Carbon cycling in peatlands — A review of processes and controls

Christian Blodau

Abstract: Covering only 3% of the land area, northern peatlands store about 30% of the global soil carbon and account for 5 to 10% of the global methane burden to the atmosphere. A review of the literature on net ecosystem exchange, net primary productivity, carbon mineralization, methane emissions, and dissolved organic carbon dynamics indicates that peatlands can be both C sources and sinks. The temporal and spatial variability of fluxes is large, but a substantial portion of this variation can be explained by environmental and ecological variables. Uncertainty in predictions about carbon dynamics under changing environmental conditions arises from a number of knowledge gaps: (*i*) the understanding of how organic matter is mineralized and partitioned into carbon dioxide, methane, and dissolved organic carbon is insufficient; (*ii*) little is known about the consequences of long-term and short-term disturbances, such as elevated carbon dioxide concentrations, nitrogen and sulfur deposition, fire, and droughts, on the individual components of the carbon cycle; (*iii*) models that capture the dynamic interaction of the processes and their controls have not been developed yet, with the notable exception of methane dynamics.

Key words: peatlands, carbon cycle, organic matter, carbon dioxide, methane, climate change.

Résumé : Couvrant seulement 3 % de la surface terrestre, les tourbières nordiques constituent environ 30 % du carbone global du sol, et représentent 5 à 10 % de la charge en méthane vers l'atmosphère. Une revue de la littérature sur les échanges nets de l'écosystème, la productivité primaire, la minéralisation du carbone, les émissions de méthane, et la dynamique du carbone dissout indique que les tourbières peuvent à la fois agir comme source et comme puit de C. La variabilité spatio - temporelle des flux est grande, mais une portion substantielle de cette variation peut s'expliquer par des variables environnementales et écologiques. L'incertitude des prédictions portant sur la dynamique du carbone sous des conditions changeantes de l'environnement, proviennent de plusieurs connaissances déficientes. (*i*) La compréhension du processus de la minéralisation de la matière organique et la partition en dioxyde de carbone, méthane et carbone organique dissout, est insuffisante. (*ii*) On connaît peu de choses sur les conséquences à court et à long terme de perturbations telles que les teneurs élevées en dioxyde de carbone, les dépôts d'azote et de soufre ainsi que le feu et les sécheresses, sur les composantes individuelles du cycle du carbone. (*iii*) Aucun modèle n'a encore été développé pour saisir l'interaction dynamique des processus et leur contrôle, sauf l'exception notoire qui est celle de la dynamique du méthane.

Mots clés : tourbières, cycle du carbone, matière organique, dioxyde de carbone, méthane, changement climatique.

[Traduit par la Rédaction]

Received 1 November 2001. Accepted 16 May 2002. Published on the NRC Research Press Web site at `http://er.nrc.ca/` on 21 June 2002.

C. Blodau.[1] Department of Geography and Centre for Climate and Global Change Research, McGill University, 805 Sherbrooke Street West, QC H3A 2K6, Canada.

[1] Present Address: Department of Hydrology and Limnological Research Station, University of Bayreuth, D-95444 Bayreuth, Germany (email: christian.blodau@uni-bayreuth.de).

 DOI: 10.1139/A02-004

Relevance of carbon cycling in peatlands

Northern peatlands play an important role in the global carbon (C) cycle. Although they cover only 3% of the land area (Maltby and Immirzi 1993), they store about 30% of the global soil C, equivalent to about 455 Pg (Gorham 1991; Dean and Gorham 1991). Northern peatlands developed within a few thousand years following the end of the last glaciation (Harden et al. 1992). The accumulation of organic matter is caused by anoxic conditions in the waterlogged peat masses and by the stability of peat forming plant litter (Glaser 1987). Northern peatlands mainly function as long-term sinks for atmospheric carbon dioxide (CO_2) and sources of atmospheric methane (CH_4). As is seen from atmospheric records, the development of peatlands has significantly lowered atmospheric CO_2 and raised CH_4 concentrations since the end of the last glaciation (Blunier et al. 1995; Fung et al. 1991).

Measured CO_2 and CH_4 exchange rates between peatlands and the atmosphere strongly vary both geographically and seasonally (Moore et al. 1998), necessitating an effort to understand the processes that produce and consume trace gases in peatlands and the factors that control the exchange rates.

The principal controls on the C cycle are soil temperature, plant community structure, position of redox boundaries associated with the water table, and the chemical composition of plant tissues and peat (Bubier et al. 1993, 1995; Whiting and Chanton 1993; Yavitt et al. 1997). Empirical models that incorporate these controls can explain much of the variation in seasonal CH_4 exchange rates and reflect average differences in environmental and ecological variables within and between peatlands (Moore et al. 1998).

On smaller spatiotemporal scales and for CO_2 exchange in general, much less variation in exchange rates can be explained by environmental and ecological variables (e.g., Bellisario et al. 1999; Moore et al. 1994; Shannon and White 1994). Changes in the frequency and intensity of weather related events, such as the local water table lowering during droughts, may be a consequence of climate change. The consequences of these changes are at present not clear, but might be significant. It has been demonstrated, for instance, that fluctuating water table levels can increase C mineralization rates by a factor of 1.5 to 3 (Aerts and Ludwig 1997).

Such observations raise concern about the accuracy of trace gas exchange scenarios that are based on average changes in environmental and ecological variables, rather than disturbances. Controls on other processes in the C cycle, such as mineralization of organic C and release of dissolved organic carbon (DOC), have also not been substantiated in studies based on dynamic scenarios.

The coupling between carbon, nitrogen (N), and sulfur (S) cycling in peatlands is also increasingly drawing attention. Deposition experiments demonstrated that increased N deposition increased primary production rates in peatlands (Li and Vitt 1997; Rochefort et al. 1990), which might alter C sequestration rates (Schindler and Bayley 1993). It has also been hypothesized that, in analogy to forest ecosystems, N deposition might alter organic matter mineralization rates in peatlands. Increased sulfate deposition rates have been conjectured to be the cause for relatively small CH_4 production and large sulfate reduction rates in oligotrophic peatlands in eastern North America and England (Nedwell and Watson 1995; Watson and Nedwell 1998). In incubation and field experiments sulfate addition often results in decreased potential production and emission rates of CH_4 (Dise and Verry 2001; Watson and Nedwell 1998; Yavitt et al. 1987).

In 1991, Gorham wrote “given the diversity of possible responses by boreal and subarctic peatlands to climatic warming, it is impossible at present to predict their future contributions to the global carbon cycle”. This probably still holds true, but more recently much has been learned about the processes involved in the C cycling in peatlands and also about possible responses to environmental changes. This work provides a review of much of this progress.

Peatlands

Peatlands are defined as any area with a waterlogged predominantly organic substrate of at least 30–40 cm thickness (Glaser 1987). Peatlands have been classified based on several criteria, e.g., vegetation characteristics, geomorphology, hydrology, chemistry, stratigraphy, and peat characteristics, or on combinations of these criteria. This has resulted in complex classification systems (Moore and Bellamy 1974; Mitsch and Gosselink 1993). In North America four basic types, ombrotrophic bogs, minerotrophic fens, intermediate or "poor" fens, and calcareous fens, are distinguished. These types differ with respect to pH, base cation concentrations, dominating vegetation, and hydrologic dynamics (Glaser 1987; Mullen et al. 2000; Vitt et al. 1995). Ponds and beaver ponds also constitute important peatland components (Belyea and Lancaster 2002; Hamilton et al. 1994; Roulet et al. 1997).

Peatlands are structured both horizontally and vertically. Vertical peat profiles consist of a saturated zone, in which oxygen is depleted and organic matter is anaerobically decomposed ("catotelm"). On top of the catotelm a surface layer ("acrotelm") can be found (Clymo 1984). This layer is often oxic but can seasonally be saturated and anoxic. The acrotelm consists of a productive layer, a litter layer, and a collapse layer in which the macrostructure of the plants is lost (Warner 1996). Acrotelm and catotelm store approximately 98.5% of the total C in peatlands (Gorham 1991). Carbon stored in vegetation contributes on average only about 1.5% ($\sim$2000 g m^{-2}) to the C pool, but this contribution may vary substantially (350 to 6000 g m^{-2} (Grigal et al. 1985)). Horizontally, peatlands are structured on different scales. "Microtopes" are developed mainly within the vegetation layer and the acrotelm. A typical example is the often observed hummocks and hollows, which represent elevated and indented areas on the scale of a square metre and display distinct vegetation associations (Rochefort et al. 1990; Warner 1996). Individual, more or less homogeneous peatlands, such as bogs and fens, have been defined as mesotopes. "Peatland complexes" or macrotopes encompass many individual peatlands and can cover hundreds or even thousands of square kilometres.

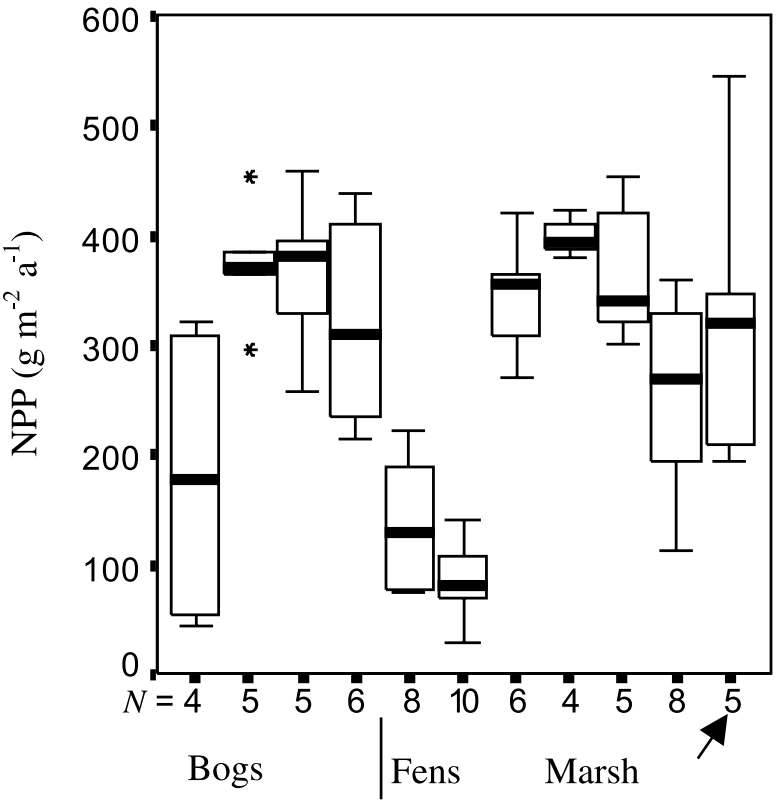
Net primary production

Rates of net primary production

Net primary production (NPP) has been estimated in all types of northern peatlands, by direct biomass measurements or as part of net ecosystem exchange studies (Frolking et al. 1998). Often the contribution of the different vegetation units was also quantified (Szumigalski and Bayley 1997). The reported values for aboveground net production vary over more than two orders of magnitude, from about 5 g m^{-2} a^{-1} dry weight to more than 1000 g m^{-2} a^{-1}, covering average values for the full range of global ecosystems (Melillo et al. 1993). Values between 100 and 400 g m^{-2} a^{-1}seem most common (Fig. 1). The NPP of northern peatlands is therefore lower than that of most other ecosystems relevant to the global C cycle, but it is of a similar magnitude as the NPP of boreal forests (Melillo et al. 1993). A problem with these values, which were determined by seasonal growth, arises from the fact that generally only aboveground production was determined. The belowground contribution of vascular plants in peatlands is probably a very important component of the C cycle, accounting for about 30–50% of the vascular plant production(Backeus 1990; Moore et al. 2002). Also, if graminoid plants are abundant, accounting for the life history of the vegetation can become important for determining the seasonal NPP due to high shoot mortalities throughout the vegetation period. Bernard and MacDonald (1974) found for *Carex lacustris*, a sedge characteristic of shallow waters bordering swamps and lakes, that NPP increased from 857 to 1580 g m^{-2} $a^{-1}$when shoots dying during the vegetation period were considered.

The variance in NPP within sites, within peatland types, and within climatic zones is typically large (Bartsch and Moore 1985; Klinger et al. 1994; Moore 1989*a*, 1989*b*; Szumigalski and Bailey 1997). The NPP also varies strongly on an annual basis (Moore 1989*b*; Rochefort et al. 1990), which might provide an explanation for some of the variance found among studies. Although peatland types, such

Fig. 1. Variability of rates of NPP (C) within and between northern peatlands covering peatlands in the Hudson Bay Lowlands (Klinger et al. 1994), western Canada (Szumigalski and Bayley 1997), and northern Quebec (Bartsch and Moore 1985). Boxes represent the intra-site variability of NPP. The central crossbar represents the median; the boxes, the 75th and 25th percentile; the upper and lower bars, the 90th percentile; the asterisks, extreme values of the displayed data set.



as bogs and fens, cannot be clearly separated with respect to NPP (Fig. 1), it seems that photosynthetic activity in bogs is on average about 25 % lower than in fens (Frolking et al. 1998).

Controls on net primary production

The NPP in northern peatlands is mainly controlled by the level of photosynthetic radiation (PAR), by the hydrologic regime, and by the availability of N and phosphorus. The NPP and mean water table level are believed to be positively correlated, based on results from field studies (Forrest and Smith 1975; Moore 1989*b*; Szumigalski and Bayley 1997). There is also experimental evidence for such a correlation. Lowering the water table levels from 7 to 37 cm significantly decreased the NPP of *Sphagnum* sp. in greenhouse experiments (Williams et al. 1999). However, the response of NPP to the water table position is not straightforward to predict because individual vegetation types, such as herbs and shrubs, respond differently to this control. Long-term succession of the vegetation communities may also offset short-term effects of changes in water table levels (Szumigalski and Bayley 1997). Mean annual temperature (MAT) might currently account for about 30 to 40% of variance across peatland *Sphagnum* related NPP across the climatic zones (Moore 1989*b*). Mean monthly summer temperatures are also positively correlated with the standing crop in sedge fens (Gorham 1974).

In pristine oligotrophic peatlands, N is mostly retained by the vegetation and the belowground turnover is dominated by organic forms of N (Hemond 1983; Urban and Eisenreich 1988). This is probably also true for many more minerotrophic wetlands (Li and Vitt 1997; Rochefort et al. 1990; Vitt et al. 1995). At low background deposition rates of N, the NPP of peatland forming mosses can temporarily increase as a response to an increased experimental N deposition level (Li and Vitt 1997; Rochefort et al. 1990). However, such a response does not always occur (Tamm 1954; van der Heijden et al. 2000; Williams et al. 1999; Williams and Silcock 1997). Elevated N deposition levels can even be detrimental to the primary production of *Sphagnum* when other factors limit the growth rate and nutrient imbalances develop (van der Heijden et al. 2000).

For other sites with larger background inputs of atmospheric N it was concluded that the NPP was not limited by N availability (Hemond 1983) and that instead phosphorus was limiting the NPP (Tamm 1954; Williams et al. 1999; Williams and Silcock 1997). Nitrogen saturation, which is characterized by the through-flow of mineral N, has recently been proposed to occur in peatlands that receive more than about 18 kg N ha a^{-1} (Lamers et al. 2000). Lamers and colleagues' hypothesis was based on a simple mass balance consideration of annual biomass synthesis, N deposition level, and C/N ratios of 40–50, which prevail in *Sphagnum*. This hypothesis is supported by experimental studies (Williams et al. 1999).

Elevated levels of atmospheric CO_2 are also likely to affect the NPP of peatlands. Short-term, physiologically oriented laboratory studies demonstrated a stimulation of *Sphagnum* mosses and shrubs by elevated CO_2 concentrations (Paffen and Roelofs 1991; Silvola et al. 1993; van der Heijden et al. 2000), but responses vary among species and over time (Jauhiainen et al. 1993). The response of mosses is also a function of the nutrient status and will probably have ramifications for the quality of the plant detritus (van der Heijden et al. 2000).

In conclusion, higher water table levels, temperatures, and N availability probably increase the NPP in peatlands where N is in short supply. In cases where higher levels of N are supplied from the groundwater or atmospheric deposition, phosphorus availability might become a limiting factor for the NPP. The long-term effect of elevated CO_2 concentrations cannot be quantified yet, due to both the occurrence of nutrient interactions and physiological responses and the lack of long-term ecosystem manipulation studies.

Carbon mineralization

Carbon mineralization rates

Carbon dioxide production is the result of the mineralization of soil organic C and plant respiration. Both processes might occur at similar rates in peatlands (Moore et al. 1998), but there is some uncertainty in this hypothesis, since both processes are difficult to separate in situ.

In peatlands C mineralization proceeds slowly compared to most other ecosystems. In organic matter decomposition studies, exponential decay constants (-0.05 to -1.2 a^{-1}) are on average lower than for plant residues and labile organic matter in terrestrial soils (-0.1 to -4.2 a^{-1}, Aiwa et al. 1998; Jenkinson 1977; Trumbore 1993) and in coastal marine sediments (-0.5 to -8.8 a^{-1}, Berner 1980; Martens and Klump 1984). They are, on the other hand, larger than in deep sea marine sediments (-10^{-2} to -10^{-4} a^{-1}) (Emerson et al. 1985; Heggie et al. 1987). In peatlands, litter bags filled with *Carex*, *Sphagnum*, *Betula*, and other litter lost between 3 and 47% of mass per year, if the reported values are recalculated for a 1-year period (Bartsch and Moore 1985; Clymo 1978; Johnson and Damman 1991; Moore 1989*a*; Verhoeven and Toth 1995). On average the mass loss amounted to about 20% based on a 1-year period. It has to be kept in mind, though, that the remaining mass decreases exponentially, rather than linearly. This probably introduced some variability in these figures. Lower (about 5% per year) and less variable values were obtained in two long-term studies of peat decomposition under laboratory conditions (Hogg 1993; Updegraff et al. 1996). Nonvascular species such as *Sphagnum* sp. decompose slower than vascular species (Bartsch and Moore 1985; Moore 1989*b*; Verhoeven and Toth

1995). Decomposition rates have also been reported to vary by a factor 2–3 among different *Sphagnum* species (Rochefort et al. 1990).

Controls on carbon mineralization rates

Carbon mineralization rates depend on the availability of oxygen associated with the depth of the water table, the microbial activity in the peat, the soil temperature, the type of vegetation, and the chemical characteristics of the peat (Johnson and Damman 1991; Moore and Dalva 1993; Updegraff et al. 1996; Yavitt et al. 1997). Under normal peat temperature ranges, CO_2 production rates increase by a factor of 2–3 for every 10°C temperature increase (Q_{10}) (McKenzie et al. 1998; Moore and Dalva 1993; Yavitt et al. 1997). Smaller and larger Q_{10} values have also been reported (Russell and Voroney 1998; Scanlon 1998; Updegraff et al. 1996; von Hulzen et al. 1999). The Q_{10} values vary with depth and among areas in peatlands (Scanlon 1998). It is at present not clear what controls the temperature dependency of C mineralization rates.

The experimental response of CO_2 production rates to changes in redox conditions is very variable. In incubation and column studies, aerobic–anaerobic ratios of C mineralization may range from 1.2 to 6 (Aerts and Ludwig 1997; Moore and Knowles 1989; Moore and Dalva 1993; Öquist and Sundh 1998; Updegraff et al. 1996; Yavitt et al. 1997). By comparison of CO_2 production rates in incubations with long-term in situ C accumulation rates it has also been inferred that rates increase up to a factor 200 when stable, previously anaerobic peat from lower depths is incubated in flasks under aerobic conditions (Hogg 1993). Fluctuations in redox conditions may also have a net effect on CO_2 production rates. In laboratory column studies periodic changes in aeration or water table increased cumulative C mineralization rates by a factor of 1.5 to 3 (Aerts and Ludwig 1997). Similar results have also been reported from long-term litterbag decomposition studies under field conditions (Belyea 1996). These increased cumulative CO_2 production rates might be caused not only by larger aerobic CO_2 production rates but by mineralization pulses after disturbance, as observed in drying–wetting experiments with soils (Bottner 1985; Clein and Schimel 1994; Kieft et al. 1987). The increased CO_2 production after disturbance may be caused by redox-induced chemical breakdown and enhanced recycling of biomass (Aller 1994; Kieft et al. 1987). Activation of exo-enzymes after short-term exposure to O_2 can also have a pronounced effect on C mineralization rates (Freeman et al. 1997).

Many other chemical controls on C mineralization rates have been documented. Nitrogen and phosphorus concentrations in the litter of *Sphagnum* have the potential to influence C mineralization rates (Bartsch and Moore 1985; Hogg et al. 1994). Carbon mineralization rates were often found to be correlated to chemical parameters such as the contents of water soluble carbohydrates (Updegraff et al. 1996), acid-soluble organic matter and carbohydrates (Updegraff et al. 1996; Yavitt et al. 1997), the C/N and lignin/N ratios, or lignin contents (Best and Jacobs 1997; Bartsch and Moore 1985; Updegraff et al. 1996). The predictive capacity of such parameters may be limited to individual peatlands. Across the temperate and boreal zone of North America, the lignin/N ratio, which is used in many terrestrial ecosystem models (e.g., Schimel et al. 1996), was not found to be a strong predictor of C mineralization rates (Yavitt et al. 1997). There is also evidence that individual environmental and chemical controls strongly interact with each other (Amaral and Knowles 1994; Updegraff et al. 1996).

Low C mineralization rates in peatlands and differences in C mineralization rates between litter of different moss species may also be a result of inhibitors of microbial activity. Homogenates of freshly ground *Sphagnum* plants have been shown to slow down the decomposition of *Sphagnum* and *Carex* litter (Verhoeven and Toth 1995). The authors speculated that antibiotic properties of certain compounds contained in *Sphagnum* might be responsible for this effect.

The study of decomposition rates has suggested that C mineralization rates result from the interplay of plants and water table fluctuations. Carbon mineralization rates not only decrease with the age of the peat (Hogg 1993) but they also differ between hummocks and hollows (Belyea 1996; Johnson et al. 1990). These differences are partly caused by the species distribution within the microtopography

(Johnson and Damman 1991). While the (potential) decomposability of the organic material decreases with age and depth, actual decomposition rates seem to be largest close to the water table (Belyea 1996). This finding has been attributed to optimum conditions of aeration, water, and nutrient availability. The decomposition process itself also provides an important feedback on the maintenance of anaerobic conditions, since the loss of the plant structure decreases the hydraulic conductivity. This initiates the development of the catotelm and the existence of a perched water table (Johnson et al. 1990). A perched water table is, in turn, a prerequisite for low rates of anaerobic C mineralization.

Overall, higher temperatures, lower water tables, fluctuating water tables, minerotrophic conditions, and the predominance of vascular, especially graminoid plants, seem to sustain larger C mineralization rates. Although these controls have been identified, it is difficult to establish well-constrained quantitative relationships between these controls and C mineralization rates due to the outlined large variance in the experimental response of CO_2 production rates to these controls.

A portion of this variance may be caused by differences in the experimental conditions under which rates were determined and by the history of the peat prior to experimentation. This can be concluded by drawing the analogy to studies in which peat was exposed to changes as they often occur during sampling or in incubations. Significant effects of redox conditions on CO_2 production rates occurred when the changes in water table levels were large and when the incubation periods were long (Bergmann 1998; Moore and Dalva 1993, 1997). Conversely C mineralization rates were not significantly affected by small changes in water tables (Best and Jacobs 1997; Freeman et al. 1993, 1996) and when the incubation periods were short (Yavitt et al. 1997).

However, there are also more fundamental problems. High-resolution measurements of C mineralization rates have not been carried out under dynamic conditions and in undisturbed soils. In situ litter decomposition studies have not provided the control and the time resolution necessary for the quantification of the effects of environmental variables. Little is still known about the quantitative in situ effect of temperature, water table level, and water potential fluctuations on C mineralization rates and on the microbial communities involved in this process. The effects of amplitude, duration, and frequency of such fluctuations have not been investigated. Studies that address these effects are needed to assess the consequences of climate change on this component of C cycling.

Methane dynamics

Methane exchange with the atmosphere

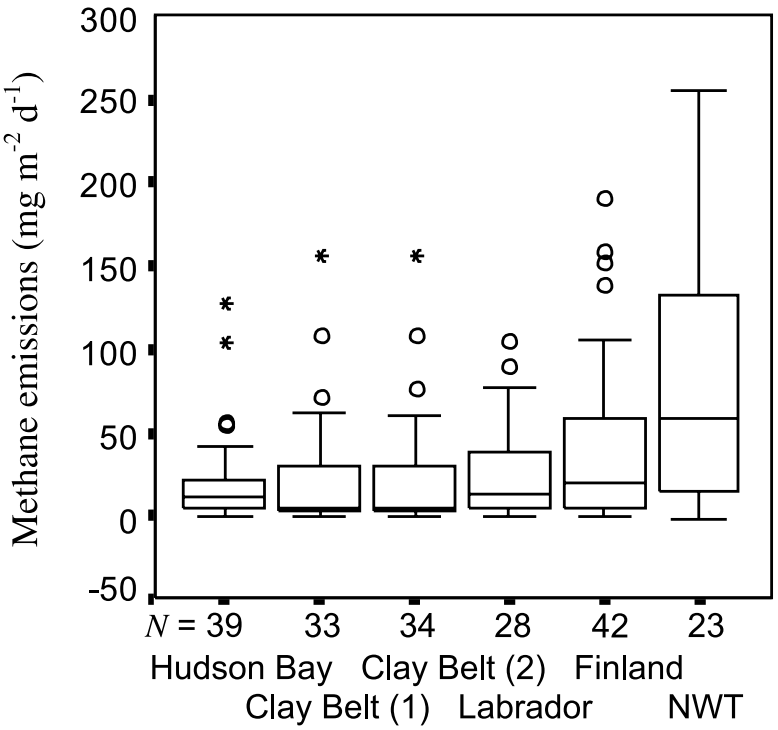
Methane fluxes between peatlands and the atmosphere may range from slight uptake to emissions of more than 1000 mg m^{-2} d^{-1} (Klinger et al. 1994; Yavitt et al. 1990*a*). Fluxes are temporally and spatially highly variable (Fig. 2; Bubier et al. 1993; Moore et al. 1990, 1994, 1998; Roulet et al. 1997; Yavitt et al. 1990*b*). Average emissions of 5 to 80 mg m^{-2} d^{-1} are most common in northern peatlands. The flux distributions are skewed to larger values, but values over 100–200 mg m^{-2} $d^{-1}$are unusual and restricted to ponds (Hamilton et al. 1994; Roulet et al. 1997; Scott et al. 1999; Sugimoto and Fujita 1997; Waddington and Roulet 1996; Yavitt et al. 1990*b*). These areas contribute proportionally more to the overall emissions than their relatively small surface area suggests. Beaver activity is hence an important biological factor for CH_4 emissions from northern peatlands (Naiman et al. 1990). Fens generally are stronger emitters than bogs because the anaerobic zone is on average closer to the peatland surface (Moore et al. 1990). Within bogs significant emissions are restricted to lawns and hollows (Bubier et al. 1993; Klinger et al. 1994; Waddington and Roulet 1996).

Controls on CH_4 production, consumption, and emissions

Environmental and chemical variables

Methane production depends directly on the microbial activity in the peat and indirectly on the soil temperature, the type of vegetation, the chemical characteristics of the peat, and on the position of redox

Fig. 2. Variability of rates of methane emissions (C) within and between northern peatland regions (Moore et al. 1994; Bubier 1995; Bubier et al. 1993; Nykaenen et al. 1998; Liblik et al. 1997; data were recalculated for a 150 d period). The central crossbar represents the median; the boxes, the 75th and 25th percentile; the upper and lower bars, the 90th percentile; the asterisks, extreme values of the displayed data set.



boundaries associated with the water table (Bubier et al. 1993, 1995; Whiting and Chanton 1993; Yavitt et al. 1997). Strictly anaerobic conditions are obligatory for CH_4 production, since methanogens are obligate anaerobes (Fetzer et al. 1993). Methane production and emission might also be influenced by the reduction of sulfate (Dise and Verry 2001; Nedwell and Watson 1995; Watson and Nedwell 1998; Wieder et al. 1990) because sulfate reducers can successfully compete with methanogens for organic substrates (Kristjanson et al. 1982; Lovley and Klug 1983). The sulfate availability in peatlands is influenced by the atmospheric input and by the reoxidation of reduced inorganic and organic S, which occurs during water table fluctuations (Bayley et al. 1986; Devito and Hill 1999; Mandernack et al. 2000).

Soil acidity controlled CH_4 production in laboratory studies (Dunfield et al. 1993; Valentine et al. 1994). Optimum pH values for methanogenesis were found to be about 6–7. A dependency of CH_4 production rates on pH could not be found in the field (Moore et al. 1994) possibly due to an adaptation of populations to acidity (Updegraff et al. 1996). Additions of either easily fermentable substrates (glucose and leaf leachate) or fermentation products (ethanol, formate, acetate, methanol, and H_2) to peat often resulted in increased CH_4 production rates, indicating substrate limitation of CH_4 production (Amaral and Knowles 1994; Bergmann 1998; Valentine et al. 1994). Acetate might be the major substrate for methanogens in peatlands (Hornibrook et al. 1997). Under acidic conditions, high concentrations of fermentation products, in particular acetic acid, can inhibit methanogenesis (Bergmann 1998; Yavitt et al. 1987). The addition of micronutrients such as Ni, Fe, Co, and Na, can increase CH_4 production rates in oligotrophic peatlands (Basiliko and Yavitt 2001). Several organic matter characteristics, such as the

lignin/N ratio, were also found to correlate with potential CH_4 production rates (Updegraff et al. 1996; Valentine et al. 1994; Yavitt et al. 1997).

Studies of the effects of water table levels and temperature on CH_4 production in peat soils and exchange with the atmosphere have focussed on the potential production rates in disturbed samples (e.g., Kettunen et al. 1999; Öquist and Sundh 1998; Yavitt et al. 1987, 1990*a*, 1997) and on the net exchange of trace gases from peat columns with the atmosphere (e.g., Aerts and Ludwig 1997; Moore and Knowles 1989; Moore and Dalva 1993). These studies demonstrated that CH_4 production and emission exponentially decrease with lower water tables, and variance could generally be explained fairly well.

The temperature dependency of CH_4 production (Q_{10} = 4.1) is on average steeper than of CO_2 production (Q_{10} = 2–2.5) and shows a large range of Q_{10} values from 1.1 to 28 (Segers 1998). Presently this phenomenon is not fully explained. "Anomalous behavior" of methanogens and interactions between substrate and temperature effects have been conjectured (Segers 1998). Methanogens have a narrow substrate spectrum, which makes them depend on fermentation processes (Conrad 1999), and they are also inferior competitors when other electron acceptors are abundant (Achtnich et al. 1995). Modeling of incubation scale data, which simulated the interaction of these components, has suggested that the variable temperature response could be a result of the competition of methanogenesis and electron accepting processes, the growth of methanogenic populations, and the provision of substrates by fermentation (von Hulzen et al. 1999).

Methane emissions in the field are controlled by the topography, which influences the hydrologic regime and the vegetation patterns within peatlands (Waddington and Roulet 1996). Net ecosystem productivity and dominating plant species were found to correlate to CH_4 emissions on the landscape scale when water table levels are closer than about 20 cm to the peatland surface (Bubier 1995; Bubier et al. 1995; Whiting and Chanton 1993). These relationships reflect that plant communities supply substrates for CH_4 production, may allow for conduit transport of CH_4, and indicate average water table levels (Bubier 1995).

Empirical models that are based on water table levels, peat temperatures, and vegetation characteristics can therefore explain much of the variation in seasonal CH_4 exchange rates and reflect average differences in environmental and ecological variables within and between peatlands (Dise et al. 1993; Moore et al. 1998). The regression slopes of such relationships between cumulated CH_4 emissions and seasonally averaged water tables levels are fairly similar (Bubier et al. 1993; 1995; Moosavi et al. 1996; Moore et al. 1994; Nykaenen et al. 1998). These regression slopes indicate that lowering water table level by 1 cm lowers the logarithm of seasonal CH_4 emission by about 2–5%.

Interactions among controlling variables

The relationship among methane emissions, dominating plant types, and water tables is scale dependent. Statistical models are regionally valid (Bubier et al. 1995), but they are weak when the available data are lumped together (Moore et al. 1998). Methane emissions also vary among regions in the northern hemisphere and tend to increase with latitude (Fig. 2), although primary production, which is one of the landscape level controls on CH_4 emissions (Whiting and Chanton 1993), tends to decrease with latitude (Moore 1989*b*). Other variables such as average water table levels and peat temperature cannot explain regional differences in CH_4 emissions (Moore et al. 1998).

Also on smaller spatial and temporal scales, little of the variation in CH_4 exchange rates can be explained by water table levels, peat temperature, and other variables (Kettunen et al. 1996; Bellisario et al. 1999; Moore et al. 1994; Shannon and White 1994). This is probably a consequence of the interaction among production, consumption, storage, and transport of gases in the peat. On time-scales of weeks to months, equilibrium among these processes might not be reached when environmental controls vary. It can therefore be hypothesized that biogeochemical process rates in the peat are to a varying degree decoupled from fluxes to the atmosphere. This would explain why fluxes measured in field studies were

decoupled from controls on CH_4 production (Kettunen et al. 1996; Bellisario et al. 1999; Moore et al. 1994; Shannon and White 1994). It also explains that better correlation between environmental variables and CH_4 exchange rates have been obtained by cumulating exchange rates of CH_4 (e.g., Moore et al. 1998), which eliminates time lags in process rates, storage, and transport effects.

Indeed there is support for such an interpretation. Öquist and Sundh (1998) and Kettunen et al. (1999) demonstrated that the onset of methanogenesis in surface layers of peat soils is not inhibited by oxic periods, but that time lags occur. In bacterial suspensions, oxygen does not impair the viability of cells and 0.5 to 10% of the active biomass might even survive desiccation, but it reduces potential production rates (Fetzer et al. 1993). Mayer and Conrad (1990) also noted that the initiation of CH_4 production in paddy soils is retarded when soil is stored under aerated but moist conditions. These observations suggest that CH_4 production rates in zones that are exposed to water table fluctuations show a "memory" for previous conditions, which would cause variable CH_4 production rates at a particular location after the onset of anaerobic conditions. Moreover, the buildup of dissolved CH_4 in the peat might require relatively long time periods (Kettunen et al. 1996).

Methanotrophic bacteria in aerobic soil reoxidize methane to CO_2 (Edwards et al. 1998). Since methanotrophic bacteria are dependent on both oxygen and CH_4 as substrates, reoxidation of methane is mostly located within about 25 cm around the oxic–anoxic interface (Segers 1998). Methane oxidation activity is probably not affected by the delayed response to changes in oxygen availability described above. In several studies large aerobic CH_4 oxidation potentials were found in previously anaerobic peat (Moore et al. 1994; Yavitt et al. 1990*a*), probably resulting from the capacity of methanotrophs to survive anaerobiosis (Edwards et al. 1998). With respect to climate change, temperature effects on CH_4 consumption (Q_{10} = 1.9) are on average smaller than on methane production (Q_{10} = 4.1; Segers 1998). Increasing mean annual temperatures could therefore cause increasing CH_4 emissions, assuming other controls remain unchanged (Moore et al. 1998).

Since CH_4 is oxidized once it reaches aerobic soil layers, CH_4 emission rates critically depend on rates of transportation. Transportation rates greatly increase when water tables decrease, since diffusion rates in the pore gas space are much larger than in pore water (Lerman 1979). Through the degassing of stored CH_4, decreasing water table levels can thus result in temporarily increasing CH_4 emissions (Kettunen et al. 1996; Moore et al. 1990; Shannon and White 1994). Large rates of CH_4 emissions also occur if plant root conduit and ebullition (bubbling) prevail (Fechner-Levy and Hemond 1996; Shannon and White 1994; Schimel 1995). Up to 90% of CH_4 emissions may be via root transport where sedges are the dominating plants (Schimel 1995). The resulting fast transportation velocities greatly reduce the residence time of CH_4 in the aerated zone of peat soils and reduce the fraction of the produced CH_4 that is oxidized. It has consequently been demonstrated that the onset of significant CH_4 emissions is bound to the development of annual plant roots in the spring (Shannon and White 1994; Shannon et al. 1996). Methane transported by advection and diffusion moves more slowly and is prone to reoxidation, causing emission rates to be low.

Roots can, however, also mediate the transportation of oxygen into the anaerobic zone. This oxygen locally reoxidizes CH_4 in the rhizosphere (Dannenberg and Conrad 1999). The relative importance of either process is probably a function of root density and plant type. Large root densities may cause increased CH_4 oxidation rates (Arah and Stephen 1998).

Modeling of CH_4 emissions from various peatlands has suggested that simple relationships between environmental variables and CH_4 emissions will generally not exist on the time-scale at which environmental variables typically vary (Walter and Heimann 2000). Walter and Heimann's model explains how emissions result from the interaction of production, transportation, and oxidation. However, so far it is not possible to predict CH_4 emissions without site-specific tuning because biogeochemical processes and characteristics affecting CH_4 production have not been included in this and other models.

Biogeochemical suppression of methane production

Biogeochemical processes and especially the availability of inorganic electron acceptors might have important consequences for C cycling in wetlands (Roden and Wetzel 1996; Wieder et al. 1990). It has been suggested, based on field studies and laboratory assays, that CH_4 production and emissions in peatlands can be suppressed under high atmospheric deposition levels of sulfate (Nedwell and Watson 1995; Watson and Nedwell 1998). This is supported by Dise and Verry's (2001) finding that sulfate addition decreased CH_4 emission rates from a peatland when exchange data were cumulated over time.

Usually, it is assumed that such an effect results from methanogenic and sulfidogenic activity being competitive (e.g., Nedwell and Watson 1995). Sulfate reduction will then predominate, due to thermodynamic and kinetic reasons, when sulfate is sufficiently available (Achtnich et al. 1995; Kristjanson et al. 1982). Similarly, reduction of ferric iron oxides may decrease both sulfate reduction and methanogenesis in southern and agricultural wetlands (Achtnich et al. 1995; Roden and Wetzel 1996). Studies that report on iron reduction rates in northern peatlands are not available to date.

A general problem with the "competitive suppression hypothesis" is that in oligotrophic peatlands sulfate pools are small even under severely S-polluted conditions. ^{35}S-radiotracer assays of sulfate reduction suggested that sulfate pools are being turned over within days (Nedwell and Watson 1995; Wieder et al. 1990). If SO_4^{2-} is not recycled in the peat, potential sulfate reduction rates would equal the atmospheric deposition, which is 10–150 mmol S m^{-2} a^{-1} (Lindfors et al. 1992; Sisterson et al. 1994). This is a small quantity compared to average potential CH_4 production rates (1365 $\pm$ 1733 (mean $\pm$ SD) mmol C m^{-2} a^{-1}) and compared to in situ average emissions from peatlands (762 $\pm$ 1157 mmol C m^{-2} a^{-1}) (Fig. 2).

Except for water table fluctuations that occur primarily during the summer (Bayley et al. 1986; Devito and Hill 1999) no effective recycling mechanism for sulfate has been empirically demonstrated in peatlands. The only other documented potential mechanism would involve recycling with oxygen in the rhizosphere of graminoid plants (Wind and Conrad 1997), which could be effective in fens and oceanic and blanket bogs, which also have a considerable cover of graminoids (Forrest and Smith 1975). However, it is probably irrelevant in continental bogs because of the absence of large numbers of graminoid plants. There is, however, mounting evidence from ^{34}S and isotopic studies (Mandernack et al. 2000) and from the above rate measurements that such a recycling must occur. With respect to CH_4 production rates, the processes involved in recycling might be more important than different levels of sulfate deposition.

The reduction of CH_4 production despite low sulfate concentrations could be explained by the presence of organic electron acceptors. It has been demonstrated that quinones, which are contained in humic substances and which have been extracted from peats (Coates et al. 1998), oxidize both H_2S and acetate (Curtis and Reinhard 1994; Dunnivant et al. 1992; Lovley et al. 1996; Scott et al. 1998). The quinones are in the process transformed into radical semiquinones and into hydroquinones, which can be analytically identified (Scott et al. 1998). The process itself is microbially mediated through bacteria of the genus *Geobacter*, which has been isolated both from marine sediments and from freshwater wetlands (Coates et al. 1998; Lovley et al. 1996). If significant, this novel pathway of C mineralization would have important consequences for our understanding of C cycling in peatlands. It would imply that humification and DOC production directly contribute to C mineralization rates. It would also explain the recurring contradiction of large sulfate reduction rates despite very small sulfate pools, and it could explain the generally low contribution of CH_4 production to anaerobic C mineralization.

Dissolved organic carbon

Microorganisms can take up only small dissolved organic molecules with molecular weights below about 600 g mol^{-1} (Fenchel et al. 1998). Anaerobic respiration further relies on a relatively small consortium of simple molecules (Fenchel et al. 1998). Carbon mineralization and CH_4 production

processes consequently depend on the production of DOC. The DOC is also important with respect to exchange processes with adjacent ecosystems and it is further of importance for the mobilization of metals such as aluminum (Helmer et al. 1990) and iron (Chin et al. 1998; Moore 1988). Export of DOC influences the acidity (Gorham et al. 1986; Urban et al. 1989), the metal dynamics (Driscoll et al. 1988), and the primary production of surface waters in northern regions (Effler et al. 1985).

Dissolved organic carbon concentrations between 20 and 60 mg L^{-1} have been reported for most northern peatlands. The DOC fluxes from the atmosphere (0.8–2.8 g m^{-2} a^{-1}; Dalva and Moore 1991; Koprivnjak and Moore 1992; McKnight et al. 1985; Urban et al. 1989) and from adjacent upland soils (0.3–4.8 g m^{-2} a^{-1}; Rivers et al. 1998; Urban et al. 1989) into peatlands are usually small. Peatlands export DOC to discharging streams at rates between 1 and 50 g m^{-2} a^{-1} (Dillon and Molot 1997; Koprivnjak and Moore 1992; Moore 1987, 1988; Urban et al. 1989). Within peatland complexes beaverponds may be sinks for DOC at ranges of –4 to –18 g m^{-2} a^{-1} (Devito et al. 1989). Overall, the rate of DOC export is small compared to both NPP and soil respiration fluxes in northern peatlands, as has been noted before (Gorham 1995).

The controls on DOC production and export in peatlands are poorly understood, but temperature and runoff seem to be important factors. Increases in DOC concentrations were observed during summers (Dalva and Moore 1991; Moore 1989*a*; Waddington and Roulet 1997). Higher temperatures, therefore, seem to accelerate DOC production compared to DOC consumption and may be due to increased microbial and plant mediated DOC release (Moore and Dalva 2001). Concentration effects due to evaporation might also play a role in this phenomenon. The DOC release is probably also physicochemically controlled, since DOC export from a peatland was found to correlate with runoff ($n = 23$, $r^2 = 0.80$; Urban et al. 1989). Contact of peat with water poor in DOC also releases DOC from the peat matrix (Moore and Dalva 2001). The movement of DOC within peatlands is hydrologically induced and can be substantial (Siegel et al. 1995; Waddington and Roulet 1997). As a consequence, "young" and labile dissolved organic matter from the acrotelm can enter larger depths and sustain fast rates of C mineralization (Chanton et al. 1995).

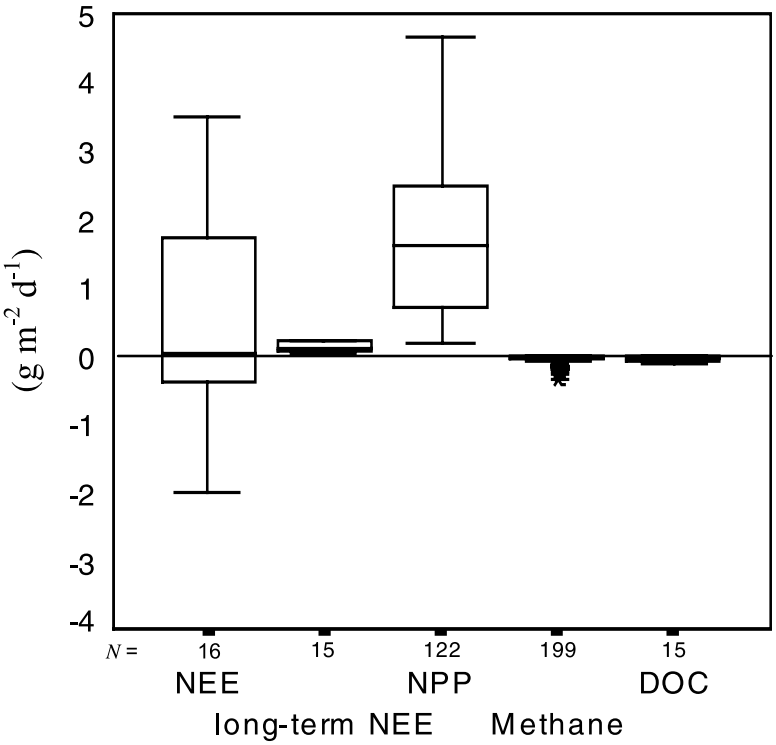
In comparison to soils and sediments, not much work has been done with respect to the chemical properties of DOC and to the determination of intermediates in the microbial decomposition process. Only a few molecular weight distribution measurements (Chin et al. 1998; Moore 1988), acid–base and structural properties (Hruska et al. 1996; McKnight et al. 1985; Urban et al. 1989), and seasonal measurements of acetate and fatty acids have been reported (Amaral and Knowles 1994; Shannon and White 1996).

This is probably one reason why DOC dynamics in peatlands are at present poorly understood. Dissolved organic carbon represents several groups of compounds, including cell residues, fermentation products, and humic and fulvic substances, which derive from different sources and differ in their bioavailability and ecological function. The concentration of fermentation products as acetate, for example, can be highly variable seasonally and is tightly coupled to the activity of fermentative bacteria, sulfate reducers, and methanogens (Amaral and Knowles 1994; Avery et al. 1999; Shannon and White 1996). Acetate concentrations in peatlands can at times exceed 1 mmol L^{-1} or 60 mg L^{-1}, whereas at other times acetate is nearly absent in pore waters (Shannon and White 1996; Blodau et al. 2002). This is probably not the case for humic and fulvic substances, which represent complex and relatively stable macromolecules (McKnight et al. 1985). Thus the parameter "DOC" summarizes diverse compounds that differ in their dynamics. To understand the role of DOC in the C cycle of peatlands these functional differences have to be taken into account.

The carbon balance of peatlands

Northern peatlands have sequestered atmospheric C at rates between 0.03 and 0.29 g m^{-2} d^{-1} (Botch et al. 1995). The average rate has been about 0.15–0.19 g m^{-2} d^{-1} (Dean and Gorham 1991; Gorham 1991). This value is very small compared to the turnover of C within the vegetation and the

Fig. 3. Summary of previously discussed rates of NEE (C) (Table 1), long-term carbon balance (Botch et al. 1995), NPP, methane fluxes, and DOC export (g m^{-2} d^{-1}). Summer NEE, NPP, and methane fluxes from the discussed sources were recalculated for a vegetation period of 150 d, if not otherwise reported, the other fluxes were recalculated for a 365 d period. The central crossbar represents the median; the boxes, the 75th and 25th percentile; the upper and lower bars, the 90th percentile; the asterisks, extreme values of the displayed data set.



soils (Fig. 3). The C balance of peatlands is not surprisingly quite variable on short time-scales (Table 1). Seasonal net ecosystem exchange (NEE) measurements indicate that at present peatlands can be both sources and sinks of CO_2 to the atmosphere and that differences in seasonal NEE are large compared to long-term C accumulation rates (Dean and Gorham 1991; Gorham 1991; Klinger et al. 1994; Schraeder et al. 1994; Shurpali et al. 1994).

The C balance of peatlands is primarily the result of C mineralization and net primary production rates. As previously shown, other terms in the balance are quantitatively subordinate. In the short term, the C balance is thus controlled by the effect of environmental variables on C mineralization and NPP. Based on the reviewed studies, it seems probable that higher water table levels, temperatures, PAR levels, and N availability increase the NPP in most peatlands. A larger productivity can also be expected when vascular plants increase in relative abundance compared to mosses. The response of C mineralization rates to the same changes is less certain. Higher temperatures and an increasing abundance of vascular plants will probably increase rates. Fluctuating water tables might also increase C mineralization rates (Aerts and Ludwig 1997). However, if water tables increase and remain stable, C mineralization rates will probably decrease.

Net ecosystem exchange studies have indicated that CO_2 is released in winter, early in spring, and late in fall when the vegetation is inactive but soil respiration continues, and taken up in summer when photosynthesis is strong (Alm et al. 1999; Carroll and Crill 1997; Frolking et al. 1998; Roehm and Roulet 2002). Winter release of CO_2 can be between 10 and 30% of the total annual CO_2 emissions and,

Table 1. Selected NEE as reported in the literature. Seasonal rates were converted to daily rates, based on a 150 d period if no other information was provided. Reported temperature (Δ temp.) and precipitation (Δ prec.) deviation from the seasonal average are also shown.

Type	Rate ($g\ m^{-2}d^{-1}$)	Technique	Δ temp. (°C)	Δ prec. (%)	Source
Tundra wet	-0.27 ± 0.25	Chamber	(> 0)		Oechel et al. 1993
Tundra dry	-2.0 ± 1.44	Chamber	(> 0)		Oechel et al. 1993
Fen	−1.1	Gradient	+2.0	−55	Schraeder et al. 1994
Fen	−0.90	Eddy	+1.5	−37	Schraeder et al. 1994
Fen	+2.7	Eddy	+0.5	+20	Schraeder et al. 1994
Fen	+0.03	Chamber			Whiting 1994
Fen	−0.51	Chamber			Klinger et al. 1994
Fen	+0.15	Chamber			Klinger et al. 1994
Fen	-0.13 ± 0.10	Chamber			Whiting 1994
Fen	−0.8	Chamber	+1.1	89	Carroll and Crill 1997
Mixture	+0.08	Eddy			Rivers et al. 1998
Bog	+0.08	Chamber			Waddington and Roulet 1996
Bog	−0.48	Eddy	+1.3	−19	Shurpali et al. 1994
Bog	+0.22	Eddy	−0.2	+16	Shurpali et al. 1994
Bog	+1.7 (July)	Eddy			Neumann et al. 1994
Bog	-0.058 ± 0.15	Chamber			Whiting 1994
Bog	−0.23	Chamber			Klinger et al. 1994
Pond	−11.5	Stag. film			Hamilton et al. 1994
Pond	−10.3	Stag. film			Hamilton et al. 1994
Pond	−3.5	Stag. film			Hamilton et al. 1994
All	+0.19	Deposits			Gorham 1991; Dean and Gorham 1991
All	+0.15	Deposits			Gorham 1991; Dean and Gorham 1991

therefore, constitutes an important contribution to the carbon balance of peatlands (Alm et al. 1999). Based on some observations (Table 1) it has been suggested that hot and dry summer weather shifts the balance and C is released from peatlands, since respiration is probably enhanced by water table drawdowns and higher temperatures, while vegetation suffers from heat stress and water deficiency (Carroll and Crill 1997; Schraeder et al. 1994).

The first continuous multi-year C balance of a northern bog does not provide evidence for these suggestions because C budgets were nearly identical among years despite very different weather conditions (Roulet 2001)[2]. Interannual differences in the onset of snow melt and in the weather early in the vegetation period have also been suggested as factors influencing the C balance (Griffis et al. 2000). Other factors, such as the effects of fire and permafrost degradation on the C balance of peatlands, are only beginning to be investigated (Robinson and Moore 2000; Wieder 2001) but are likely to be very important as global warming progresses (Gorham 1995).

Conclusion and research directions

Several studies have addressed how the C cycle and the C balance of peatlands will react to incrementally changing environmental conditions (Moore et al. 1998; Roulet et al. 1992; Waddington et al. 1998), but their predictions are uncertain. This uncertainty is on the one hand a result of the complexity of the processes that are involved in the C cycle and on the other hand a result of deficiencies in our

[2]Roulet, N.T. 2001. Personal communication.

understanding of the processes themselves. A better quantitative understanding of C cycling in peatlands is hampered by methodological difficulties, which are a pervasive phenomenon in biogeochemistry and environmental microbiology (Madsen 1998).

Field-scale studies of undisturbed peatlands do not allow for a clear identification of the processes and controls that underlie observed net processes on the ecosystem scale. There are narrow limits to the statistical prediction of interacting processes by simple relationships, as has been demonstrated for CH_4 production (von Hulzen et al. 1999) and methane emissions (Walter and Heimann 2000). These limits are a result of the dynamic interplay among processes, storage and transport, and the controlling environmental factors. The second problem associated with this type of studies is that environmental variables are usually not controlled and varied. Because of co-varying and interacting environmental factors it will remain very difficult to establish causal relationships between processes and potential controls.

Controls that have been derived from incubation-scale experiments with soils and sediments cannot easily be related back to the field scale, since critical components such as vegetation are excluded from the experiment and since it is usually not known when the chosen experimental conditions prevail in situ. Little is also known about the effects of laboratory techniques on the determined rates and controls, since biogeochemical processes in intact soils have rarely been reported.

Uncertainty also arises from the impact of environmental change occurring on time scales of years to decades. Such impacts are experimentally difficult to investigate. This applies to deposition effects of N and S on C cycling in peatlands. In deposition experiments it has, for example, been demonstrated that the response of NPP changes considerably over a period of 4 years (Rochefort et al. 1990). Phenomena such as the reduction of CH_4 production by sulfate reduction might be the result of decades of S and N pollution. The incremental invasion of vascular plants in areas that have been previously devoid of them, as is currently occurring in the subarctic of Northwestern Canada (Sturm et al. 2001), and changes in fire frequency and deterioration of permafrost can also alter C cycling of peatlands in the long term (Robinson and Moore 2000; Wieder 2001).

The primary interest in the C cycling of peatlands is due to their important role in the global C cycle and the large variations in CO_2 and CH_4 exchange rates between peatlands and the atmosphere. This variability indicates that the peatland C cycle is susceptible to environmental change (Moore et al. 1998). To make progress towards quantitative predictions of CO_2 and CH_4 exchange rates, and to mitigate some of the above outlined scientific obstacles, several types of studies seem promising.

(*i*) Quantification of controls. Previously identified controls on individual processes need to be substantiated under more realistic conditions. Mesocosm studies that include all components of the C cycle, including the vegetation, provide an experimental regime that is useful for such studies and allows for the study of interacting processes. Mesocosms can be manipulated and controlled with respect to temperature, water table levels, light levels, and chemical inputs. From the combination of exchange rate, pore gas and water measurements, and internal mass balances, pool sizes, turnover rates, and response times of processes can be determined and related to changes in environmental variables (Blodau and Moore 2002; Beckmann and Lloyd 2001).

(*ii*) Connecting processes, controls, and exchange. The processes that drive exchange rates have to be related to exchange rates on the time scale at which significant changes occur. Such studies must accomplish the simultaneous determination of environmental variables, in situ process rates, and CO_2 and CH_4 exchange rates with the atmosphere. Mechanistically oriented studies, such as those of Shannon and White (1994), Shannon et al. (1996), and Walter et al. (1996), in which in situ CH_4 exchange rates were related to pool sizes of acetate, sulfate, and methane, the phenology of vascular plants, and environmental variables such as temperature and water table levels have greatly enhanced the understanding of methane dynamics. This approach should be expanded towards both the study of C mineralization and root respiration and also the determination of

subsurface process rates, rather than pool sizes. Based on this approach it could be possible to substantiate causal and quantitative relationships between driving environmental variables and exchange rates and to come to a better understanding of the sources of variance in exchange rates.

(*iii*) Ecosystem manipulation experiments. Long-term ecosystem manipulation experiments have produced insight into the effects of eutrophication, acidification, and land use change on forest ecosystems and northern lakes (Likens and Bormann 1995; Schindler et al. 1985) and are currently shedding new insight on the response of forest ecosystems to elevated atmospheric CO_2 concentrations (Orem et al. 2001; Schlesinger and Lichter 2001). Smaller manipulation experiments have provided much useful information about the effects of water table levels (Dise et al. 1993), N and S deposition (Dise and Verry 2001; Li and Vitt 1997; Rochefort et al. 1990), and temperature (Granberg 1998) on peatlands. Realistic long-term climate change manipulation studies do not seem to have been undertaken in the investigation of C cycling in peatlands, but would be necessary to quantify the long-term effects of environmental variables such as elevated CO_2, temperature, N deposition, and water table levels. Studies that address disturbances such as fire and permafrost melting, fluctuations in water table levels, and in the length of vegetation periods will also be necessary to extrapolate results from controlled experiments.

(*iv*) Modeling. Recently, mathematical modeling has arguably made the largest contribution to the understanding of CH_4 cycling in peatlands. These studies shed new insight into the effects of roots (Arah and Stephen 1998), terminal electron acceptors (Segers and Kengen 1998), responses to environmental controls (von Hulzen et al. 1999), the significance of processes at different scales (Segers 1999), and the interaction of processes and controls at the ecosystem level (Granberg et al. 1997; Walter and Heimann 2000). The next step must be the incorporation of factors that influence rates of C mineralization and the fraction of C mineralization used in the production of CH_4. Possible factors are peat age (Hogg et al. 1993), substrate characteristics (Valentine et al. 1994), micro-nutrient availability (Basiliko and Yavitt 2001), time lags in the microbial response (Kettunen et al. 1999), the utilization of electron acceptors (Segers and Kengen 1998), the effect of enzyme activity (Freeman et al. 1996), and in situ concentration effects that might slow down or increase CO_2 and CH_4 production rates (Blodau 2002).[3]

At the biogeochemical process level, no mechanistic models have been published that are linked to other processes within the C cycle and with respect to the C cycle as a whole. A pertinent problem of complex environmental models is parameter uncertainty and over-parameterization (e.g., Sogn et al. 1995). The utility of future modeling projects will therefore also depend on whether empirical data about process rates are available, so that not only model results but also quantities, which are calculated within the models, can be compared to real world data (Walter and Heimann 2000).

Much of this research cannot be accomplished by individuals and disciplinary research. The success of studies that push our scientific understanding of C cycling in peatlands beyond what we already know will, therefore, critically depend on interdisciplinary collaboration among ecologists, palaeoecologists, hydrologists, biogeochemists, and modelers.

Acknowledgements

I would like to thank T.R. Moore, C.L. Roehm, N. Basiliko, and E. Gorham for helpful discussions and their comments on the manuscript.

[3]Blodau, C. 2002. Unpublished data.

References

Achtnich, C., Bak, F., and Conrad, R. 1995. Competition for electron donors among nitrate reducers, ferric iron reducers, sulfate reducers, and methanogens in anoxic paddy soil. Biol. Fert. Soils, **19**: 65–72.

Aerts, R., and Ludwig, F. 1997. Water-table changes and nutritional status affect trace gas emissions from laboratory columns of peatland soils. Soil. Biol. Biochem. **29**: 1691–1698.

Aiwa, H.A., Rice, C.W., and Sotomayor, D. 1998. Carbon and nitrogen mineralization in tallgrass prairie and agricultural soil profiles. Soil. Sci. Soc. Am. J. **62**: 942–951.

Aller, R.C. 1994. Bioturbation and remineralization of sedimentary organic matter: effects of redox oscillation. Chem. Geol. **114**: 331–345.

Alm, J., Saarnio, S., Nykanen, H., Silvola, J., and Martikainen, P.J. 1999. Winter CO_2, CH_4 and N_2O fluxes on some natural and drained boreal peatlands. Biogeochemistry, **44**: 163–186.

Amaral, J.A., and Knowles, R. 1994. Methane metabolism in a temperate swamp. Appl. Environ. Microbiol. **60**: 3945–3951.

Arah, J.R.M., and Stephen, K.D. 1998. A model of the processes leading to methane emission from peatland. Atmos. Environ. **32**: 3257–3264.

Avery, G.B., Shannon, R.D., White, J.R., Martens, C.S., and Alperin, M.J. 1999. Effect of seasonal changes in the pathways of methanogenesis on the $\delta^{13}C$ values of pore water methane in a Michigan peatland. Global Biogeochem. Cycles, **13**: 475–484.

Backeus, I. 1990. Production and depth distribution of fine roots in a boreal open bog. Ann. Bot. Fennici, **27**: 261–265.

Bartsch, I., and Moore, T.R. 1985. A preliminary investigation of primary production and decomposition in four peatlands near Schefferville, Quebec. Can. J. Bot. **63**: 1241–1248.

Bayley, S.E., Behr, R.S., and Kelly, C.A. 1986. Retention and Release of S from a freshwater wetland. Water Air Soil Pollut. **31**: 101–114.

Beckmann, M., and Lloyd, D. 2001. Mass spectrometric monitoring of gases (CO_2, CH_4, O_2) in a mesotrophic peat core from Kopparas mire, Sweden. Global Change Biol. **7**: 171–180.

Bellisario, L.M., Bubier, J.L., Moore, T.R., and Chanton, J.B. 1999. Controls on CH_4 emissions from a northern peatland. Global Biogeochem. Cycles, **13**: 81–91.

Belyea, L.R. 1996. Separating the effects of litter quality and microenvironment on decomposition rates in a patterned peatland. Oikos, **77**: 529–539.

Belyea, L.R., and Lancaster, J. 2002. Inferring landscape dynamics of bog pools from scaling relationships. J. Ecol. **90**: 223–234.

Bergmann, I. 1998. Microbial carbon mineralisation in peat from a boreal mixed mire. Ph.D. thesis, Acta Universitatis Agriculturae Sueciae, Silvestria 74. Umea, Sweden.

Berner, R.A. 1980. A rate model for organic matter decomposition during bacterial sulfate reduction in marine sediments. *In* Biogeochemistry of organic matter at the sediment–water interface. CNRS Int. Colloq. : 35–45.

Best, E.P.H., and Jacobs, F.H.H. 1997. The influence of raised water table levels on carbon dioxide and methane production in ditch dissected peat grasslands in the Netherlands. Ecol. Eng. **8**: 129–144.

Blodau, C., and Moore, T.R. 2002. Experimental response of peatland carbon dynamics to a water table fluctuation. Aquat. Sci. In press.

Blodau, C., Roehm, C.L., and Moore, T.R. 2002. Iron, sulfur and dissolved carbon dynamics in a northern peatland. Arch. Hydrobiol. In press.

Blunier, T., Chappelaz, J., Schwander, J., Stauffer, B., and Raynaud, D. 1995. Variations in atmospheric methane concentrations during the Holocene epoch. Nature, **374**: 46–49.

Botch, M.S., Kobak, K.I., Vinson, T.S., and Kolchugina, T.P. 1995. Carbon pools and accumulation in peatlands of the former Soviet Union. Global Biogeochem. Cycles, **9**: 37–46.

Bottner, P. 1985. Response of microbial biomass to alternate moist and dry conditions in a soil incubated with ^{14}C- and ^{15}N-labelled plant material. Soil Biol. Biochem. **17**: 329–337.

Bubier, J.L. 1995. The relationship of vegetation to methane emission and hydrochemical gradients in northern peatlands. J. Ecol. **83**: 403–420.

Bubier, J.L., Moore, T.R., and Roulet, N.T. 1993. Methane emissions from wetlands in the midboreal region of northern Ontario, Canada. Ecology, **74**: 2240–2254.

Bubier, J.L., Moore, T.R., and Juggins, S. 1995. Predicting methane emission from bryophyte distribution in northern peatlands. Ecology, **76**: 677–693.

Carroll, P., and Crill, P. 1997. Carbon balance of a temperate poor fen. Global Biogeochem. Cycles, **11**: 349–356.

Chanton, J.P., Bauer, J.E., Glaser, P.A., Siegel, D.I., Kelley, C., Tyler, S.C., Romanowitz, E.H., and Lazarus, A. 1995. Radiocarbon evidence for the substrates supporting methane formation within northern Minnesota peatlands. Geochim. Cosmochim. Acta, **59**: 3663–3668.

Chin, Y.P., Traina, S.J., Swank, C.R., and Backhus, D. 1998. Abundance and properties of dissolved organic matter in pore waters of a fresh water wetland. Limnol. Oceanogr. **43**: 1287–1296.

Clein, J.S., and Schimel, J.P. 1994. Reduction in microbial activity in birch litter due to drying and rewetting events. Soil Biol. Biochem. **26**: 403–406.

Clymo, R.S. 1978. A model of peat bog growth. *In* Production ecology of some British moors and montane grasslands. *Edited by* O.W. Heal and D.F. Perkins. Ecological Studies 27, Springer Verlag, Berlin, Germany.

Clymo, R.S. 1984. The limits to peat bog growth. Philos. Trans. R. Soc. Lond. B, **303**: 605–654.

Coates, J.D., Ellis, D.J., Blunthariis, E.L., Gaw, C.V., Roden, E.E., and Lovley, D.R. 1998. Recovery of humic-reducing bacteria from a diversity of environments. Appl. Environ. Microbiol. **64**:1504–1509.

Conrad, R. 1999. Contribution of hydrogen to methane production and control of hydrogen concentrations in methanogenic soils and sediments. FEMS Microbiol. Ecol. **28**: 193–202.

Curtis, G.P., and Reinhard, M. 1994. Reductive dehalogenation of hexachloroethane, carbon tetrachloride, and bromoform by anthrahydroquinone disulfonate and humic acid. Environ. Sci. Technol. **28**: 2393–2401.

Dalva, M., and Moore, T.R. 1991. Sources and sinks of dissolved organic carbon in a forested swamp catchment. Biogeochemistry, **15**: 1–19.

Dannenberg, S., and Conrad, R. 1999. Effect of rice plants on methane production and rhizospheric metabolism in paddy soil. Biogeochemistry, **45**: 53–71.

Dean, W.E., and Gorham, E. 1991. Magnitude and significance of carbon burial in lakes, reservoirs, and peatlands. Geology, **26**: 535–538.

Devito, K.J., and Hill, A.R. 1999. Sulphate mobilization and pore water chemistry in relation to groundwater hydrology and summer drought in two conifer swamps on the Canadian Shield. Water Air Soil Pollut. **113**: 97–114.

Devito, K.J., Dillon, P.J., and Lazerte, B.D. 1989. Phosphorus and nitrogen retention in five Precambrian shield wetlands. Biogeochemistry, **8**: 185–204.

Dillon, P.J., and Molot, L.A. 1997. Effect of landscape form on export of dissolved organic carbon, iron, and phosphorus from forested stream catchments. Water Resour. Res. **33**: 2591–2600.

Dise, N.B., and Verry, E.S. 2001. Suppression of peatland methane emissions by cumulative sulfate deposition in simulated acid rain. Biogeochemistry, **53**: 143–160.

Dise, N.B., Gorham, E., and Verry, E.S. 1993. Environmental factors controlling methane emissions from peatlands in northern Minnesota. J. Geophys. Res. **98**(D): 10583–10594.

Driscoll, C.T., Fuller, R.D., and Simone, D.M. 1988. Longitudinal variations in trace metal concentrations in a northern forested ecosystem. J. Environ. Qual. **17**: 101–107.

Dunfield, P., Knowles, R., Dumont, R.T., and Moore, T.R. 1993. Methane production and consumption in temperate and subarctic peat soils: response to temperature and pH. Soil Biol. Biochem. **25**: 321–326.

Dunnivant, F.M., Schwarzenbach, R., and Macalady, D.L. 1992. Reduction of substituted nitrobenzenes in aqueous solutions containing natural organic mater. Environ. Sci. Technol. **26**: 2133–2141.

Edwards, C., Hales, B.A., Hall, G.H., McDonald, I.R., Murrell, J.C., Pickup, R., Ritchie, D.A., Saunders, J.R., Simon, B.M., and Upton, M. 1998. Microbiological processes in the terrestrial carbon cycle: Methane cycling in peat. Atmos. Environ. **32**: 3427–3255.

Effler, S.W., Schafran, G.C., and Driscoll, C.W. 1985. Partitioning light attenuation in an acidic lake. Can. J. Fish. Aquat. Sci. **42**: 1707–1711.

Emerson, S., Fischer, K., Reimers, C., and Heggie, D. 1985. Organic carbon dynamics and preservation in deep sea sediments. Deep-Sea Res. **32**: 1–21.

Fechner-Levy, E.J., and Hemond, H.F. 1996. Trapped methane volume and potential effects on methane ebullition in a northern peatland. Limnol. Oceanogr. **41**: 1375–1383.

Fenchel, T., King, G.M., and Blackburn, T.H. 1998. Bacterial Biogeochemistry, Academic Press, London, U.K.

Fetzer, S., Bak, F., and Conrad, R. 1993. Sensitivity of methanogenic bacteria from paddy soil to oxygen and desiccation. FEMS Microbiol. Ecol. **12**: 107–115.

Ford, T.E., and Naiman, R.J. 1989. Groundwater–surface water relationships in boreal forest watersheds: Dissolved organic carbon and inorganic nutrient dynamics. Can. J. Fish. Aquat. Sci. **46**: 41–49.

Forrest, G.I., and Smith, R.A.H. 1975. The productivity of a range of blanket bog vegetation types in the northern Pennines. J. Ecol. **59**: 453–479.

Freeman, C., Lock, M.A., and Reynolds, B. 1993. Fluxes of CO_2, CH_4 and N_2O from a Welsh peatland following simulation of water table draw-down: potential feedback to climate change. Biogeochemistry, **19**: 51–60.

Freeman, C., Liska, G., Ostle, N.J., Lock, M.A., Reynolds, B., and Hudson, J. 1996. Microbial activity and enzymic decomposition processes following peatland water table drawdown. Plant Soil, **180**: 121–127.

Freeman, C., Liska, G., Ostle, N.J., Lock, M.A., Hughes, S., Reynolds, B., and Hudson, J. 1997. Enzymes and biogeochemical cycling in wetlands during a simulated drought. Biogeochemistry **39**: 177–187.

Frolking, S.E., Bubier, J.L., Moore, T.R., Ball, T., Bellisario, L.M., Bhardwaj, A., Carroll, P., Crill, P.M., Lafleur, P.M., McCaughey, J.H., Roulet, N.T., Suyker, A.E., Verma, S.E., and Waddington, J.M. 1998. Relationships between ecosystem productivity and photosynthetically active radiation for northern peatlands. Global Biogeochem. Cycles, **12**: 115–126.

Fung, I., John, J., Lerner, J., Mathews, M., Prather, M., Steele, L., and Frazer, P. 1991. Global budgets of atmospheric methane: results from a three-dimensional global model synthesis. J. Geophys. Res. **6**: 13033–13065.

Glaser, P.H. 1987. The ecology of patterned boreal peatlands of northern Minnesota: a community profile. Biol. Rep. 85 (7.14). U.S. Fish and Wildl. Serv., Washington, D.C. 98 p.

Gorham, E. 1974. The relationship between standing crop in sedge meadows and summer temperature. J. Ecol. **62**: 487–491.

Gorham, E. 1991. Northern peatlands: Role in the global carbon cycle and probable response to climate warming. Ecol. Appl. **1**: 182–193.

Gorham, E. 1995. The biogeochemistry of northern peatlands and its possible responses to global warming. *In* Biotic feedbacks in the global climatic systems. *Edited by* G.M. Woodwell and F.T. McKenzie. Oxford University Press, New York, N.Y.

Gorham, E., Underwood, J.K., Martin, F.B., and Ogden, J.G., III. 1986. Natural and anthropogenic causes of lake acidification in Nova Scotia. Nature, **234**: 451–453.

Granberg, G. 1998. Environmental control of methane emission from boreal mires: experimental data and model simulations. Ph.D. dissertation, Acta Universitatis Agriculturae Sueciae, Silvestria 83. Umea, Sweden.

Granberg, G., Mikkela, C., Sundh, I., Svensson, B.H., and Nilsson, M. 1997. Sources of spatial variation in methane emissions from mires in northern Sweden: A mechanistic approach in statistical modeling. Global Biogeochem. Cycles, **11**: 135–150.

Griffis, T.J., Rouse, W.R., and Waddington, J.M. 2000. Interannual variability of net ecosystem exchange at a subarctic fen. Global Biogeochem. Cycles, **14**: 1109–1121.

Grigal, D.F., Buttleman, C.G., and Kernick, L.K. 1985. Biomass and productivity of the woody strata of forested bogs in northern Minnesota. Can. J. Bot. **63**: 2416–2424.

Hamilton, J.D., Kelly, C.A., Rudd, J.W.M, Hesslein, R.H., and Roulet, N.T. 1994. Flux to the atmosphere of CH_4 and CO_2 from wetland ponds on the Hudson Bay lowlands (HBLs). J. Geophys. Res. **99**: 1495–1510.

Harden, J.W., Sundquist, E.T., Stallard, R.F., and Mark, R.K. 1992. Dynamics of soil carbon during deglaciation of the Laurentide ice sheet. Science, **258**: 1921–1924.

Heggie, D., Maris, C., Hudson, A., Dymond, J., Beach, R., and Cullen, J. 1987. Organic carbon oxidation and preservation in NW Atlantic continental margin sediments. *In* Geology and geochemistry of Abyssal Plains. Geol. Soc. Spec. Publ. **31**: 215–236.

Helmer, E.H., Urban, N.R., Eisenreich, S.J. 1990. Aluminum chemistry in peatland waters. Biogeochemistry, **9**: 247–276.

Hemond, H.F. 1983. The nitrogen budget of Thoreau's bog. Ecology, **64**: 99–109.

Hogg, H.E. 1993. Decay potential of hummock and hollow Sphagnum peats at different depths in a Swedish raised mire. Oikos, **66**: 269–278.

Hogg, E.H., Malmer, N., and Wallen, B. 1994. Microsite and regional variation in the potential decay rate of *Sphagnum magellanicum* in south Swedish bogs. Ecography, **17**: 50–59.

Hornibrook, E.R.C., Longstaff, F.J., and Frye, W.S. 1997. Spatial distribution of microbial methane production pathways in temperate zone wetland soils: Stable carbon and hydrogen isotope evidence. Geochim. Cosmochim. Acta, **61**: 745–753.

Hruska, J., Johnson, C.E., and Kram, P. 1996. Role of organic solutes in the chemistry of acid-impacted bog waters of the western Czech Republic. Wat. Resour. Res. **32**: 2841–2851.

Jauhiainen, J., Vasander, H., and Silvola, J. 1993. Differences in response of two Sphagnum species to elevated CO_2 and nitrogen input. Suo, **43**: 211–215.

Jenkinson, D.S. 1977. Studies on the decomposition of plant material in soil. V. The effects of plant cover and soil type on the loss of carbon from ^{14}C labelled ryegrass decomposing under field conditions. J. Soil Sci. **28**: 424–434.

Johnson, L.C., and Damman, A.W.H. 1991. Species-controlled sphagnum decay on a south Swedish mire. Oikos, **61**: 234–242.

Johnson, L.C., Damman, A.W.H., and Malmer, N. 1990. Sphagnum macrostructure as an indicator of decay and compaction in peat cores from an ombrotrophic south Swedish peat bog. J. Ecol. **78**: 633–647.

Kettunen, A., Kaitala, V., Alm, J., Silvola, J., Nykänen, H., and Martikainen, P.J. 1996. Cross-correlation analysis of the dynamics of methane emissions from a boreal peatland. Global Biogeochem. Cycles, **10**: 457–471.

Kettunen, A., Kaitala, V., Lehtinen, A., Lohila, A., Alm, J., Silvola, J., and Martikainen, P.J. 1999. Methane production and oxidation potentials in relation to water table fluctuations in two boreal mires. Soil Biol. Biochem. **31**: 1741–1749.

Kieft, T.L., Soroker, E., and Firestone, M.K. 1987. Microbial biomass response to a rapid increase in water potential when dry soil is wetted. Soil Biol. Biochem. **19**: 119–126.

Klinger, L.F., Zimmermann, P.R., Greenberg, J.P., Heidt, L.E., and Guenther, A.B. 1994. Carbon trace gas fluxes along a successional gradient in the Hudson Bay lowland. J. Geophys. Res. **99**(D1): 1469–1494.

Koprivnjak, J.F., and Moore, T.R. 1992. Sources, sinks and fluxes of dissolved organic carbon in subarctic fen catchments. Arct. Alp. Res. **24**: 204–210.

Kristjanson, J.K., Schoenheit, P., and Thauer, R.K. 1982. Different Ks values for hydrogen of methanogenic bacteria and sulfate reducing bacteria: An explanation for the apparent inhibition of methanogenesis by sulfate. Arch. Microbiol. **131**: 278–282.

Lamers, L.P., Bobbinck, R., and Roelofs, J.G. 2000. Natural nitrogen filter fails in polluted raised bogs. Global Change Biol. **6**: 583–586.

Lerman, A. 1979. Geochemical processes. John Wiley and Sons, New York, N.Y.

Li, Y., and Vitt, D.H. 1997. Patterns of retention and utilization of aerially deposited nitrogen in boreal peatlands. Ecoscience, **4**: 106–116.

Liblik, L.K., Moore, T.R., Bubier, J.L., and Robinson, S.D. 1997. Methane emissions from wetlands in the zone of discontinuous permafrost: Fort Simpson, North West Territories, Canada. Global Biogeochem. Cycles, **11**: 485–494.

Lindfors, V., Joffre, S.M., and Damski, J. 1992. Meteorological variability of the wet and dry deposition of sulphur and nitrogen compounds over the Baltic Sea. Water Air Soil Pollut. **66**: 1–28.

Lovley, D.R., and Klug, M.J. 1983. Sulfate reducers can outcompete methanogens at freshwater sulfate concentrations. Appl. Environ. Microbiol. **54**: 187–192.

Lovley, D.R., Coates, J.D., Blunt Harris, E.L., Phillips, E.J.P., and Woodward, J.C. 1996. Humic substances as electron-acceptors for microbial respiration. Nature, **382**: 445–448.

Madsen, E.L. 1998. Epistemology of environmental microbiology. Environ. Sci. Technol. **32**: 429–439.

Maltby, E., and Immirzi, P. 1993. Carbon dynamics in peatlands and other wetland soils, regional and global perspectives. Chemosphere, **27**: 999–1023.

Mandernack, K.W., Lynch, L., Krouse, H.R., and Morgan, M.D. 2000. Sulfur Cycling in wetland peat of the new Jersey Pinelands and its effect on stream water chemistry. Geochim. Cosmochim. Acta, **64**: 3949–3964.

Martens, C.S., and Klump, J.V. 1984. Biogeochemical cycling in an organic-rich coastal marine basin 4. An organic carbon budget for sediments dominated by sulfate reduction and methanogenesis. Geochim. Cosmochim. Acta, **48**: 1987–2004.

Mayer, H.P., and Conrad, R. 1990. Factors influencing the population of methanogenic bacteria and the initiation of methane production upon flooding of paddy soil. FEMS Microbiol. Ecol. **73**: 103–112.

McKenzie, C., Schiff, S., Aravena, R., Kelly, C., and St. Louis, V. 1998. Effect of temperature on production of CH_4 and CO_2 from peat in a natural and flooded boreal forest wetland. Clim. Change, **40**: 247–266.

McKnight, D., Thurman, E.M., and Wershaw, R.L. 1985. Biogeochemistry of aquatic humic substances in Thorau's bog, Concord, Massachusetts. Ecology, **66**: 1339–1352.

Melillo, J.M., McGuire, A.D., Kicklighter, D.W., Moore, B.M., III, Vorosmarty, C.J., and Schloss, A.L. 1993. Global climate change and terrestrial net primary production. Nature, **363**: 234–240.

Mitsch, W.J., and Gosselink, J.G. 1993. Wetlands, Van Nostrand Reinhold, New York, N.Y.

Moore, P.D., and Bellamy, P.J. 1974. Peatlands, Elek Science, London, U.K.

Moore, T.R. 1987. Patterns of dissolved organic matter in subarctic peatlands. Earth Surf. Processes Landforms, **12**: 387–397.

Moore, T.R. 1988. Dissolved iron and organic matter in northern peatlands. Soil Sci. **145**: 70–76.

Moore, T.R. 1989*a*. Plant production, decomposition, and carbon efflux in a subarctic patterned fen. Arct. Alp. Res. **21**: 156–162.

Moore, T.R. 1989*b*. Growth and net production of Sphagnum at five sites fen sites, subarctic eastern Canada. Can. J. Bot. **67**: 1203–1207.

Moore, T.R., and Dalva, M. 1993. The influence of temperature and water table on carbon dioxide and methane emissions from laboratory columns of peatland soils. J. Soil Sci. **44**: 651–664.

Moore, T.R., and Dalva, M. 1997. Methane and carbon dioxide exchange potentials of peat soils in aerobic and anaerobic laboratory incubations. Soil. Biol. Biochem. **29**: 1157–1164.

Moore, T.R., and Dalva, M. 2001. Some controls on the release of dissolved organic carbon by plant tissues and soils. Soil Sci. **166**: 38–47.

Moore, T.R., and Knowles, R. 1989. The influence of water table levels on methane and carbon dioxide emissions from peatland soils. Can. J. Soil. Sci. **69**: 33–38.

Moore, T.R., Roulet, N.T., and Knowles, R. 1990. Spatial and temporal variations of methane flux from subarctic/northern boreal fens. Global Biogeochem. Cycles, **4**: 29–46.

Moore, T.R., Heyes, A., and Roulet, N.T. 1994. Methane emissions from wetlands, southern Hudson Bay Lowland. J. Geophys. Res. **99**: 1455–67.

Moore, T.R., Roulet, N.T., and Waddington, J.M. 1998. Uncertainty in predicting the effect of climatic change on the carbon cycle of Canadian Peatlands. Clim. Change, **40**: 229–245.

Moore, T.R, Bubier, J.L., Frolking, S.E., Lafleur, P.M., and Roulet, N.T. 2002. Plant Biomass and production and CO_2 exchange in an ombrotrophic bog. J. Ecol. **90**: 25–36.

Moosavi, S.C., Crill, P.M., Pullmann, E.R., Funk, D.W., and Peterson, K.M. 1996. Controls on CH_4 flux from an Alaskan boreal wetland. Global Biogeochem. Cycles, **10**: 287–296.

Mullen, S.F., Janssen, J.A., and Gorham, E. 2000. Acidity of and the concentration of major and minor metals in the surface waters of bryophyte assemblages from 20 North American bogs and fens. Can. J. Bot. **78**: 718–727.

Naiman, R.J., Manning, T., and Johnston, C.A. 1990. Beaver population fluctuations and tropospheric methane emissions in boreal wetlands. Biogeochemistry, **10**: 1–15.

Nedwell, D., and Watson, A. 1995. CH_4 production, oxidation and emissions in a U.K. ombrotrophic peat bog: Influence of SO_4^{2-} from acid rain. Soil Biol. Biochem. **27**: 893–903.

Neumann, H.H., and den Hartog, G. 1994. Carbon dioxide fluxes over a raised bog at the Kinosheo Lake tower site during the Northern Wetlands Study (NOWES). J. Geophys. Res. **99**(D1): 1529–1538.

Nykaenen, H., Alm, J., Silvola, J., and Tolonen, K. 1998. Methane fluxes on boreal peatlands of different fertility and the effect of long-term experimental lowering of the water table on flux rates. Global Biogeochem. Cycles, **12**: 53–69.

Oechel, W.C., Hastings, S.J., Vourlitis, G., Jenkins, M., Riechers, G., and Gruhlke, N. 1993. Recent change of arctic tundra ecosystems from a net carbon dioxide sink to a source. Nature, **361**: 520–523.

Öquist, M., and Sundh, I. 1998. Effects of a transient oxic period on mineralization of organic matter to CH_4 and CO_2 in anoxic peat incubations. Geomicrobiology, **15**: 325–333.

Orem, R., Ellsworth, D.S., Johnsen, K.H., Phillips, N., Ewers, B.E., Maier, C., Schäfer K.V.R., McCarthy, H., Hendrey, G., McNulty, S.G., and Katut, G.G. 2001. Soil fertility limits carbon sequestration by forest ecosystems in a CO_2 enriched atmosphere. Nature, **411**: 469–471.

Paffen, B.G.P., Roelofs, J.G.M. 1991. Impact of carbon dioxide and ammonium on the growth of submerged *Sphagnum cuspidatum*. Aquat. Bot. **40**: 61–71.

Rivers, J.S., Siegel, D.J., Chasar, L.S., Chanton, J.P., Glaser, P.H., Roulet, N.T., and McKenzie, J.M. 1998. A stochastic appraisal of the annual carbon budget of a large circumboreal peatland, Rapid River watershed, northern Minnesota. Global Biogeochem. Cycles, **12**: 715–727.

Robinson, S.D., Moore, T.R. 2000. The influence of permafrost and fire upon carbon accumulation in high boreal peatlands, Northwest Territories, Canada. Arct. Antarct. Alp. Res. **32**: 155–166.

Rochefort, L., Vitt, D.H., and Bayley, S.E. 1990. Growth, production, and decomposition dynamics of *Sphagnum* under natural and experimentally acidified conditions. Ecology, **7**: 1986–2000.

Roehm, C.L., and Roulet, N.T. 2002. The seasonal contribution of CO_2 fluxes in the annual budget of a northern bog. Global Biogeochem. Cycles, in press.

Roulet, N.T., Moore, T.R., Bubier, J., and Lafleur, P. 1992. Northern fens: methane flux and climatic change. Tellus, **44**(B): 100–115.

Roulet, N.T., Crill, P.M., Comer, N.T., Dove, A., and Boubonniere, R.A. 1997. CO_2 and CH_4 flux between a boreal beaver pond and the atmosphere. J. Geophys. Res. **103**(D24): 29313–29319.

Russell, C.A., and Voroney, R.P. 1998. Carbon dioxide efflux from the floor of a boreal aspen forest. I. Relationship to environmental variables and estimates of C respired. Can. J. Soil Sci. **78**: 301–310.

Scanlon, D. 1998. Carbon dioxide production due to the subsurface decomposition of peat in a Canadian Bog, poor fen and beaver pond margin. MSc thesis, McGill University, Montreal, Canada.

Schimel, J.P. 1995. Plant transport and methane production as controls on methane flux from arctic wet meadow tundra. Biogeochemistry, **28**: 183–200.

Schimel, D.S., Braswell, B.H., McKeown, R., Ojima, D.S., Parton, W.J., and Pulliam, W. 1996. Climate and nitrogen controls on the geography and timescales of terrestrial biogeochemical cycling. Global Biogeochem. Cycles, **10**: 677–692.

Schindler, D.W., Mills, K.H., Malley, D.F., Findlay, D.D., Shearer, J.A., Davies, I.J., Turner, M.A., Linsey, G.A., and Cruikshank, D.R. 1985. Long term ecosystem stress: the effect of years of experimental acidification on a small lake. Science, **228**: 1395–1401.

Schindler, D.W., and Bayley, S.E. 1993. The biosphere as an increasing sink for atmospheric carbon: Estimates from increased nitrogen deposition. Global Biogeochem. Cycles, **7**: 717–733.

Schlesinger, W.H., and Lichter, J. 2001. Limited carbon storage in soil and litter of experimental forest plots under increased atmospheric CO_2. Nature, **411**: 466–469.

Schraeder, C.P., Rouse, W.R., Griffis, T.J., Boudreau, L.D., and Blanken, P.D. 1994. Carbon dioxide fluxes in a northern fen during a hot dry summer. Global Biogeochem. Cycles, **12**: 729–740.

Scott, D.T., McKnight, D.M., Blunt-Harris, E.L., Kolesar, S.E., and Lovley, D.R. 1998. Quinone moieties act as electron acceptors in the reduction of humic substances by humics-reducing microorganisms. Environ. Sci. Technol. **32**: 2984–2989.

Scott, K.J., and Kelly, C.A., and Rudd, J.W.M. 1999. The importance of floating peat to methane fluxes from flooded peatlands. Biogeochemistry, **47**: 187–202.

Segers, R. 1998. Methane production and methane consumption: a review of processes underlying wetland methane fluxes. Biogeochemistry, **41**: 23–51.

Segers, R. 1999. Wetlands methane fluxes: Upscaling from kinetics via a single root and a soil layer to the plot. Ph.D. dissertation, Wageningen University, Wageningen, The Netherlands.

Segers, R., and Kengen, S.W.M. 1998. Methane production as a function of anaerobic carbon mineralization: A process model. Soil. Biol. Biochem. **30**: 1107–1117.

Shannon, R.D., and White, J.R. 1994. A three year study of controls on methane emissions from two Michigan peatlands. Biogeochemistry, **27**: 35–60.

Shannon, R.D., and White, J.R. 1996. The effects of spatial and temporal variations in acetate and sulfate on methane cycling in two Michigan peatlands. Limnol. Oceanogr. **41**: 435–443.

Shannon, R.D., White, J.R., Lawson, J.E., and Gilmour, B.S. 1996. Methane efflux from emergent vegetation in peatlands. J. Ecol. **84**: 239–246.

Shurpali, N.J., Verma, S.B., and Kim, J. 1994. Carbon dioxide exchange in a peatland ecosystem. J. Geophys. Res. **100**(D7): 14319–14326.

Siegel, D.I., Reeve, A.S., Glaser, P.H., and Romanowicz. E.A. 1995. Climate driven flushing of pore water in peatlands. Nature, **374**: 531–533.

Sisterson, D.L., Bowersox, V.C., and Olsen, A.R. 1994. A review of spatial and temporal trends of precipitation composition for North America for the period 1979–1987. *In* Acid rain, current situation and remedies. *Edited by* J. Rose. Gordon and Breach Science Publishers, Yverdon, Switzerland.

Silvola, J., and Ahlholm, U. 1993. Effects of CO_2 concentration and nutrient status on growth, growth rhythm and biomass partitioning in a willow, *Salix phylicifolia*. Oikos, **67**: 227–234.

Sogn, T.A., Sandvik, G.A., and Abrahamsen, G. 1995. Nutrient balance in scots pine (*Pinus sylvestris* L.) forest 4. Testing the nutrient cycling model (NuCM). Water Air Soil Pollut. **85**: 1161–1166.

Sturm, M., Racine, C., and Tape, K. 2001. Increasing shrub abundance in the Arctic. Nature, **411**: 546.

Sugimoto, A., and Fujita, N. 1997. Characteristics of methane emission from different vegetations on a wetland. Tellus, **49**(B): 382–392.

Szumigalski, A.R., and Bayley, S.E. 1997. Net aboveground primary production along a peatland gradient in central Alberta in relation to environmental factors. Ecoscience, **4**(3): 385–393.

Tamm, C.O. 1954. Some observations on the nutrient turn-over in a bog community dominated by *Eriophorum Vaginatum* L. Oikos, **5**: 189–194.

Trumbore, S.E. 1993. Comparison of carbon dynamics in tropical and temperate soils using radiocarbon measurements. Global Biogeochem. Cycles, **7**: 275–290.

Updegraff, K., Pastor, J., Bridgham, S.D., and Johnston, C.A. 1996. Environmental and substrate controls over carbon and nitrogen mineralization in northern wetlands. Ecol. Appl. **5**: 151–163.

Urban, N.R., and Eisenreich, S.J. 1988. Nitrogen Cycling in a forested bog. Can. J. Bot. **66**: 435–449.

Urban, N.R., Bayley, S.E., and Eisenreich, S.J. 1989. Export of dissolved organic carbon and acidity from peatlands. Wat. Res. Res. **25**: 1619–1628.

Valentine, D.W., Holland, E.A., and Schimel, D.S. 1994. Ecosystem and physiological controls over methane production in northern wetlands. J. Geophys. Res. **99**: 1565–1571.

van der Heijden, E., Verbeek, S.K., Kuiper, P.J.C. 2000. Elevated atmospheric CO_2 and increased nitrogen deposition: effects on C and N metabolism and growth of the peat moss *Sphagnum recurvum* P. Beauv. Var. *Mucronatum* (Russ.) Warnst. Global Change Biol. **6**. 201–212.

Verhoeven, J.T.A., and Toth, E. 1995. Decomposition of Carex and Sphagnum litter in fens: Effect of litter quality and inhibition by living tissue homogenates. Soil Biol. Biochem. **27**: 271–275.

Vitt, D.H., Bayley, S.E., and Jin, T.L. 1995. Seasonal variation in water chemistry over a bog-rich fen gradient in Continental Western Canada. Can. J. Fish. Aquat. Sci. **52**: 587–606.

von Hulzen, J.B., Segers, R., van Bodegom, P.M., and Leffelaar, P.A. 1999. Temperature effects on soil methane production: an explanation for observed variability. Soil Biol. Biochem. **31**: 1919–1929.

Waddington, J.M., and Roulet, N.T. 1996. Atmosphere-wetland exchanges: Scale dependency of CO_2 and CH_4 exchange on the developmental topography of a peatland. Global Biogeochem. Cycles, **10**: 233–245.

Waddington, J.M., and Roulet, N.T. 1997. Groundwater flow and dissolved carbon movement in a boreal peatland. J. Hydrol. **191**: 122–138.

Waddington, J.M., Griffis, T.J., and Rouse, W.R. 1998. Northern Canadian Wetlands: Net Ecosystem CO_2 exchange and climatic change. Clim. Change, **40**: 267–275.

Walter, B., and Heimann, M. 2000. A process based climate sensitive model to derive methane emissions from natural wetlands: Application to five wetland sites, sensitivity to model parameters, and climate. Global Biogeochem. Cycles, **14**: 745–765.

Walter, B.P., Heimann, M., Shannon, R.D., and White, J.R. 1996. A process-based model to derive methane emissions from natural wetlands. Geophys. Res. Lett. **23**: 3731–3734.

Warner, B.G. 1996. Vertical gradients in peatlands. Wetlands, Environmental Gradients, Boundaries, and Buffers. *Edited by* G. Mulamoottil, B.G. Warner, and E.A. McBean. Lewis Publishers, Boca Raton, Fla., U.S.A.

Watson, A., and Nedwell, D.B. 1998. Methane production and emission from peat: the influence of anions (sulphate, nitrate) from acid rain. Atmos. Environ. **32**: 3239–3245.

Whiting, G.J. 1994. CO_2 exchange in the Hudson Bay lowlands: Community characteristics and multispectral reflectance properties. J. Geophys. Res. **99**(D1) : 1519–1528.

Whiting, G.J., and Chanton, J.P. 1993. Primary production control of methane emissions from wetlands. Nature, **364**: 794–795.

Wieder, K. 2001. Preliminary regional carbon budget for the peatland region of boreal, continental, Western Canada. 7th Symposium on the Biogeochemistry of Wetlands, Duke University, Wetland Center, Durham, N.C.

Wieder, R.K., Yavitt, J.B., and Lang, G.E. 1990. Methane production and sulfate reduction in two Appalachian Peatlands. Biogeochemistry, **10**: 81–104.

Williams, B.L., and Silcock, D.J. 1997. Nutrient and microbial changes in the peat profile beneath *Sphagnum magellanicum* in response to additions of ammonium nitrate. J. Appl. Ecol. **34**: 961–970.

Williams, B.L., Butler, A., Grosvernier, P., Francez, A.J., Gilbert, D., Ilomets, M., Jauhainen J., Matthey, Y., Silcock, D.J., and Vasander, H. 1999. The fate of NH_4NO_3 added to *Sphagnum magellanicum* carpets at five European mire sites. Biogeochemistry, **45**: 73–93.

Wind, T., and Conrad, R. 1997. Localization of sulfate reduction in planted and unplanted rice field soil. Biogeochemistry, **37**: 253–278.

Yavitt, J.B., Downey, D.M., Lancaster, E., and Lang, G.E. 1990 *a*. Methane consumption in decomposing *Sphagnum* derived peat. Soil Biol. Biochem. **22**: 441–447.

Yavitt, J.B., Lang, G.E., and Sexstone, A.J. 1990*b*. Methane Fluxes in wetland and forest soils, beaverponds, and low order streams of a temperate forest. J. Geophy. Res. **95**(D13): 22463–22474.

Yavitt, J.B., Lang, G.E., and Wieder, R.K. 1987. Control of carbon mineralization to CH_4 and CO_2 in anaerobic, *Sphagnum* derived peat from Big Run Bog, West Virginia. Biogeochemistry, **4**: 141–157.

Yavitt, J.B., Williams, C.J., and Wieder, R.K. 1997. Production of methane and carbon dioxide in peatland ecosystems across North America: Effects of temperature, aeration, and organic chemistry of the peat. Geomicrobiol. J. **14**: 299–316.