</sub> emissions when the concentration of CH<sub>4</sub> in their rooting zone is high [*Kutzbach et al.*,

2004]; vegetation can have a larger effect on CH<sub>4</sub> production when the rhizosphere is mostly anoxic. *Kutzbach et al.* [2004] measured much higher CH<sub>4</sub> fluxes when the water table was above the soil surface. *Von Fischer et al.* [2010] found that soil saturation and water-table depth are the best predictors of spatial CH<sub>4</sub> variability in an Arctic coastal tundra. Interestingly, soil saturation limits diffusion rates of CH<sub>4</sub> through the soil itself, as well as oxygen diffusion rates, which may mean that increased soil saturation requires alternative transport mechanisms [*Kutzbach et al.*, 2004].

#### **4.6 Implications for climate change**

Because peatlands are an important source of atmospheric CH<sub>4</sub> [*Vasander and Kettunen*, 2006], any future changes in these ecosystems will most likely result in feedbacks that may either enhance or reduce the greenhouse effect. In order for climate models to improve their predictions of future conditions, controls on CH<sub>4</sub> emissions from peatlands need to be thoroughly understood. As discussed, CH<sub>4</sub> fluxes from plots in Sallie's Fen with *C. rostrata* are larger than those from sites from which the *C. rostrata* was removed. Though most CH<sub>4</sub> fluxes in this study were measured in late morning, *von Fischer et al.* [2010] determined that CH<sub>4</sub> flux rates are generally stable over a six-hour time period and thus that an individual flux measurement can be representative of the daily rate of CH<sub>4</sub> emission through diffusive pathways. In addition, because a large percent of the annual CH<sub>4</sub> flux occurs during the peak growing season, vegetation-related controls most likely dominate annual fluxes and thus are important to consider in climate models [*von Fischer et al.*, 2010]. *Riutta et al.* [2007] also conclude that plant

community is very important in predicting CH<sub>4</sub> flux, even across otherwise homogenous sites.

*C. rostrata* and other sedges are generally found in waterlogged environments, and thus a decrease in precipitation could shift the dominant vegetation species to one that prefers a drier environment [Strack *et al.*, 2006; Breeuwer *et al.*, 2009]. Changes in the seasonal patterns of precipitation may lead to a lower water-table depth in some peatlands [Frolking *et al.*, in press]. If shrubs take over areas that were previously dominated by sedges, the most likely effect would be a negative feedback on warming, because shrubs do not have the same CH<sub>4</sub>-emission enhancing effect as that of *C. rostrata* [Thomas *et al.*, 1996]. Alternatively, vegetation shifts could occur in the opposite direction, especially since some studies predict a trend for increased precipitation in boreal and subarctic peatlands [Frolking *et al.*, in press]. If precipitation increases and sites become wetter *C. rostrata* may invade [Anderson, 2008] and CH<sub>4</sub> emissions might increase, in the more-anoxic environment especially because of the enhancing effect of *C. rostrata*. Finally, as the climate warms and permafrost melt creates water-logged sites, *C. rostrata* and other sedges are likely to colonize those areas [Frolking *et al.*, in press].

In addition, changes in seasonality will most likely affect CH<sub>4</sub> emissions from sedge-dominated sites. We observed a strong seasonal trend in CH<sub>4</sub> flux, so a longer summer or warmer fall could lead to larger total CH<sub>4</sub> emissions. These data indicate a strong correlation between air temperature and CH<sub>4</sub> flux regardless of the presence or absence of *C. rostrata*. Models consistently predict warming for temperate and boreal peatlands [Frolking *et al.*, in press] and which would increase CH<sub>4</sub> emissions, if



saturation conditions do not change. All of these components could affect the role of CH<sub>4</sub> in global climate and thus all are important to consider. Determining the contributions of methanogenesis, methanotrophy, and CH<sub>4</sub> transport to the net measured emissions provides valuable information for improving model predictions CH<sub>4</sub> fluxes and how they may respond to precipitation and temperature changes, especially if CH<sub>4</sub> transport is less dependent on water-table depth than the microbial processes are. Essentially, climate may have differing effects on these CH<sub>4</sub>-related processes, so it is crucial to quantify the impacts separately.

#### **4.7 Future work**

Three field seasons of data for this vegetation-removal experiment is a valuable series, but increasing the amount of data collected will strengthen the conclusions drawn from these results. 2010 was the first year in which spring through winter data were collected (i.e. from the initial sedge green-up through *C. rostrata* senescence), so additional spring and winter data would be useful for statistical purposes and for understanding of inter-annual variability. Previous vegetation removal experiments have mainly focused on CH<sub>4</sub> emissions during the summer months [e.g. *Kelker and Chanton.*, 1997; *King et al.*, 1998; *Verville et al.*, 1998; *Strack et al.*, 2006] so the beginning and end of the growing season are especially important to monitor.

Natural variability contributes to some ambiguity in the results, which in turn complicates isolating the relative contributions of oxidation, production, and transport to the observed differences in CH<sub>4</sub> emissions from the control and experimental sites. However, estimating diffusive fluxes allowed quantification of the role of *C. rostrata*

transport in Sallie's Fen. Production and oxidation can be examined using stable-isotope composition of CH<sub>4</sub> samples, though field conditions in 2010 were not ideal for collecting the necessary porewater samples around the *C. rostrata* rhizosphere. The hope for 2011 is to obtain isotope data spanning a longer time period and closer to the peat surface, in order to investigate possible differences between the control and experimental plots.

Measuring *in situ* oxidation rates would also add to the understanding of individual processes occurring in the two sets of plots. Various techniques are possible, such as applying an oxidation inhibitor (i.e. preventing methanotrophs from oxidizing CH<sub>4</sub>) and measuring CH<sub>4</sub> fluxes before and after [Moosavi and Crill, 1998]. However, CH<sub>3</sub>F and other oxidation inhibitors may also inhibit methanogenesis, complicating their use [Frenzel and Karofeld, 2000].

Another important consideration is that *C. rostrata* is only one of the many sedge species that occur in peatlands. Other sedges, and many other wetland and aquatic species such as *Eriophorum* or *Phragmites*, also enhance CH<sub>4</sub> emissions [e.g. Waddington *et al.*, 1996; King *et al.*, 1998; Verville *et al.*, 1998; Arkebauer *et al.*, 2001]. To thoroughly understand the effect of sedges in the current or future CH<sub>4</sub> cycle, manipulation experiments need to be conducted at sites dominated by different sedge species.

## CONCLUSIONS

There is a strong positive relationship between *C. rostrata* green area and CH<sub>4</sub> flux, meaning that the presence of *C. rostrata* increases CH<sub>4</sub> emissions from Sallie's Fen. Removing the aboveground *C. rostrata* biomass caused an immediate decrease in CH<sub>4</sub> emissions that persisted for the rest of the growing season and continued over the next two years of the study, with summer CH<sub>4</sub> flux from the experimental plots averaging 53-75% of the magnitude of the control CH<sub>4</sub> fluxes, depending on the year. The difference in mean summer CH<sub>4</sub> flux from the control plots with *C. rostrata* and the experimental plots without *C. rostrata* increased over time. Despite having similar amounts of *C. rostrata* green leaf area in spring and fall, the largest treatment effects on CH<sub>4</sub> flux occurred in summer and fall.

Model results show that in the *C. rostrata*-dominated control plots, not all CH<sub>4</sub> flux can be accounted for through diffusion up the peat column. Instead, transport through the aerenchyma of *C. rostrata* is estimated to be responsible for 35-74% of total summer emissions. The percentage of daily CH<sub>4</sub> flux attributed to *C. rostrata* transport is correlated with the *C. rostrata* green leaf area. There were no observable differences in potential CH<sub>4</sub> production or potential CH<sub>4</sub> oxidation between the treatments in 2010.

Air temperature, peat temperature, and water-table depth are all significant predictors of CH<sub>4</sub> flux in the regression model. However, even when combined with *C. rostrata* green area, these controls only explained 34.6% of the observed variability in CH<sub>4</sub> emissions so more investigation is necessary to explain the remaining variability.

Moreover, large inter-annual variability in vegetation distribution and biomass, water-table depth, and temperature was observed in this study. Thus, it is crucial to have multi-year studies to thoroughly understand the interactions among these factors and how they can be incorporated into models to predict CH<sub>4</sub> emissions under changing conditions.

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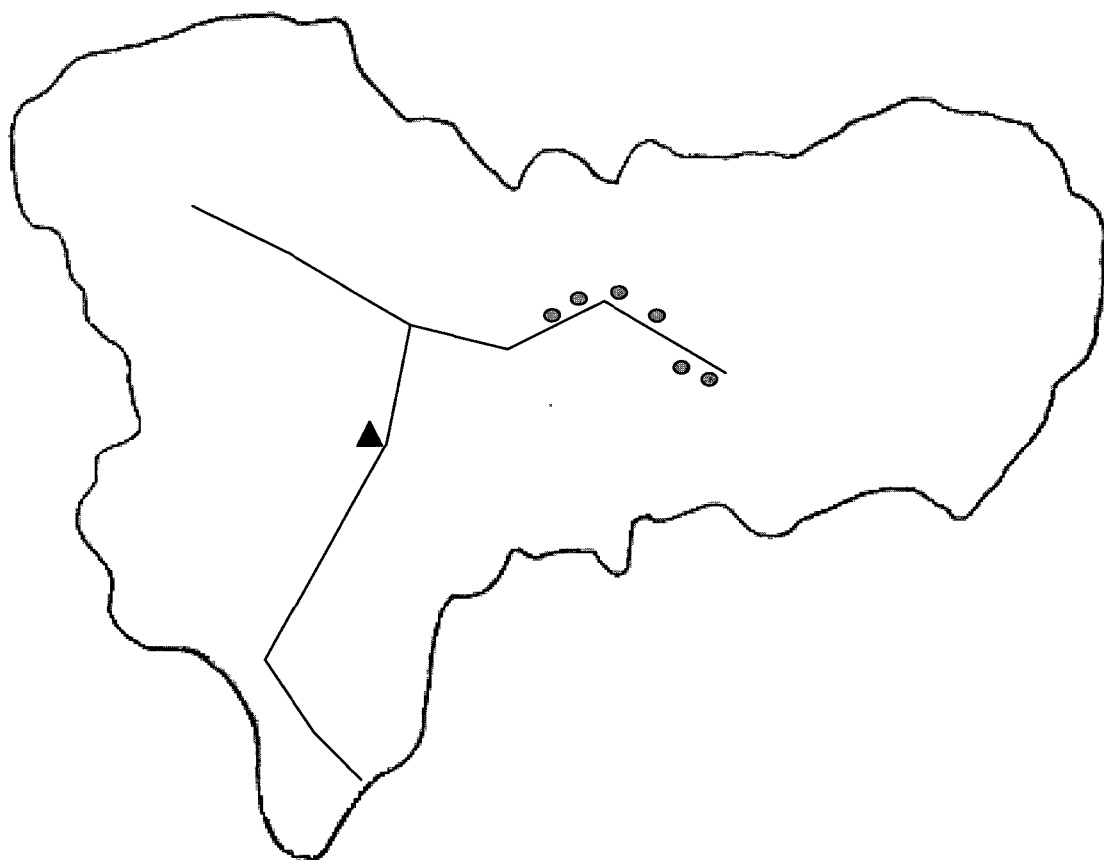
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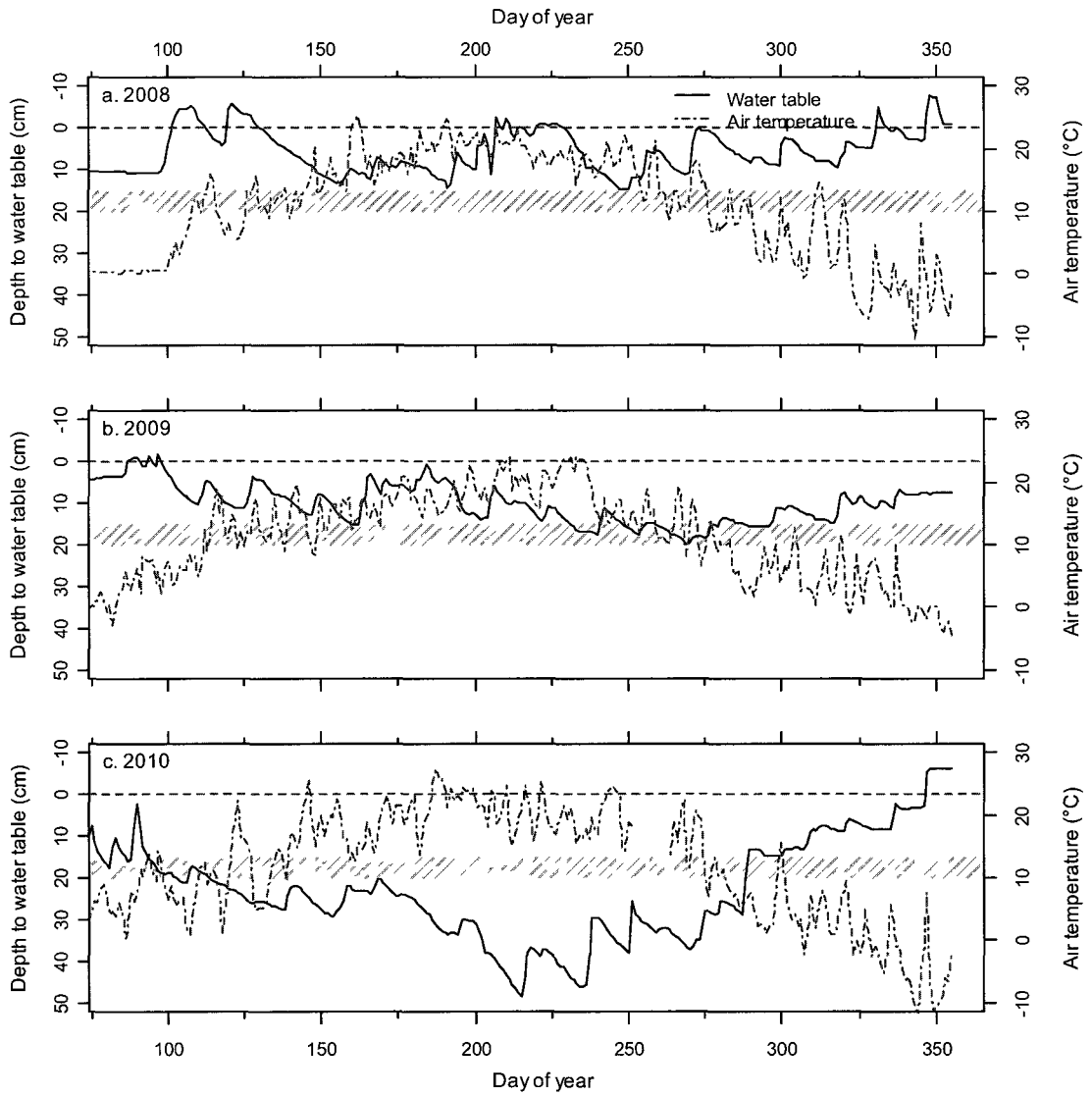
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## FIGURES

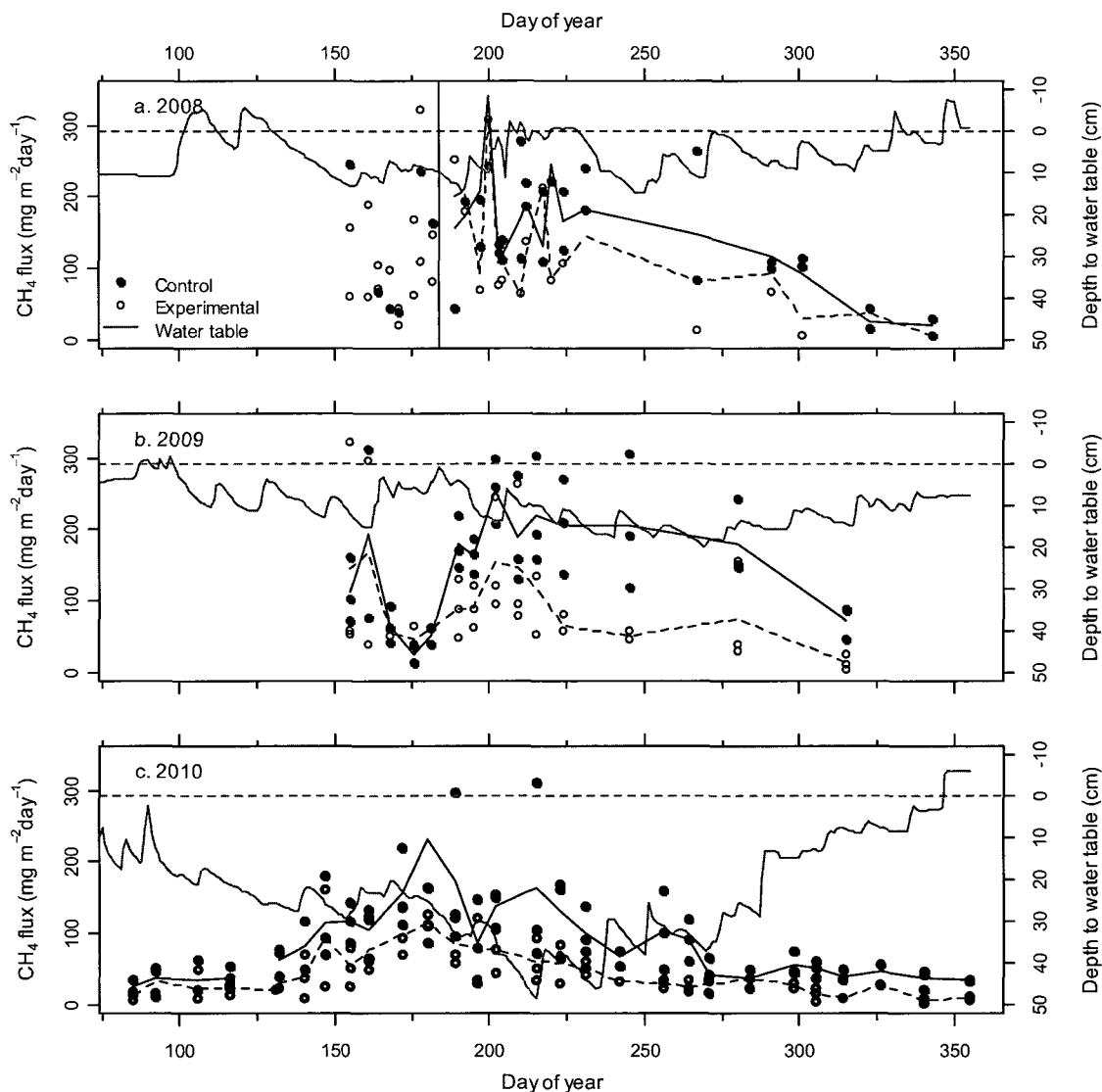


**Figure 1.** Map of Sallie's Fen showing the placement of the six plots used in this study (dots), as well as the meteorological station (triangle).

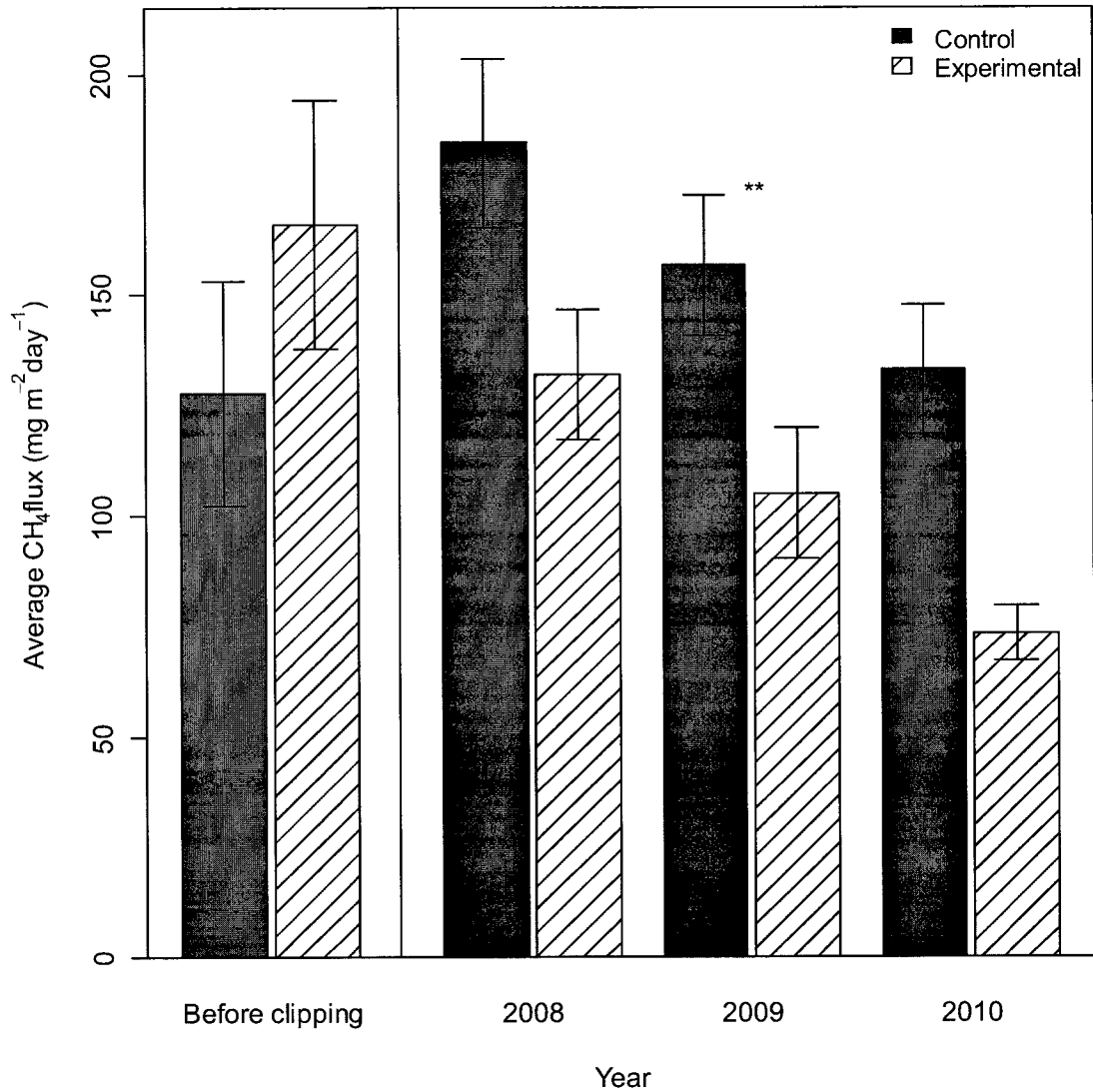




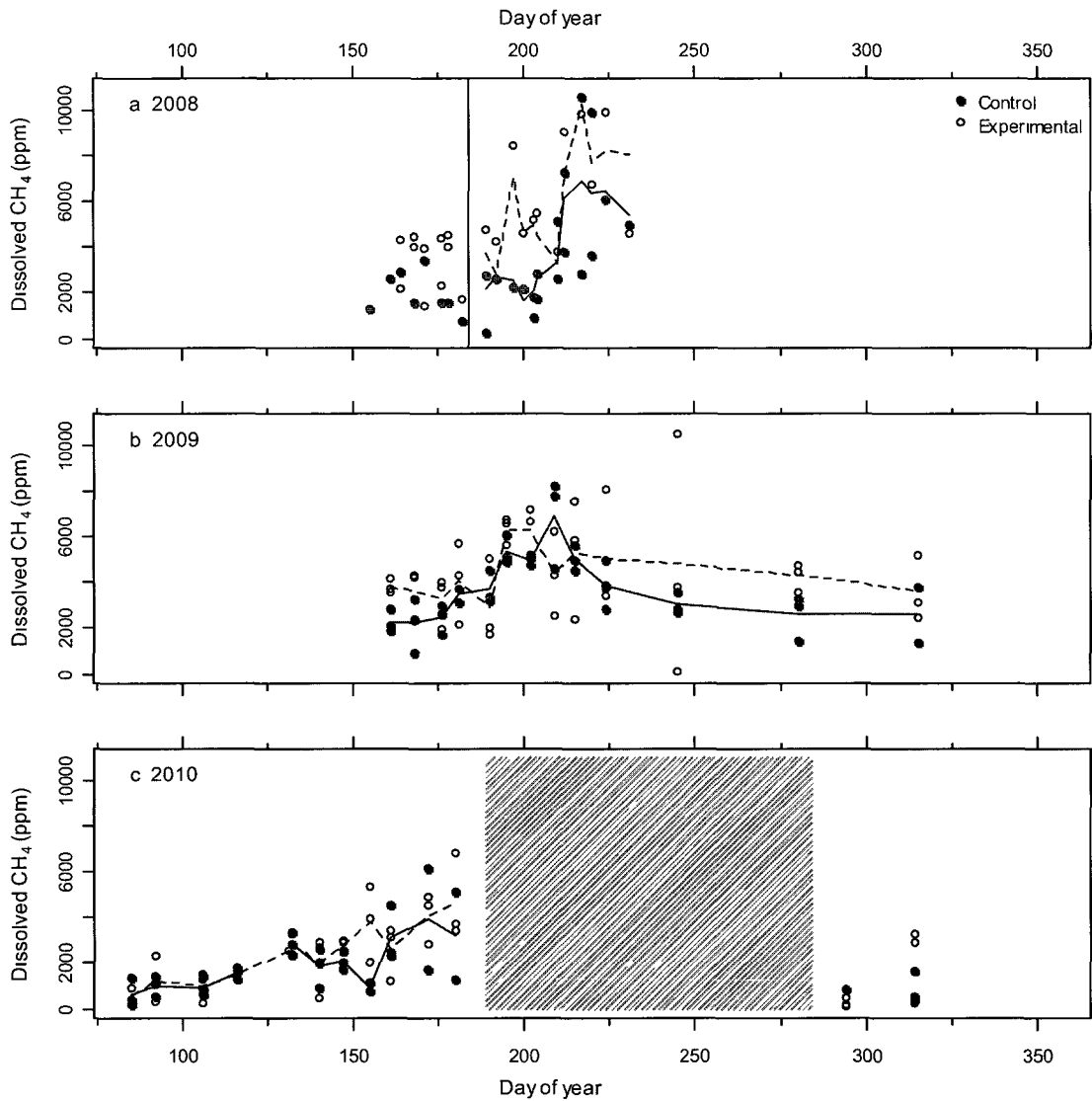
**Figure 2.** Time series of daily mean water-table depth (black) and air temperature (grey) in 2008 (a), 2009 (b), and 2010 (c). The shaded area indicates the approximate depth of the majority of *C. rostrata* roots (15-20 cm). The dotted line indicates the peat surface.



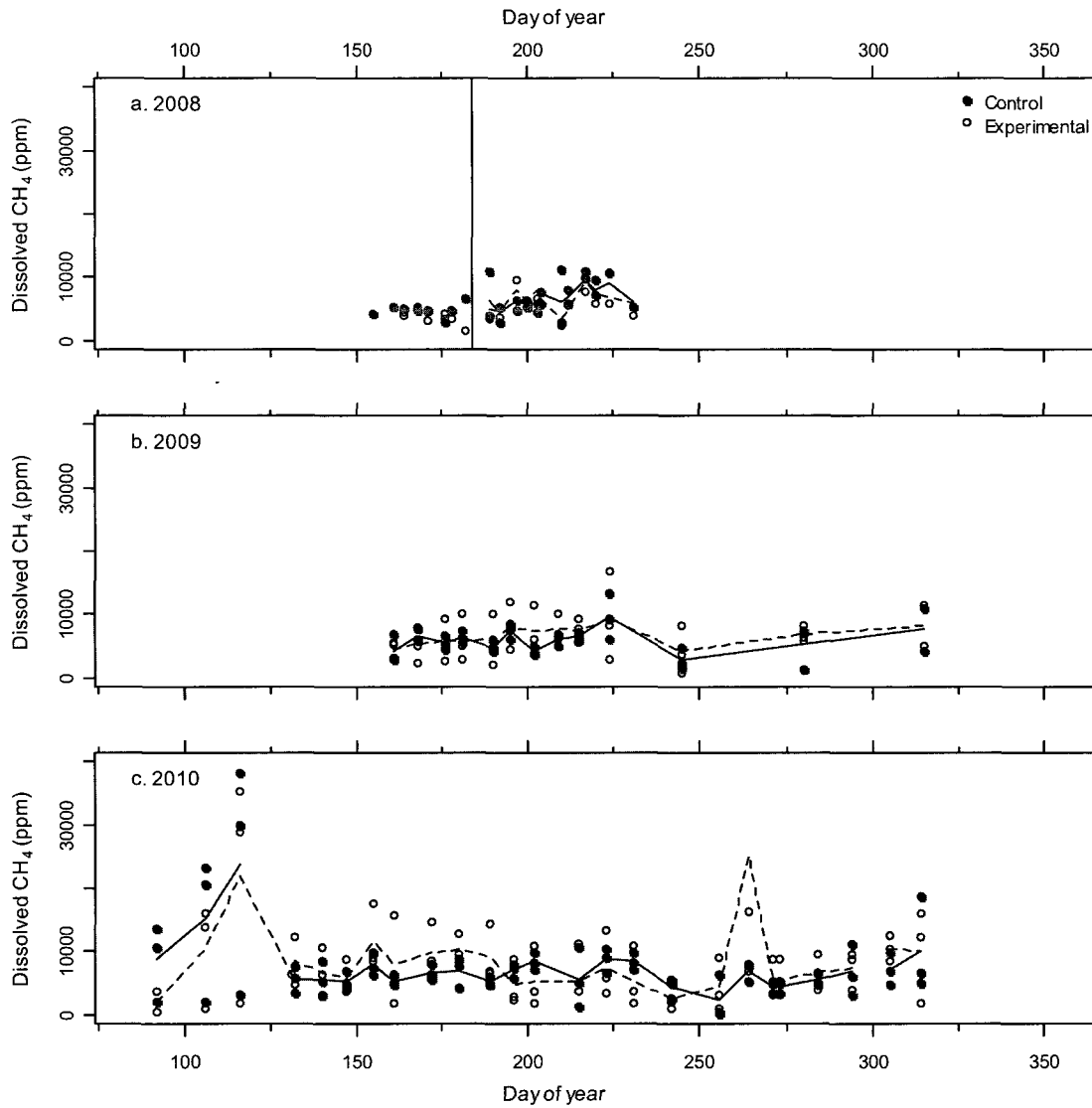
**Figure 3.** Time series of all CH<sub>4</sub> fluxes (black) and mean daily water-table depth (grey) in 2008 (a), 2009 (b), and 2010 (c) including daily CH<sub>4</sub> fluxes from all six plots (points) and daily mean CH<sub>4</sub> flux per treatment (lines). Solid circles and lines indicate the control plots; open circles and dashed lines indicate the experimental plots. The vertical line in (a) divides the calibration period from the implementation of the clipping experiment. The dotted line indicates the peat surface.



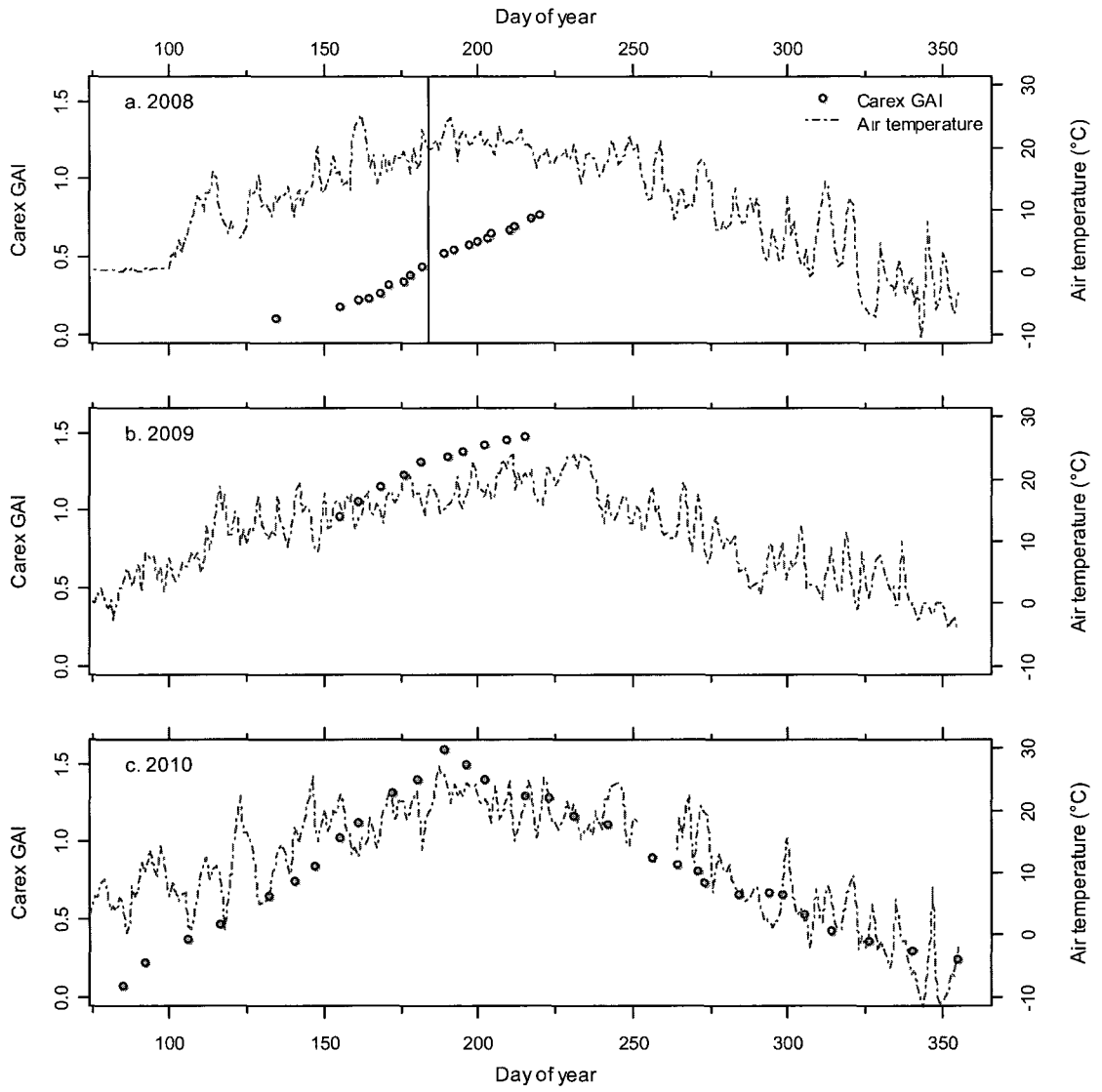
**Figure 4.** Mean summer CH<sub>4</sub> flux for control (solid) and experimental (striped) plots. Averages were calculated per collar and then averaged together by treatment. Grey bars are mean CH<sub>4</sub> flux in June 2008, before the clipping experiment was implemented. 2008 means include July and August; 2009 and 2010 means include June through August. Stars indicate significant differences between treatments, using an n of 3 (\* p<0.10; \*\* p<0.05; \*\*\* p<0.01).



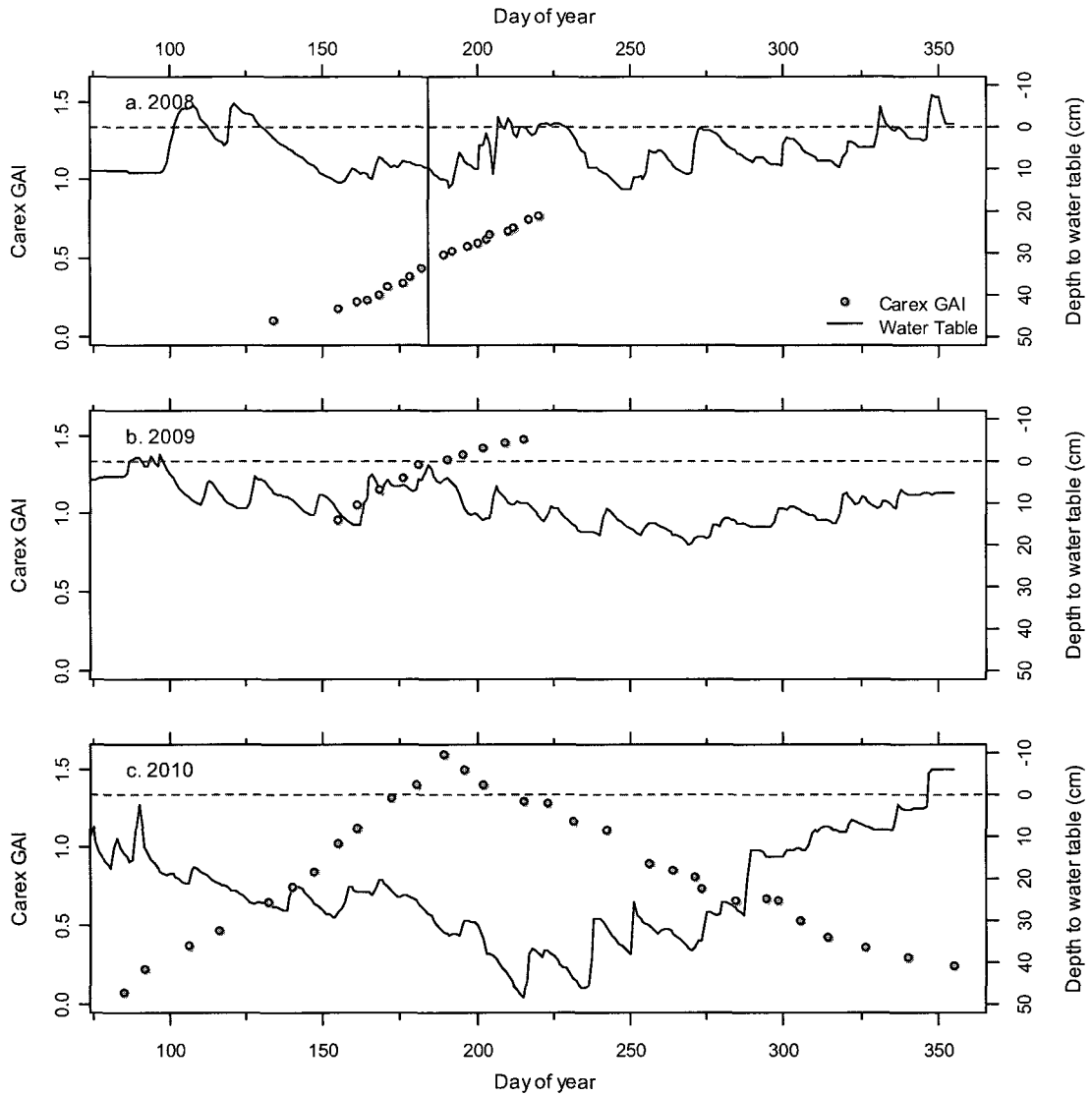
**Figure 5.** Time series of all dissolved CH<sub>4</sub> concentrations at 18 cm below the peat surface in 2008 (a), 2009 (b), and 2010 (c) including daily measured CH<sub>4</sub> concentrations from all six plots (points) and daily mean dissolved CH<sub>4</sub> concentrations per treatment (lines). Solid circles and lines indicate the control plots; open circles and dashed lines indicate the experimental plots. The vertical line in (a) divides the calibration period from the implementation of the clipping experiment. The shaded area in (c) indicates the portion of summer 2010 when the water table was too low to collect 18 cm porewater.



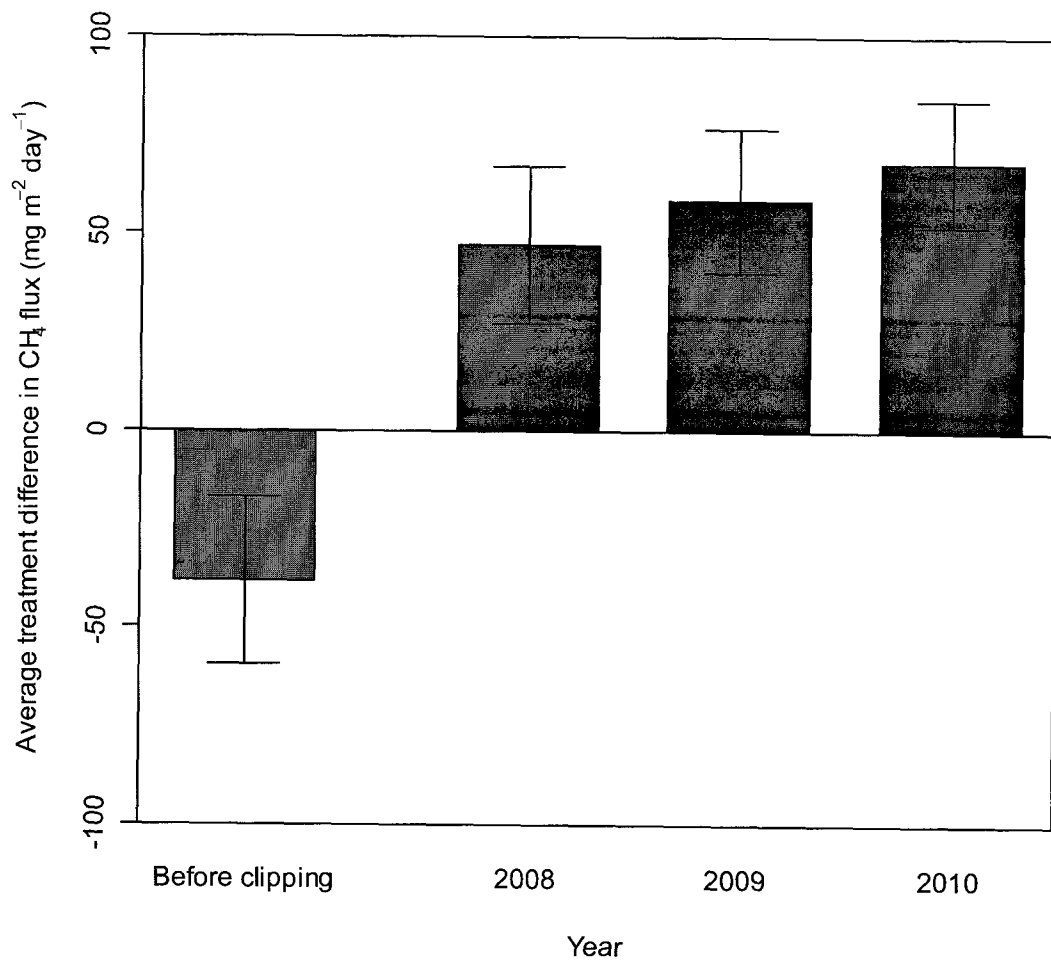
**Figure 6.** Time series of all dissolved CH<sub>4</sub> concentrations at 60 cm below the peat surface in 2008 (a), 2009 (b), and 2010 (c) including daily measured CH<sub>4</sub> concentrations from all six plots (points) and daily mean dissolved CH<sub>4</sub> concentrations per treatment (lines). Solid circles and lines indicate the control plots; open circles and dashed lines indicate the experimental plots. The vertical line in (a) divides the calibration period from the implementation of the clipping experiment.



**Figure 7.** Time series of mean *C. rostrata* Green Area Index (GAI) for control plots (points) and mean daily air temperature (dashed line) in 2008 (a), 2009 (b), and 2010 (c).

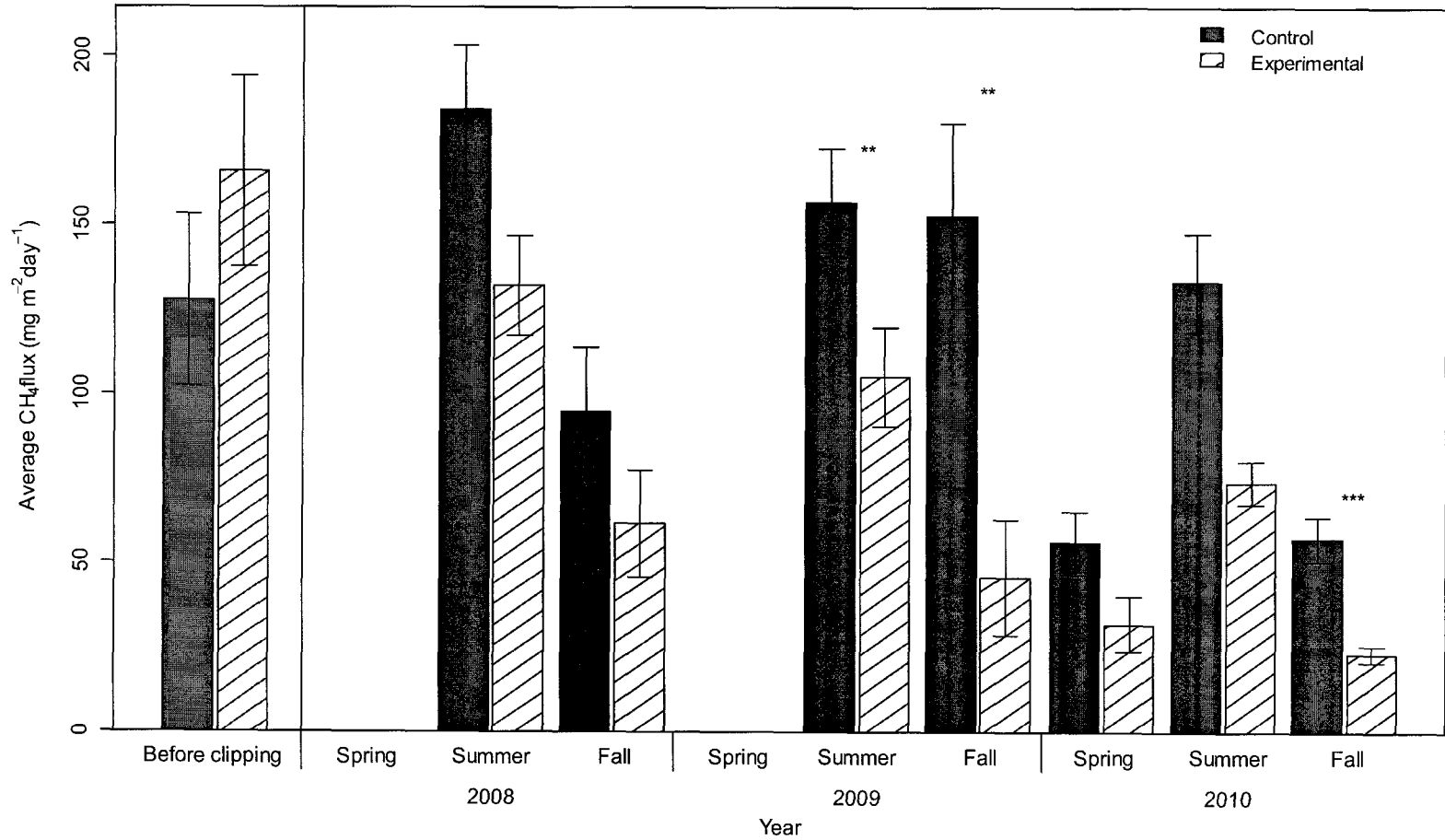


**Figure 8.** Time series of mean *C. rostrata* Green Area Index (GAI) for control plots (points) and mean daily water-table depth (line) in 2008 (a), 2009 (b), and 2010 (c). The dotted line indicates the peat surface.

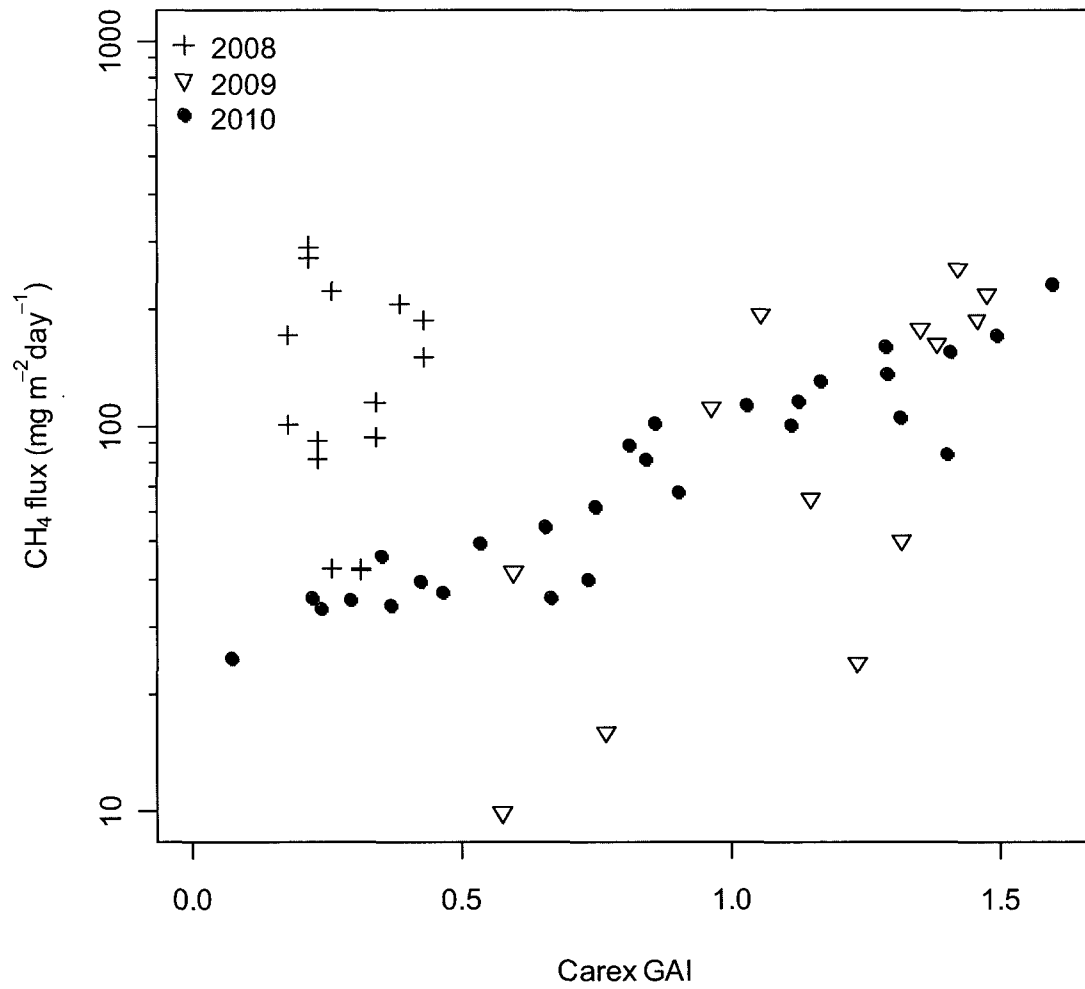


**Figure 9.** Mean difference in summer CH<sub>4</sub> flux between control and experimental plots in 2008, 2009, and 2010. The light grey bar is the difference between designated control and experimental plots in June 2008, before the clipping experiment was implemented. Positive numbers indicate larger fluxes from the control plots. Error bars indicate standard error.

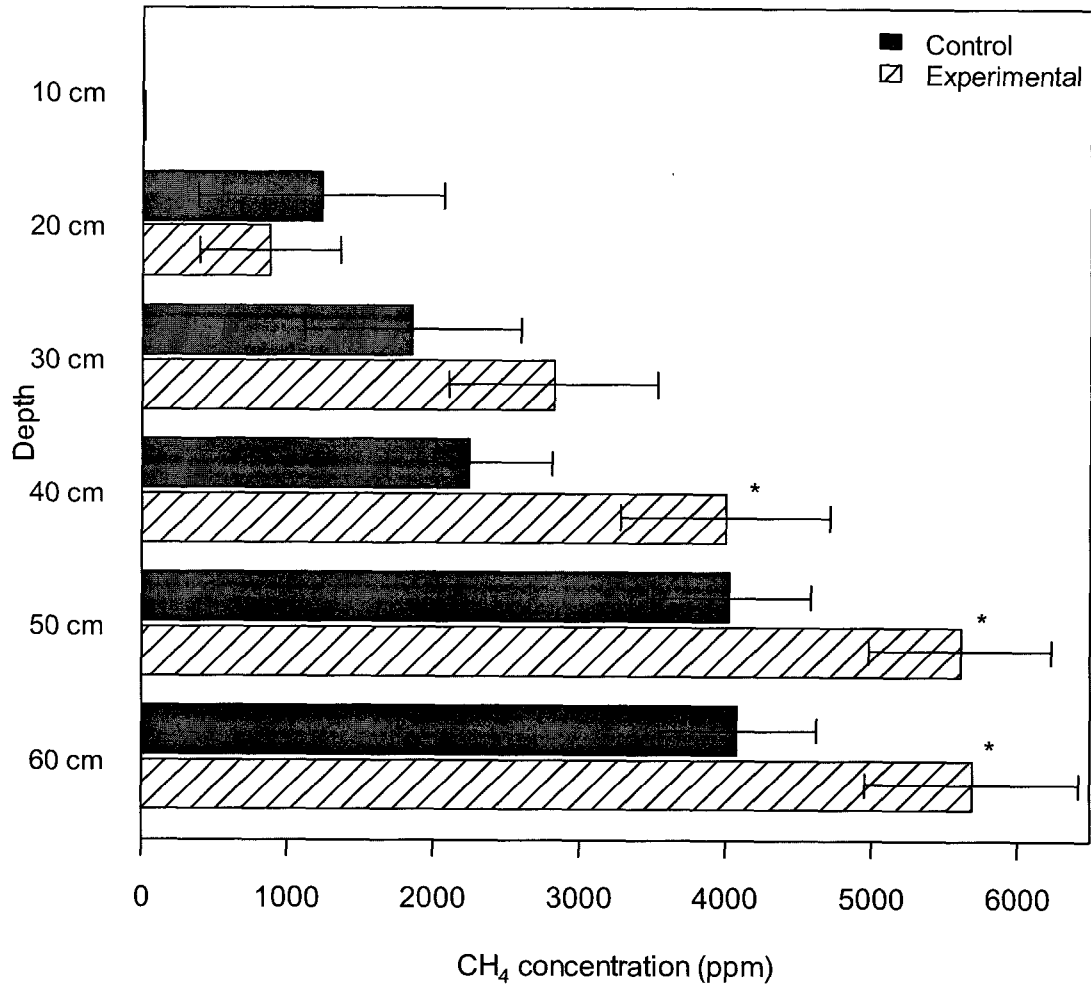




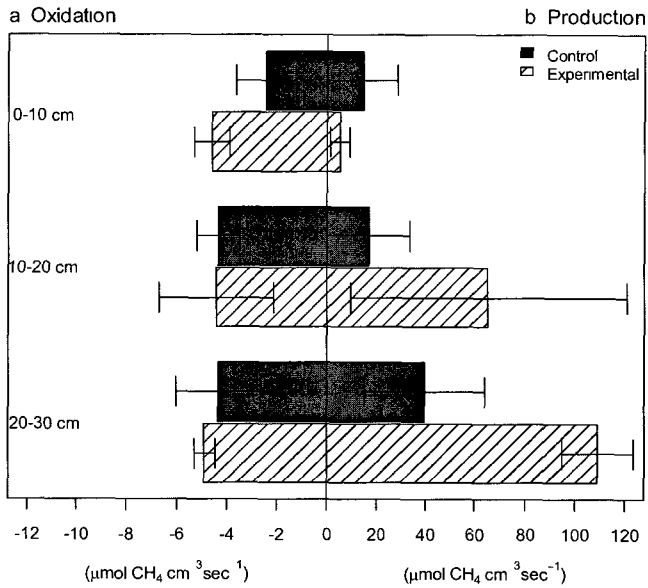
**Figure 10.** Mean seasonal CH<sub>4</sub> flux for control (solid) and experiment (striped) plots. Seasonal averages were calculated per collar and then averaged together by treatment. Light grey bars are mean CH<sub>4</sub> flux in June 2008, before the clipping experiment was implemented. Spring means include March through May, summer means include June through August, and fall means include September through November. Stars indicate significant differences between treatments, using an n of 3 (\* p<0.10; \*\* p<0.05; \*\*\* p<0.01).



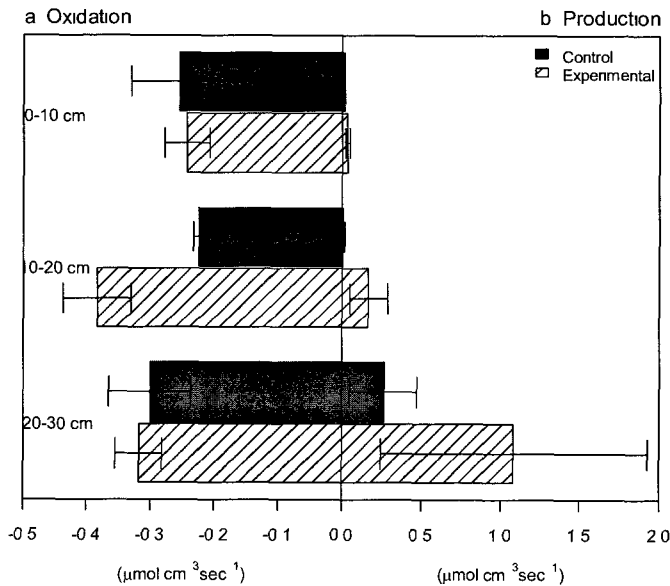
**Figure 11.** Correlation between *C. rostrata* Green Area Index (GAI) and daily mean CH<sub>4</sub> flux (plotted on log scale) for control plots in 2008 (crosses;  $r = 0.45$ ), 2009 (triangles;  $r = 0.33$ ), and 2010 (dots;  $r = 0.94$ ).



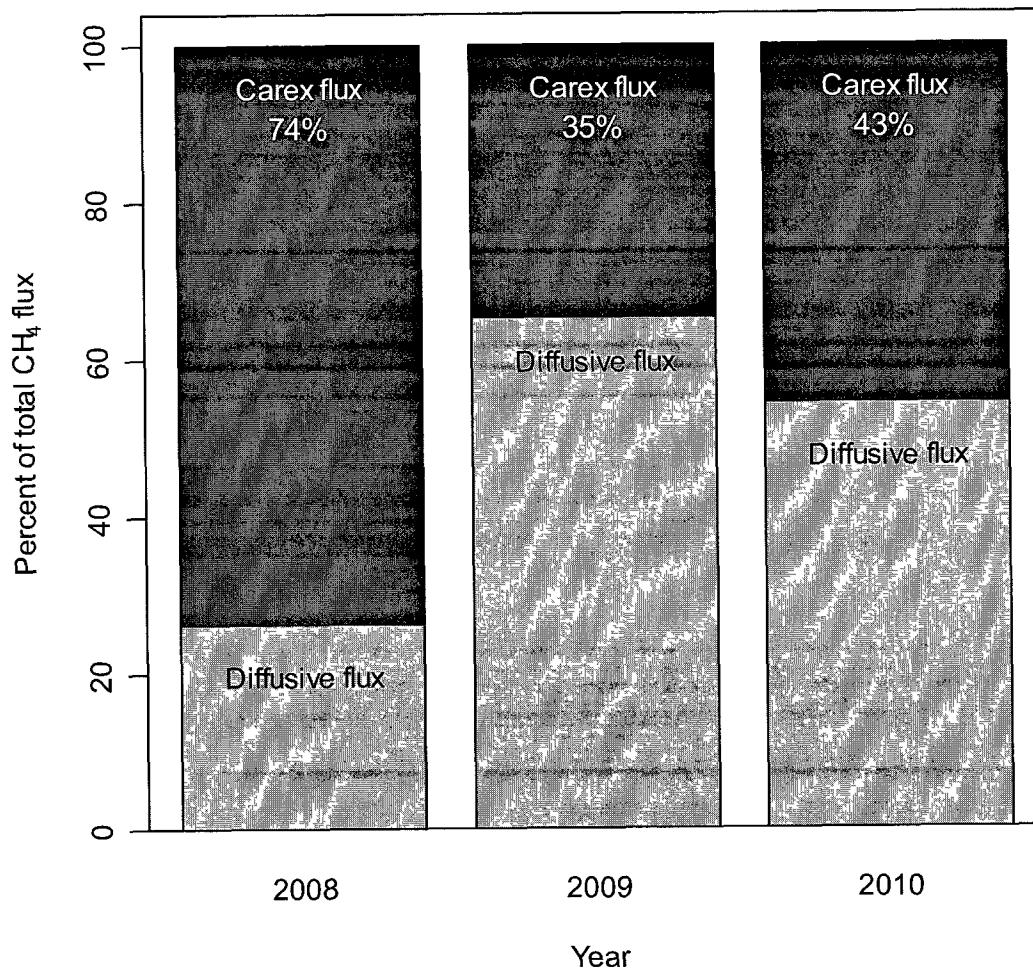
**Figure 12.** Mean concentrations of CH<sub>4</sub> at 10 to 60 cm below the peat surface during summer 2010 in control (solid) and experimental (striped) plots. Error bars indicate standard error. The mean water-table depth during this period was 32.8 cm below the peat surface. All 10 and 20 cm samples were taken from unsaturated peat, 30 and 40 cm samples were taken from both unsaturated and saturated peat, depending on the day's water-table depth, and 50 and 60 cm samples were always below the water table. Stars indicate significant differences between treatments.



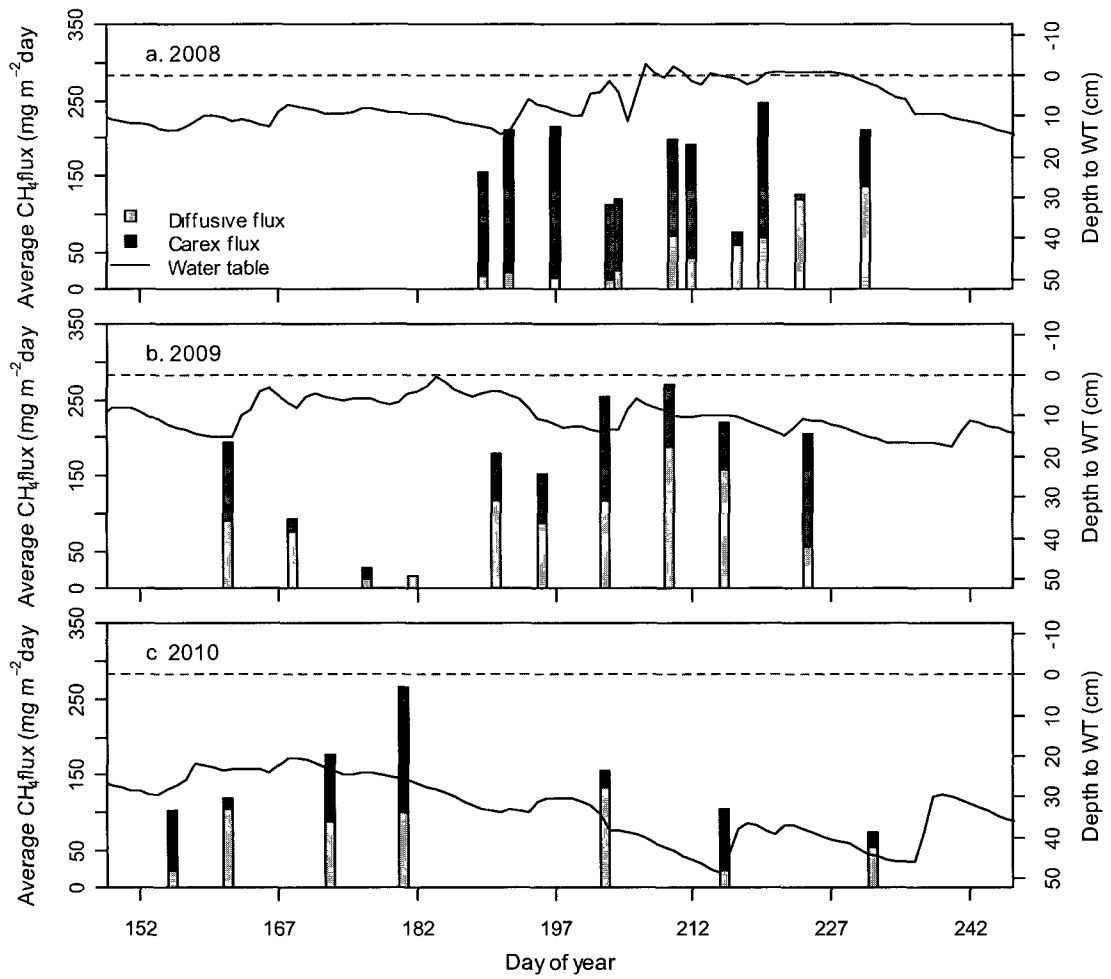
**Figure 13.** Measured potential  $\text{CH}_4$  oxidation (a) and potential  $\text{CH}_4$  production (b) at three depths in control (solid) and experimental (striped) plots from cores collected on June 28, 2010. Error bars indicate standard error. Due to higher rates of production than oxidation, the scale for (b) is ten times larger than the scale for (a).



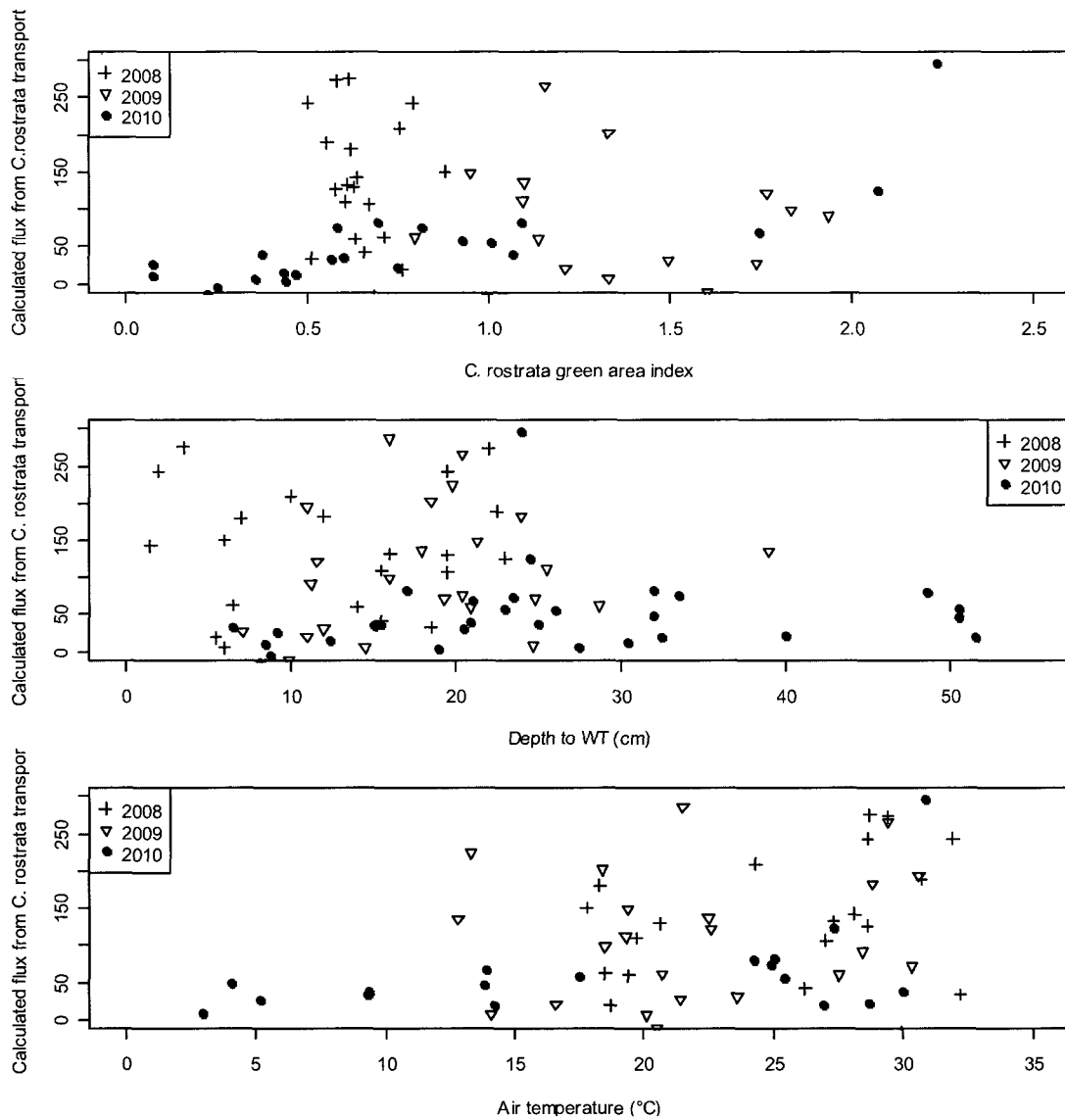
**Figure 14.** Measured potential  $\text{CH}_4$  oxidation (a) and potential  $\text{CH}_4$  production (b) at three depths in control (solid) and experimental (striped) plots from cores collected on July 27, 2010. Error bars indicate standard error. Due to higher rates of production than oxidation, the scale for (b) is four times larger than the scale for (a).



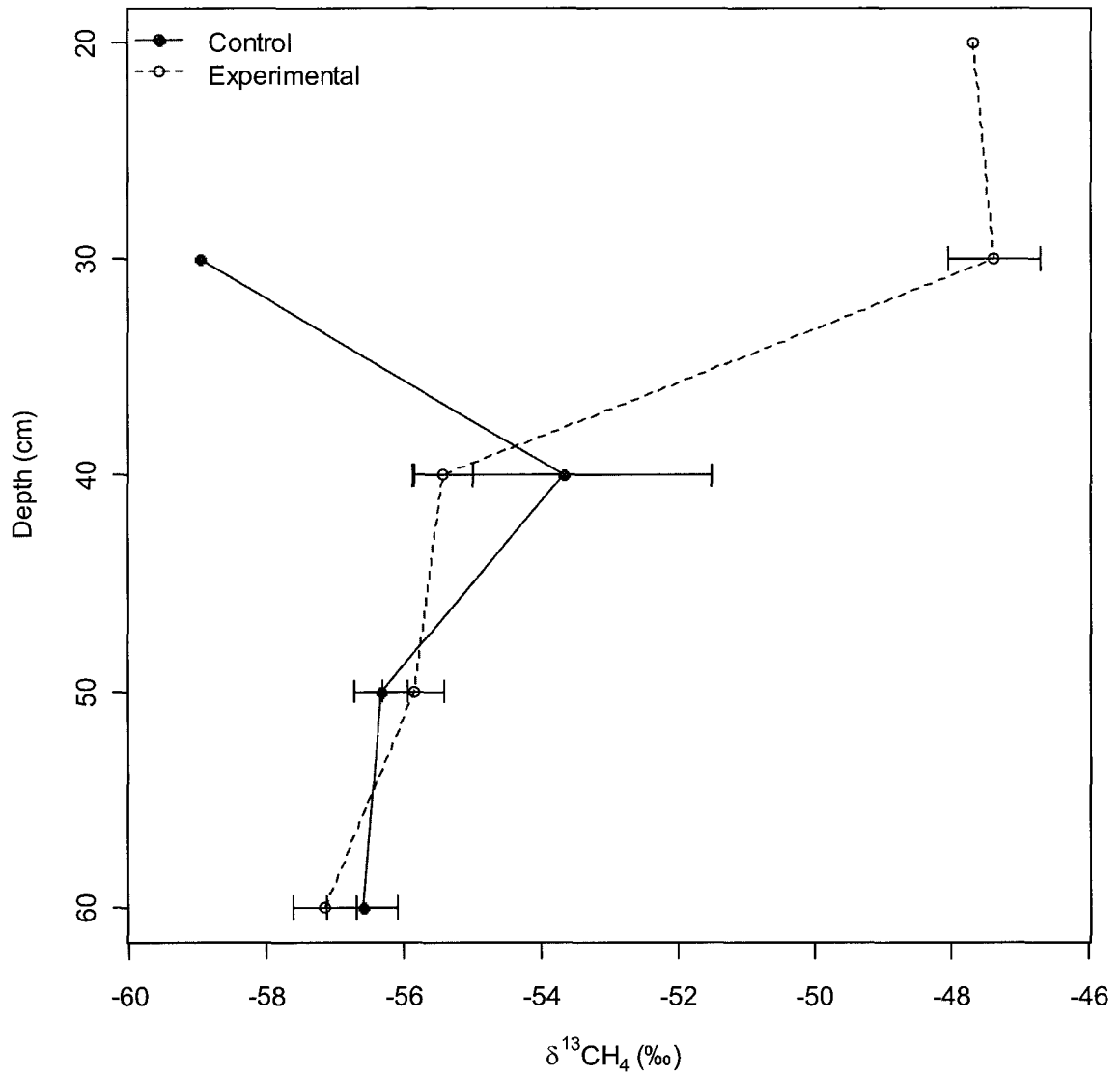
**Figure 15.** Mean percent of total measured CH<sub>4</sub> flux from control plots estimated to have been emitted through *C. rostrata* transport (dark grey) compared to diffusion (light grey) for 2008, 2009, and 2010. Data included in the mean are only from the summer months (June, July, and August).



**Figure 16.** Mean daily  $\text{CH}_4$  fluxes from control plots in summer 2008 (a), 2009 (b), and 2010 (c) shown as the sum of estimated diffusive  $\text{CH}_4$  flux (light grey) and estimated  $\text{CH}_4$  emitted through plant transport (dark grey). The black line indicates daily water-table depth; the dotted line indicates the peat surface.



**Figure 17.** Scatterplots of the estimated amount of CH<sub>4</sub> emitted through *C. rostrata* transport and *C. rostrata* green area (top), depth to water table (middle), and air temperature (bottom) in 2008 (crosses), 2009 (triangles), and 2010 (dots). Across all three years, *C. rostrata* flux is only significantly correlated with air temperature ( $r = 0.41$ ,  $p = 0.001$ ).



**Figure 18.** Mean dissolved  $\text{CH}_4$   $^{13}\text{C}$  signatures at 20-60 cm below the peat surface in control (solid) and experimental (dashed) plots.. Samples were collected between 23 July and 21 October, 2010. Error bars indicate standard error for depths with more than one measurement.



## TABLES

**Table 1.** Summary of daily air temperature and water-table depth in 2008, 2009, and 2010.

		<b>Year</b>		
		2008	2009	2010
<b>Air temperature (°C)</b>				
Spring	Minimum	-0.5	-2.8	0.0
	Mean	6.0	7.5	4.7
	Maximum	20.3	19.7	25.9
Summer	Minimum	13.3	12.0	12.7
	Mean	19.3	18.4	20.0
	Maximum	25.2	24.0	27.4
Fall	Minimum	-7.3	-0.9	-5.3
	Mean	8.6	8.4	8.1
	Maximum	22.1	19.4	24.4
<b>Depth to water table (cm)</b>				
Spring	Minimum	1.9	2.2	2.4
	Mean	13.0	9.9	19.7
	Maximum	19.9	16.8	28.3
Summer	Minimum	5.1	4.5	20.3
	Mean	14.5	14.0	32.8
	Maximum	21.9	21.5	48.5
Fall	Minimum	2.6	11.5	-6.1
	Mean	14.2	18.0	16.9
	Maximum	22.6	23.8	38.0

**Table 2.** T-test results comparing treatment means of CH<sub>4</sub> measurements, *C. rostrata* green area index, and environmental variables in 2008, 2009, and 2010. 2008 data are only after clipping. Means were calculated per collar and then per treatment.

Measurement		t	df	Sig.
CH <sub>4</sub> flux	2008	2.065	4	0.108
	2009	3.089	4	0.037
	2010	2.262	4	0.087
18 cm porewater CH <sub>4</sub>	2008	-2.283	4	0.085
	2009	-1.013	4	0.368
	2010	-0.853	4	0.442
60 cm porewater CH <sub>4</sub>	2008	0.579	4	0.594
	2009	-0.435	4	0.686
	2010	-0.390	4	0.717
<i>C. rostrata</i> GAI	2008	27.201	4	<0.001
	2009	6.782	4	0.002
	2010	3.615	4	0.023
Water-table depth	2008	0.228	4	0.831
	2009	1.924	4	0.127
	2010	1.660	4	0.172
10 cm temperature	2008	0.884	4	0.426
	2009	-0.500	4	0.643
	2010	0.520	4	0.630

**Table 3.** Average peak *C. rostrata* biomass in control collars in 2008, 2009, and 2010.

Year	Date	Biomass (g m <sup>-2</sup> )
2008	7 Aug	96.3
2009	3 Aug	171.9
2010	8 Jul	184.7

**Table 4.** T-test results comparing treatment means of CH<sub>4</sub> flux, by season. 2008 data are only after clipping. Means were calculated per collar and then per treatment.

Year	Season	t	df	Sig.
2008	Spring			
	Summer	2.018	4	0.114
	Fall	1.496	4	0.209
2009	Spring			
	Summer	2.885	4	0.045
	Fall	2.83	4	0.047
2010	Spring	1.644	4	0.176
	Summer	1.683	4	0.168
	Fall	5.024	4	0.007

**Table 5.** Correlation coefficients among CH<sub>4</sub> measurements, *C. rostrata* green area, and environmental variables across all three years. Italics indicates significance at  $\alpha = 0.05$ ; bold indicates significance at  $\alpha = 0.01$ .

	lnCH <sub>4</sub> Flux	18cm CH <sub>4</sub>	60cm CH <sub>4</sub>	Carex GAI	Water Table	Air Temp	10cm Temp
All plots							
ln CH <sub>4</sub> Flux	1	<b>0.353</b>	<b>-0.156</b>	<b>0.360</b>	-0.085	<b>0.569</b>	<b>0.465</b>
18cm CH <sub>4</sub>		1	-0.069	-0.021	<b>-0.333</b>	0.100	0.030
60cm CH <sub>4</sub>			1	-0.106	-0.007	-0.051	-0.026
Control plots only (after clipping only)							
ln CH <sub>4</sub> Flux	1	<b>0.537</b>	<b>-0.192</b>	<b>0.467</b>	<b>-0.166</b>	<b>0.635</b>	<b>0.466</b>
18cm CH <sub>4</sub>		1	-0.121	<b>0.491</b>	<b>-0.349</b>	<b>0.250</b>	0.100
60cm CH <sub>4</sub>			1	-0.194	-0.191	0.101	0.002
Experimental plots only (after clipping only)							
ln CH <sub>4</sub> Flux	1	<b>0.423</b>	-0.114	---	-0.124	<b>0.684</b>	<b>0.520</b>
18cm CH <sub>4</sub>		1	-0.117	---	<b>-0.295</b>	0.271	-0.023
60cm CH <sub>4</sub>			1	---	0.107	-0.088	-0.046
Calculated fluxes							
Total <i>C. rostrata</i> flux		<b>0.0319</b>	-0.248	0.211	-0.187	<b>0.410</b>	0.033
Percent <i>C. rostrata</i> flux		-0.133	-0.196	<b>-0.307</b>	0.011	0.030	-0.155

**Table 6.** Summary of final models from multiple linear regressions of ln CH<sub>4</sub> flux, 18 cm dissolved CH<sub>4</sub>, and *C. rostrata* GAI, using data from control plots only. Numbers refer to model coefficients. Italics indicate significance at  $\alpha = 0.05$ ; bold indicates significance at  $\alpha = 0.01$ .

	$\beta_0$	Carex GAI	Water Table	Air Temp.	10 cm Temp.	R <sup>2</sup>	Model Sig.
ln CH <sub>4</sub> flux	<b>3.595</b>	<b>0.341</b>	-0.012	<b>0.033</b>	0.016	0.346	<0.001
18 cm CH <sub>4</sub>	<b>3.260</b>	<b>1629</b>	73.4			0.204	<0.001
<i>C. rostrata</i> GAI	0.305		0.007	<b>0.016</b>		0.097	<0.001

## APPENDIX

Year	Day	Collar	Treatment	CH <sub>4</sub> flux (mg m <sup>-2</sup> day <sup>-1</sup> )	Temperature (°C) Air 10cm	Depth to water table (cm)	<i>C. rostrata</i> GAI (m <sup>2</sup> m <sup>-2</sup> )	Porewater CH <sub>4</sub> (ppm) 18 cm	Porewater CH <sub>4</sub> (ppm) 60cm
2008	134	LG 1	Before clipping				0.200		
2008	134	LG 2	Before clipping				0.144		
2008	134	LG 3	Before clipping				0.237		
2008	134	LG 4	Before clipping				0.075		
2008	134	LG 5	Before clipping				0.094		
2008	134	LG 6	Before clipping				0.406		
2008	155	LG 1	Before clipping	61.1	27.3	13.0			
2008	155	LG 2	Before clipping	47.6	23.6	13.0			
2008	155	LG 3	Before clipping	156.8	22.9	12.0			
2008	155	LG 4	Before clipping	9.7	24.8	16.5			
2008	155	LG 5	Before clipping	245.8	24.9	14.4		1307	4164
2008	155	LG 6	Before clipping	300.0	21.6	18.7			
2008	161	LG 1	Before clipping	60.4	31.6	21.5			
2008	161	LG 2	Before clipping	109.9	31.0	25.3			
2008	161	LG 3	Before clipping	189.1	37.0	20.0			
2008	161	LG 4	Before clipping	186.1	30.7	23.8			
2008	161	LG 5	Before clipping	580.0	27.2	22.0		2632	5266
2008	161	LG 6	Before clipping	563.6	28.1	24.1			
2008	164	LG 1	Before clipping	72.6	24.0	18.8	0.377	4329	3952
2008	164	LG 2	Before clipping	90.5	27.6	17.7	0.195	2004	4199
2008	164	LG 3	Before clipping	103.6	25.4	18.8	0.487	2158	4339
2008	164	LG 4	Before clipping	90.1	25.8	17.3	0.229	3961	5134
2008	164	LG 5	Before clipping	66.0	27.2	20.0	0.277	2884	4968
2008	164	LG 6	Before clipping	97.9	26.7	19.0	0.865	4165	5715
2008	168	LG 1	Before clipping	406.5	16.9	14.1		4492	5295
2008	168	LG 2	Before clipping	25.2	15.1	15.3		1583	3089
2008	168	LG 3	Before clipping	97.4	24.1	15.8		4045	5027
2008	168	LG 4	Before clipping	59.8	24.1	16.7		4955	4909
2008	168	LG 5	Before clipping	42.8	27.5	15.0		1609	4774
2008	168	LG 6	Before clipping	166.1	86.0	20.0		1100	4958
2008	171	LG 1	Before clipping	43.7	21.6	14.0		3944	4541
2008	171	LG 2	Before clipping	64.8	21.4	15.4		3520	3779

Year	Day	Collar	Treatment	CH <sub>4</sub> flux (mg m <sup>-2</sup> day <sup>-1</sup> )	Temperature (°C)		Depth to water table (cm)	<i>C. rostrata</i> GAI (m <sup>2</sup> m <sup>-2</sup> )	Porewater CH <sub>4</sub> (ppm)	
					Air	10cm			18 cm	60cm
2008	171	LG 3	Before clipping	19.3	24.1	15.5	11.5		4045	5027
2008	171	LG 4	Before clipping	23.2	27.7	16.3	14.0		4955	4909
2008	171	LG 5	Before clipping	40.0	29.8	18.1	13.5		1609	4774
2008	171	LG 6	Before clipping	63.4	30.6	16.0	17.0		1100	4958
2008	176	LG 1	Before clipping	61.6	24.1	16.6	15.5	0.491	3944	4541
2008	176	LG 2	Before clipping	156.7	24.2	20.2	18.0	0.341	3520	3779
2008	176	LG 3	Before clipping	169.1	30.2	17.0	11.5	0.550	1458	3035
2008	176	LG 4	Before clipping	30.1	25.9	19.4	13.5	0.342	4034	4632
2008	176	LG 5	Before clipping		26.4	16.9	13.5	0.343	3445	4658
2008	176	LG 6	Before clipping		25.4	17.2	20.0	1.028	2487	4761
2008	178	LG 1	Before clipping	108.3	22.8	15.1	16.5		4408	4175
2008	178	LG 2	Before clipping	147.8	20.7	16.8	18.0		2720	4117
2008	178	LG 3	Before clipping	323.1	19.9	15.7	10.5		2319	3302
2008	178	LG 4	Before clipping	234.2	21.1	18.2	14.5		857	4393
2008	178	LG 5	Before clipping	237.1	19.8	17.4	14.5		1583	2720
2008	178	LG 6	Before clipping	191.4	19.7	17.4	18.5		602	4542
2008	182	LG 1	Before clipping	80.2	27.2	19.9	16.5		4564	4550
2008	182	LG 2	Before clipping	142.5	26.3	19.9	18.5		4457	4300
2008	182	LG 3	Before clipping	147.5	26.6	17.0	11.0		4023	3391
2008	182	LG 4	Before clipping	145.9	31.9	22.5	14.5		4511	4334
2008	182	LG 5	Before clipping	162.6	30.0	22.3	15.5		1583	4722
2008	182	LG 6	Before clipping	333.9	27.6	17.7	16.0		1551	5137
2008	171	LG 3	Before clipping	19.3	24.1	15.5	11.5			
2008	171	LG 4	Before clipping	23.2	27.7	16.3	14.0			3526
2008	171	LG 5	Before clipping	40.0	29.8	18.1	13.5		1760	1495
2008	171	LG 6	Before clipping	63.4	30.6	16.0	17.0			
2008	176	LG 1	Before clipping	61.6	24.1	16.6	15.5	0.491	802	6670
2008	176	LG 2	Before clipping	156.7	24.2	20.2	18.0	0.341		
2008	189	LG 1	Experimental		27.2	21.4	21.0		2997	4145
2008	189	LG 2	Control		30.2	18.2	23.0	0.545	2754	3821
2008	189	LG 3	Experimental	149.1	29.1	19.6	16.0		4767	3264
2008	189	LG 4	Control	44.2	32.2	23.3	18.5	0.513	3492	4138

Year	Day	Collar	Treatment	CH <sub>4</sub> flux (mg m <sup>-2</sup> day <sup>-1</sup> )	Temperature (°C)		Depth to water table (cm)	<i>C. rostrata</i> GAI (m <sup>2</sup> m <sup>-2</sup> )	Porewater CH <sub>4</sub> (ppm)	
					Air	10cm			18 cm	60cm
2008	189	LG 5	Control	268.2	31.9	20.9	19.5	0.502	255	10795
2008	189	LG 6	Experimental	251.7	32.2	21.9	21.5		3456	7252
2008	192	LG 1	Experimental	55.0	25.3	20.4	20.5		480	4444
2008	192	LG 2	Control	194.6	30.7	19.7	22.5		2637	2794
2008	192	LG 3	Experimental	389.7	26.3	19.6	16.0		4251	3644
2008	192	LG 4	Control		26.6	21.2	18.0		2684	5339
2008	192	LG 5	Control	151.4	27.1	24.0	19.5			5109
2008	192	LG 6	Experimental	180.7	27.1	22.3	21.0		3895	5649
2008	197	LG 1	Experimental	99.7	26.3	18.6	24.5		6978	6249
2008	197	LG 2	Control	196.7	27.9	19.3	26.0			4732
2008	197	LG 3	Experimental	110.5	28.8	18.4	20.5		8447	9425
2008	197	LG 4	Control	130.1	28.6	18.9	23.0		2893	8276
2008	197	LG 5	Control	300.4	29.4	19.5	22.0		2254	6311
2008	197	LG 6	Experimental	68.5	28.1	18.6	25.5		5649	8245
2008	200	LG 1	Experimental		28.6	17.8	27.0			6460
2008	200	LG 2	Control	686.7	28.2	19.3	29.0	0.586		5211
2008	200	LG 3	Experimental		28.4	18.4	23.0		4621	6376
2008	200	LG 4	Control	242.1	30.4	21.5	26.5	0.599	1134	5635
2008	200	LG 5	Control	93.5	31.9	20.5	24.5	0.604	2148	6103
2008	200	LG 6	Experimental	309.0	33.0	21.6	27.5			6005
2008	203	LG 1	Experimental	90.1	20.9	18.6	17.0		7114	8628
2008	203	LG 2	Control	131.8	20.6	23.5	19.5		1845	5710
2008	203	LG 3	Experimental	153.8	20.4	18.9	13.5		5170	6668
2008	203	LG 4	Control	120.0	19.7	19.9	15.5		3459	7298
2008	203	LG 5	Control	85.6	19.4	19.7	14.0		904	4530
2008	203	LG 6	Experimental	75.9	19.6	19.0	18.5		2679	8820
2008	204	LG 1	Experimental	98.2			17.5		5906	7310
2008	204	LG 2	Control	111.1			19.5		2862	5828
2008	204	LG 3	Experimental	145.0			13.5		5477	5627
2008	204	LG 4	Control	140.6			16.0		3188	8445
2008	204	LG 5	Control	106.1			15.5		1768	7782
2008	204	LG 6	Experimental	84.4			19.0		2323	

Year	Day	Collar	Treatment	CH <sub>4</sub> flux (mg m <sup>-2</sup> day <sup>-1</sup> )	Temperature (°C)		Depth to water table (cm)	<i>C. rostrata</i> GAI (m <sup>2</sup> m <sup>-2</sup> )	Porewater CH <sub>4</sub> (ppm)	
					Air	10cm			18 cm	60cm
2008	210	LG 1	Experimental		23.7	17.4	4.0		3684	3740
2008	210	LG 2	Control	113.4	23.5	17.9	6.0		2654	2882
2008	210	LG 3	Experimental	57.2	25.7	18.3	0.5		3808	2372
2008	210	LG 4	Control	278.7	27.0	18.5	3.5		2273	4020
2008	210	LG 5	Control	118.3	27.3	18.9	8.5		5130	11060
2008	210	LG 6	Experimental	65.1	28.1	18.8	6.0		2459	4185
2008	212	LG 1	Experimental	114.3	27.1	17.1	8.5		7489	8880
2008	212	LG 2	Control	220.4	26.2	16.8	10.0		7275	5792
2008	212	LG 3	Experimental	91.4	31.5	17.9	5.0		9066	5621
2008	212	LG 4	Control	187.9	28.7	20.0	7.0		7511	6721
2008	212	LG 5	Control	165.0	29.9	19.5	6.5		3778	7796
2008	212	LG 6	Experimental	138.0	30.0	19.2	10.0		5069	21
2008	217	LG 1	Experimental		24.8	17.3	8.0		10710	11005
2008	217	LG 2	Control	208.0	20.9	18.2	10.0		10625	9720
2008	217	LG 3	Experimental		27.3	17.8	4.0		9839	7702
2008	217	LG 4	Control	109.3	24.5	19.0	6.5		7244	7835
2008	217	LG 5	Control	76.5	24.3	19.5	5.5		2814	10841
2008	217	LG 6	Experimental	213.4	24.7	18.5	9.5		10403	8967
2008	220	LG 1	Experimental	77.2	19.1	16.8	5.0		10479	10401
2008	220	LG 2	Control	223.0	18.3	17.0	6.0	0.880	9899	7116
2008	220	LG 3	Experimental	94.5	18.0	17.0	-0.5		6762	5899
2008	220	LG 4	Control	221.2	18.5	17.6	1.5	0.636	5667	6902
2008	220	LG 5	Control	295.2	18.7	17.7	2.0	0.790	3686	9484
2008	220	LG 6	Experimental	83.6	18.3	17.7	14.0		5875	6024
2008	224	LG 1	Experimental		18.6	16.9	2.5		8774	7475
2008	224	LG 2	Control	208.6	17.0	17.6	5.0		6124	10576
2008	224	LG 3	Experimental	102.4	17.5	18.3	-0.5		9931	5683
2008	224	LG 4	Control	125.2	17.8	17.4	6.0		6837	7468
2008	224	LG 5	Control	163.8	18.1	18.6	1.5			
2008	224	LG 6	Experimental	106.5	17.3	18.1	5.5		6070	7722
2008	231	LG 1	Experimental	122.6	26.2	16.0	8.5		10583	6708
2008	231	LG 2	Control	239.8	28.1	17.0	12.0		4949	5189



Year	Day	Collar	Treatment	CH <sub>4</sub> flux (mg m <sup>-2</sup> day <sup>-1</sup> )	Temperature (°C)		Depth to water table (cm)	<i>C. rostrata</i> GAI (m <sup>2</sup> m <sup>-2</sup> )	Porewater CH <sub>4</sub> (ppm)	
					Air	10cm			18 cm	60cm
2008	231	LG 3	Experimental	166.4	28.1	17.6	5.5		4634	3857
2008	231	LG 4	Control	183.0	28.6	19.7	8.0		5964	7005
2008	231	LG 5	Control	125.0			8.0			
2008	231	LG 6	Experimental				10.0		8942	6879
2008	267	LG 1	Experimental	80.3	20.0	10.3				
2008	267	LG 2	Control	263.8	21.4	11.7				
2008	267	LG 3	Experimental	150.2	19.8	10.8				
2008	267	LG 4	Control	84.5	20.1	10.9				
2008	267	LG 5	Control	91.8	20.0	10.9				
2008	267	LG 6	Experimental	12.1	21.9	13.1				
2008	291	LG 1	Experimental	41.5	12.4	6.9				
2008	291	LG 2	Control	100.7	12.4	8.6				
2008	291	LG 3	Experimental	166.3	12.2	10.8				
2008	291	LG 4	Control	108.4	14.4	10.9				
2008	291	LG 5	Control	136.6	13.1	10.9				
2008	291	LG 6	Experimental	67.5	13.4	13.1				
2008	301	LG 1	Experimental	46.7	23.0	7.2				
2008	301	LG 2	Control	102.4	24.0	7.3				
2008	301	LG 3	Experimental	32.5	25.2	6.3				
2008	301	LG 4	Control	115.0	24.5	6.7				
2008	301	LG 5	Control	61.0	20.9	8.7				
2008	301	LG 6	Experimental	6.7	23.5	8.3				
2008	323	LG 1	Experimental	36.7	5.3	5.8				
2008	323	LG 2	Control	15.2	4.8	5.8				
2008	323	LG 3	Experimental	35.9	4.8	6.8				
2008	323	LG 4	Control	43.3	3.1	6.2				
2008	323	LG 5	Control	12.5	6.2	7.2				
2008	323	LG 6	Experimental		6.8	6.7				
2008	343	LG 1	Experimental	7.2	-11.1	-0.5				
2008	343	LG 2	Control	30.5	-10.6	-0.6				
2008	343	LG 3	Experimental	6.2	-10.0	-0.5				
2008	343	LG 4	Control	6.6	-10.2	-1.5				

Year	Day	Collar	Treatment	CH <sub>4</sub> flux (mg m <sup>-2</sup> day <sup>-1</sup> )	Temperature (°C)		Depth to water table (cm)	<i>C. rostrata</i> GAI (m <sup>2</sup> m <sup>-2</sup> )	Porewater CH <sub>4</sub> (ppm)	
					Air	10cm			18 cm	60cm
2008	343	LG 5	Control	23.2	-8.9	-0.4				
2008	343	LG 6	Experimental	5.8	-7.6	-0.1				
2009	155	LG 1	Experimental	51.9	26	14	16.0			
2009	155	LG 2	Control	101.9	20.7	15.2	28.7	0.795		
2009	155	LG 3	Experimental	57.1	17	13.4	14.1			
2009	155	LG 4	Control	161.7	16.1	12.4	18.2	1.146		
2009	155	LG 5	Control	71.1	19.4	15	21.3	0.951		
2009	155	LG 6	Experimental	322.2	20.1	15.4	20.0			
2009	161	LG 1	Experimental	38.5	13.1	12			4175	5470
2009	161	LG 2	Control	76.6	16.1	12			2129	2903
2009	161	LG 3	Experimental		15.7	12.1			3708	2932
2009	161	LG 4	Control		12.2	12			1852	3019
2009	161	LG 5	Control	312.7	12.2	12.9			2849	6810
2009	161	LG 6	Experimental	297.2	12.2	12.8			3578	5175
2009	168	LG 1	Experimental	51.6	19.9	11.5	9.5		4274	4991
2009	168	LG 2	Control	40.0	21.3	11	22.6	0.850	3298	5853
2009	168	LG 3	Experimental	59.9	22.3	10.9	8.2		4324	2369
2009	168	LG 4	Control	93.1	23.6	11.2	12.0	1.496	2435	6170
2009	168	LG 5	Control	61.7	26.2	13	14.0	1.104	959	7724
2009	168	LG 6	Experimental		26	13.6	11.8		2340	8003
2009	176	LG 1	Experimental	64.8	20	13.9	6.5		4004	5289
2009	176	LG 2	Control	12.4	20.5	13.7	11.5		2617	4382
2009	176	LG 3	Experimental	39.9	23.2	14.5	4.5		3787	2532
2009	176	LG 4	Control	36.2	20.5	13.7	9.9		2988	5325
2009	176	LG 5	Control		18.5	14.2	8.9		1709	6633
2009	176	LG 6	Experimental	32.0	17.8	13.7	8.9		1958	9336
2009	181	LG 1	Experimental		16.2	16.5	5.0		5719	4893
2009	181	LG 2	Control	63.0	16.9	16.5	17.1		3717	5575
2009	181	LG 3	Experimental		15.9	13.2	3.1		4316	2784
2009	181	LG 4	Control	38.0	15.4	13.4	7.1		3700	6282
2009	181	LG 5	Control		14.3	13.5	10.1		3102	7274
2009	181	LG 6	Experimental	59.1	15.4	14.2	7.5		2208	10011

Year	Day	Collar	Treatment	CH <sub>4</sub> flux (mg m <sup>-2</sup> day <sup>-1</sup> )	Temperature (°C)		Depth to water table (cm)	<i>C. rostrata</i> GAI (m <sup>2</sup> m <sup>-2</sup> )	Porewater CH <sub>4</sub> (ppm)	
					Air	10cm			18 cm	60cm
2009	190	LG 1	Experimental	129.9	18	13.4	5.1		5042	5933
2009	190	LG 2	Control	218.9	22.5	13.2	17.9		3208	4570
2009	190	LG 3	Experimental	87.8	20.9	14	3.3		2061	2073
2009	190	LG 4	Control	171.3	21.4	13.9	7.1		3374	4034
2009	190	LG 5	Control	145.9	16.6	14	11.0		4526	5797
2009	190	LG 6	Experimental	48.3	18.4	13.6	7.8		1750	10020
2009	195	LG 1	Experimental	87.3	22.4	14.5	9.6		6583	7276
2009	195	LG 2	Control	185.9	20.3	15.4	21.8	1.051	5128	6017
2009	195	LG 3	Experimental	62.0	21.6	15.4	7.3		6766	4370
2009	195	LG 4	Control	166.7	22.6	14.7	11.6	1.766	4930	7793
2009	195	LG 5	Control	137.5	20.1	16.2	14.5	1.331	6081	8437
2009	195	LG 6	Experimental	121.5	19.2	16.1	12.4		5632	11972
2009	202	LG 1	Experimental	121.3	19.8	15.2	13.0		6653	6107
2009	202	LG 2	Control	206.9	19.3	17.1	25.5		5217	4887
2009	202	LG 3	Experimental	244.5	20.5	16.6	11.1		7196	4863
2009	202	LG 4	Control	260.1	18.5	16.6	16.0		4743	3900
2009	202	LG 5	Control	298.4	18.4	17.8	18.5		5031	3730
2009	202	LG 6	Experimental	96.2	19.3	17.9	15.1		5030	11350
2009	209	LG 1	Experimental	94.4	27.5	17.5	9.1		6206	6662
2009	209	LG 2	Control	130.4	27.5	17.6	20.9		4631	4879
2009	209	LG 3	Experimental	265.1	27.3	18.1	7.1		4297	6043
2009	209	LG 4	Control	276.4	27.5	17.3	11.2		8226	6475
2009	209	LG 5	Control	158.7	27.3	17.9	13.8		7757	6979
2009	209	LG 6	Experimental	77.7	27.2	18.1	10.8		2569	10104
2009	215	LG 1	Experimental	52.6	28.7	17.8	8.6		7603	7576
2009	215	LG 2	Control	304.6	29.4	17.8	20.4	1.157	5664	7057
2009	215	LG 3	Experimental	134.6	28.4	18.5	5.4		5901	5504
2009	215	LG 4	Control	194.8	28.4	20.5	11.2	1.936	4541	6604
2009	215	LG 5	Control	158.5	25.3	16.3	13.8	1.328	5002	5848
2009	215	LG 6	Experimental	158.5	25.3	16.3	9.1		2382	9274
2009	224	LG 1	Experimental	57.5	26.3	20	16.9		8083	8188
2009	224	LG 2	Control	209.7	28.8	19.7	24.0		3847	5965

Year	Day	Collar	Treatment	CH <sub>4</sub> flux (mg m <sup>-2</sup> day <sup>-1</sup> )	Temperature (°C)		Depth to water table (cm)	<i>C. rostrata</i> GAI (m <sup>2</sup> m <sup>-2</sup> )	Porewater CH <sub>4</sub> (ppm)	
					Air	10cm			18 cm	60cm
2009	224	LG 3	Experimental	57.5	24.5	28	7.2		3695	2746
2009	224	LG 4	Control	271.5	30.6	20.4	11.0		4963	9148
2009	224	LG 5	Control	137.7	30.3	21.5	19.3		2810	13389
2009	224	LG 6	Experimental	80.2	25	21.9	14.1		3399	16806
2009	245	LG 1	Experimental	45.7	21	15.5	14.8		111	3510
2009	245	LG 2	Control	190.5	18	20	26.5		2712	2191
2009	245	LG 3	Experimental	56.8	20	17.5	11.3		10504	8272
2009	245	LG 4	Control	306.0	21.5	14.5	16.0		3585	1544
2009	245	LG 5	Control	118.6	21	12.5	19.6		2817	4813
2009	245	LG 6	Experimental		20	15	16.4		3783	561
2009	280	LG 1	Experimental	38.8	12.9	11.7	17.0		4462	8166
2009	280	LG 2	Control	147.9	12.8	11.7	39.0		1456	1246
2009	280	LG 3	Experimental	29.1	14	11.6	15.6		4778	5651
2009	280	LG 4	Control	242.2	13.3	13.6	19.8		3006	7468
2009	280	LG 5	Control	151.8	14.1	12.5	24.7		3317	7097
2009	280	LG 6	Experimental	157.0	14.4	11.9	19.4		3612	6367
2009	315	LG 1	Experimental	2.7			19.2		5235	
2009	315	LG 2	Control	45.1			32.1			
2009	315	LG 3	Experimental	10.4			18.1		3116	4977
2009	315	LG 4	Control	88.6			20.4		3831	4297
2009	315	LG 5	Control	84.7			24.8		1393	10839
2009	315	LG 6	Experimental	25.4			21.5		2504	11522
2010	85	LG 1	Experimental	13.4	4	3.6	8.3			
2010	85	LG 2	Control		2.5	3.4	18.9	0.066	1362	
2010	85	LG 3	Experimental	16.5	6	4.6	8.2		904	
2010	85	LG 4	Control	34.0	5.2	4.4	9.2	0.077	383	
2010	85	LG 5	Control	15.9	3	5.5	8.5	0.077	199	
2010	85	LG 6	Experimental	5.2	5.7	6.3	8.9		165	
2010	92	LG 1	Experimental				7.2		2330	3542
2010	92	LG 2	Control	51.5			17.6		1414	2044
2010	92	LG 3	Experimental	48.5			5.7		1068	504
2010	92	LG 4	Control	46.4			8.8		1141	13687

Year	Day	Collar	Treatment	CH <sub>4</sub> flux (mg m <sup>-2</sup> day <sup>-1</sup> )	Temperature (°C)		Depth to water table (cm)	<i>C. rostrata</i> GAI (m <sup>2</sup> m <sup>-2</sup> )	Porewater CH <sub>4</sub> (ppm)	
					Air	10cm			18 cm	60cm
2010	92	LG 5	Control	9.8			8.2		545	10488
2010	92	LG 6	Experimental	14.7			9.4		323	
2010	106	LG 1	Experimental	9.0			15.1		276	13708
2010	106	LG 2	Control	19.1			27.1	0.303	1428	1891
2010	106	LG 3	Experimental	8.6			13.5		1489	939
2010	106	LG 4	Control	20.5			12.4	0.434	824	20552
2010	106	LG 5	Control	62.8			20.9	0.377	613	23268
2010	106	LG 6	Experimental	47.9			16.0		1317	16101
2010	116	LG 1	Experimental	23.8			25.0		1696	28936
2010	116	LG 2	Control	22.8			27.5		1268	3120
2010	116	LG 3	Experimental	14.0			14.5		1522	1807
2010	116	LG 4	Control	52.4			15.0		1835	29833
2010	116	LG 5	Control	36.0			19.0		1671	38245
2010	116	LG 6	Experimental	26.4			16.5		1356	35239
2010	131	LG 1	Experimental	19.5			19.0		2573	6279
2010	132	LG 2	Control	37.9			30.5		3380	3314
2010	132	LG 3	Experimental	22.3			18.5		3317	4651
2010	132	LG 4	Control	76.3			23.0		2870	5816
2010	132	LG 5	Control	70.8			20.5		2387	7725
2010	132	LG 6	Experimental	38.0			19.0		2331	12204
2010	140	LG 1	Experimental	8.6			12.0		2728	6214
2010	140	LG 2	Control				26.5		2023	3139
2010	140	LG 3	Experimental	36.9			13.0		2890	2753
2010	140	LG 4	Control	115.2			17.0		2650	5257
2010	140	LG 5	Control	48.8			17.0		957	8373
2010	140	LG 6	Experimental	68.3			13.5		476	10617
2010	147	LG 1	Experimental	24.3			19.5		2962	4940
2010	147	LG 2	Control	92.1			33.5		2048	4111
2010	147	LG 3	Experimental				19.0		2459	3555
2010	147	LG 4	Control	180.5			23.5		2524	4591
2010	147	LG 5	Control	70.4			23.5		1723	6747
2010	147	LG 6	Experimental	160.3			20.5		2890	8673

Year	Day	Collar	Treatment	CH <sub>4</sub> flux (mg m <sup>-2</sup> day <sup>-1</sup> )	Temperature (°C)		Depth to water table (cm)	<i>C. rostrata</i> GAI (m <sup>2</sup> m <sup>-2</sup> )	Porewater CH <sub>4</sub> (ppm)	
					Air	10cm			18 cm	60cm
2010	155	LG 1	Experimental	25.8	26.6	16.2	20.5		5363	8926
2010	155	LG 2	Control	86.9	25	18.4	32.0		766	6327
2010	155	LG 3	Experimental	51.2	26.2	17.1	17.0		3966	8448
2010	155	LG 4	Control	143.1	24.2	17	23.0			7352
2010	155	LG 5	Control	117.1	24.9	20.3	23.5		1110	9703
2010	155	LG 6	Experimental	78.6	27.1	18.9	23.5		2051	17669
2010	161	LG 1	Experimental	58.8	13.6	55	18.0		3148	5964
2010	161	LG 2	Control	64.2	14.2	55.8	32.5		2338	4737
2010	161	LG 3	Experimental	48.8	13.1	54.7	17.5		3409	1850
2010	161	LG 4	Control	133.3	13.9	55.5	21.0		4563	4881
2010	161	LG 5	Control	119.5	13.7	57.9	29.5		2467	6214
2010	161	LG 6	Experimental	124.4	13.3	56.8	18.5		1239	15678
2010	172	LG 1	Experimental	92.3	28.2	16.7	23.0		4896	8558
2010	172	LG 2	Control	111.4	29.6	21.1	33.5			6420
2010	172	LG 3	Experimental	69.3	28.8	16.1	19.5		4512	5941
2010	172	LG 4	Control	219.1	27.3	17.3	24.5		6159	5513
2010	172	LG 5	Control	137.1	25.4	20.7	26.0		1719	7793
2010	172	LG 6	Experimental	134.0	32.2	18.8	24.0		2843	14636
2010	180	LG 1	Experimental	108.9	27.1	18.8	23.0		6859	9636
2010	180	LG 2	Control	163.2	29.6	22.4	34.5			7572
2010	180	LG 3	Experimental	110.9	28.9	24.6	23.0		3713	8236
2010	180	LG 4	Control	448.9	30.8	17.8	24.0		5129	4226
2010	180	LG 5	Control	85.4	30	19.7	25.0		1293	8629
2010	180	LG 6	Experimental	124.5	31.4	20.2	21.0		3443	12831
2010	189	LG 1	Experimental	57.2	25.8	20.8	28.5			6809
2010	189	LG 2	Control	95.0	29.5	23.8	40.5	1.029		5023
2010	189	LG 3	Experimental	68.3	30.4	20.8	28.5			6707
2010	189	LG 4	Control	297.4	29	20.4	30.0	2.561		4805
2010	189	LG 5	Control	125.8	28.7	24.2	35.5	1.193		6031
2010	189	LG 6	Experimental	122.1	29.7	24	31.5			14301
2010	196	LG 1	Experimental		26.1	19.6	28.5			2332
2010	196	LG 2	Control	78.4	24.8	21.9	37.5			5893

Year	Day	Collar	Treatment	CH <sub>4</sub> flux (mg m <sup>-2</sup> day <sup>-1</sup> )	Temperature (°C)		Depth to water table (cm)	<i>C. rostrata</i> GAI (m <sup>2</sup> m <sup>-2</sup> )	Porewater CH <sub>4</sub> (ppm)	
					Air	10cm			18 cm	60cm
2010	196	LG 3	Experimental	34.9	27.1	20.9	30.0			2928
2010	196	LG 4	Control	147.3	28.1	20.7	27.5			7866
2010	196	LG 5	Control	29.4	27.1	22.3	30.0			7485
2010	196	LG 6	Experimental	121.8	26.1	21.3	26.0			8753
2010	202	LG 1	Experimental	44.3	26.9	18.5	28.5			1731
2010	202	LG 2	Control	154.5	28.7	18.1	40.0			8307
2010	202	LG 3	Experimental	76.9	27.8	23.4	29.5			3574
2010	202	LG 4	Control	149.1	28.8	19.5	31.0			9733
2010	202	LG 5	Control	107.1	29.2	22.7	31.5			7227
2010	202	LG 6	Experimental	104.4	30.3	18.8	32.5			10772
2010	215	LG 1	Experimental	51.4	22.1	17.2	36.0			3587
2010	215	LG 2	Control	103.9	24.2	16.9	48.5			5065
2010	215	LG 3	Experimental	92.9	24.6	18.1	29.0			1270
2010	215	LG 4	Control	310.7	26.2	16.9	39.0			1101
2010	215	LG 5	Control	71.6	27	21.6	27.5			10608
2010	215	LG 6	Experimental	34.7	26.8	23.6	31.0			11173
2010	223	LG 1	Experimental		23.2	18.2	35.5			5838
2010	223	LG 2	Control	63.9	24.9	18.8	46.5			8862
2010	223	LG 3	Experimental	30.5	24.7	18.1	31.0			3336
2010	223	LG 4	Control	160.9	26.5	18.7	36.0			6670
2010	223	LG 5	Control	167.5	26.3	22.2	36.0			10245
2010	223	LG 6	Experimental	82.9	27.8	19.3	32.0			13237
2010	231	LG 1	Experimental	58.9	25.1	16.6	40.0			1731
2010	231	LG 2	Control	73.6	26.9	17.8	51.5			8307
2010	231	LG 3	Experimental	41.9	25.1	20.1	39.5			3574
2010	231	LG 4	Control	137.5	28.6	17.7	42.5			9733
2010	231	LG 5	Control	90.9	27.9	22.2	40.0			7227
2010	231	LG 6	Experimental	50.3	29.2	18.3	41.0			10772
2010	242	LG 1	Experimental		26.2	15.2	41.5			4836
2010	242	LG 2	Control	74.1	26.8	16.6	27.5			5021
2010	242	LG 3	Experimental	31.2	26.6	17.6	29.0			2105
2010	242	LG 4	Control	52.3	30.6	18.1	40.5			2576

Year	Day	Collar	Treatment	CH <sub>4</sub> flux (mg m <sup>-2</sup> day <sup>-1</sup> )	Temperature (°C)		Depth to water table (cm)	<i>C. rostrata</i> GAI (m <sup>2</sup> m <sup>-2</sup> )	Porewater CH <sub>4</sub> (ppm)	
					Air	10cm			18 cm	60cm
2010	242	LG 5	Control	74.7	30.3	17.7	31.5			5521
2010	242	LG 6	Experimental		30.2	18.1	29.0			1015
2010	256	LG 1	Experimental	34.6	15.1	12.8	36.0			
2010	256	LG 2	Control	47.9	13.8	13.6	50.5			
2010	256	LG 3	Experimental	29.4	14.2	13.4	35.5			872
2010	256	LG 4	Control	157.5	14.6	13.6	40.0			398
2010	256	LG 5	Control	99.4	14.6	14.3	38.5			3066
2010	256	LG 6	Experimental	23.2	15.3	14.3	37.5			93
2010	264	LG 1	Experimental	22.7	15.3	10.3	37.5			6397
2010	264	LG 2	Control	90.2	17.5	10.1	50.5			9018
2010	264	LG 3	Experimental	16.9	17.1	11.4	65.0			51921
2010	264	LG 4	Control	119.4	20.3	10.2	40.0			7950
2010	264	LG 5	Control	59.1	20.3	12.3	42.5			6792
2010	264	LG 6	Experimental	33.3	19.8	12.3	35.0			5160
2010	271	LG 1	Experimental	37.2	11.9	12.7	41.0			7720
2010	271	LG 2	Control	40.1	11.6	13.8	54.0			16193
2010	271	LG 3	Experimental	15.0	11.6	13.6	38.5			4613
2010	271	LG 4	Control	65.0	11.9	13.5	41.0			5182
2010	271	LG 5	Control	14.8	12.1	14.5	44.5			3006
2010	271	LG 6	Experimental	30.9	12.3	13.7	38.0			3248
2010	273	LG 1	Experimental				38.0			4860
2010	273	LG 2	Control				50.5			8740
2010	273	LG 3	Experimental				37.5			4613
2010	273	LG 4	Control				41.0			5182
2010	273	LG 5	Control				37.5			3006
2010	273	LG 6	Experimental				38.3			3248
2010	284	LG 1	Experimental		12.6	4.8	31.0			4860
2010	284	LG 2	Control	49.3	14.8	6.2	44.5			8740
2010	284	LG 3	Experimental	36.5	14.7	8	30.5			3921
2010	284	LG 4	Control	35.4	14.7	6.8	34.0			4605
2010	284	LG 5	Control	23.0	15.7	7.9	33.0			6319
2010	284	LG 6	Experimental		18.7	8.4	31.0			5012



Year	Day	Collar	Treatment	CH <sub>4</sub> flux (mg m <sup>-2</sup> day <sup>-1</sup> )	Temperature (°C)		Depth to water table (cm)	<i>C. rostrata</i> GAI (m <sup>2</sup> m <sup>-2</sup> )	Porewater CH <sub>4</sub> (ppm)	
					Air	10cm			18 cm	60cm
2010	294	LG 1	Experimental				20.5		461	3761
2010	294	LG 2	Control				33.0			6035
2010	294	LG 3	Experimental				19.0		198	9482
2010	294	LG 4	Control				25.0		861	3103
2010	294	LG 5	Control				22.5			11187
2010	294	LG 6	Experimental				20.5		107	8698
2010	298	LG 1	Experimental		8.3	6.3	22.0			
2010	298	LG 2	Control	46.3	7.6	6.2	34.5			
2010	298	LG 3	Experimental	30.5	8.1	6.5	21.0			
2010	298	LG 4	Control	44.6	9.4	6.8	35.0			
2010	298	LG 5	Control	73.4	10.5	6.7	23.0			
2010	298	LG 6	Experimental	22.3	10.6	6.7	22.0			
2010	305	LG 1	Experimental	21.8	4.9	4.4	19.5			12486
2010	305	LG 2	Control	51.3	4.1	3.2	32.0			6809
2010	305	LG 3	Experimental	3.9	5.8	4.8	19.0			8422
2010	305	LG 4	Control	37.5	7.9	5.7	20.0			4802
2010	305	LG 5	Control	60.2	7.9	3.7	20.0			9904
2010	305	LG 6	Experimental	14.3	9.2	5.8	20.5			10298
2010	314	LG 1	Experimental		7.7	6.8	12.5		3269	12103
2010	314	LG 2	Control	34.3	7.4	6.7	27.0		1691	18713
2010	314	LG 3	Experimental	8.2	8.9	6.9	13.5		2886	1770
2010	314	LG 4	Control	35.5	9.3	7.0	6.5		577	6517
2010	314	LG 5	Control	48.8	9.4	7.4	15.5		417	5079
2010	314	LG 6	Experimental	7.3	9.2	7.1	13.5		296	15952
2010	326	LG 1	Experimental		2.0	1.3	17.5			
2010	326	LG 2	Control	28.2	1.3	1.9	27.0			
2010	326	LG 3	Experimental		0.9	0.1	17.0			
2010	326	LG 4	Control	54.5	1.8	1.7	21.0			
2010	326	LG 5	Control	54.8	1.4	2.6	20.0			
2010	326	LG 6	Experimental	26.9	2.1	2.2	16.5			
2010	340	LG 1	Experimental	9.3	-1.4	0.2	18.5			
2010	340	LG 2	Control	18.7	-2.3	0.3	27.5			

Year	Day	Collar	Treatment	CH <sub>4</sub> flux (mg m <sup>-2</sup> day <sup>-1</sup> )	Temperature (°C)		Depth to water table (cm)	<i>C. rostrata</i> GAI (m <sup>2</sup> m <sup>-2</sup> )	Porewater CH <sub>4</sub> (ppm)	
					Air	10cm			18 cm	60cm
2010	340	LG 3	Experimental	1.8	-2.2	-0.8	13.5			
2010	340	LG 4	Control	46.0	-2.2	1.0	19			
2010	340	LG 5	Control	40.8	-2.6	1.3	17			
2010	340	LG 6	Experimental	5.5	-2.6	-1.0	16.7			
2010	355	LG 1	Experimental	10.7	0.7	-0.6	27.0			
2010	355	LG 2	Control		0.3	-0.6	25.5			
2010	355	LG 3	Experimental		1.1	-0.4	15.0			
2010	355	LG 4	Control	35.3	1.5	-0.2	20.0			
2010	355	LG 5	Control	31.7	1.9	-0.1	19.0			
2010	355	LG 6	Experimental	6.9	1.7	0.0	16.5			