INTERANNUAL AND SEASONAL VARIATION OF METHANE FLUX

FROM A TEMPERATE PEATLAND AND POSSIBLE

ENVIRONMENTAL CONTROLS

by

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ABSTRACT

This study examined the sub-seasonal, seasonal and interannual variations in net ecosystem CO_2 exchange (NEE) and CH_4 effluxes and possible links between the two processes in an attempt to determine the environmental controls responsible for the variations. We measured NEE_{max}, CH_4 fluxes, water table level, and meteorological data from the summer (1 May-31 August) for five years (2000-2004) at a temperate peatland in southern New Hampshire. We observed increasing photosynthesis and respiration values as the summer progressed. CH_4 fluxes also increased in magnitude and variability due to higher peat temperatures and episodic events as the season progressed.

When considering mean seasonal methane flux over the five year period, we found low interannual and spatial variability. However, we found high interannual variability of methane fluxes and relationships between fluxes and variables when we considered instantaneous time scales. Significant differences in methane fluxes were driven by differences in mean monthly methane fluxes. Sedge-dominated sites had the strongest relationships between methane fluxes and measures of plant productivity (NEE_{max}, $photosynthesis_{max}$, respiration), as well as environmental variables (air temperature, peat temperature, water table level). This suggests that controls on methane fluxes vary in importance over different timescales and types of vegetation.

INTRODUCTION

1. THE SIGNIFICANCE OF METHANE

Methane (CH_4) is a greenhouse gas with 62 times the global warming potential of carbon dioxide over the next 20 years (IPCC 2001). Methane concentrations have been increasing by 7.0 part per billion (ppb) per year from pre-industrial revolution concentrations. 1998 concentrations of 1745 ppb were 250% higher than pre-industrial revolution concentrations (IPCC, 2001). Although the atmospheric concentration of methane is 200 times lower than that of carbon dioxide (CO_2), it accounts for 20% of the radiative forcing of all greenhouses gases in the atmosphere (IPCC 2001). Methane is particularly important in the global climate change debate because it has a mean residence time in the atmosphere of 12 years (IPCC 2001), magnifying the radiative forcing of methane and causing a higher global warming potential from methane than from CO_2. Methane is destroyed in a reaction with OH^- radicals, forming water and potentially ozone (Tyler, 1991). Methane has a significant effect on the chemical interactions of the Earth's atmosphere, such as through the formation of ozone, another important greenhouse gas, and consequently has the potential to enhance global climate change both through its own global warming potential and through the formation of other greenhouse gases.

Methane is produced both anthropogenically and naturally. Anthropogenic sources of methane account for 60% of methane emissions while natural sources produce the rest (IPCC 2001). Of both anthropogenic and natural sources, wetlands comprise the largest single source of methane to the atmosphere (IPCC 2001; Table 1).

Wetlands are an important factor in global climate change because they store approximately one-third of global soil carbon as peat (Alm *et al.*, 1997; Gorham, 1991). Peatlands act as carbon sinks because the carbon accumulated through primary production is greater than that lost to respiration. While primary productivity is relatively low in wetlands (Bubier *et al.*, 1999; Frolking *et al.*, 1998), respiration is limited by temperature, substrate availability, water table level, and oxygen availability, leading to the accumulation of undecomposed organic matter over thousands of years.

In any given year, wetlands can be either a source or a sink of carbon to the atmosphere, depending on the moisture regime (Alm *et al.*, 1999; Aurela *et al.*, 2001; Bubier *et al.*, 2003; Carroll & Crill, 1997). When the water table is higher, anaerobic processes dominate, whereas aerobic processes will increase in importance as the water table drops. Temperature is also a factor in the carbon balance of wetlands. With global climate change, higher temperatures and changing water table levels are predicted at higher latitudes, which will most likely increase rates of ecosystem respiration and methane emissions (Carroll &

Crill, 1997; Roulet *et al.*, 1992).   Such changes would release carbon to the atmosphere that has been sequestered in the peatland for thousands of years.

Peatlands may act as a positive or negative feedback to global warming. Both the potential lowering of the water table and the increased temperature may lead to increased productivity of wetlands through increased photosynthesis, a colonization of former lagg areas, and a possible shift in species composition (Waddington *et al.*, 1998; Weltzin *et al.*, 2000). The changes in productivity might result in greater biomass, in which case wetlands may serve as a negative feedback to global climate change as they could sequester more carbon. However, both a higher temperature and a lower water table may increase respiration, causing wetlands to release more carbon to the atmosphere and consequently act as a positive feedback to global climate change.

Methane fluxes from peatlands are a net result of three processes: production, oxidation, and transport (Figure 1). The same environmental factors control the processes, which makes the relationships between methane fluxes and temperature, water table, and productivity very complex.

2. METHANE PRODUCTION

Methane (CH_4) is a trace gas that is the end product of a long string of reactions that break down organic matter in anaerobic environments. Methane formation occurs through two different pathways, bicarbonate reduction or acetate fermentation. Both processes are mitigated by methanogenic bacteria in the

absence of oxygen and other alternate electron receptors (Westermann & Ahring, 1987). The bicarbonate reduction, also known as the hydrogen pathway, uses H_2 to reduce CO_2 to a formyl group, to a methyl group, and then to methane in the following reaction.

$$4 H_2 + CO_2 \rightarrow CH_4 + 2 H_2O \qquad\qquad \Delta G_0' = -135.6 \text{ kJ/mol } CH_4$$

The other mechanism of methane formation is acetate fermentation, or the acetate pathway. This process involves the conversion of acetate to methyl and then to methane in the following equation.

$$C_2H_3OO^- + H^+ \rightarrow CH_4 + CO_2 \qquad\qquad \Delta G_0' = -31.0 \text{ kJ/mol } CH_4$$

The hydrogen pathway and the acetate pathway differ in their importance to methane production. The reduction of carbon dioxide via the hydrogen pathway to form methane becomes more important with peat depth as labile carbon is less available (Chasar *et al.*, 2000; Popp *et al.*, 1999), but is relatively unimportant in most peatlands with high amount of labile carbon. Where labile carbon is readily available, acetate fermentation is the dominant pathway of methane formation in many peatlands. Acetate fermentation accounts for 85-90% of methane produced in ecosystems with low temperatures (Avery *et al.*, 1999). Acetate is formed from labile carbon in the peat, from root exudates, organic matter, and recent photosynthates in plant roots (King & Reeburgh, 2002; van Hulzen *et al.*, 1999).

Older reviews concluded that much of the substrate for methanogenesis was derived from peat decomposition (Panikov, 1999), but more recent research

has shown that recently fixed carbon is an important source of substrate for methanogens. King and Reeburg (2002) found a fraction of isotopically labeled carbon taken up as CO_2 during photosynthesis is released as methane as soon as two hours after uptake as vascular plants allocate recently fixed carbon to their roots. Similarly, isotopically labeled acetate was emitted as methane at the highest rates between 72 and 240 hours after addition (Ström *et al.*, 2003), indicating that labile carbon is used very quickly. The rapid turnover of the carbon substrates to methane indicates the importance of recently fixed carbon to methane production.

Substrate availability is the key determinant of methane production. If either acetate or labile carbon is available in the absence of alternate electron acceptors in anoxic conditions, methane production will occur given that populations of methanogenic bacteria are present. Methanogens are active only under anoxic conditions, so the production of methane is dependent on the water table level. Although methanogens can survive dry periods with a low water table levels, they generally do not produce any methane during these periods (Blodau & Moore, 2003a; Moore & Dalva, 1993).

3. METHANE OXIDATION

Methane fluxes are the net result of methane production in the anaerobic zone of the peat, and methane oxidation in the aerobic peat layers. Methane oxidation or methanotrophy occurs in aerobic environments as anaerobically

produced methane is oxidized by methanotrophic bacteria to form CO_2 in the following equation.

$$CH_4 + 2\ O_2 \rightarrow CO_2 + 2\ H_2O$$
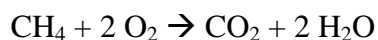
Methane oxidation has a significant impact on methane fluxes. Oxidation may consume up to 90% of methane produced in a peatland (King, 1990a). The proportion of methane oxidized is dependent on the concentration of methane in the peat (Moosavi & Crill, 1998; Sundh *et al.*, 1995), which is dependent on the diffusion. However, methane can also be transported through other mechanisms and bypass oxidation, increasing the net efflux from the system.

4. METHANE TRANSPORT

The methane flux that is measured is a combination of three different transport mechanisms, diffusion through the peat, ebullition or episodic fluxes, and plant mediated transport. Diffusion contributes a much smaller proportion to methane fluxes than plant mediated transport and ebullition (Chasar *et al.*, 2000; Dove *et al.*, 1999), but this is dependent on the environmental conditions and vegetation within a peatland.

Methane diffusion through the peat is a passive physical process. Methane travels from the anaerobic zone of the peat at or below water table depth and through the aerobic zone of the peat. The methane efflux is significantly less than the methane that is produced due to methane oxidation in the aerobic zone. The relative importance of these two processes is controlled by the water table. Areas

with a low water table level both produce less methane due to the reduced anaerobic zone (and presumably less labile C), and oxidize more methane due to the increased aerobic zone, resulting in a lower net methane flux.

Ebullition and episodic fluxes contribute significantly to methane fluxes. Ebullition, or bubbling of gases, occurs in saturated areas where the water table is above the peat surface. Episodic fluxes are significantly higher than average fluxes at a site where inundation does not occur. Ebullition and episodic fluxes are significant contributors to annual methane fluxes because they are emitted as pulses that are too large to be fully oxidized, unlike methane diffusion through the peat. Christensen et al. (2003) estimated that ebullition fluxes accounted for 18-50% of total methane emissions. A possible cause of episodic fluxes is a drop in water table level (Windsor *et al.*, 1992) or a change in atmospheric pressure (Bubier *et al.*, 1993b; Moore & Dalva, 1993; Scranton *et al.*, 1993), which causes dissolved methane in the peat to be released.

Plant mediated transport of methane, the final mechanism by which methane is released to the atmosphere, has been found to account for between 48% and 97% of methane effluxes (Christensen *et al.*, 2003b; Kelker & Chanton, 1997; Shannon *et al.*, 1996). Vascular plant species have differing effects on methane emissions depending on whether a plant is aerenchymatous or not (Shannon & White, 1994). Vascular plants with aerenchymatous tissue, like sedges, have passages that allow both oxygen to travel to their roots and methane to escape to the atmosphere. Ericaceous plants such as leatherleaf do not. Plants

transport oxygen to their roots for root respiration, which also enables methane oxidation when dissolved methane in the peat is exposed to oxygen (Bellisario *et al.*, 1999; Shannon *et al.*, 1996). However, by transporting a gas to their roots, plants also enable methane to diffuse through the plant roots and bypass oxidation in the peat. Additionally, vascular plants allocate carbon to their roots, increasing the substrate available for methanogenesis.

Several studies have shown that sites with vascular vegetation have much higher methane emissions than sites where vascular vegetation has been removed or clipped (Christensen *et al.*, 2003b; Kelker & Chanton, 1997; Saarnio *et al.*, 1998; Waddington *et al.*, 1996). The strength of vascular plant control, however, is determined by species composition and the water table level. Wetland sites with sedges have been found to have the highest methane fluxes (King *et al.*, 1998), 6 to12 times higher than sphagnum sites (Saarnio *et al.*, 1998) and significantly higher than sites with ericaceous shrubs (Shannon & White, 1994). Sedges are aerenchymatous plants, and it has been well documented that the presence of sedges leads to higher methane fluxes due to their physical properties (Kelker & Chanton, 1997). However, Waddington et al. (1996) suggest that the influence of vascular plants on methane fluxes is correlated with the water table level. They also suggest that methane fluxes may only be enhanced by vascular vegetation when the water table is high, because the plant roots are more likely to reach the zone of methane production, thus contributing substrate through root exudates and enabling transport from the anaerobic zone of methane production.

5. CONTROLS ON METHANE FLUXES

The controls on methane fluxes fall into two groups: abiotic and biotic controls. The biotic controls on methane fluxes are microbial communities and vegetation while the abiotic controls are environmental factors and substrate availability. Both vegetation and environmental factors affect substrate availability, which is the all-encompassing control on methane production. Even in ideal environmental conditions, methane production will not occur without a substrate.

Biotic Controls on Methane Fluxes

Microbial populations determine the methane flux through the amount of methane produced and the amount of methane that is oxidized. This is especially pertinent for the portion of methane fluxes emitted through diffusion. The balance between production and oxidation is controlled by the water table level that dictates the size of the aerobic zone.

There are two sources of substrate for methanogens, recently fixed carbon that is released as root exudates, and other labile carbon in the peat. While methanogens use the end-products of other microbial reactions, they are still limited by both substrate and nutrients. The greatest methane production occurs in the anaerobic zone while the highest potential methane oxidation rates are at either the water table level (Moore & Dalva, 1997; Sundh *et al.*, 1995; Sundh *et al.*, 1994) or 10 cm below water table level (Kettunen *et al.*, 1999). This indicates

that both communities are able to adapt to changing water table levels, indicating the importance of water table level on methane fluxes.

Vegetation influences methane fluxes through substrate production and through plant-mediated transport. The presence of vascular vegetation has been found to increase methane emissions (Shannon & White, 1994; Shannon *et al.*, 1996; Waddington *et al.*, 1996), despite the associations described between active methane oxidizing bacteria and the rhizospheres of sedge species (Popp *et al.*, 2000) and plant fine root material (Gerard & Chanton, 1993). Methane oxidation is not as tightly coupled to vascular plants as methane production.

Many studies have linked to plant productivity and carbon assimilation to methane fluxes (Joabsson & Christensen, 2001; King *et al.*, 2002; Whiting & Chanton, 1993; Whiting *et al.*, 1991). This is probably due to carbon allocation to the plant roots and subsequent plant root exudates, which leads to increased substrate for methanogenesis (Joabsson *et al.*, 1999; King *et al.*, 2002; Ström *et al.*, 2003). Other research has shown that CH_4 fluxes are related to light-regulated root exudation (Mikkëla *et al.*, 1995) although this might also be a function of light-related oxidation processes, which are inhibited by light (King, 1990b). Van den Pol-van Dasselaar and Oenema (1999) found that plant residues in the peat surface (from 0-5cm depth) contributed to 70% of the total CH_4 production capacity of the peat, indicating that plants are crucial to the formation of substrate for methanogenesis.

The plant species composition of a wetland also affects the methane fluxes through the amount of methane transportation and the substrate production. Strom et al. (2003) found that different vegetation species had different rates of acetate production. Studies have found varying qualities of labile carbon in the peat, depending on the dominant species type (Aerts & Toet, 1997; Bergman *et al.*, 1998; Valentine *et al.*, 1994). Shrub dominated areas tend to have recalcitrant carbon sources within the peat, while the carbon found in sedge dominated areas of the peat is more labile (Yavitt & Lang, 1990). Plant species composition will definitely impact the methane fluxes from a wetland site.

Environmental Controls on Methane Production

The most important environmental controls on the methane flux are water table level and peat temperature. These environmental factors act as indirect controls on methane emissions through affecting conditions for methane production, rather than direct controls, which would be things such as substrate availability and microbial abundance. Many studies have found that accounting for differences in peat temperature and water table position accounts for much of the variation in methane emissions (Bubier *et al.*, 1995; Moore & Dalva, 1993; Updegraff, 2001).

Water Table Depth

Water table level controls the depth of the anoxic layer below the peat surface and therefore controls the zone of methane production and methane oxidation occurring in the aerobic zone of the peat above the water table. Higher methane emissions have been observed with a higher water table level, while lower emissions have been observed at lower water table levels (Aerts & Ludwig, 1997; Bubier *et al.*, 1993a; Dise *et al.*, 1993; Moore & Roulet, 1993). Several researchers have found that the water table is a major control of methane emissions and found that the seasonal average water table may be the best predictor of methane emissions (Bubier *et al.*, 1993a; Bubier, 1995; Dise *et al.*, 1993; Moore & Dalva, 1997; Waddington *et al.*, 1996).

However, the relationship between water table and methane emissions is not always direct. An inverse relationship from that which is expected and described above has been measured in several studies. High methane fluxes during a period of low water table position have been observed when the average water table was within 15 cm of the peat surface (Bellisario *et al.*, 1999; Kettunen *et al.*, 1996). Insignificant correlations between methane fluxes and water table level with small variations in the water table have been found (Moosavi & Crill, 1997; Shannon & White, 1994; Yavitt *et al.*, 1993). Van den Pol-Van Dasselaar (1999) found a 5 cm change in the water table could decrease or increase methane emissions by 30-50%. Furthermore, Kettunen et al. (2000) found that water table position did not explain any additional variability of methane fluxes than that

accounted for by peat temperature. Frolking and Crill (1994) also found that the relationships between water table level and methane fluxes did not hold true for all years of their 3-year study, depending on yearly environmental variations. These findings indicate that although the relationship between water table level and methane emissions is generally positive, it does not hold true in all cases, especially when there are small variations in water table level or it is near the peat surface.

The relationship between methane effluxes and water table level becomes less certain when the water table level experiences small fluctuations or is close to the peat surface. It is possible that with small changes in water table or with a high water table, methane fluxes become decoupled from the environmental factors. Instead fluxes become dependent on plant activities, such as plant transport and substrate production, leading to the observed correlations between plant productivity and methane emissions, which are discussed later. With small changes in water table, these processes may vary in importance. A possible explanation for the observed high emissions during periods of low water table is the efflux of methane due to a pressure gradient between the zones of production and the atmosphere (Kettunen *et al.*, 1996). Both departures from the hypothetical relationship of methane to water table indicate that the relationships between methane fluxes and environmental variables are complex.

Peat Temperature

Peat temperature is another well-documented control on methane emissions. Methane production is a microbially mitigated process, so like all microbial processes, temperature controls the rate of activity. The correlation between peat temperature and methane production has been described by many researchers (Bergman *et al.*, 2000; Christensen *et al.*, 2003a; Dise *et al.*, 1993; Frolking & Crill, 1994; Kettunen *et al.*, 2000; Shannon & White, 1994; Updegraff, 2001; van Hulzen *et al.*, 1999).

Several studies have described seasonal patterns of methane fluxes (Waddington *et al.*, 1996; Windsor *et al.*, 1992). Methane fluxes are smaller in the beginning of the season due to the lower peat temperature. As the peat warms throughout the summer season, methane fluxes increase in magnitude. In the winter, methane fluxes are 10% to 100% of their summer values (Heikkinen *et al.*, 2002).

Air temperature and water table level control peat temperature. The lagg time between changes in air temperature and peat temperature is a likely cause of the observed seasonal patterns of methane emissions (Frolking & Crill, 1994). Peat temperature has been shown to account for most of the variability in methane fluxes, especially when used with water table data, and the seasonal mean of both water table and peat temperature have been used to predict methane emissions (Bubier *et al.*, 1995). The effects of peat temperature on methane emissions are also somewhat dependent on the vegetation of a given site. Sites dominated by

vascular, aerenchymatous plants have a stronger positive relationship between methane fluxes and peat temperature at depth than other sites (Saarnio *et al.*, 1998; Shannon & White, 1994).

Storm Effects

Other environmental factors such as large storms can also play a role in methane fluxes. Large precipitation events change the water table level very quickly and air temperature, both increasing the anaerobic zone for increased methane production and possibly providing more nutrients through increasing available dissolved organic carbon (DOC). These changes are sometimes reflected through increased methane emissions with a lagg time of zero to several days and vary with peat depth (Blodau & Moore, 2003b; Kettunen *et al.*, 1996). Other studies have found that methane fluxes do not always increase from precipitation events. Frolking and Crill (1994) and Joabsson and Christensen (2001) found that methane emissions appeared to be suppressed by large rainstorms, possibly due to flooding and loss of methanogens, availability of alternate electron acceptors, or penetration of oxygen into the anaerobic peat environment.

6. PREDICTING METHANE FLUXES ON A BROADER SCALE

It is important to be able to predict methane fluxes on a broader scale because methane is an important greenhouse gas and driver of global climate

change. Wetlands are the largest single source of methane to the atmosphere, and it would therefore be beneficial to be able to determine the contribution of wetlands on a broad scale without having to measure fluxes at each individual site. Several studies have correlated methane fluxes to measures of plant productivity, species composition, and net ecosystem CO_2 exchange with the atmosphere, which suggest that broader interpretations of methane fluxes can be determined from sites where these factors are known or can be measured.

Predicting methane fluxes at scales broader than a single measurement site is difficult due to the high spatial variability of methane fluxes. Substrate availability has been shown to account for much of the variability in methane fluxes over a large scale, and when combined with temperature, the two explain much of the observed variability in methane fluxes (Bergman *et al.*, 2000; Christensen *et al.*, 2003a). Substrate availability and air temperature seemingly conflict with the importance of water table level and the control of methane fluxes that water table exerts. This may be due to differences in water table across wetlands, with water table on a broader scale. Liblik *et al.* (1997) showed that only after water table was at a sufficient level for methane production did temperature become important. Substrate and temperature can differ between areas within a wetland due to the microtopography of the wetland.

Many researchers have attributed high spatial variability in methane fluxes to differences in microtopography (Bubier *et al.*, 1993a; Heikkinen *et al.*, 2002; Van den Pol-Van Dasselaar *et al.*, 1999). Microtopography determines the height

of the peat surface above the water table, which affects the peat temperature and the species composition, and eventually methane fluxes. For example, Bubier et al. (1993) found average summer CH_4 effluxes ranging from 5.1 g m^{-2} day^{-1} for a hummock to 156.2 g m^{-2} day^{-1} for a hollow within one wetland site in Canada. High spatial variability has also been attributed to differences in substrate availability (Kettunen 2000) and vegetation differences (Christensen 2003; Van den Pol-van Dasselaar, Van Beusichem et al. 1999). Species composition determines substrate availability in the root vicinity, leading to higher rates of acetate production in root microcosms of different species (Bergman *et al.*, 1998; Ström *et al.*, 2003). The large spatial variability of methane production within sites may also be explained by a coupling between variations in water table depths and microbial population variability and size. Like methane production, methane oxidation has high spatial variability (Moosavi & Crill, 1998). This may be due to plant species composition, microtopographical differences in water table level, and even the production of methane in the anaerobic peat.

Net ecosystem productivity (NEP) is a measure of the net carbon accumulation of an ecosystem. Taken over the period of a year, the NEP will determine whether a site has been a net sink or source of carbon to the atmosphere. NEP can be measured using the net primary productivity (NPP), which can be measured by determining plant biomass, and subtracting the rates of soil and microbial respiration, as measured by a dark chamber to eliminate

photosynthesis. However, NEP is usually best described through modeling due to the difficulties measuring above and below-ground biomass.

Correlations have been found between NEP and methane fluxes across a variety of wetlands (Waddington *et al.*, 1996; Whiting & Chanton, 1993), but the correlation has only been observed in wet or inundated sites with high water table levels (Waddington *et al.*, 1996). In northern peatlands, sedge biomass and water table level have been found to be good predictors of NEP (Bellisario *et al.*, 1999). Both vascular plant biomass and water table level influence methane fluxes, which may account for the correlation between NEP and methane fluxes.

Vascular plant biomass and species composition may be another way to predict methane emissions on a broader scale. Vascular plants both enhance methane production through the addition of substrate to the peat and, depending on the species, increasing methane fluxes to the surface via passive transport. The magnitude of methane fluxes has been linked to vascular plant biomass (Bellisario *et al.*, 1999; Christensen *et al.*, 2003b; Whiting *et al.*, 1991), but has also been found to depend on the species composition (Bubier, 1995; Joabsson & Christensen, 2001). Wetland sites dominated by sedges generally have higher methane fluxes than areas that are not sedge-dominated. This is likely due to wetter conditions and root exudates that favor methane production (Bergman *et al.*, 1998), and because sedges are more efficient conduits for methane transport than ericaceous shrubs. A study by Bellisario et al. (1999) found that methane fluxes were most strongly related to the end of the season sedge biomass. Shrub

cover is generally indicative of drier conditions and subsequently, often has lower methane emissions than sedge-dominated areas (Bubier, 1995) both because shrubs generally do not transport methane as efficiently as aerenchymatous vegetation like sedges, and because the conditions for methane production are less favorable. Not only is the water table depth from the peat surface higher, but the substrate for methanogenesis from shrub-dominated wetlands is often more recalcitrant than other vegetation types (Yavitt & Lang, 1990).

Methane fluxes may also be determined by the net ecosystem CO_2 exchange (NEE) of a site. NEE is the difference between gross photosynthesis and respiration, representing the net carbon balance of a site in a given time scale, usually daily. Methane fluxes have been strongly correlated with NEE in studies (Bellisario *et al.*, 1999; Joabsson & Christensen, 2001), most likely through higher levels of plant productivity.

Similarly, methane fluxes have been correlated to photosynthesis. Photosynthesis has been tightly linked to methane fluxes, especially in wet sites (Joabsson *et al.*, 1999; Nykanen *et al.*, 2003) by studying the effects of shading treatments (Joabsson *et al.*, 1999; Ström *et al.*, 2003) and also by using a radioactive tracer (King & Reeburgh, 2002; Ström *et al.*, 2003). A definite lagg time ranging from 6 hours to a week has been observed between rates of maximum photosynthesis and maximum methane fluxes (Joabsson *et al.*, 1999; King & Reeburgh, 2002; Ström *et al.*, 2003; Waddington *et al.*, 1996). More recent research using radioactively labeled carbon has traced the path of carbon

taken up by the plants during photosynthesis through its release to the atmosphere as methane. The lagg time between CO_2 uptake and CH_4 production ranges from 4 hours to 1 week before emission (King & Reeburgh, 2002). Methane production is related to photosynthetic rates because recently fixed photosynthates are released as methane.

Finally, ecosystem respiration may be another measurement to predict methane fluxes. Ecosystem productivity, plant biomass, water table level and temperature are all significant controls on carbon loss through respiration (Bubier *et al.*, 2003), and all also control the magnitude of methane fluxes. Additionally, anaerobic potential methane production in the peat has been found to correlate with potential aerobic CO_2 production (Moore & Dalva, 1997). Because similar factors control both carbon losses as CO_2 and as CH_4, the potential exists for observing a correlation between these factors although a lower water table often corresponds to increased ecosystem respiration and decreased methane fluxes (Alm *et al.*, 1999).

7. PURPOSES OF THIS STUDY

This study examines the links between methane fluxes and environmental variables such as water table, air temperature, and peat temperature, as well as considering relationships between methane fluxes and NEE, photosynthesis, and respiration, all of which were measured simultaneously. We were also able to compare the effects of plant species composition on methane fluxes. While

several studies have taken this integrative approach to looking at methane fluxes, most have been limited to one or two growing seasons (Bellisario *et al.*, 1999; Waddington *et al.*, 1996). We had five years of measurements. This enabled us to compare differences between years, as well as time scales within years and to determine which factors controlled methane fluxes on an instantaneous basis, represented by the field measurements, as well at the seasonal level. Finally, we were able to compare different parts of the growing season, because trends in methane fluxes were very different in the early part of the growing season (May and June) than the later part of the season (July and August).

Our study site, Sallie's Fen, is a peatland located in Southern New Hampshire. In New England, wetlands are a dominant source of methane to the atmosphere (Blaha *et al.*, 1999). Sallie's Fen can be a source or sink of carbon to the atmosphere on an annual scale, depending on environmental factors (Carroll & Crill, 1997). Due to the important contributions of wetlands to methane emissions from New England, it is important to characterize the role of environmental controls on methane fluxes in temperate wetlands.

We hypothesized that methane fluxes would be correlated with environmental variables as well as measures of ecosystem carbon exchange. CH_4 emissions should be negatively correlated with greater water table depth because of the effects of lowering the water table on the balance between anaerobic methane production and aerobic methane oxidation. CH_4 should be positively

correlated with peat temperature because of the effects of peat temperature on microbial activity.

We expected to see a positive correlation between methane fluxes and full-light NEE (Bellisario *et al.*, 1999). Higher methane emissions will occur through two mechanisms: increased substrate production and increased vascular plant transport. Part of the carbon taken up by plants becomes substrate for methane production through the anaerobic decomposition and oxidation of root exudates (Bellisario *et al.*, 1999; Joabsson *et al.*, 1999; King *et al.*, 2002). Root exudates are preferentially used in methanogenesis because they are higher quality carbon substrate than the recalcitrant organic matter found in the peat (Joabsson 2001). Additionally, on a seasonal level, CH_4 emissions will be correlated with NEE due to vascular plant transport.

Similarly, methane fluxes will be positively correlated with photosynthesis. Carbon assimilation occurs during photosynthesis, which is the driving force in production of root exudates and labile carbon substrate as discussed above. Therefore, it is likely that we will observe a correlation between photosynthesis and methane emissions, although probably at a seasonal level (Bellisario *et al.*, 1999; King *et al.*, 2002).

Methane emissions will be negatively correlated with respiration. Both processes are microbially mitigated, however one is aerobic and the other anaerobic, so whether CO_2 or CH_4 is produced should be determined by the water table level. A water table level that favors the production of one would hinder

production of the other, indicating a negative relationship. However, if the sign convention is switched as it is in this study, so that both CH_4 effluxes are positive and CO_2 loss through respiration is negative, methane flux and respiration will show a positive correlation.

Methane emissions will differ with the species composition. Due to plant physiology, high sedge biomass will increase methane emissions through efficient vascular plant transport, which is one of the largest sources of methane (Christensen 2003). Shrub dominated sites will have lower methane emissions than sedge dominated sites because shrubs do not transport methane as efficiently. Both sedge and shrub sites should have higher methane emissions than sites without vascular vegetation due to production of acetate and also because they will not transport methane.

Finally, we expect methane emissions to be larger in the later part of the season. This may be due to increases in peat temperature and decreases in water table (Windsor *et al.*, 1992), which could lead to the drying of methanotrophs, the methane consuming bacteria. This may also lead to the observed increase in methane flux variability.

MATERIALS AND METHODS

Site Description

Sallie's Fen is a temperate peatland located in Barrington, NH, USA (43 12.5' N, 71 3.5' W), approximately 12 miles from Durham, NH. The fen is approximately 1.7 ha and has been classified as a mineral poor fen because it receives most of its water from runoff and rainfall, as well as through a small ephemeral stream. The pH of the fen ranges from 4.1 to 5.7. The site has been previously described by Frolking and Crill (1994) and Bubier *et al.* (2003). The fen receives an average of 1100 mm of precipitation annually. The annual average temperature is 8.1° C, and an average annual growing season temperature is 17.1° C. The biologically active season is from late April through October. Plant senescence begins in late August.   The dominant vegetation of the fen is Sphagnum moss, along with leatherleaf (*Chamaedaphne calyculata*), sedge (*Carex rostrata* and *Carex aquatilus*), alder (*Alnus incana ssp. rugosa*), cranberry (*Vaccinium Oxyccacus*) and bog lily (*Menyanthes trifoliata*). The dominant ericaceous shrubs are leatherleaf, alder, and blueberry (*Vaccinium corymbosum* and *Vaccinium angustifolium*).

Methods

NEE and CH_4 flux measurements were made at 10 sites (collars) within the Fen (Figure 2). These sites span a range of heights above the water table and vegetation types (Table 2). The vegetation is generally low lying shrubs, sedges, and sphagnum mat, although a few alder shrubs and red maple trees reach approximately 1.8 m in height. The measurement sites are defined by a permanent metal collar in the peat, which is used to lessen disturbance to the site as well as to provide a seal for the measurement chamber.

We measured net ecosystem CO_2 exchange (NEE), respiration, and methane fluxes at each site on a weekly basis. We recorded the air temperature, peat temperature at a depth of 10cm, and the pH of the surface water simultaneously. NEE was measured using the static chamber method, as described by Caroll and Crill (1997). A clear Teflon chamber (volume=4.0074 x 10^5 cm^3) was placed over a metal collar that is permanently inserted in the peat. CO_2 concentrations were measured using a LICOR-6200 infrared gas analyzer (Licor Instruments, Lincoln, NE) for a period of 2 minutes. NEE was calculated from the change in CO_2 concentration over the measurement period. NEE was measured at three light levels to mimic a photosynthetic light response curve using shrouds that blocked out approximately ½ and ¾ of the photosynthetically active radiation (PAR), although only measurements made at PAR>1000 were used to ensure maximum rates of photosynthesis (NEE_{max}). We measured

ecosystem respiration during a dark measurement of NEE using a shroud to block light.

Methane measurements were taken during the dark run to avoid changes in temperature. Five methane samples were taken every two minutes for a ten-minute period. Methane concentrations were analyzed on a Shimadzu GC-14A gas chromatograph with a flame ionization detector at 50° C using Ultra High Purity Nitrogen (UHP N_2) as a carrier gas. The column is 2m 1/16" stainless steel and packed with PoropakQ. Precision is +/- 0.5%. Fluxes were calculated using a linear regression of the change in CH_4 concentration over the 10 minute period. CH_4 fluxes showing a statistically insignificant relationship and an r^2 of less than 0.75 (n=5), 0.87 (n=4) or 0.95 (n=3) were discarded.

Meteorological data and water table data were collected continuously at Sallie's Fen using an automated meteorological (MET) station. Hourly average meteorological data and daily average water table data are used in the analysis. Water table level at each collar was determined by using the daily average water table position and adding the collar height of each individual collar (Table 2). Water table levels were calibrated and equalized using manual measurements of water table depth and depth from peat surface for all years. During periods when meteorological data were unavailable, air temperatures and precipitation data were used from a weather station in Durham, NH, approximately 12 miles away. Water table data were linearly interpolated from 7 June-6 July 2003, when data were unavailable.

Species composition and biomass estimates of each collar were made during August 2003. Species composition was measured using a quadrat and estimating percent coverage within the collar. Biomass estimates were derived from counting stem height and number of each species within the color using algorithms from previous estimations (Burrows et al. 2005).

We determined the collar height using a tube level and the nearest surface water in August 2004. We measured the difference between the height of the collar and the water and assumed that the water table was uniform throughout the whole fen. We determined that the automatically measured water table level at the MET station was the reference point on that day. Using manual measurements of the water table depth at the automatic well, we calibrated the other years to the reference point. We use water table depth to represent the collar height measurement plus the depth below the reference point.

Data Analysis

We used NEE, photosynthesis, respiration, methane flux, air temperature, peat temperature, and water table data from 1 May- 31 August (Julian days 120-242) for the years 2000-2004. NEE, photosynthesis, respiration, air temperature, peat temperature, and water table depth data are referred to as independent variables (Table 3). Respiration is recorded as a negative number because it is a loss of carbon from the system. However, methane effluxes from the system are denoted by positive numbers.

We used certain criteria for data included in our analysis. NEE measurements were corrected using corrections described by Hooper *et al.* (2002). Only NEE measurements made in full light (PAR>1000) were used to avoid the effects of shading and to estimate maximum photosynthesis (PSN_{1000}). Respiration measurements were made using a fully shaded chamber. NEE measurements with a relative humidity greater than 80% were discarded due to plant stress leading to decreased photosynthesis. A natural-log transformation was used on the methane flux data to reduce skewness and to approximate a normal distribution (Appendix 1).

The collars we sampled included collars with different vegetation types, average height above water table, and biomass. We looked at relationships between our independent variables and methane to determine differences in temporal scale, as well as differences between dominant vegetation types. We used data from individual years, and also used combined data from all years (grouped years).

To look at differences in temporal scales, we used data from all ten collars. We looked at the relationships between the independent variables and methane on a seasonal scale using instantaneous fluxes and seasonal average fluxes. Instantaneous fluxes are the measurements that were taken in the field. The seasonal averages used in the analysis were means of all variables that were calculated for each collar in a season, as well as for all collars.

We also looked at the same relationships between independent variables and methane on a sub-seasonal scale by classifying measurements as being made in the "early" or "late" season. Early season consisted of measurements from 1 May- 30 June, while late season fluxes were from 1 July-31 August. Early and late season means were calculated to compare the differences between early and late season measurements.

We determined the two main vegetation groups, sedge and leatherleaf, from a measurement of collar species composition and biomass (Table 2). Leatherleaf collars consist of the three collars with the highest leatherleaf biomass (collars 6, 2, 11). Sedge collars consist of the three collars with the highest sedge biomass (collars 5, 7, 8).

SPSS 12.0 (SPSS Inc., Chicago, Ill.) was used for statistical analysis. Collar, year, NEE, photosynthesis, respiration, water table depth, air temperature, and peat temperature were all treated as independent variables. Methane flux and the natural log of methane were the dependent variables.

One-way ANOVA tests were conducted at $\alpha=0.05$ (two-tailed) to determine the differences between the independent variables in different years. We used the same analysis to determine the differences between collars. A Bonferroni post-hoc analysis was used to determine where differences occurred between the groups.

To determine the effects of the interactions between collar and year on methane fluxes, we conducted a two-way ANOVA at $\alpha=0.01$. This also tested

the significance of the effects of collar and year on methane fluxes. A correlation matrix/Pearsons test for correlation at $\alpha=0.05$ was used to determine the correlations between independent variables (Table 4). Regression analyses were conducted at $\alpha=0.05$ for single and multiple regressions. We used regressions to determine the relationships between our independent variables (air temperature, peat temperature, water table depth, NEE, photosynthesis, and respiration) and also correlation with methane fluxes. We used the Pearsons test for correlation to determine the inherent relationships between the factors we measured.

Multiple regressions included parameters for NEE, photosynthesis, respiration, air temperature, peat temperature, and water table level. In some cases, collar was added as a secondary explanatory variable. We modeled methane fluxes using all the independent variables as well as collar and year.

RESULTS

Differences among years

Environmental Variables. We observed differing air temperature, precipitation, and water table level among the years during the study period (Table 5). July and August had a higher mean monthly air temperature than May and June by an average of 2-3 °C. Mean seasonal air temperature is highest in 2001 and lowest in 2004. Water table level fell over the course of the summer, dropping as little as 13 cm over the season in 2001 and as much as 45 cm in 2002 (Figure 3). Cumulative precipitation was similar among all years except 2004 but varied in its timing and amount (Table 5, Figure 4).

Measured Variables. Measured variables differed among years and months (Table 6). Results of a one-way ANOVA (α=.01) indicated significant differences among years for photosynthesis ($F_{(4, 382)}$=3.831, p=.005) and methane fluxes ($F_{(4, 382)}$= 4.180, p=.003). A Bonferroni post-hoc analysis revealed no significant differences among photosynthesis measurements in individual years, indicating there were simply differences among years. The same analyses revealed significantly different methane fluxes between 2000 and 2002.

Within years, NEE, photosynthesis, and respiration showed a seasonal pattern. NEE showed a seasonal pattern of increasing values through mid-season

and then beginning to decline toward the end of the season (Figure 5), ranging from values of -0.57 μmol CO_2 m^{-2} s^{-1} to a peak value of 14.51 μmol CO_2 m^{-2} $s^{-1.}$ The components of NEE, photosynthesis and respiration, also increased in magnitude over the season (Figure 6). Photosynthesis values range from 3.8 μmol CO_2 m^{-2} s^{-1} to 22.2 μmol CO_2 m^{-2} s^{-1}, and followed the expected seasonal pattern with lower values in the beginning of the season, peak values during the mid-season (approximately day 180), and decreasing values at the end of the summer season as senescence began. Respiration values for Sallie's Fen ranged from -1.3 μmol CO_2 m^{-2} s^{-1} to -12.9 μmol CO_2 m^{-2} s^{-1}. Respiration showed similar patterns to NEE and photosynthesis, increasing throughout the season but not decreasing at the end of the season. Methane fluxes increased in magnitude and variability during the season (Figure 7), ranging from effluxes of 8.68 mg CH_4 m^{-2} day^{-1} on 15 August 2003 to effluxes of 3833.11 mg CH_4 m^{-2} day^{-1} on 31 July 2002. The seasonal increase is observed in all years (Figure 8), and becomes linear and normally distributed when a logarithmic transformation is applied to the methane flux (Appendix 1). We found significant differences between seasonal mean CH_4 fluxes between 2000 and 2004, and between years in July and August of several years (Figure 9, Table 6).

<u>Differences among collars</u>

The collars varied in species composition, biomass, height above water table, and location within the fen (Table 2). Similarly, mean seasonal NEE,

photosynthesis, respiration, and methane fluxes differed significantly among collars in the grouped years (Table 7, Figure 10). Collars 3, 4 and 6 had the highest mean seasonal respiration (-7.5 μmol CO_2 m^{-2} s^{-1}) and mean seasonal photosynthesis (15.3 μmol CO_2 m^{-2} s^{-1}). Collars 3, 4, and 6 were significantly different from all other collars in photosynthesis measurements and respiration values (which did not differ significantly from collar 10) (Figure 10) Collar 1 had the highest seasonal mean methane flux (680.6 mg CH_4 m^{-2} day^{-1}) which was significantly different from all collars but collar 4. Collar 7 had the lowest mean methane flux (181 mg CH_4 m^{-2} day^{-1}), which was not significantly different from any site except collar 1.

Effects of year and collar

Results of a collar by year two-way ANOVA (α=.01) indicated no significant interaction among collar and year on methane flux (Table 8). However, both collar and year individually had a significant effect on methane flux ($p<0.001$; $p=0.002$, respectively).

Correlations between variables

Using a Pearsons correlation analysis (α=.05), we found significant correlations between many pairs of the instantaneous measurements of independent variables (Table 4). The only variable without consistent correlations with other variables was NEE, which was only weakly correlated

with photosynthesis (r=0.044), and air temperature (r=-0.208). Julian day is

mostly highly correlated with methane flux (r= 0.423), followed by peat

temperature (r= 0.341), air temperature (r= 0.326), and respiration (r=0.223).

Correlations between variables and methane fluxes

Seasonal instantaneous measurements. Using seasonal instantaneous

measurements from 2000-2004, we found significant relationships (α=.05)

between methane fluxes and each of the independent variables except NEE (Table

9a) using a simple regression. Peat temperature, air temperature, and respiration

were the three factors having the highest correlation to methane fluxes over the

grouped years (r^2=0.12, 0.11, 0.10 respectively). Julian day (JD) also shows a

significant, positive correlations with methane fluxes (F (1, 385)= 83.814,

p<.001).

Air temperature was significantly positively correlated with methane flux

in 4 of 5 individual years (2000-2003), as well as all 5 years combined (Figure

11), although peat temperature had a slightly stronger r^2 (0.12 versus 0.11) in

grouped years. Similarly, respiration is significantly negatively correlated with

methane fluxes in 4 of 5 years (2000-2002, 2004) and also for all five years

(Figure 12). Water table depth was positively correlated with methane fluxes in

2000, 2002, 2004 (Table 9a). The regression between water table depth and

methane flux in the years 2000, 2002, 2004, and all years have a similar slope of

0.02, 0.03, 0.02, and 0.02, respectively (Figure 13).

Mean seasonal measurements. We did not find significant relationships between seasonal mean ln methane fluxes and seasonal mean NEE, photosynthesis, respiration, peat temperature, and water table depth when looking at grouped data from 2000-2004 (Table 9b). Mean seasonal air temperature was the only variable that expressed a significant relationship with mean seasonal methane flux in combined years (Table 9b).

When looking at individual years, mean seasonal air temperature showed a significant relationship with mean seasonal methane flux in 2001, and explained 58% of the variability in CH_4 fluxes (Table 9b). Water table depth showed a significant negative relationship with mean seasonal methane flux in 2001 and 2003 (Figure 14). Seasonal mean peat temperature showed a significant relationship with seasonal mean methane flux in 2002 (Table 9b).

Sub-seasonal Instantaneous Measurements. We found significantly lower values between the early and late season of respiration, photosynthesis, water table depth, air temperature, peat temperature, and methane flux (Table 10). Methane fluxes were more than two times higher during the late season than the early season, with very large standard deviation. Water table level during the late season was 12 cm lower than the early season. Mean air temperature and peat temperature were 2ºC and 3º C higher, respectively, than the early season.

In the early sub-season, we found significant relationships between methane fluxes and NEE, respiration, photosynthesis, air temperature, and peat temperature (Table 11a). We found no significant relationships between any

independent variables and methane fluxes in 2003 (Table 11a). We found significant correlations (α=.05) between all independent variables and methane fluxes in at least one individual year (Table 11a). NEE had a significant positive correlation with methane fluxes in 2000, photosynthesis had a significant positive correlation with ln CH_4 in 2000 and 2002, and respiration showed a significant relationship with methane fluxes in the early season of 2000, 2001, and 2002 (Table 11a).

In the late sub-season, we found significant relationships (α=.05) between methane flux and NEE, respiration, air temperature, and peat temperature in all years (Table 11b). In individual years, we found significant relationships between methane fluxes and NEE (2001, 2004), respiration (2000), air temperature (2000, 2001, 2003), and peat temperature (2001). We found no significant relationships between methane fluxes and photosynthesis and water table depth in any individual years, or all years combined.

Vegetation groups. The mean methane emissions of the collars with the highest sedge biomass were not significantly higher than methane emissions of leatherleaf dominated collars (p=0.682). Only mean respiration was significantly higher at leatherleaf collars than sedge collars using all years (p=.004), while mean water table depth was significantly lower (p=.007) at sedge collars than leatherleaf collars (Table 12).

Sedge collars showed significant relationships showed with higher correlation coefficients than all collars combined and leatherleaf collars. We

found significant correlations between methane fluxes and respiration,

photosynthesis, air temperature, peat temperature, and water table depth for all

years combined (Table 13a).   The same relationships also occurred in 2000 and

2001. They also occurred in 2002 with the exception of a relationship between

methane and photosynthesis. However, we did not see any significant

relationships between methane fluxes and the independent variables for sedge

collars in either 2003 or 2004. Water table depth accounted for anywhere from

31% of the variability of methane fluxes in all years, to 50% of the variability in

2002.

Leatherleaf collars showed significant relationships between methane

fluxes and respiration, photosynthesis, air temperature, and peat temperature for

all years combined (Table 13b). However, the correlations coefficients are lower

than sedge collars. Methane fluxes showed significant relationships with

respiration in 2002 and 2003, with air temperature in 2002 and 2003, and with

peat temperature in 2000 and 2004.

Modeling methane fluxes using multiple regression

We found that collar and year had a significant effect on methane fluxes

(Table 8), and included these as the first model. The first model using collar and

year to predict methane flux was significant at $\alpha=.05$ and had an $R^2=0.11$ (Table

14). In the second model, we included all the independent variables in addition to

collar and year. The model fit increased from an $R^2=0.11$ to 0.372 with the

addition of NEE, respiration, photosynthesis, air temperature, peat temperature, and water table depth. The coefficients for NEE, respiration, and water table depth in the regression were all significant (Table 14).

DISCUSSION

Variability among years and collars

     Yearly environmental differences. All five years of our study had slightly different environmental conditions during the measurement season of May through August (Table 5). However, some general characterizations can be made. The temperature in 2000 was near-median and it received normal amounts of precipitation (336.5 mm). 2001 was warm and dry, but the water table level did not fall until August. 2002 was also warm and showed the largest drop in water table, reaching a minimum of 54.1 cm below the peat surface in August 2002 (Figure 3). This was the lowest water table during our study period. 2003 had the median seasonal temperature but was relatively dry. 2004 was the coolest, wettest year. In August, it received nearly six times the precipitation of August 2001 (Figure 4).

     Yearly differences of measured variables. We did not find strong differences between years when we looked at a seasonal scale. Using combined data from all collars, we found no significant differences among years for NEE and respiration, and only a significant effect of year on photosynthesis. In a Bonferroni and Scheffe post-hoc analysis, photosynthesis did not show significant differences between any individual years. This indicates that significant pair-wise

differences between years do not occur, however, there may be differences between groups of years. For example, 2000 and 2001 have lower seasonal mean photosynthesis than 2003 and 2004, while 2002 has intermediate values. Environmental conditions are not identical within these pairs of years (Table 5), indicating that some other factor affected photosynthesis. Because photosynthesis is higher in 2003 and 2004, conditions may have become more favorable for some plant species. Bubier *et al.* (2003) found differing moisture and temperature regimes favored different plant species, meaning that a combination of air temperature and water table level may have increased productivity of different species and increased the overall photosynthesis. When mean photosynthesis is broken down by collar and year (Table 7), we see significant differences at two collars between 2000 and 2003, which may explain some of the interannual variation when collars are grouped.

Monthly differences between years. We compared monthly mean measurements between years to determine control on measures of plant productivity at a lesser time scale. We found significant differences of monthly values among years. NEE measurements are significantly different between June 2000 and 2001 and other years (Table 6a). Additionally, we found differences in mean seasonal photosynthesis in these years. When comparing the minimum monthly mean NEE and photosynthesis in June, we found correlations between low NEE measurements and low photosynthesis measurements. These differences

in NEE seem to be driven by differences in photosynthesis between these years (Table 6c) because there are no significant differences between respiration values.

Although 2000 and 2001 show similar values of plant productivity (NEE, respiration, photosynthesis), they do not have similar environmental conditions. 2000 is cool in May and June with a median water table level, while 2001 shows warm temperatures and a high water table level. This leads us to believe that monthly differences in NEE are not related to environmental variables that we measured and are driven by differences photosynthesis, not respiration. Differences in NEE and photosynthesis between years may be related to the amount of photosynthetically active radiation (PAR) received or number of sunny days during the month instead of other environmental conditions. If 2000 and 2001 had a similar number of sunny days and neither were impacted by environmental conditions, plant productivity might have been the similar, like our measurements indicate. Unfortunately, we did not measure the number of days with ideal growing conditions. This does also indicate that environmental conditions may not limit plant productivity in May and June.

Highest mean seasonal values of NEE, respiration, and photosynthesis occur in 2003 and 2004. This appears to be counter-intuitive because these years appear to have very different environmental conditions. 2004 is cool and wet with the highest mean seasonal water table average, while 2003 is dryer and warmer. The only similarity in the measured environmental variable is a dry June, which corresponds with the month where the significant differences in NEE

and photosynthesis occur. Previous research has found that warmer and drier conditions as predicted by global climate change models (GCMs) may increase plant productivity (Waddington *et al.*, 1998; Weltzin *et al.*, 2000). We found that drier conditions will result in higher values of photosynthesis and respiration, but also that the NEE during maximum PAR is also higher, indicating higher productivity. It is possible that if we had been able to measure May 2003, we would not have found such similar values, which is another explanation for why we find similar values of plant productivity despite varying environmental conditions.

Methane flux values. Mean seasonal methane fluxes ranged from 203.7 to 423.3 mg CH_4 m^{-2} day^{-1} from 2000-2004. Instantaneous methane fluxes varied 400-fold, ranging from 8.9 to 3833.1 mg CH_4 m^{-2} day^{-1}. The highest mean monthly methane fluxes occurred in August 2001 and 2002 (634.1 mg CH_4 m^{-2} day^{-1} and 622.1 mg CH_4 m^{-2} day^{-1}, respectively). Monthly average methane fluxes are in the range of fluxes reported by Frolking & Crill (1994) at the same site, and also those reported by Bellisario *et al*. (1999) at a peatland complex in Canada.

We found significant differences among years for mean seasonal methane fluxes, with significant differences between two individual years, 2000 and 2002 (Table 6c). This may have been due to differences in environmental variables between these two years. Cumulative precipitation was very similar but varied in its distribution among months. 2000 received over 113 mm of precipitation in

July, while precipitation was 20.8 mm in July 2002 (Table 5). Similarly, the mean water table depth for August 2002 was 45.4 cm below peat surface, while the water table depth for August 2000 was 15.4 cm. Furthermore, when we looked at methane fluxes on a sub-seasonal level, we found no significant differences between the early parts of the seasons in 2000 and 2002 (Figure 9, Appendix 3a). However, there were significant differences between the methane fluxes in the late sub-season (Appendix 3b), suggesting that the differences between the years were driven by the significantly higher mean seasonal methane fluxes in the later part of 2002 that correlated with the exceptionally dry period with a low water table level. Windsor *et al.* (1992) described a pressure gradient that occurs with a drop in the water table level, increasing methane fluxes for a short period of time (<2 days). We found consistently higher methane fluxes throughout the rest of the season in 2002 (Figure 7), not simply a period of a few days. This could be because the water table kept decreasing (Figure 3). A previous study by Frolking & Crill (1994), conducted at Sallie's Fen, found the interannual variability of methane fluxes were related to differences in environmental variables.

Differences among collars. Differences among collars of the measured variables were evident at a seasonal scale. The mean methane flux for collar 1 was significantly higher than all other collars except collar 4 (Figure 10). Collar 1 was located near the lag of the fen (Figure 2) and was the wettest collar (Table 2), so theoretically it should produce the most methane (Bartlett *et al*. 1992;

Reeburgh *et al*. 1998). Despite being the wettest collar, it has no sedge biomass
as would be expected in a wetter collar.

Seasonal mean methane fluxes were the highest in 2002 in all sites except
collars 6 and 2. While the differences between the years is non-significant, it is
interesting that these collars show higher mean seasonal methane fluxes in
different years. Collars 2 and 6 are not spatially close to each other (Figure 2) and
have quite different heights (Table 2). However, these are both collars that have
substantial leatherleaf biomass. We don't see this behavior at other collars with
high leatherleaf biomass, perhaps because none of the years are significantly
different from eachother.

Collar groups. The groupings that we used to differentiate collars by
vegetation type did not necessarily reflect the groups evidenced by the mean
collar measurements (Figure 10). We grouped collars by whether they had the
largest amount of sedge or leatherleaf biomass relative to the other collars. This
was not always the dominant species; collar 6 is dominated by a small white pine
tree.

Natural groupings were evident when we looked at the values of the
measured variables. For example, collars 3, 4, and 6 never differed significantly
from each other in measurements of NEE, respiration, or photosynthesis. Collars
4 and 6 had large amounts of woody biomass in the form of a few alder shrubs
and a white pine sapling, respectively. Collar 3 is very close in proximity to
collar 4 (Figure 2), and has similar water table level, but has no woody biomass

other than leatherleaf (Table 2). Additionally, collars 2, 5, and 8 had similar

values in mean measured variables for the grouped years (Figure 10), especially

NEE and respiration. Collars 5 and 8 are classified as sedge collars, but collar 2 is

classified as a leatherleaf collar and has no sedge biomass (Table 2). When

further broken down, maximum and minimum mean annual measurements do not

correspond between these collars. Finally, methane fluxes are not significantly

different among most collars, with the exception of collar 1 (Figure 10). The

spatial variability disappears except for lag sites (collar 1) with differing biomass

and water table when using a long time scale of measurements to account for the

interannual variability. Additionally, future research should group collars by their

height above the water table to determine the differences among wetter collars

and drier collar, even though differences seemed to disappear over a longer time

scale.

Predicting Methane Fluxes

    Time scales. We found differing relationships among the independent

variables and methane fluxes depending on the length of time we considered. We

looked at the seasonal scale using seasonal mean measurements and instantaneous

measurements. We also looked for relationships at the sub-seasonal scale,

looking at the early sub-season (May and June) and the late sub-season (July and

August).   We also looked at an interannual scale, using five individual years as

well as grouped years (2000-2004).

Seasonal mean methane fluxes. Relationships between methane fluxes and environmental variables and measured variables were significant depending on the time scale we used. Seasonal mean measurements showed no relationships with the measured variables (Table 9b), indicating that productivity at the seasonal scale is not correlated with seasonal mean methane fluxes.

In the five grouped years, there was a weakly correlated relationship between seasonal mean air temperature and seasonal mean methane flux. In the five individual years, seasonal mean measurements only showed significant relationships with mean methane fluxes and the environmental variables: water table, air temperature, and peat temperature (Table 9b). These relationships explained much of the variability in methane flux measurements (r^2=0.41-0.58), but were not consistent throughout the years and were not observed in 2000 or 2004, which were the coolest and wettest consistently throughout the summer (Table 5). Because these years were consistently wet, we did not observe large decreases in the water table level (Figure 3). Water table level variations over the season were less than 25 cm in these two years, which may have reduced a pressure gradient that forces methane fluxes to diffuse. Additionally, if air temperatures were low and water table was high, peat temperature probably remained low, and conditions were not favorable for methanogenesis and other microbial activity.

Seasonal mean methane fluxes were only correlated with environmental variables in individual years, indicating that the environmental variables are more

important than measured variables on a seasonal mean basis. Lack of significant

relationships between seasonal mean methane fluxes and environmental variables

in cool, wet years indicate that certain parameters that we did not measure may

significantly relate to and pose some sort of limitation on methane fluxes. This

might be microbial population size, either of methanogens or methanotrophs. Net

ecosystem productivity for all species over the course of the season might be

reduced in cool wet years due to fewer days with full sunshine, resulting in less

available substrate for methanogens. If these biotic processes are limited by

temperature and sunshine, methane fluxes will most likely not correlated directly

to environmental variables, like we have observed.

Seasonal instantaneous methane fluxes. Relationships between methane

fluxes and the independent variables were more common when we looked at

instantaneous fluxes. At a seasonal instantaneous scale, we found significant

relationships between methane fluxes and all independent variables except NEE

(Table 9a). We also observed relationships between methane fluxes and nearly all

the variables in 2000 and 2002. Respiration showed significant relationships with

methane fluxes in 4 of 5 individual years. The slopes of the regression between

respiration and methane fluxes varied between individual years, as did the

correlation coefficient (Figure 12, Appendix 2a). Similarly, the slopes of the

relationship between methane flux and air temperature were different between

individual years, and the r^2 of the relationships between the variables increased

from the grouped years to 2001 and 2002 (Figure 11). At an instantaneous scale,

the significance of relationships and the slope of the regression lines between independent variables and methane fluxes vary widely among years for most factors (Appendix 2a). This emphasizes the high interannual variability that we find at the instantaneous scale when trying to predict relationships between methane, plant productivity, and environmental factors, even when statistically significant relationships exist. However, we do not find significant differences between many measures of plant productivity when we consider a full-season time scale, only differing degrees of correlation and differing slopes of the relationships.

Differences between early and late sub-season. Because patterns between methane fluxes and independent variables were not consistent among years and only explained 28% of variability at the most, we looked at a sub-seasonal scale to further explain methane flux variability. We observed significant differences between the two parts of the season, the early and late sub-season (Table 10), which may be the reason we are finding low correlations between the independent variables and methane fluxes at the seasonal scale. Early and late sub-seasons also differed in the relationships between the factors that I considered and methane emissions (Table 11). Differences between the early and late sub-season may be due to increases in peat temperature and decreases in water table, which could lead to the drying of methanotrophs, the methane consuming bacteria. This may also lead to the observed increase in methane flux variability (Figure 7).

Sub-season methane fluxes. The early sub-season showed stronger relationships with more independent variables than the late season for all grouped years (Table 11). Methane fluxes in the early season were significantly correlated with ecosystem respiration in the grouped years, as well as in 2000, 2001, and 2002. Methane fluxes in the late season were significantly correlated with air temperature in the grouped years and 2000, 2001, and 2003 (Table 11b). In the late season, respiration is only significantly correlated with methane flux in 2000 and the grouped years. Respiration is a significant predictor of methane flux in individual years in the early part of the season, and not in the later part of the season in most years, indicating that respiration varies in importance during different parts of the sub-season.

Similarly, other independent variables are predictors of methane fluxes in the early season and not in the late season (Table 11). The fewer observed relationships between independent variables and methane fluxes during the late sub-season could be due simply to the high variability of methane fluxes (Figure 7), or due to differences in environmental variables (Table 5). It also could be a function of accumulated differences in environmental conditions and plant productivity that result in high interannual variability of relationships with methane. Differences between the early and late sub-season of the strongest and most consistent predictors of methane fluxes indicate that the independent variables vary in importance to methane fluxes within the same growing season.

Minimum and maximum monthly methane fluxes. We further broke down the sub-season and looked at correlations between maximum and minimum mean monthly methane fluxes and environmental and measured variables during the five year period. There were no significant differences in any of our measured variables in the earlier part of the season, indicating that the timing of snowmelt and spring may not influence fluxes on a monthly scale by May and June.

In May and June, high methane fluxes corresponded with high plant productivity (NEE and photosynthesis) (Table 6). Similarly, low methane fluxes in May, June, and July corresponded to the lowest plant productivity. We did not observe correlations between productivity and methane fluxes in August. Low respiration values correlated with low methane fluxes in May and July, but not June or August.

Both minimum and maximum mean monthly plant productivity measurements (as measured by full-light NEE) are positively correlated with minimum and maximum methane fluxes in May and June (Table 6). July shows correlations between minimum plant productivity and minimum methane fluxes, but not between high plant productivity and high methane fluxes. July also shows a correlation between minimum methane fluxes, minimum respiration, and minimum temperature. July appears to be a transition time with correlations between low methane fluxes and productivity as well as environmental factors, perhaps because we see correlations also between low air temperature and low respiration. There do not seem to be any correlations between methane fluxes and

plant productivity in August, corresponding with our results indicating a relationship between methane fluxes and environmental variables in the late sub-season but not with other variables (Table 11b). This indicates that plant productivity controls methane fluxes in the early part of the season but not as much in the late part of the season.

In the early part of season, the water table is much higher than the later part of the season. Waddington *et al.* (1996) found that plant productivity enhanced methane fluxes only in wet sites with a water table near the surface, like Sallie's Fen (mean WTD= 9 to 24 cm).

We observed correlations between high methane fluxes and high air temperatures in May, July, and August. This is what we expected to find because higher temperatures stimulate higher microbial activity and higher rates of methanogenesis (Dise *et al.*, 1993; Frolking & Crill, 1994). However, we found the opposite trend in June.

Additionally, we found that high methane fluxes were correlated with low precipitation, while low fluxes were correlated to higher precipitation. The highest methane fluxes showed correlations with the lowest water table level in both July 2002 and August 2001 and 2002. Joabsson & Christensen (2001) found that large precipitation events suppressed methane fluxes and destroyed relationships between plant productivity and methane fluxes. The lowest mean monthly flux in August, 2003, coincides with a water table increase (Figure 3) and a steady receipt of precipitation (Figure 4). Wetter conditions are predicted to

produce higher methane fluxes due to a change in water table level that favors anaerobic respiration, although generally we did not see strong correlations between mean monthly methane fluxes (Table 6d) and mean monthly water table level (Table 5). Measurements of maximum photosynthesis and NEE may not be effectively and accurately capturing plant productivity if wetter conditions correspond with increased precipitation and fewer days in which maximum photosynthesis occurs. This seems to indicate that using net ecosystem productivity (NEP) to approximate plant productivity might be more appropriate and effective. NEP would be more reflective of productivity on a longer time scale than a short period of measurements made at full-light during the day.

Vegetation Groups. Even when broken down to a sub-seasonal level, methane fluxes are still not easily and consistently predicted across all five years of the study. We thought this might be due to the high collar variability (Table 7), so we grouped the collars by vegetation type. Collar classification was based on species biomass within the collar. These groups didn't necessarily reflect the natural groupings based on the mean measurements over the five year period (Figure 10). However, methane fluxes were more highly and consistently correlated with independent variables in sedge collars than all collars combined for 2000-2002 as well as the grouped years (Table 13). In the leatherleaf collars, methane fluxes were significantly correlated with environmental variables, photosynthesis, and respiration in individual years. However, there were fewer significant relationships between the independent variables and methane fluxes.

Correlations between methane fluxes and air temperature seem to be limited to years with high air temperatures and low precipitation in July and August. This implies that methane fluxes are coupled with environmental conditions through late-season conditions only in warm, dry years.

Sedge collars. Methane fluxes from sedge collars were not significantly correlated with plant productivity or environmental variables in 2003 or 2004. Maximum mean seasonal NEE and maximum (in magnitude) respiration were recorded in these two years for sedge collars (Table 7), while maximum methane fluxes occurred in 2002 for all three collars that comprise the sedge group. 2003 and 2004 are similar and differ from other years because these two years receive more than twice as much precipitation in August as they did in July (Table 5). When we look at where fluxes from these two years fall relative to the other years, we find that methane fluxes in 2003 and 2004 are lower than other years in the later part of the season after day 210 (Appendix 4). In 2003, these low fluxes correspond with an increase in water table level following a precipitation event. Similarly, in 2004, low fluxes correspond to a large precipitation event. If the precipitation event does not directly suppress fluxes, the decrease in atmospheric pressure may affect the diffusion gradient (Bubier *et al.*, 1993b; Moore & Dalva, 1993; Scranton *et al.*, 1993), reducing the methane flux to the atmosphere via diffusion. Storm events combined with high respiration and NEE may have may have altered relationships between plant productivity, environmental conditions, and methane fluxes.

Differences between sedge and leatherleaf groups. We hypothesized that we would see higher methane fluxes in sedge collars than leatherleaf collars (Shannon *et al*. 1994; King *et al*. 1998). This was not the case. Mean seasonal methane fluxes were not significantly different between the two vegetation groups (Table 12). However, the relationships between methane fluxes and independent variables are much stronger in the sedge collars than the leatherleaf collars (Table 13). Methane fluxes were highly positively correlated with water table depth at sedge collars (Appendix 5). We would expect to find an contradicting relationship for several reasons. Findings by Waddington *et al*. (1996) indicate sedges decrease in importance of transporting methane during periods of low water table level. Sedges also have lower rates of photosynthesis in dry years (Bubier *et al*. 2003), so they would not allocate as much carbon to their roots as during more productive years, meaning that there would be less substrate for methanogenesis. We might be finding increasing methane fluxes with decreasing water table level because we are using instantaneous measurements for the whole season, which also showed a the opposite relationship with methane flux than what we expected. It may also be due to the pressure gradient that forces methane stored in the peat to diffuse increases the rate of transport through the sedge plants, increasing methane fluxes.

Multiple Regression. Single variable relationships between methane fluxes and environmental and measured variables did not completely explain the variability of the observed methane fluxes. Many individual variables had a

correlation coefficient (r) of approximately 0.3 in the grouped years, and thus only explained approximately 15% of the variability of methane fluxes (Table 4). Additionally, we demonstrated that both collar and year had significant effects on methane flux (Table 8). To determine the cumulative effect of all the variables and account for the variability due to differing environmental conditions in different years and collars, we constructed the multiple regression.

Predictors of methane fluxes. The combined effects of collar and year explained some (r^2=0.11) of the variability in methane fluxes, while when the independent variables were added, the fit increased to r^2 =0.372 (Table 14). This is much higher than any individual r^2 from the seasonal instantaneous measurements. The results indicate that it is appropriate to use an integrative approach to model methane fluxes at a seasonal instantaneous scale that incorporates environmental variables and measured variables, and accounts for collar and year variability. However, to determine the effects of year and collar it is necessary to have detailed measurements over a longer measurement period.

The fit of the model might have been increased not by adding other factors that we measured, although rates of production and rates of oxidation might have been helpful. Model fit might have increased had we reduced the number of measurements we used by simply modeling smaller groups such as shrub collars, sedge collars, early sub-season, late sub-season, dry collars, and wet collars. Other possibilities for groups are to model by seasonal mean values, as well as biomass measurements.

When we included the independent variables in the model in addition to year and collar, photosynthesis was excluded as a predictor and air temperature was included as a non-significant predictor (Table 14). Air temperature is significantly correlated with methane fluxes in four of five individual years at a seasonal instantaneous scale. Photosynthesis shows relationships with methane fluxes in two individual years and grouped years, while NEE shows significant correlations with methane fluxes only in 2000. Both air temperature and photosynthesis were replaced from the model due to the high correlations with other variables that were significant in the model (Table 4). This indicates that all environmental and measured variables are important to predicting methane fluxes, although some were excluded from the model.

Julian day as a predictor of methane fluxes. In addition to the multiple regression, Julian day seems to be an excellent predictor of methane fluxes (Table 9a). This might be because Julian day is the best proxy for the seasonal environmental conditions, like the increases in air and peat temperature, and the water table drop due to decreased precipitation and increased evapotranspiration (Table 4). Additionally, photosynthesis, respiration, and methane fluxes all show seasonal patterns, which are all correlated with Julian day (Table 4. Julian day may be another way to predict methane fluxes for modeling purposes, although more study is necessary.

Relationships between independent variables and methane fluxes

Hypothesized relationships. We expected to see simple relationships

between independent variables and methane fluxes that would be consistent

among the years of our study. We didn't anticipate finding differing relationships

between the temporal scales of the study like we did, or high interannual

variability of these relationships.

Net ecosystem exchange and methane fluxes. We did not see significant

relationships between methane and NEE when we looked at data from all collars

on a seasonal time scale, using either seasonal instantaneous measurements and

seasonal mean measurements. However, when we separated the data into early

and late season or by vegetation type and did not combine multiple years**,** we

observed a correlation between instantaneous measurements of NEE and CH_4

(Table 11). Additionally, methane flux had a significant, positive relationship

with NEE in the early season for 2000-2005 as well as 2000, but had a significant,

negative relationship with NEE in the late season using the grouped years and

2001 (Table 11). This reflects the general decrease of NEE measurements

between July and August of all years and underscores the high variability of

relationships between the independent variables and methane fluxes.

Furthermore, we found that a monthly scale is probably better than a sub-seasonal

scale at predicting methane fluxes when we looked at correlations between plant

productivity and methane fluxes on a monthly basis. We also found that NEP

might be a better predictor of primary productivity and more indicative of overall

productivity over the course of the whole summer in conditions that are wetter and result in less sunlight.

We may not observe relationships between NEE and methane fluxes at a seasonal instantaneous scale due to the possibilities of a lag time between peak NEE and peak methane fluxes. We expected to see a lag time between NEE measurements during full-light and peak methane effluxes (Bellisario *et al*. 1999; King *et al*. 2002; Strom *et al*. 2003) due to the plant production of substrate. There is a lag between production and methanogenesis, and more lag before methane transport occurs. Our measurements and analysis really had no way to quantify the lag time.

NEE, photosynthesis, and sedge collars. We expected to observe a correlation between NEE and methane fluxes at sedge collars, despite the lag time between high NEE and methane fluxes (Waddington *et al*. 1996; King *et al*. 1998; Joabsson *et al*. 2001). Sedges are very efficient in methane transport, as well as root carbon allocation (Yavitt *et al.* 1990). Higher NEE can indicate higher primary productivity, and subsequent input of methanogenic substrate (Joabsson *et al.* 1999; King *et al*. 2002; Strom *et al*. 2003) as well as higher potential for methane transport via vascular plants (Shannon *et al*. 1996). We did not observe a significant relationship between NEE and methane flux at sedge collars, but we did observe a correlation between photosynthesis and methane flux (Table 13).

Photosynthesis and methane fluxes. Photosynthesis had a significant positive correlation with the simultaneously measured methane flux (Table 4).

The relationships were the most highly correlated in the early sub-season and in the sedge collars (Table 13a). This may have been because maximum photosynthesis has been occurring for longer than the 2 hour lag time for methane production found by King & Reeburg (2002). Subsequently, the recently-fixed photosynthates may have been available to the methanogens for methane production through the mechanisms described for NEE above. Maximum photosynthesis measurements may better reduce the lag time between plant production and methane production.

Water table depth and methane fluxes. The relationship between methane and water table depth varies depending on the time scale. We expected to see a negative relationship between increasing water table depth and methane fluxes as the lower water table level favors aerobic respiration and methane oxidation (Bubier *et al*. 1993; Dise *et al*. 1993; Moore *et al*. 1993; Aerts *et al*. 1997). When looking at seasonal instantaneous scale, we see positive correlations between water table depth and methane flux in the grouped years and several individual years (Figure 13), indicating that a lower water table position produces higher methane flux at the instantaneous scale. Bellisario *et al*. (1999) also found inverse relationships from those expected between water table level and methane flux. However, we see significant negative correlations between water table depth and methane flux in 2001 and 2003 at the seasonal average scale with higher correlation coefficients (Figure 14). Neither 2001 nor 2003 show significant relationships at the seasonal instantaneous scale. 2001 and 2003 are

both dry years with similar temperatures in July and August (Table 5), and show the expected relationship of decreasing methane fluxes with decreasing water table level.

Finally, the collar with the highest water table level (collar 1) consistently shows the highest mean seasonal methane fluxes (Table 6), indicating that average water table position still determines methane fluxes, but there might be other factors that affect the relationship. Collar 1 receives the least sun, spending many mornings and late afternoons in shade and consequently has a low biomass. Higher methane fluxes from this site indicate that water table controls methane fluxes at this wet site, not plant productivity.

Water table depth, methane flux, and the sub-season. Early sub-season fluxes show both positive and negative correlations between methane flux and water table depth, but no significant relationships were observed during the late sub-season (Table 11b). The sign change of the relationship between water table depth and methane flux between the instantaneous scale and the seasonal scale indicates that water table depth is a better predictor of methane flux at the seasonal scale than the instantaneous scale, which is similar to findings by many researchers (Bubier *et al*. 1993; Dise *et al*. 1993; Bubier 1995; Waddington *et al*. 1996; Moore *et al.* 1997). We may be seeing positive relationships between water table depth and methane flux at the seasonal instantaneous scale because the water table is relatively close to the peat surface (e.g. Kettunen *et al*. 1996).

Respiration and methane fluxes. We expected to see a positive relationship between respiration and methane flux, when methane efflux was represented by positive numbers and respiration was represented by negative numbers because respiration and methane production are affected by water table depth in opposite ways (Alm *et al*. 1999). However, we observed a negative correlation between respiration and methane flux (Table 4) that was consistent across time scales and species groups (Table 9, 11, 12). Respiration was correlated with methane fluxes at a seasonal instantaneous scale in many individual years. Respiration has been correlated to water table level, temperature, and plant productivity (Bubier 2003). The same factors also control methane fluxes (Bubier *et al*. 1995, Joabsson *et al*. 2001). However, different types of microbes produce methane and CO_2 and the fundamental difference is the use of aerobic or anaerobic respiration. The significant correlations with methane fluxes at a seasonal instantaneous time scale indicate that similar conditions favor both anaerobic and aerobic respiration, which is also indicated by the significant increase in methane fluxes with increasing WTD.

However, when considering longer time scales, such as mean seasonal values, there are no correlations between respiration and methane flux. This could be because significant, strong correlations between the two processes are observed during the early sub-season, but only weakly during the late sub-season in fewer years (Table 11).

Air temperature and methane fluxes. Air temperature shows a significant relationship with methane fluxes on an instantaneous scale in the grouped years, as well as four of five individual years (Figure 11). Methane fluxes are also significantly related to air temperature at all the time scales I looked at, from instantaneous, to partial season for both early and late halves, to full season . Numerous studies have found relationships between temperature and methane flux, so it is understandable that relationships with temperature are observable at all scales.

Peat Temperature and methane fluxes. Peat temperature was also positively correlated with methane fluxes (Table 4). While peat temperature was significantly correlated with methane fluxes over many different time scales, air temperature was often more strongly correlated with methane fluxes. Due to the significant correlations between air temperature, water table depth, and peat temperature, we only thoroughly discussed air temperature and water table depth because of the ease of measurement.

Implications for global climate change

Peatlands have the potential to be either a positive or negative feedback to global climate change. The contributions of Sallie's Fen to global warming are unclear. We might expect to find increasing productivity with warmer, drier future climates because we found significant positive relationships between photosynthesis and air temperature and also between photo and water table depth

(Table 4). We found significant positive correlations between respiration and water table depth and air temperature, indicating that increases in water table depth and air temperature will lead to higher values of respiration (Table 4). NEE, however, the best measure of the carbon balance over the measurement period, was not significantly correlated with water table depth but was significantly negatively related to air temperature (Table 4), indicating that at higher temperatures would decrease carbon storage in Sallie's Fen.

Similarly, implications of global climate change and higher air temperatures and projected low water table levels for methane fluxes are unclear. We found significant positive relationships between methane fluxes and air temperature as well as water table depth at a seasonal instantaneous scale (Table 4). We found significant positive relationships between methane fluxes and air temperature using seasonal means of grouped years (Table 9b). A lower water table level will also affect methane fluxes on differing time scales. An increase in water table depth significantly correlated with higher methane fluxes on an instantaneous time scale. However, on a seasonal average time scale, we found the opposite. We found that an increase in water table depth significantly correlated with a decrease in methane fluxes in dry years showed no relationship. The early sub-season showed high interannual variability in relationships, while the late sub-season showed no relationships at all (Table 11). Temperature increases will lead to higher methane fluxes, but effects of a lower water table level are unclear due to the differing relationships at different time scales. It is

likely though, that if conditions are drier overall throughout the summer, and we

do not observe drops in the water table (as in 2002), methane fluxes will decrease

because of the decrease of methane fluxes found with increasing water table depth

at a seasonal average time scale.

Using the multiple regression to attempt to estimate methane fluxes due to

global warming. We used the correlation coefficients of NEE and respiration

with water table depth and air temperature to assign a direction to changes in

methane fluxes. With increases in water table depth, increases in air temperature,

corresponding increases in peat temperature and corresponding increases in NEE

and respiration, we expect to see larger methane fluxes. However, as

demonstrated before, instantaneous increases in methane fluxes do not necessarily

translate into higher seasonal mean measurements. Additionally, each collar

might not see increased methane fluxes due to high spatial variability (Figure 10).

CONCLUSIONS

The importance of environmental conditions and measurements of plant

productivity to predicting methane fluxes varies depending on time scale. When

looking at multiple years as a group and combining multiple sites, we find low

spatial and interannual variability. Significant differences in methane fluxes can

be attributed to differences in water table, with significant differences in one year

and at one site. However, if we look at smaller temporal and spatial scales by looking at individual years and individual sites, we find increased variability in controls on methane fluxes. Additionally, factors such as plant productivity become important controls on methane fluxes. At the mean seasonal scale, differences in methane fluxes seem to be driven by environmental controls in warm years, and differences in biotic processes of methane formation in cool, wet years. Differing environmental conditions between years creates favorable years for some vegetation types represented by sites, but there are no significant differences over a long time period.

Furthermore, environmental and measured variables affect methane fluxes a varying scales. Seasonal instantaneous methane fluxes are highly correlated with both measures of plant productivity, respiration, and environmental variables. Due to correlations with environmental and measured variables, seasonal instantaneous methane fluxes vary highly among years, sites, and within years. Julian day is one factor that seems to incorporate temporal changes of both environmental conditions and changing plant productivity, and correlates strongly with methane fluxes.

Variability in seasonal instantaneous measurements can also be eliminated by dividing measurements into sub-season or monthly measurements that accommodate the relative importance controls. Both plant productivity and environmental controls affect methane fluxes in May and June (the early sub-season), while fluxes in July and August (the late sub-season) are mainly affected

by environmental controls. These two parts of the season are significantly different, which may lead to few observed relationships at the seasonal scale.

Grouping data by vegetation type was another way to reduce spatial and temporal variability of instantaneous methane fluxes. Sedge collars showed strong relationships with plant productivity and environmental variables, despite not having significantly different methane fluxes from leatherleaf collars. Leatherleaf collars showed significant positive correlations with environmental variables that were most prominent in years with a dry, warm July and August. Environmental conditions clearly impacted methane fluxes. Warm and dry conditions resulted in higher values of photosynthesis, respiration. It is unclear whether this resulted in an higher NEP than cooler, wetter conditions, which makes it difficult to directly link NEE, photosynthesis, and methane fluxes. Methane fluxes showed stronger correlation with plant productivity on a seasonal instantaneous scale than a seasonal mean scale, and these correlations were due to correlations between productivity and methane fluxes in May and June. In the later summer, with higher air temperatures and lower water table level, correlations between methane fluxes and plant productivity disappeared.

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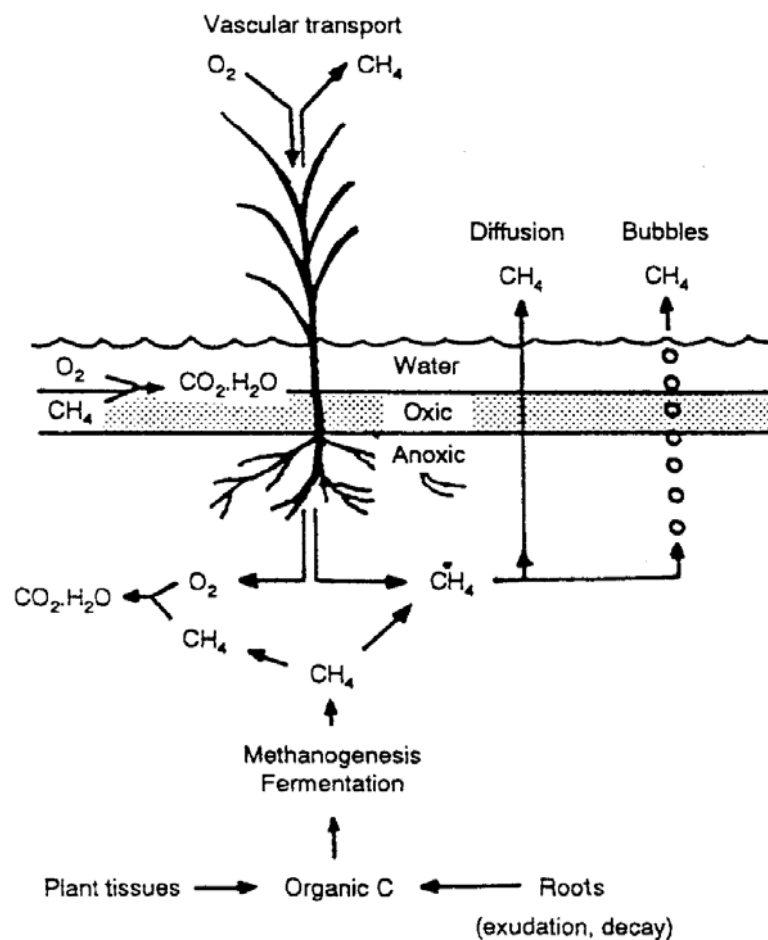
Figure 1. Diagram showing the pathways of methane production, and the pathways of methane release (Conrad 1989).
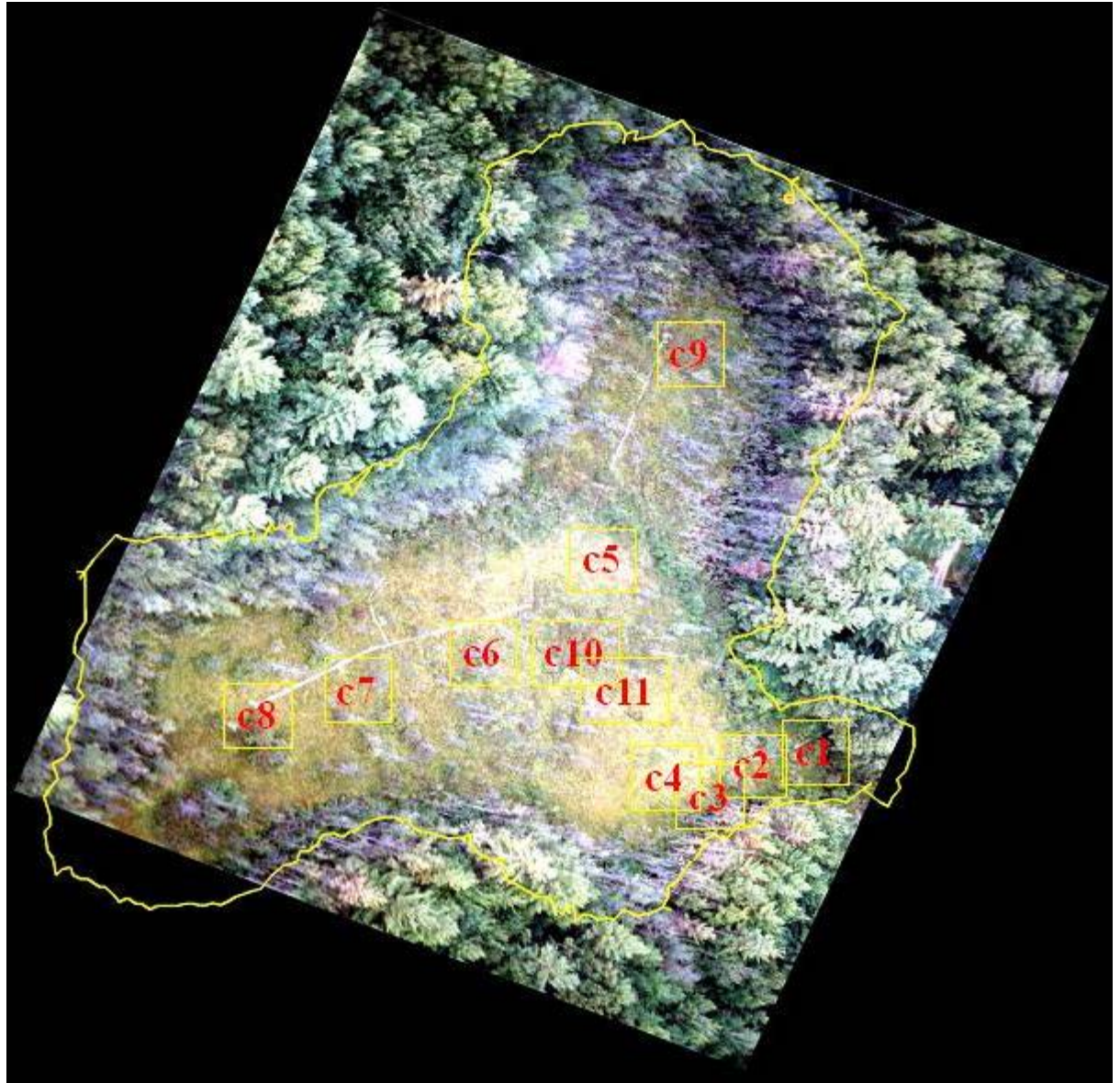
Figure 2. Aerial photo of Sallie's Fen, Barrington, NH. Squares indicate
collars described in Table 1.
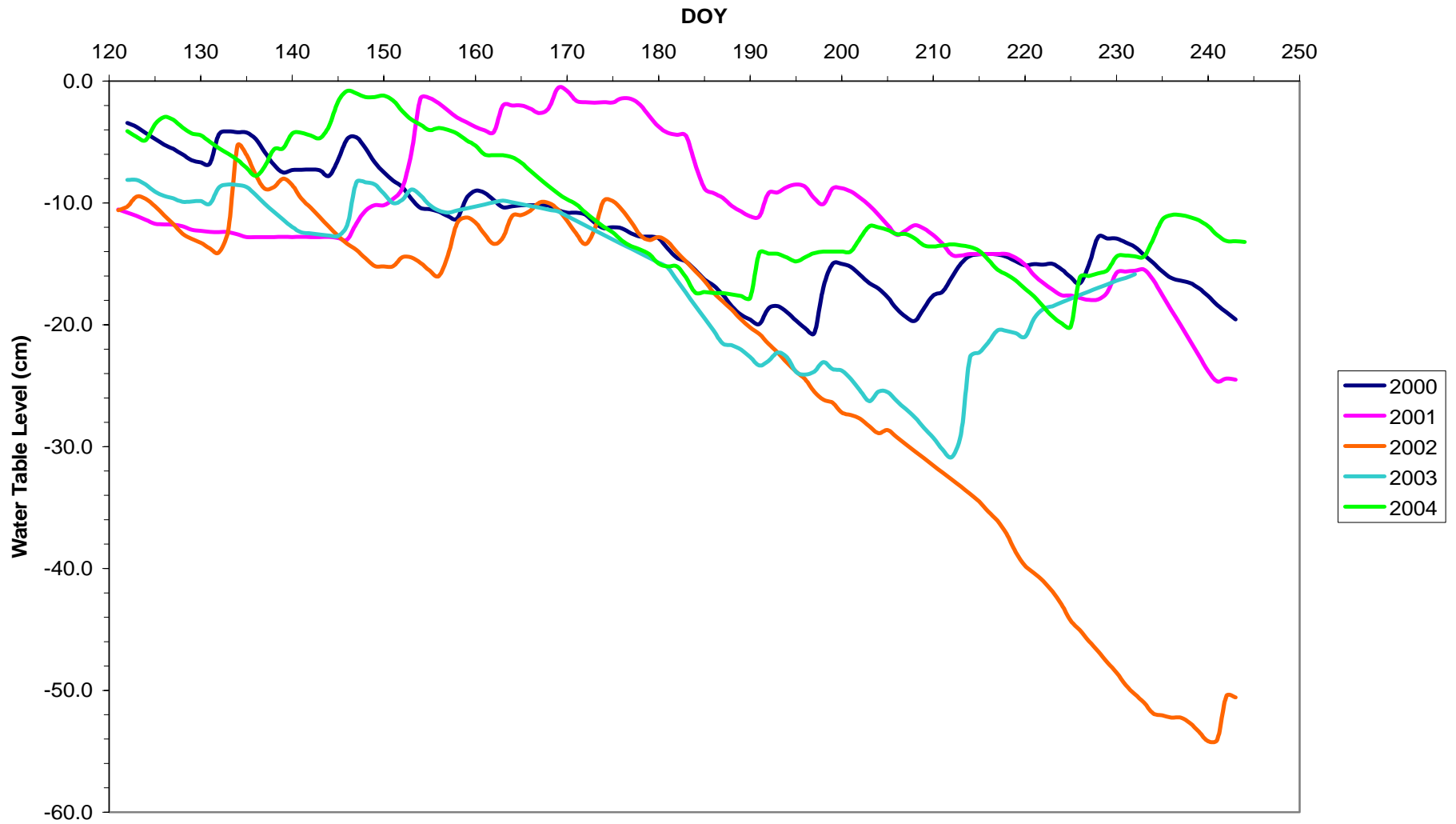
Figure 3. Mean daily water table level relative to peat surface from 1 May (day 121) through 31 August (day 245), 2000-2004.
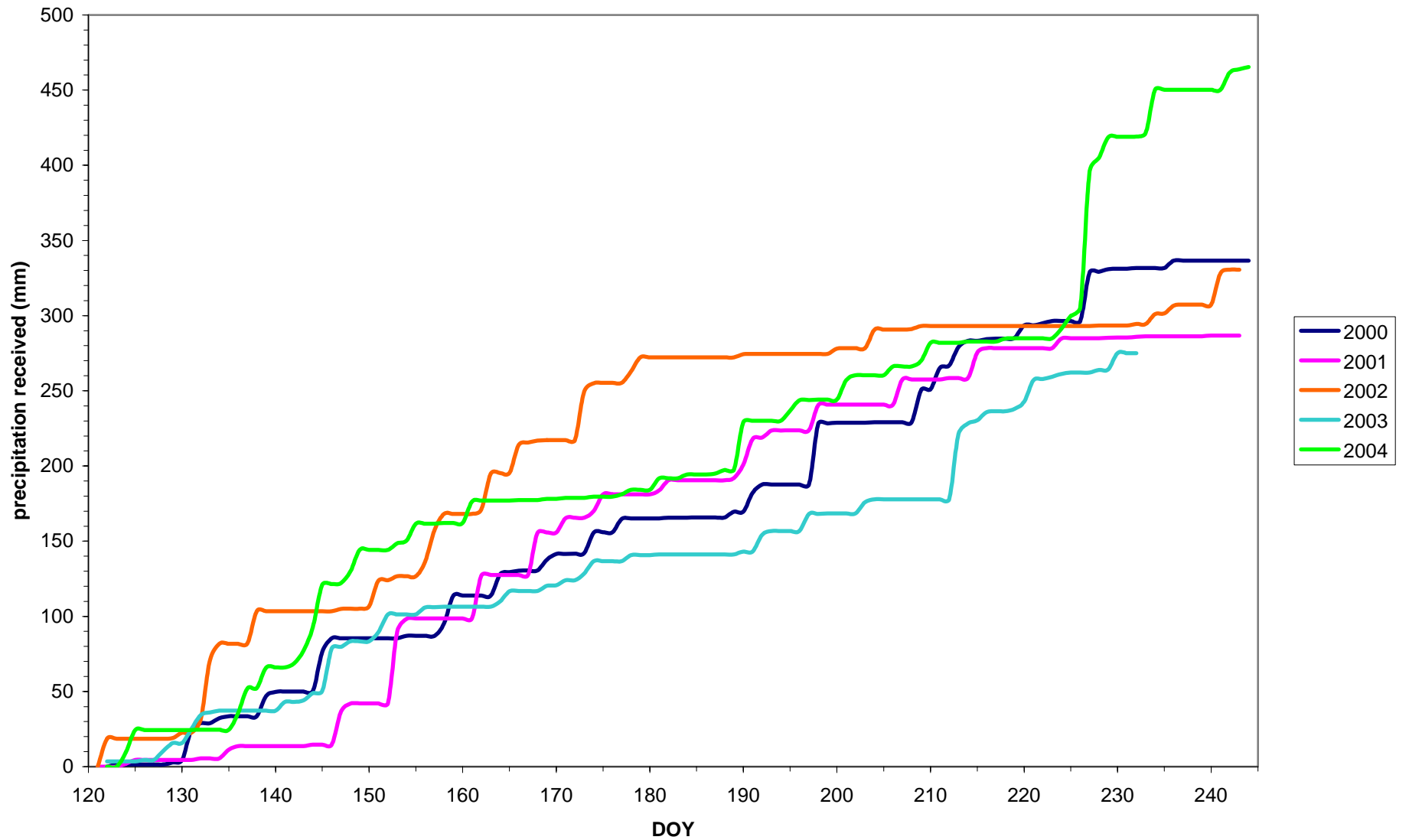
Figure 4. Cumulative precipitation from 1 May (day 121) through 31 August (day 245), 2000-2004.
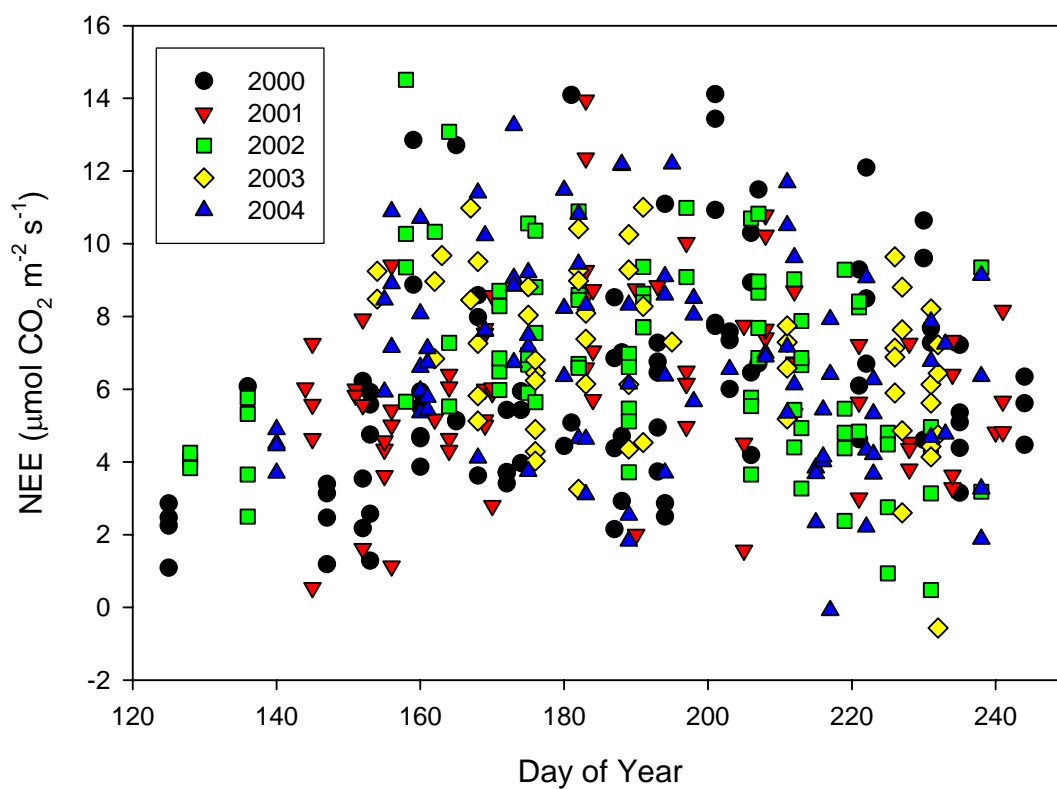
Figure 5. Seasonal pattern of NEE, 2000-2004.
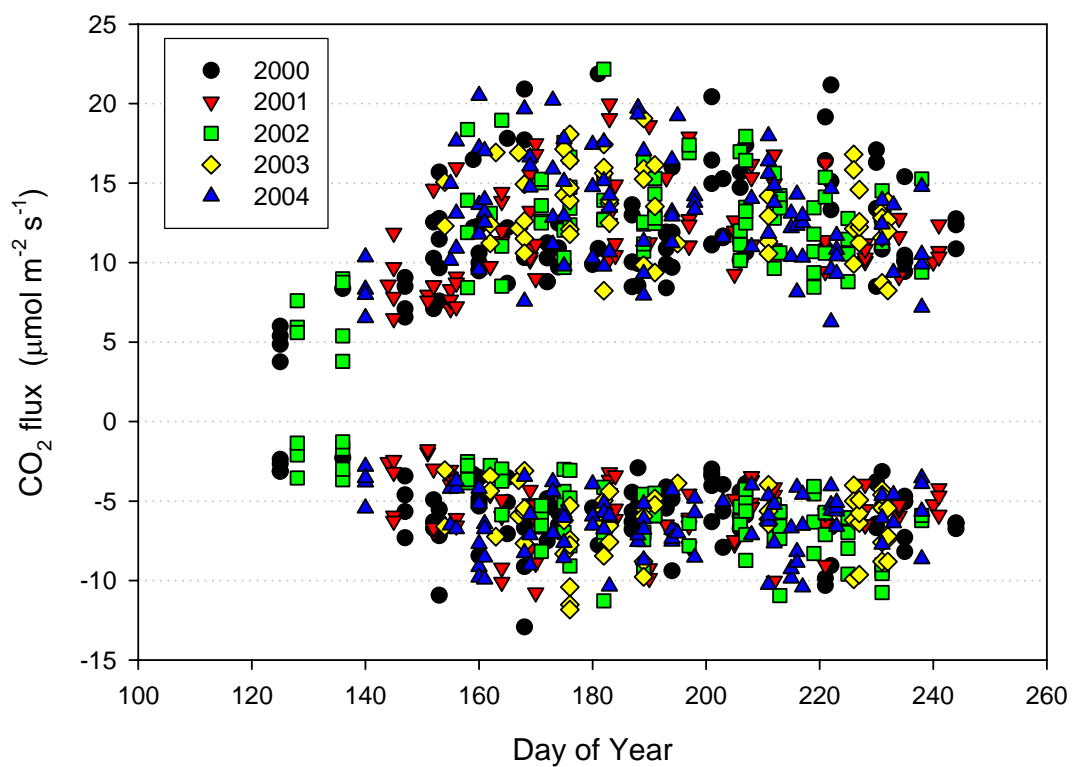
Figure 6. Seasonal pattern of photosynthesis and respiration, 2000-2004. Positive values indicate photosynthesis. Negative values indicate respiration.
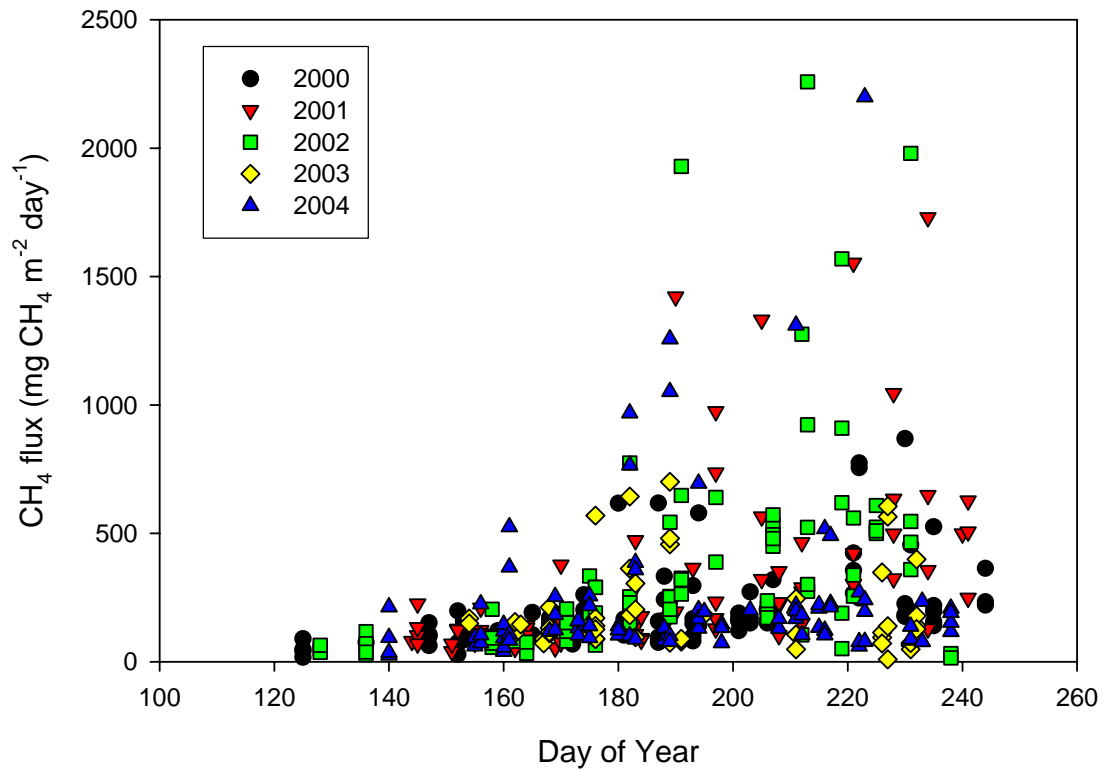
Figure 7. Seasonal pattern of methane fluxes, 2000-2004.
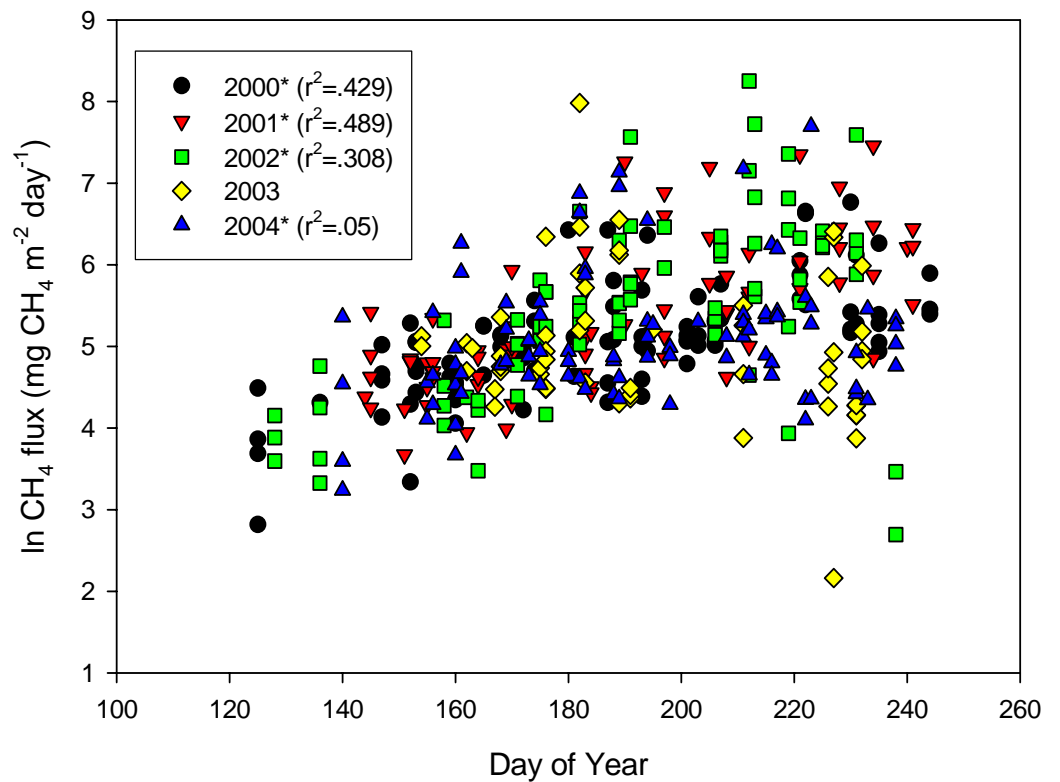
Figure 8. Seasonal pattern of ln CH_4 flux, 2000-2004.
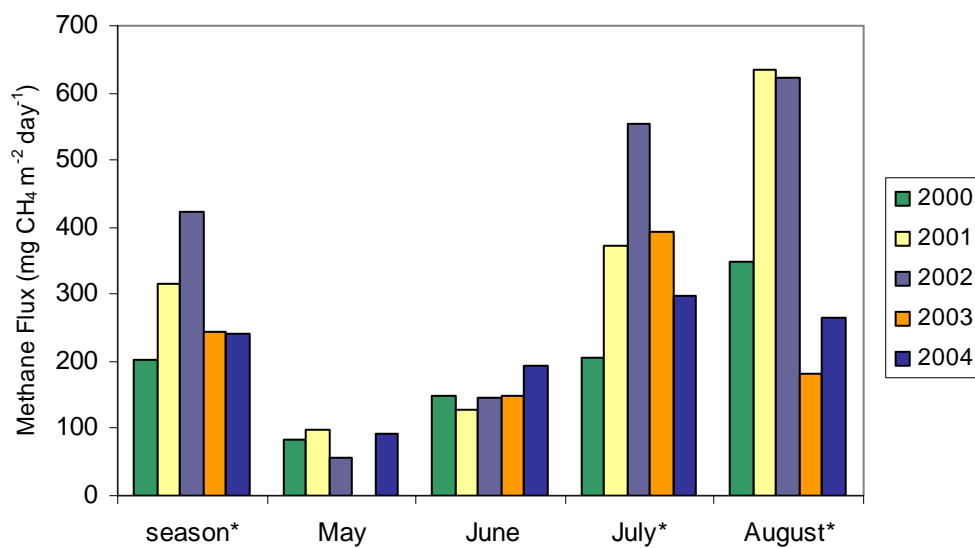
Figure 9. Seasonal mean and monthly CH$_4$ flux among years. * indicates significant difference between years

(a)

Mean NEE (μmol CO_2 m^{-2} s^{-1})

(b)

Mean respiration (μmol CO_2 m^{-2} s^{-1})
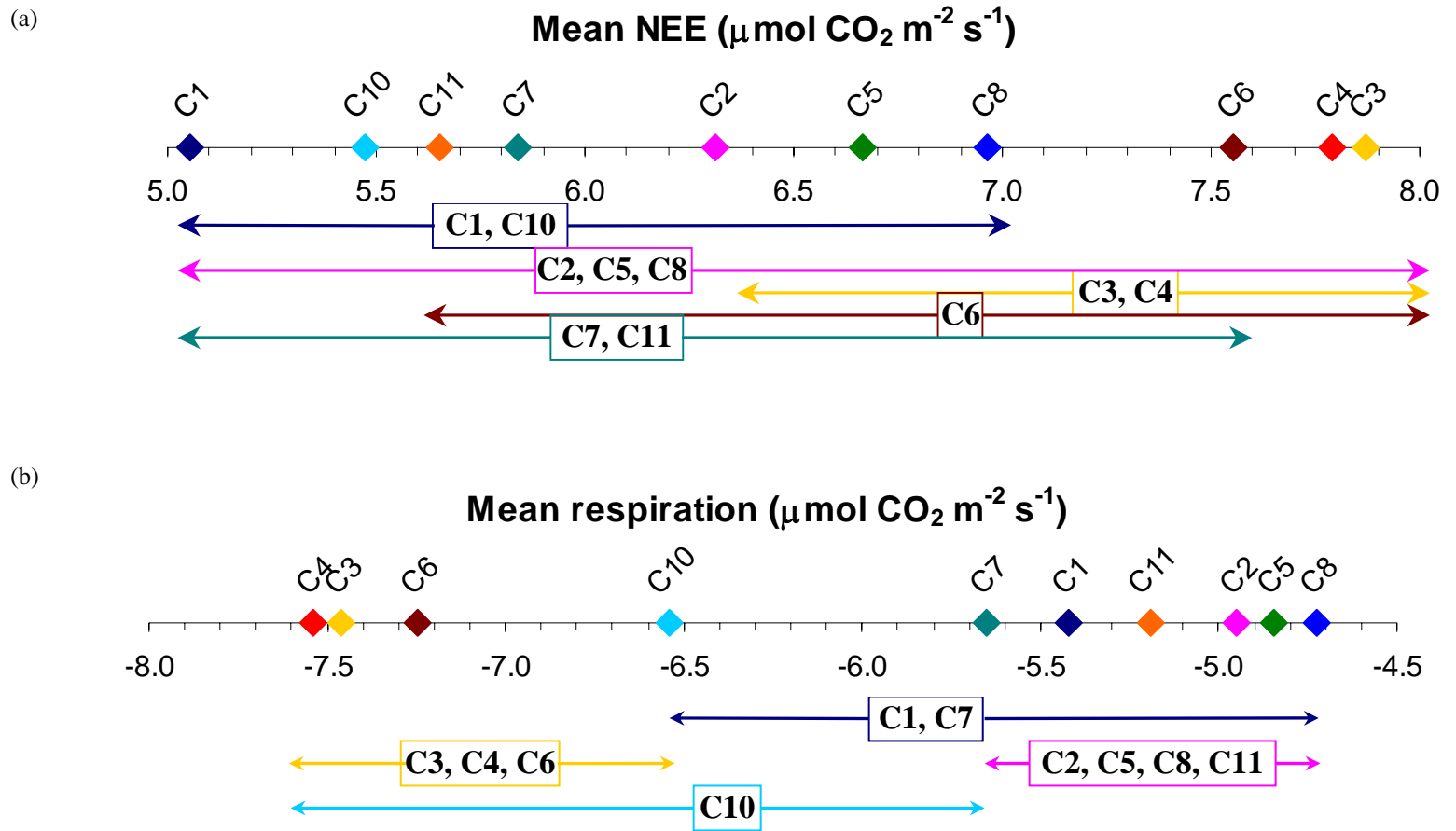
Figure 10. Mean values of (a) NEE at PAR >1000, (b) respiration, (c) photosynthesis, and (d) ln CH_4 flux by collar. Arrow intervals denote not-significantly different means between collars with values within intervals and the collars indicated in the box within the interval arrow.

(c)

Mean photosynthesis (μmol CO_2 m^{-2} s^{-1})

(d)

Mean ln CH_4 flux (mg CH_4 m^{-2} day^{-1})
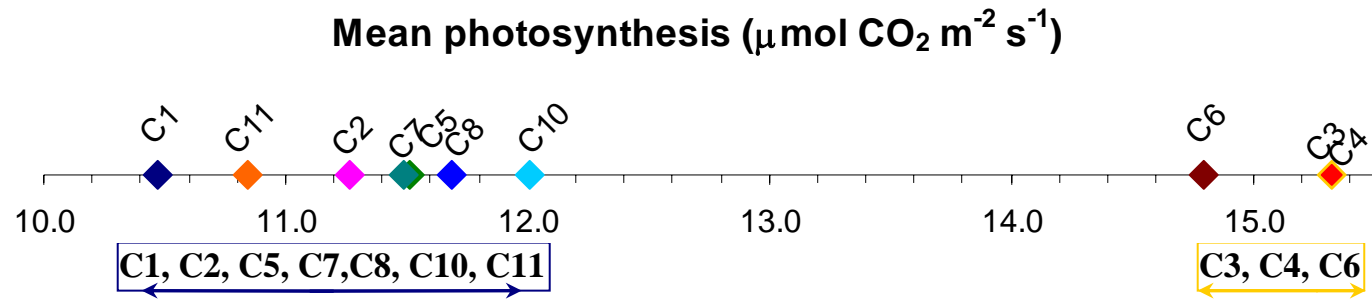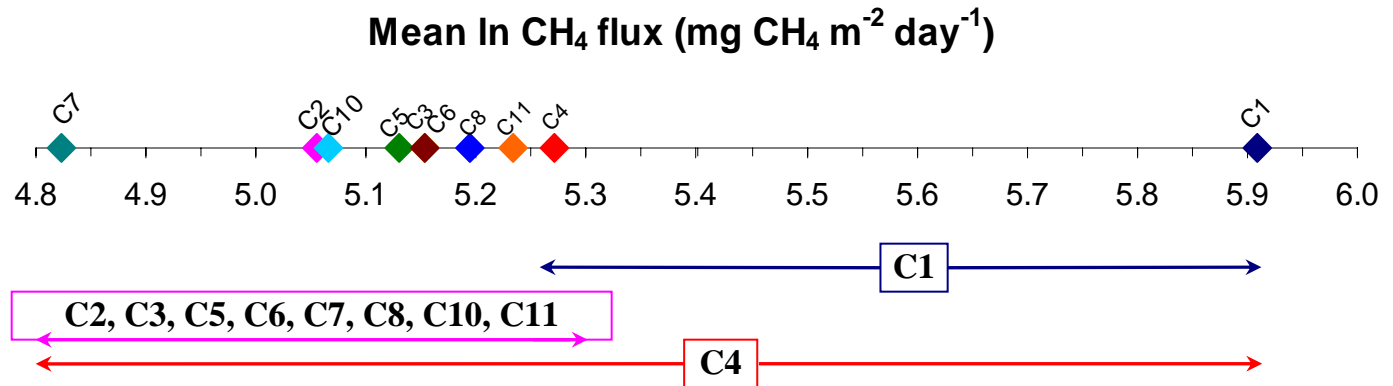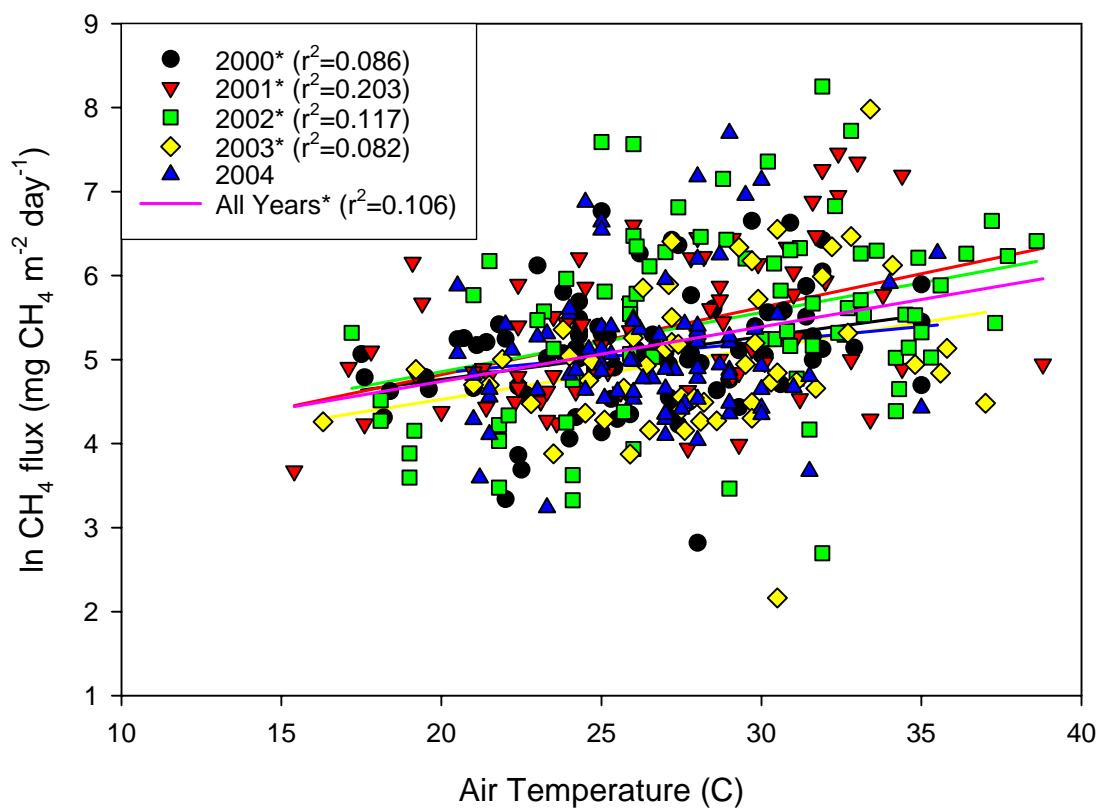
Figure 11. Seasonal instantaneous air temperature versus ln CH_4 flux, 2000-2004 and all years combined.
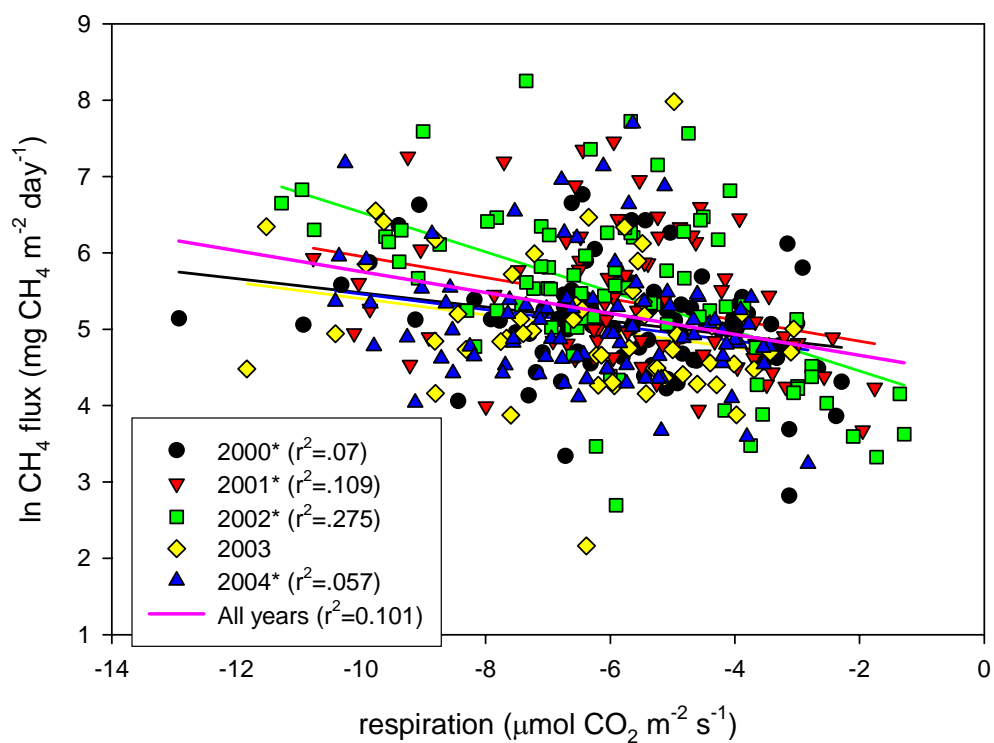
Figure 12. Seasonal instantaneous respiration versus ln CH_4 flux, 2000-2004.
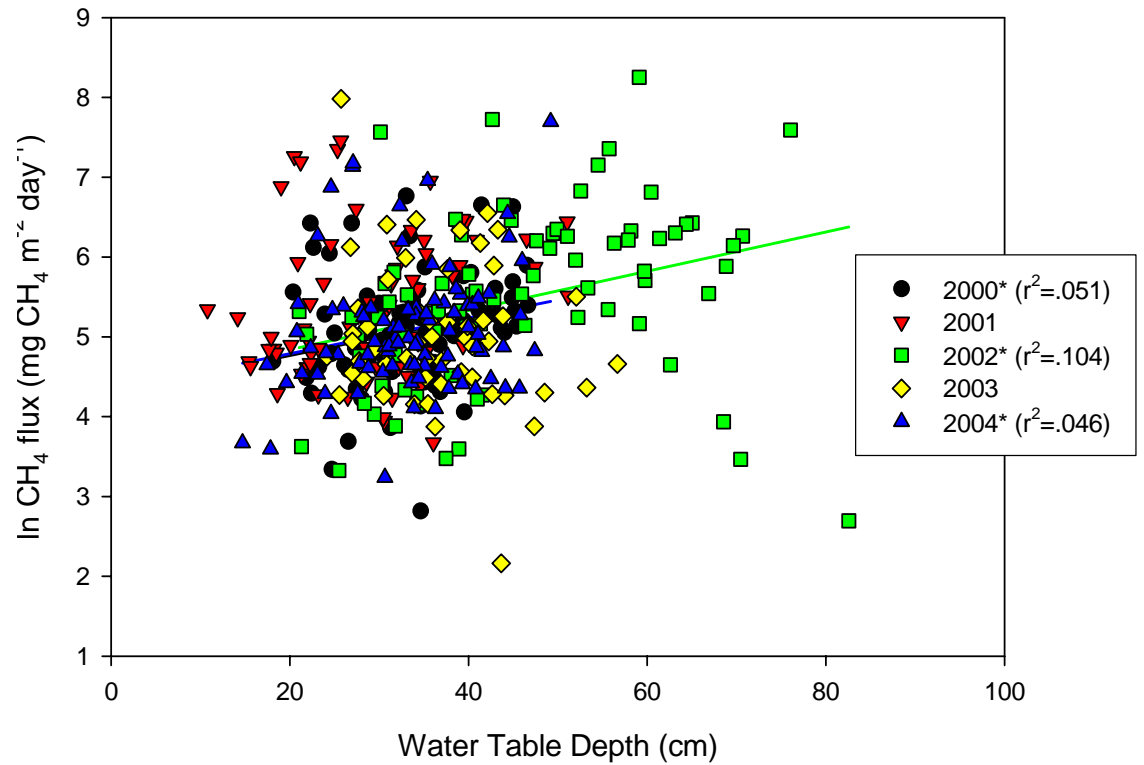
Figure 13. Seasonal instantaneous water table depth versus ln CH$_4$ flux, 2000-2004.
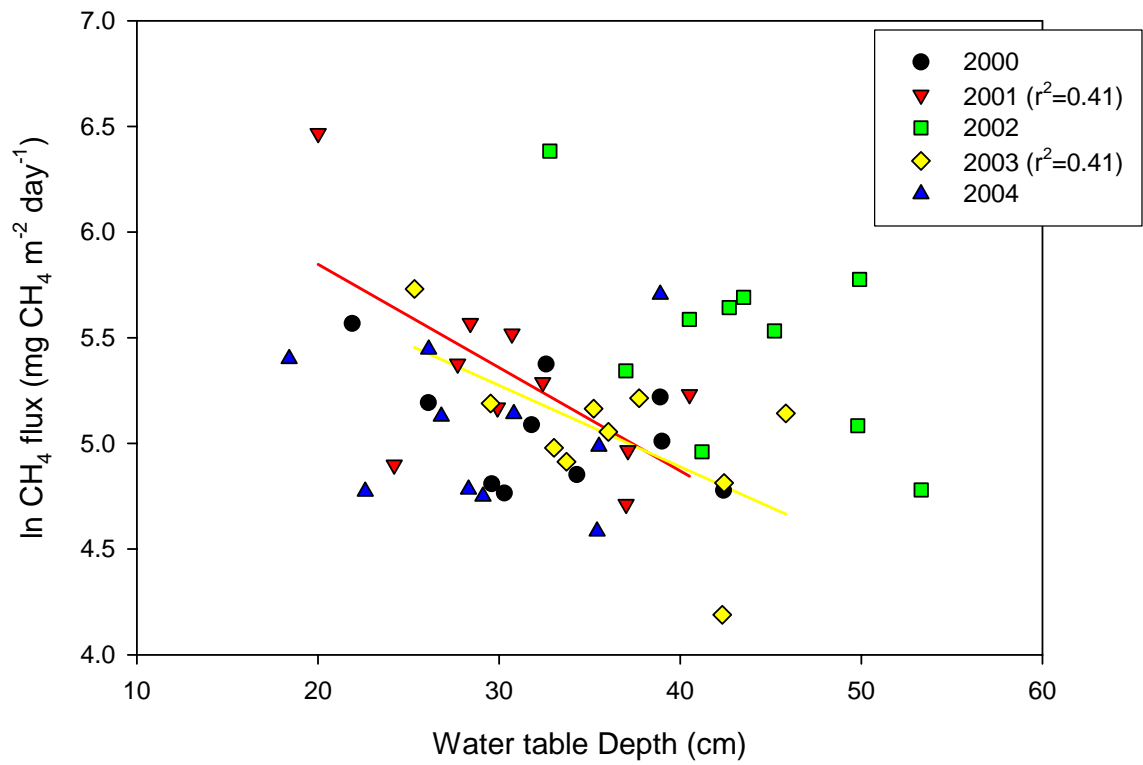
Figure 14. Mean seasonal water table depth versus mean seasonal ln CH$_4$ flux, 2000-2004.

Table 1. Estimates of components of the global methane budget in Tg CH_4 yr^{-1} (IPCC 2001).

Reference:	Fung et al. (1991)	Hein et al. (1997)	Lelieveld et al. (1998)	Houweling et al. (1999)	Mosier et al. (1998a)	Olivier et al. (1999)	Cao et al. (1998)	SAR	TAR[a]
Base year:	1980s	–	1992	–	1994	1990	–	1980s	1998
Natural sources									
Wetlands	115	237	225[c]	145			92		
Termites	20	–	20	20					
Ocean	10	–	15	15					
Hydrates	5	–	10	–					
Anthropogenic sources									
Energy	75	97	110	89		109			
Landfills	40	35	40	73		36			
Ruminants	80	90[b]	115	93	80	93[b]			
Waste treatment	–	[b]	25	–	14	[b]			
Rice agriculture	100	88	[c]	–	25-54	60		53	
Biomass burning	55	40	40	40	34	23			
Other	–	–	–	20	15				
Total source	500	587	600					597	598
Imbalance (trend)								+37	+22
Sinks									
Soils	10	–	30	30	44			30	30
Tropospheric OH	450	489	510					490	506
Stratospheric loss	–	46	40					40	40
Total sink	460	535	580					560	576

[a] TAR budget based on 1,745 ppb, 2.78 Tg/ppb, lifetime of 8.4 yr, and an imbalance of +8 ppb/yr.
[b] Waste treatment included under ruminants.
[c] Rice included under wetlands.

Table 2. Description of collars.

				Species Composition		
Collar	n	Height above water table (cm)	Dry Biomass (g m^{-3})	Sedge dry biomass (g m^{-3})	Leatherleaf dry biomass (g m^{-3})	Other woody Spp. dry biomass (g m^{-3})
1	32	9.4	170.4	0	81.2	78.6
2	34	17.8	210.4	0	128.6	51.4
3	42	19.3	221.6	23.5	24.0	0
4	37	20.1	1065.1	0	27.5	972.7
5	43	26.5	326.2	185.5	46.3	88.3
6	36	29.9	595.3	0	161.1	403.2
7	42	26.4	209.1	57.8	78.2	31.6
8	38	21.8	251.6	44.8	80.2	85.1
10	39	13.6	241.4	21.2	111.9	80.7
11	43	17.1	213.1	18.3	162.3	0

Table 3. Groups used in analysis

	Independent Variables		Dependent Variables
	Environmental	Measured	
	Air Temperature (°C)	NEE (μmol CO_2 m^{-2} s^{-1})	ln CH_4 flux (mg CH_4 m^{-2} day^{-1})
	Peat Temperature (°C)	Photosynthesis (μmol CO_2 m^{-2} s^{-1})	
	Water Table Depth (cm)	Respiration (μmol CO_2 m^{-2} s^{-1})	

Table 4. Correlations (r) between independent variables at a seasonal, instantaneous scale. Bold indicates significance ($\alpha=.05$)

	JD	NEE	photo	respiration	Tair	T10cm	WTD	ln CH4
JD	1	0.017	**-0.238**	**0.159**	**0.316**	**0.511**	**0.467**	**0.423**
NEE		1	**0.044**	0.792	**-0.208**	0.029	0.06	-0.026
photo			1	**-0.575**	**0.164**	**0.24**	**0.151**	**0.172**
respiration				1	**-0.547**	**-0.354**	**-0.166**	**-0.317**
air temp					1	**0.466**	**0.195**	**0.326**
peat temp						1	**0.37**	**0.341**
WTD							1	**0.223**

Table 5. Monthly and seasonal mean (a) air temperature, (b) water table depth;
Seasonal cumulative and monthly precipitation (c).

year	season	May	June	July	August
air temperature (°C)					
2000	16.7	12.3	17.5	18.6	18.6
2001	18.3	13.6	19.4	19.0	21.0
2002	17.8	12.1	16.8	21.3	21.0
2003	17.0	11.4	17.4	20.5	19.9
2004	15.8	12.9	16.2	18.8	20.4
mean[1]	25.29	20.56	25.28	28.06	26.94

year	season	May	June	July	August
water table depth (cm below peat surface)					
2000	-12.5	-5.9	-11.1	-17.6	-15.4
2001	-10.6	-12.0	-2.6	-10.0	-17.6
2002	-23.4	-11.2	-12.3	-24.3	-45.4
2003	-15.9	-10.0	-11.4	-23.9	-19.4
2004	-9.0	-4.0	-8.8	-14.5	-14.7

year	season	May	June	July	August
cumulative precipitation (mm)					
2000	336.5	85.3	80.3	113.5	57.4
2001	286.8	42.2	141.7	74.7	28.2
2002	330.5	123.7	148.6	20.8	37.3
2003	275.1	89.4	51.8	36.6	97.3
2004	465.4	144.3	47.5	90.2	183.4
mean[1]	333.50	91.69	90.93	64.26	86.61

[1] Mean reflects 30-year mean temperature and precipitation for 1971-2001 at Epping, NH (U.S. Climate Normals 1971-2000, www.ncdc.noaa.gov/normals.html).

Table 6. Seasonal and monthly mean measurements for (a) NEE, (b) respiration, (c) photosynthesis, (d) methane flux. * represents significant differences between years; [a,b] represent no significant differences between individual years at $\alpha=0.01$ level.

NEE (μmol CO_2 m^{-2} s^{-1})					
year	season	May	June*	July	August
2000	6.1	3.1	5.9[a]	7.1	6.9
2001	6.1	4.9	5.4[a]	7.5	5.3
2002	6.7	4.2	8.3[b]	7.5	5.0
2003	6.9		7.4[ab]	7.4	5.9
2004	6.8	4.4	7.9[b]	7.6	5.0

Respiration (μmol CO_2 m^{-2} s^{-1})					
Year	season	May	June	July*	August
2000	-5.7	-4.4	-6.3	-5.2[a]	-6.4
2001	-5.6	-3.4	-5.9	-5.9[a]	-5.7
2002	-5.9	-2.4	-5.0	-6.4[a]	-7.1
2003	-6.4		-6.6	-6.1[a]	-6.6
2004	-6.3	-3.9	-6.4	-6.7[a]	-6.3

Photosynthesis (μmol CO_2 m^{-2} s^{-1})					
Year	season*	May	June*	July	August
2000	11.8[a]	7.5	12.1[ab]	12.3	13.3
2001	11.7[a]	8.4	11.3[a]	13.4	11.1
2002	12.6[a]	6.6	13.3[abc]	13.9	12.2
2003	13.3[a]		13.9[bc]	13.5	12.4
2004	13.2[a]	8.3	14.3[c]	14.2	11.3

Methane Flux (mg CH_4 m^{-2} day^{-1})					
Year	season*	May	June	July*	August*
2000	203.7[a]	82.0	149.4	206.4[a]	348.8[abe]
2001	316.2[ab]	97.7	128.3	371.4[b]	634.1[ab]
2002	423.3[b]	57.2	146.4	554.5[ab]	622.1[ab]
2003	244.0[ab]		150.3	392.3[ab]	182.8[cd]
2004	241.0[ab]	92.1	192.5	299.2[ab]	266.0[acd]

Table 7. Mean annual values of (a) NEE, (b) respiration, (c) photosynthesis, and (d) methane flux by individual collars. Parentheses indicate standard deviation.

(a) NEE

collar	2000	2001	2002	2003	2004	Grouped years[1]
1*	5.18 (1.8)[ab]	2.41 (1.8)[a]	8.95 (3.3)[b]	4.48 (1.1)[ab]	5.52 (2.6)[ab]	5.1 (2.9)
2	5.68 (2.7)	6.26 (1.3)	6.48 (2.6)	7.90 (1.1)	4.37 (2.3)	6.3 (2.3)
3	8.90 (3.4)	8.56 (2.6)	6.72 (2.6)	7.96 (2.7)	7.40 (3.6)	7.9 (3.0)
4	7.15 (4.0)	8.27 (3.1)	6.91 (2.2)	7.69 (2.2)	8.94 (2.3)	7.8 (2.9)
5*	5.51 (2.5)	6.75 (1.5)	7.65 (1.9)	8.87 (1.4)	5.67 (1.2)	6.7 (2.1)
6	6.69 (4.6)	8.11 (0.8)	8.74 (1.9)	8.21 (2.7)	6.77 (2.9)	7.6 (3.0)
7	5.30 (1.7)	4.90 (0.8)	5.29 (1.5)	6.45 (1.8)	7.28 (2.7)	5.8 (2.0)
8	5.86 (2.5)	6.07 (1.3)	7.41 (3.5)	7.64 (0.8)	8.25 (2.6)	7.0 (2.5)
10	7.56 (3.2)	5.28 (1.4)	3.41 (2.8)	4.37 (2.7)	6.14 (3.4)	5.5 (3.1)
11	4.13 (1.9)	5.38 (1.5)	6.20 (1.9)	6.33 (1.5)	6.35 (2.1)	5.7 (1.9)

(b) Respiration

collar	2000	2001	2002	2003	2004	Grouped years[1]
1*	-5.09 (1.3)	-6.86 (1.1)	-5.14 (1.0)	-4.69 (0.7)	-4.72 (0.9)	-5.4 (1.3)
2	-5.16 (0.7)	-4.85 (0.7)	-4.57 (1.7)	-4.86 (1.2)	-5.79 (1.7)	-5.0 (1.3)
3	-6.44 (2.0)	-7.53 (1.6)	-7.72 (2.1)	-8.16 (1.1)	-7.67 (1.4)	-7.5 (1.7)
4	-7.35 (1.6)	-8.26 (2.3)	-7.15 (1.9)	-8.31 (1.6)	-7.16 (1.6)	-7.5 (1.8)
5	-4.59 (1.2)	-3.88 (1.2)	-5.57 (1.7)	-5.47 (1.5)	-4.77 (1.1)	-4.8 (1.4)
6	-8.12 (3.1)	-6.52 (1.1)	-5.91 (2.9)	-7.89 (2.7)	-7.73 (1.8)	-7.2 (2.5)
7	-6.04 (1.7)	-4.65 (1.8)	-5.12 (1.8)	-6.97 (3.2)	-5.84 (1.4)	-5.7 (2.0)
8	-4.47 (1.2)	-3.90 (1.2)	-4.61 (1.8)	-5.31 (0.5)	-5.69 (0.9)	-4.7 (1.3)
10	-5.65 (1.8)	-5.23 (1.3)	-7.19 (3.0)	-7.63 (2.1)	-7.33 (2.3)	-6.5 (2.3)
11	-4.63 (1.3)	-4.74 (1.3)	-5.78 (1.6)	-5.69 (1.4)	-5.30 (1.4)	-5.2 (1.4)

(c) Photosynthesis

collar	2000	2001	2002	2003	2004	Grouped years[1]
1*	10.26 (0.6)^a	9.27 (2.0)^a	14.09 (2.4)^b	9.17 (0.8)^a	10.25 (2.0)^{ab}	10.5 (2.3)
2	10.85 (2.6)	11.11 (1.0)	11.04 (2.5)	12.76 (1.6)	10.16 (3.1)	11.3 (2.2)
3*	15.33 (2.7)^a	16.09 (2.4)^{ab}	14.44 (2.9)^{ab}	16.12 (2.7)^b	15.07 (3.4)^{ab}	15.3 (2.8)
4	14.50 (3.5)	16.54 (1.5)	14.06 (2.5)	15.99 (1.6)	16.10 (2.6)	15.3 (2.7)
5*	10.10 (2.8)^a	10.63 (1.6)^{ab}	13.23 (2.2)ab	14.34 (10.4)^b	10.44 (1.2)^{ab}	11.5 (2.5)
6	14.80 (6.2)	14.64 (1.3)	14.66 (4.0)	16.10 (0.8)	14.51 (3.2)	14.8 (3.8)
7	11.34 (2.7)	9.55 (1.9)	10.41 (2.3)	13.42 (2.8)	13.12 (3.8)	11.5 (3.1)
8	10.33 (2.7)	9.97 (1.9)	12.02 (4.8)	12.95 (1.0)	13.94 (3.3)	11.7 (3.3)
10	13.21 (2.9)	10.51 (2.1)	10.60 (3.5)	12.00 (2.5)	13.48 (3.0)	12.0 (3.0)
11*	8.75 (2.2)	10.12 (1.1)	11.98 (0.9)	12.02 (1.3)	11.65 (2.6)	10.8 (2.2)

(d) Methane fluxes

collar	2000	2001	2002	2003	2004	Grouped Years[1]
1	322.9 (209)	946.1 (664)	1015.5 (1002)	888.0 (1372)	445.6 (526)	680.6 (1.2)
2	157.8 (166)	403.8 (370)	276.2 (269)	186.5 (204)	335.6 (478)	266.6 (1.0)
3	171.6 (57)	195.9 (102)	376.6 (271)	223.4 (179)	128.3 (49)	214.9 (0.6)
4	310.1 (264)	285.3 (143)	342.5 (185)	256.2 (276)	123.8 (58)	260.5 (0.8)
5*	164.4 (67)	147.8 (45)	476.6 (575)	149.7 (153)	152.7 (45)	222.3 (0.6)
6	197.7 (235)	237.1 (150)	219.0 (261)	231.2 (227)	475.1 (601)	295.9 (1.1)
7	239.2 (209)	183.2 (218)	601.0 (1152)	90.6 (49)	112.1 (56)	181.1 (1.0)
8	153.1 (80)	308.4 (268)	433.3 (471)	234.5 (196)	196.5 (90)	259.2 (0.8)
10	186.0 (48)	150.0 (85)	273.3 (185)	223.8 (183)	255.0 (377)	191.0 (0.7)
11	128.2 (44)	249.1 (150)	421.8 (523)	171.3 (107)	291.2 (223)	247.2 (0.7)

*Indicates significant differences between years at indicated collar (α=.01)
[1]Indicates significant differences between collars (α=.01). See Figure 9.

Table 8. Collar x Year Two-way ANOVA of ln methane fluxes.

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	62.882[a]	49	1.283	1.805	.001
Intercept	9632.899	1	9632.899	13551.12	.000
collar	21.924	9	2.436	3.427	**.000**
year	12.002	4	3.001	4.221	**.002**
collar * year	29.625	36	.823	1.158	.252
Error	239.559	337	.711		
Total	10764.210	387			
Corrected Total	302.441	386			

[a]R Squared = .208 (Adjusted R Squared = .093)

Table 9. Correlation coefficients (r) of independent variables versus ln CH_4 for
(a) seasonal instantaneous, (b) seasonal mean   Bold indicates significant
relationships (α=.05, two-tailed).

(a) seasonal instantaneous

	all years	2000	2001	2002	2003	2004
JD	**0.42**	**0.66**	**0.70**	**0.56**	-0.15	**0.22**
NEE	-0.03	**0.33**	-0.08	-0.09	-0.09	-0.20
respiration	**-0.32**	**-0.26**	**-0.33**	**-0.52**	-0.25	**-0.24**
photo	**0.17**	**0.42**	0.15	**0.28**	0.12	-0.04
air T	**0.33**	**0.29**	**0.45**	**0.34**	**0.29**	0.14
peat T	**0.34**	**0.52**	**0.44**	**0.36**	0.04	0.19
WTD	**0.22**	**0.23**	0.18	**0.32**	-0.17	**0.21**

(b) seasonal mean

	all years	2000	2001	2002	2003	2004
NEE	-0.14	0.18	-0.44	0.33	-0.33	-0.35
respiration	-0.02	-0.12	-0.39	-0.07	0.14	0.16
photo	-0.08	0.17	-0.08	0.38	-0.31	-0.30
air T	**0.30**	0.22	**0.76**	-0.34	0.24	0.58
peat T	0.06	0.27	0.41	**-0.64**	0.12	-0.41
WTD	-0.16	-0.50	**-0.64**	-0.58	**-0.64**	0.01

Table 10. Differences between early (May, June) and late sub-season (July, August) values for all collars in all years.

	early sub-season		late sub-season		
	mean	S.D.	mean	S.D.	p-value
NEE	6.33	2.74	6.65	2.70	0.283
Respiration	-5.57	2.31	-6.21	1.78	**0.005**
Photosynthesis	11.90	3.81	12.87	2.90	**0.011**
Water table depth	13.37	5.90	25.09	9.33	**0.000**
Air temperature	25.97	4.86	27.87	3.94	**0.000**
Peat temperature	15.02	4.44	18.90	3.26	**0.000**
Methane flux	132.33	89.16	384.67	469.91	**0.000**

Table 11. Correlation coefficients (r) of independent variables versus ln CH_4 for (a) early sub-season, (b) late sub-season. Bold indicates significant relationships (α=.05, two-tailed).

 (a) early sub-season instantaneous

	all years	2000	2001	2002	2003	2004
JD	**0.52**	**0.64**	0.25	**0.67**	0.01	**0.39**
NEE	**0.18**	**0.34**	-0.18	0.37	-0.45	0.14
respiration	**-0.44**	**-0.33**	**-0.48**	**-0.68**	-0.35	-0.32
photo	**0.39**	**0.43**	0.24	**0.62**	0.02	0.26
air T	**0.33**	0.30	**0.37**	**0.41**	0.22	0.32
peat T	**0.22**	**0.41**	0.23	0.18	-0.14	0.16
WTD	0.01	-0.06	**-0.50**	-0.02	0.32	**0.34**

(b) late sub-season instantaneous

	all years	2000	2001	2002	2003	2004
JD	-0.01	**0.35**	**0.40**	-0.03	**-0.38**	-0.18
NEE	**-0.16**	0.08	**-0.43**	-0.16	-0.02	**-0.27**
respiration	**-0.22**	**-0.29**	-0.28	-0.18	-0.28	-0.18
photo	-0.02	0.24	-0.23	-0.03	0.17	-0.15
air T	**0.25**	**0.32**	**0.64**	-0.06	**0.46**	-0.06
peat T	**0.17**	0.26	**0.34**	-0.03	0.06	0.06
WTD	0.04	0.06	0.00	-0.14	-0.31	-0.03

Table 12. Means and standard deviations for sedge and leatherleaf collars for all years, 2000-2004. Bold indicates significant differences (α=.05) between the two groups at the p-value indicated.

	Sedge		Leatherleaf		
	mean	S.D.	mean	S.D.	p
NEE	6.46	2.23	6.46	2.51	0.993
Respiration	-5.08	1.62	-5.77	2.04	**0.004**
photo	11.54	2.94	12.23	3.31	0.090
Water table	39.93	9.26	36.29	11.23	**0.007**
Methane flux	5.08	0.85	5.15	0.92	0.495

Table 13. Correlation coefficients (r) of independent variables versus ln CH_4 for (a) sedge collars, (b) leatherleaf collars. Bold indicates significant relationships (α=.05, two-tailed).

(a) sedge collars (seasonal instantaneous)

	all years	2000	2001	2002	2003	2004
JD	**0.54**	**0.78**	**0.86**	**0.82**	-0.12	**0.42**
NEE	0.08	0.35	0.28	-0.19	0.45	0.16
respiration	**-0.33**	**-0.38**	**-0.55**	**-0.65**	0.10	-0.25
photo	**0.24**	**0.50**	**0.67**	0.21	0.29	0.22
air T	**0.34**	**0.45**	**0.67**	**0.43**	-0.11	-0.07
peat T	**0.54**	**0.68**	**0.77**	**0.79**	-0.13	0.12
WTD	**0.56**	**0.72**	**0.56**	**0.71**	-0.09	0.14

(b) leatherleaf collars (seasonal instantaneous)

	all years	2000	2001	2002	2003	2004
JD	**0.35**	**0.76**	**0.74**	0.21	-0.13	0.15
NEE	0.00	**0.58**	-0.23	-0.14	-0.25	-0.24
respiration	**-0.35**	-0.28	0.00	**-0.53**	**-0.59**	-0.30
photo	**0.22**	**0.55**	-0.19	0.25	0.34	0.99
air T	**0.27**	0.12	0.07	**0.42**	**0.47**	0.30
peat T	**0.23**	**0.41**	0.13	0.25	-0.14	**0.41**
WTD	0.09	0.35	**0.58**	-0.04	-0.16	0.38

Table 14. Coefficients, R^2, t-scores, p-values for multiple regression with independent variables collar, year (model 1), and collar, year, NEE, photosynthesis, respiration, water table, air temperature, and peat temperature (model 2), with methane as the dependent variable, using seasonal instantaneous data.

Model Summary

Model	R	R^2	Std. Error of the Estimate
1[a]	.331[a]	.110	.85381
2[b]	.610[b]	.372	.72194

ANOVA

Model		Sum of Squares	df	Mean Square	F	Sig.
1[a]	Regression	33.197	13	2.554	3.503	.000[a]
	Residual	268.998	369	.729		
	Total	302.195	382			
2[b]	Regression	112.479	18	6.249	11.989	.000[b]
	Residual	189.716	364	.521		
	Total	302.195	382			

Coefficients[b]

Model	variable	Coefficients		t	Sig.
		B	Std. Error		
2	**NEE**	**.033**	**.015**	**2.168**	**.031**
	respiration	**-.168**	**.029**	**-5.809**	**.000**
	Tair	.002	.012	.136	.892
	T10cm	**.022**	**.011**	**1.969**	**.050**
	WTD	**.030**	**.005**	**5.612**	**.000**

[a] Predictors: (Constant), year, collar
[b] Predictors: (Constant), year, collar, T10cm, NEE, Tair, Water table depth (WTD), respiration (photo excluded)

Appendix 1. Histogram showing the distribution of methane fluxes (a) before and (b) following a log transformation.

(a)

Mean = 284.908
Std. Dev. = 389.4648
N = 387

CH4 flux (mg/m2)

(b)

Mean = 5.1993
Std. Dev. = 0.88517
N = 387

ln CH4
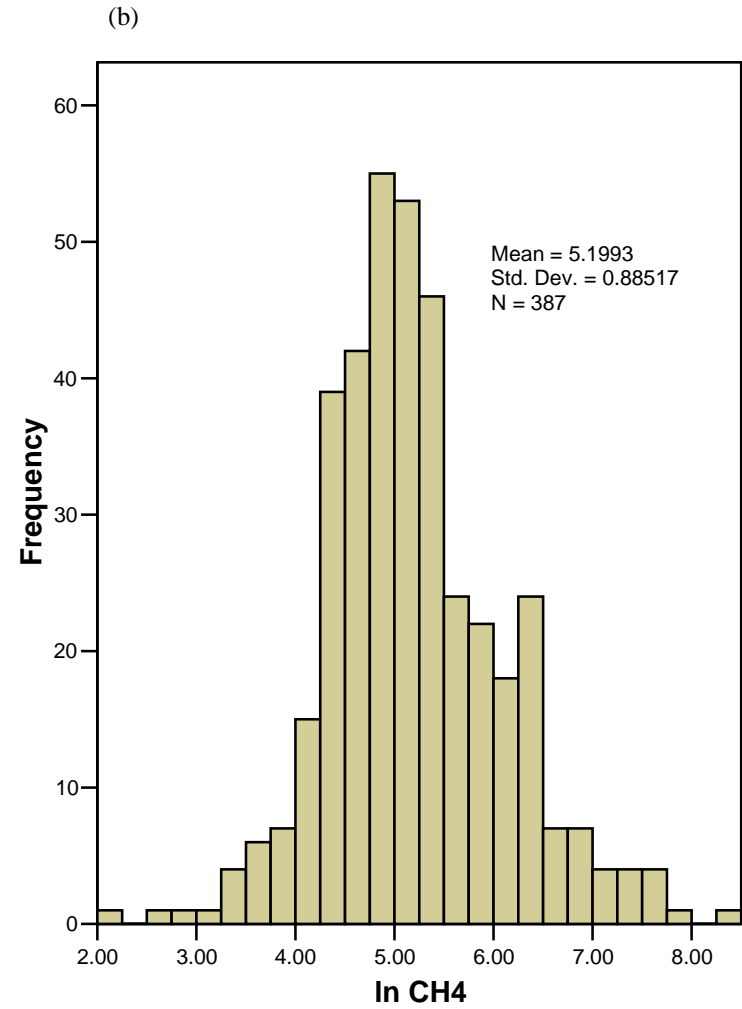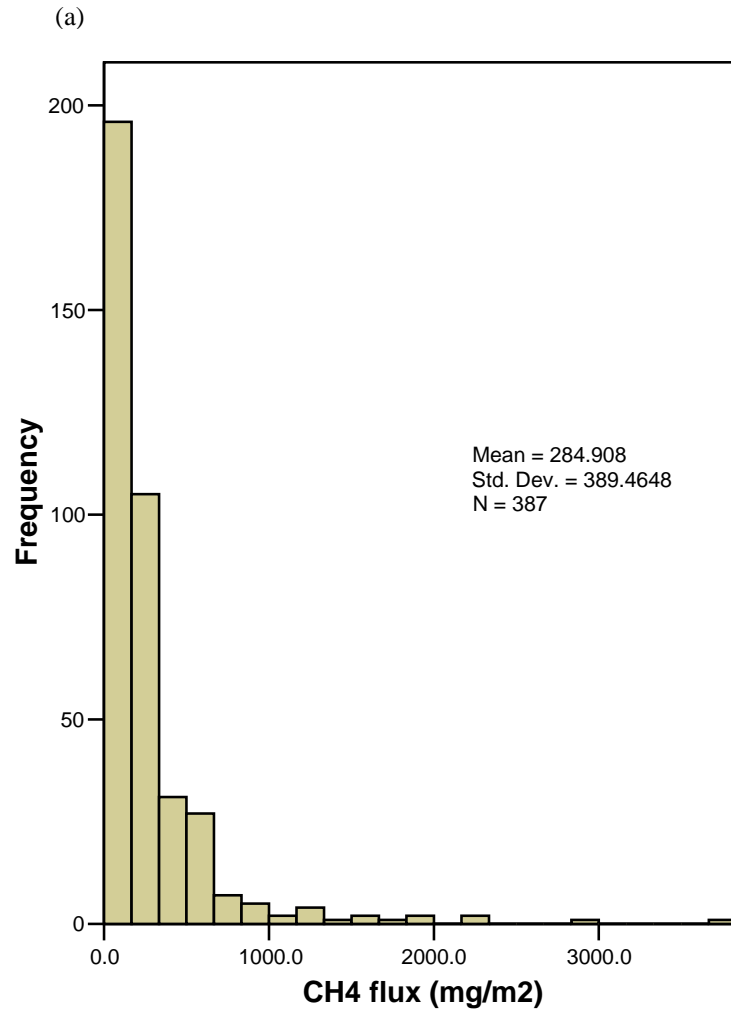
Appendix 2. Regression coefficients of independent variables versus ln CH_4 for (a) seasonal instantaneous, (b) seasonal mean, (c) early sub-season, (d) late sub-season, (e) sedge collars, (f) leatherleaf collars. Bold indicates significant relationships ($\alpha=.05$).

(a) seasonal instantaneous

ln CH4 vs.	all years		2000		2001		2002		2003		2004	
	slope	r^2	slope	r^2	slope	r^2	slope	r^2	slope	r^2	slope	r^2
JD	**0.01**	**0.18**	**0.01**	**0.43**	**0.02**	**0.49**	**0.02**	**0.31**	-0.01	0.02	**0.01**	**0.05**
NEE	-0.01	0.00	**0.08**	**0.11**	-0.03	0.01	-0.04	0.01	-0.04	0.01	-0.06	0.04
respiration	**-0.14**	**0.10**	**-0.10**	**0.07**	**-0.01**	**0.11**	**-0.26**	**0.28**	-0.11	0.06	**-0.10**	**0.06**
photo	**0.05**	**0.03**	**0.08**	**0.18**	0.04	0.02	**0.10**	**0.08**	0.04	0.01	-0.01	0.00
air T	**0.07**	**0.11**	**0.05**	**0.09**	**0.08**	**0.20**	**0.07**	**0.12**	**0.06**	**0.08**	0.04	0.02
peat T	**0.07**	**0.12**	**0.08**	**0.27**	**0.09**	**0.20**	**0.08**	**0.13**	0.01	0.00	0.04	0.04
WTD	**0.02**	**0.05**	**0.02**	**0.05**	0.02	0.03	**0.03**	**0.10**	-0.02	0.03	**0.02**	**0.05**

(b) seasonal mean

ln CH4 vs.	all years		2000		2001		2002		2003		2004	
	slope	r^2	slope	r^2	slope	r^2	slope	r^2	slope	r^2	slope	r^2
NEE	-0.04	0.02	0.04	0.03	-0.12	0.19	0.09	0.11	-0.08	0.11	-0.09	0.12
respiration	-0.01	0.00	-0.03	0.01	-0.13	0.15	-0.03	0.00	0.04	0.02	0.05	0.03
photo	-0.02	0.07	0.02	0.03	-0.01	0.01	0.10	0.14	-0.05	0.10	-0.05	0.09
air T	**0.07**	**0.09**	0.04	0.05	**0.19**	**0.58**	-0.08	0.12	0.06	0.06	0.20	0.33
peat T	0.01	0.03	0.05	0.08	0.13	0.17	**-0.17**	**0.41**	0.03	0.01	-0.19	0.17
WTD	-0.01	0.03	-0.02	0.25	**-0.05**	**0.41**	-0.04	0.34	**-0.04**	**0.41**	0.00	0.00

(c) early sub-season instantaneous

ln CH4 vs.	all years slope	all years r²	2000 slope	2000 r²	2001 slope	2001 r²	2002 slope	2002 r²	2003 slope	2003 r²	2004 slope	2004 r²
JD	**0.02**	**0.27**	**0.03**	**0.41**	0.01	0.06	**0.03**	**0.45**	0.00	0.00	**0.02**	**0.15**
NEE	**0.04**	**0.03**	**0.07**	**0.11**	-0.04	0.03	0.09	0.14	-0.10	0.20	0.04	0.02
respiration	**-0.11**	**0.19**	**-0.09**	**0.11**	**-0.09**	**0.23**	**-0.23**	**0.46**	-0.06	0.13	-0.10	0.10
photo	**0.06**	**0.16**	**0.07**	**0.19**	0.04	0.06	**0.11**	**0.39**	0.00	0.00	0.04	0.07
air T	**0.04**	**0.11**	0.04	0.09	**0.03**	**0.14**	**0.06**	**0.17**	0.02	0.05	0.05	0.11
peat T	**0.03**	**0.05**	**0.05**	**0.17**	0.02	0.05	0.03	0.03	-0.01	0.02	0.03	0.03
WTD	0.00	0.00	-0.01	0.00	**-0.03**	**0.25**	0.00	0.00	0.03	0.10	**0.03**	**0.12**

(d) late sub-season instantaneous

ln CH4 vs.	all years slope	all years r²	2000 slope	2000 r²	2001 slope	2001 r²	2002 slope	2002 r²	2003 slope	2003 r²	2004 slope	2004 r²
JD	0.00	0.00	**0.01**	**0.12**	**0.02**	**0.16**	0.00	0.00	**-0.02**	**0.14**	-0.01	0.03
NEE	**-0.05**	**0.03**	0.02	0.01	**-0.13**	**0.18**	-0.06	0.03	-0.01	0.00	**-0.08**	**0.07**
respiration	**-0.11**	**0.05**	**-0.10**	**0.09**	-0.13	0.08	-0.10	0.03	-0.17	0.08	-0.09	0.03
photo	-0.01	0.00	0.04	0.06	-0.06	0.05	-0.01	0.00	0.07	0.03	-0.04	0.02
air T	**0.06**	**0.06**	**0.05**	**0.10**	**0.11**	**0.41**	-0.02	0.00	**0.19**	**0.22**	-0.02	0.00
peat T	**0.05**	**0.03**	0.06	0.07	**0.10**	**0.11**	-0.01	0.00	0.02	0.00	0.02	0.00
WTD	0.00	0.00	0.01	0.00	0.00	0.00	-0.01	0.02	-0.04	0.10	0.00	0.00

(e) sedge collars (seasonal instantaneous)

ln CH4 vs.	all years slope	all years r^2	2000 slope	2000 r^2	2001 slope	2001 r^2	2002 slope	2002 r^2	2003 slope	2003 r^2	2004 slope	2004 r^2
JD	**0.02**	**0.29**	**0.01**	**0.60**	**0.02**	**0.75**	**0.03**	**0.67**	0.00	0.02	**0.01**	**0.18**
NEE	0.03	0.01	0.09	0.12	0.18	0.08	-0.09	0.03	0.24	0.20	0.03	0.03
respiration	**-0.17**	**0.11**	**-0.15**	**0.15**	**-0.34**	**0.30**	**-0.43**	**0.42**	0.04	0.01	-0.11	0.06
photo	**0.07**	**0.06**	**0.11**	**0.25**	**0.33**	**0.45**	0.07	0.04	0.14	0.09	0.04	0.05
air T	**0.07**	**0.12**	**0.07**	**0.21**	**0.12**	**0.46**	**0.10**	**0.19**	-0.02	0.01	-0.01	0.01
peat T	**0.10**	**0.29**	**0.08**	**0.46**	**0.16**	**0.60**	**0.18**	**0.62**	-0.03	0.02	0.02	0.01
WTD	**0.05**	**0.31**	**0.07**	**0.51**	**0.06**	**0.32**	**0.06**	**0.50**	-0.01	0.01	0.02	0.02

(f) leatherleaf collars (seasonal instantaneous)

ln CH4 vs.	all years slope	all years r^2	2000 slope	2000 r^2	2001 slope	2001 r^2	2002 slope	2002 r^2	2003 slope	2003 r^2	2004 slope	2004 r^2
JD	**0.01**	**0.12**	**0.02**	**0.59**	**0.02**	**0.55**	0.01	0.04	0.00	0.02	0.00	0.02
NEE	0.00	0.00	**0.13**	**0.33**	-0.11	0.06	-0.07	0.02	-0.09	0.06	-0.08	0.06
respiration	**-0.16**	**0.12**	-0.08	0.08	0.00	0.00	**-0.29**	**0.28**	**-0.21**	**0.35**	-0.14	0.09
photo	**0.06**	**0.05**	**0.09**	**0.31**	-0.07	0.04	0.09	0.07	0.11	0.11	0.00	0.00
air T	**0.06**	**0.08**	0.03	0.02	0.01	0.00	**0.09**	**0.18**	**0.07**	**0.22**	0.08	0.09
peat T	**0.05**	**0.05**	**0.07**	**0.17**	0.03	0.02	0.06	0.06	-0.03	0.02	**0.08**	**0.17**
WTD	0.01	0.01	0.04	0.12	**0.06**	**0.34**	0.00	0.00	-0.02	0.03	0.04	0.15

Appendix 3. Means of variables and methane fluxes between years for all collars on the sub-seasonal scale for (a) early season and (b) late season.

(a) early sub-season

year	NEE		Respiration		Photosynthesis		ln CH$_4$ flux	
	Mean*	S.D.	Mean[§]	S.D.	Mean[+]	S.D.	Mean	S.D.
2000	5.0[a]	3.0	-5.7[ab]	2.2	10.7[a]	4.0	4.7	0.6
2001	5.3[ab]	2.0	-5.3[ab]	2.3	10.6[a]	3.1	4.7	0.5
2002	7.3[bc]	2.9	-4.3[a]	2.1	11.6[ab]	4.0	4.6	0.7
2003	7.4[bc]	2.0	-6.6[b]	2.6	13.9[b]	2.3	4.9	0.4
2004	7.4[c]	2.4	-6.1[b]	2.0	13.6[b]	3.7	4.8	0.6

*[§][+] Denotes significant differences between years using two-tailed ANOVA (α=.05) and Scheffe's post-hoc analysis. [a,b,c] denote statistically similar groups.
* (F= 7.349, d.f.=152, p< 0.001)
[§] (F= 3.786, d.f.=152, p= 0.006)
[+] (F= 5.553, d.f.=152, p< 0.001)

(b) late sub-season

year	NEE		Respiration		Photosynthesis		ln CH4 flux	
	Mean	S.D.	Mean*	S.D.	Mean	S.D.	Mean[§]	S.D.
2000	7.0	2.8	-5.7	1.8	12.7	3.2	5.4[ac]	0.6
2001	6.7	2.6	-5.8	1.7	12.6	2.9	5.8[ab]	0.8
2002	6.4	2.6	-6.7	1.8	13.1	2.6	5.9[b]	1.0
2003	6.7	2.4	-6.3	1.7	13.0	2.6	5.1[ac]	1.1
2004	6.4	3.0	-6.4	1.7	12.9	3.2	5.3[c]	0.8

*[§] Denotes significant differences between years using two-tailed ANOVA (α=.05). [a,b,c] denote statistically similar groups.
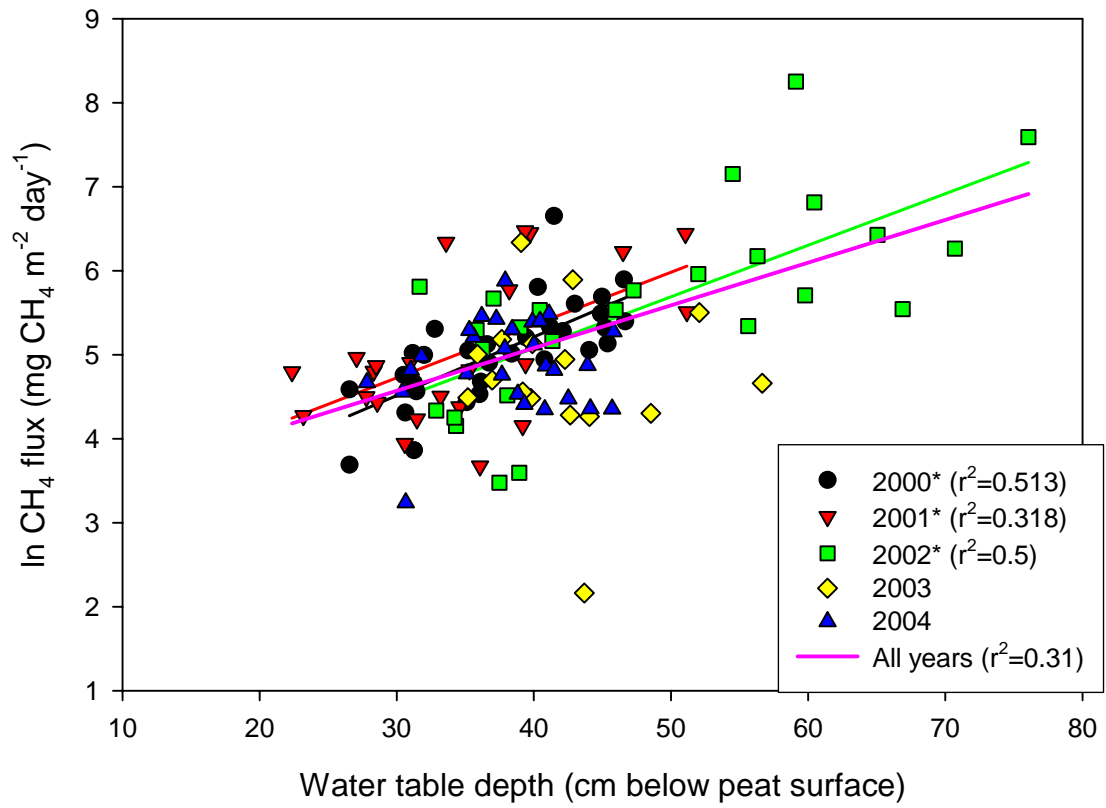* (F= 2.940, d.f.=233, p= 0.021)
[§] (F= 8.027, d.f.=233, p< 0.001)

Appendix 4.   Methane flux vs. Julian day for sedge collars in individual years. Regression line
(black) indicates best fit based on all years.
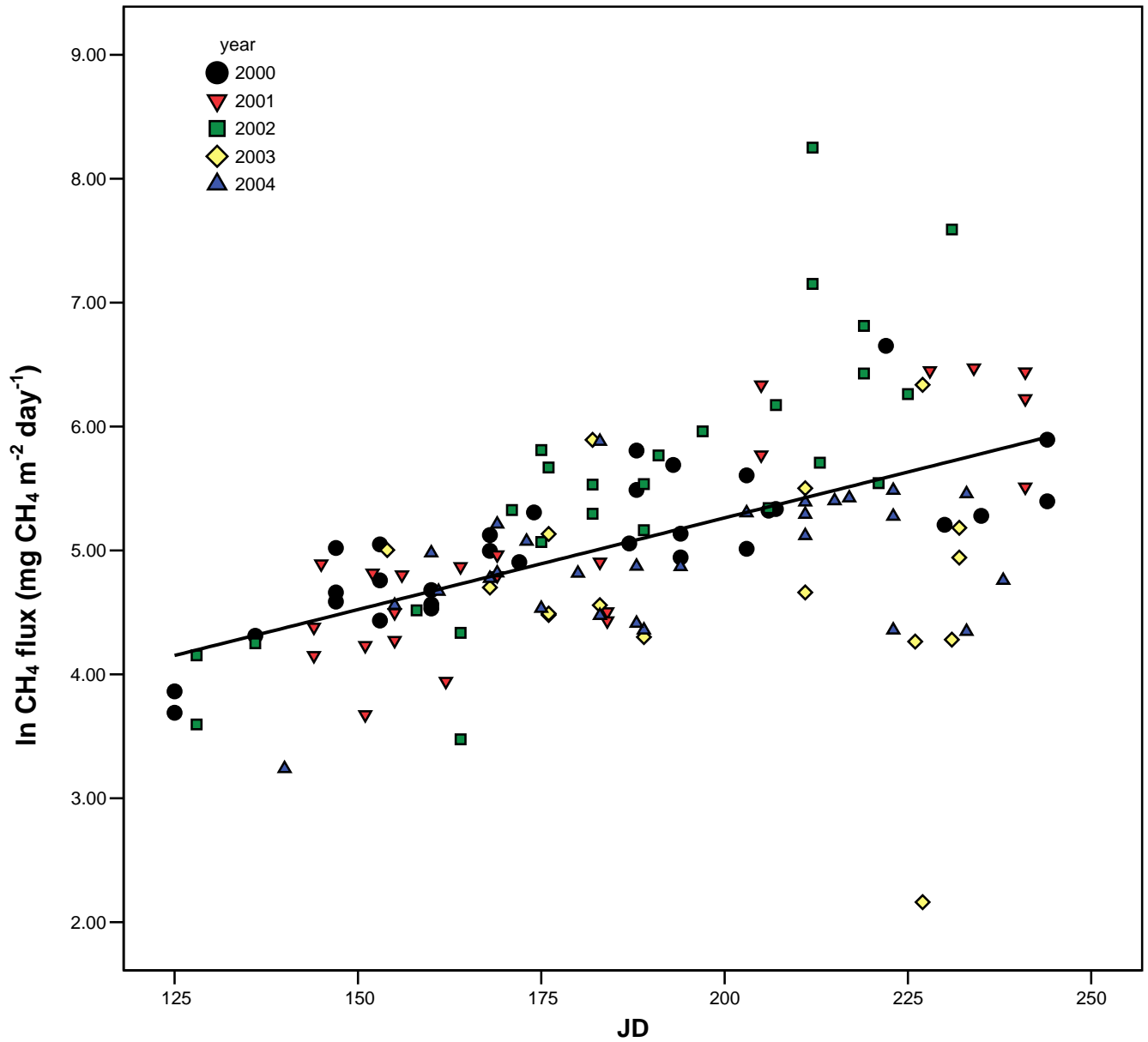
Appendix 5. Water table depth of sedge collars versus mean seasonal ln CH_4 flux, 2000-2004. * denotes significance of relationship.

Appendix 6. Correlations (r) of simple regressions between variables listed and ln CH$_4$ fluxes at different time scales and vegetation types for grouped years (2000-2004). Bold denotes significance (α=.05)

	Seasonal Instantaneous	Seasonal Mean	Early Season	Late Season	Sedge Collars	Leatherleaf Collars
JD	**0.42**		**0.52**	-0.01	**0.54**	**0.35**
NEE$_{max}$	-0.03	-0.14	**0.18**	**-0.16**	0.08	0.00
respiration	**-0.32**	-0.02	**-0.44**	**-0.22**	**-0.33**	**-0.35**
photo	**0.17**	-0.08	**0.39**	-0.02	**0.24**	**0.22**
air T	**0.33**	**0.30**	**0.33**	**0.25**	**0.34**	**0.27**
peat T	**0.34**	0.06	**0.22**	**0.17**	**0.54**	**0.23**
WTD	**0.22**	-0.16	0.01	0.04	**0.56**	0.09