

Methane flux from northern wetlands and tundra

An ecosystem source modelling approach

T. R. Christensen, I. C. Prentice, J. Kaplan, A. Haxeltine & S. Sitch

To cite this article: T. R. Christensen, I. C. Prentice, J. Kaplan, A. Haxeltine & S. Sitch (1996) Methane flux from northern wetlands and tundra, *Tellus B: Chemical and Physical Meteorology*, 48:5, 652-661, DOI: [10.3402/tellusb.v48i5.15938](https://doi.org/10.3402/tellusb.v48i5.15938)

To link to this article: <https://doi.org/10.3402/tellusb.v48i5.15938>



© 1996 The Author(s). Published by Taylor & Francis.



Published online: 18 Jan 2017.



Submit your article to this journal [↗](#)



Article views: 197



View related articles [↗](#)



Citing articles: 12 View citing articles [↗](#)

Methane flux from northern wetlands and tundra

An ecosystem source modelling approach

By T. R. CHRISTENSEN†*, I. C. PRENTICE, J. KAPLAN, A. HAXELTINE AND S. SITCH, *Global Systems Group, Department of Ecology, Lund University, Ecology Building, S-223 62 Lund, Sweden*;
†*Department of Plant Ecology, Botanical Institute, Copenhagen, University Øster Farimagsgade 2D, DK-1353 Copenhagen K, Denmark. Email: torbenrc@bot.ku.dk*

(Manuscript received 11 January 1996; in final form 11 June 1996)

ABSTRACT

The magnitude and geographical distribution of natural sources and sinks of atmospheric CH₄ in the biosphere are still poorly known. Estimates of the net contribution from northern wetlands have been lowered during recent years. According to current consensus, about 35 Tg CH₄/yr originates from northern wetlands and tundra. A process-oriented ecosystem source model for CH₄ is used here to obtain an independent estimate for this flux. The model estimates steady-state seasonal cycles of NPP and heterotrophic respiration (HR). It accounts for peatland carbon storage and then obtains CH₄ emission as a proportion of HR with the constant of proportionality (as a range) estimated from observations. The model was shown consistent with seasonal data (including winter) on NPP, soil respiration and CH₄ emission at sites spanning a range of latitudes and climates. Applied on a 1° grid basis using standard climatological and wetland distribution data sets, this approach yields a total non-forested wetland and tundra emission (> 50°N) of 8.7 ± 5.8 Tg CH₄/yr. After inclusion of forested wetlands, we estimate a total emission from northern wetlands and tundra of 20 ± 13 Tg CH₄/yr. This is somewhat lower than current atmospherically based estimates. The difference may be due to localized high emissions, which have been reported, e.g., for West Siberian wetlands but which are not well understood and not included in current models.

1. Introduction

Next to water vapour and carbon dioxide, methane (CH₄) is the most abundant greenhouse gas in the troposphere. CH₄ is estimated to have contributed 17% to the total trace gas induced radiative forcing of the global climate over the past 200 years (IPCC, 1990) and its concentration in the atmosphere has been increasing at about 0.8%/yr over the 1980s (IPCC, 1995). The rate of increase has recently shown a so far unexplained decrease (Dlugokencky et al., 1994). The anthropogenic sources of CH₄ that have mainly caused the increase are fairly well documented (Wahlen, 1993), but there is still considerable uncertainty

about the natural sources and sinks which could be altered by changes in climate. Natural wetlands are thought to be one of the largest natural sources, emitting about 110 Tg CH₄/yr (Fung et al., 1991, IPCC, 1992), but the latitudinal breakdown of this figure is highly uncertain. The first comprehensive global wetland and CH₄ emission inventory estimated that a high proportion of natural emissions, around 65 Tg CH₄/yr, arose from northern wetlands between 50° and 70°N (Matthews and Fung, 1987). This estimate was based on a few field campaigns in isolated parts of the northern wetland region. The global estimates have been lowered as more field data have become available (Aselmann and Crutzen, 1989; Fung et al., 1991; Reeburgh et al., 1994). Current estimates, based on inverse modelling of the global

* Corresponding author.

methane cycle (Taylor et al., 1991; Fung et al., 1991) and on reviews of data from field campaigns (Bartlett and Harriss, 1993; Reeburgh et al., 1994), have converged around a total emission of 35 Tg CH₄/yr from northern wetlands and tundra.

Several studies have shown empirical relationships between net primary production (NPP) of wetland ecosystems and CH₄ emissions (Clymo and Reddaway, 1971; Svensson, 1980; Aselmann and Crutzen, 1989; Whiting and Chanton, 1992; Klinger et al., 1994). Alternatively, a relationship between net ecosystem production (NEP) and CH₄ emissions was shown to apply across a large latitudinal range (Whiting and Chanton, 1993). However, the underlying processes are not as straightforward as these empirical relationships would suggest. Relevant processes include stimulation of methanogenesis by increasing substrate availability involving root exudation (Schütz et al., 1989), plant origin of accumulated peat (Nilsson and Bohlin, 1993), degree of decomposition (Svensson and Sundh, 1992) and litter input (Valentine et al., 1994). Relationships between vascular plant production and CH₄ emission, caused by plants acting as gas conduits bypassing zones of potential CH₄ oxidation in the soil, have also been found (Whiting and Chanton, 1992; Morrissey et al., 1993; Christensen, 1994; Bubier and Moore, 1994; Chanton and Whiting, 1995; Schimel, 1995), suggesting that wetland vegetation composition (vascular plants versus bryophytes) may affect CH₄ flux. A fully mechanistic approach to modelling net CH₄ flux from these ecosystems seems unachievable at present given the limited extent to which these processes have been quantified.

In this paper we apply an ecosystem CH₄ source modelling approach that is simple and process-oriented in the sense that it is based on simulation of average annual cycles of NPP, NEP and heterotrophic respiration (HR); then, empirical observations are used to constrain the proportion of HR that is released as CH₄ rather than CO₂. We use this approach to produce an independent estimate of the northern wetland contribution to the atmospheric methane budget.

2. Methods

2.1. NPP

NPP estimates are supplied by a version of the BIOME 2 model (VEMAP, 1995; Haxeltine et al.,

1996; Haxeltine and Prentice, 1996). BIOME 2 simultaneously solves for ecosystem structural attributes (foliage cover, phenology) and carbon and water fluxes. Model input consists of latitude, soil type and mean monthly climate (temperature, precipitation and sunshine hours) data on a 0.5° grid. Incident photosynthetically active radiation (PAR) is calculated as a function of latitude and sunshine hours using an algorithm described by Prentice et al. (1993). Photosynthesis is calculated as a function of the intercepted PAR and temperature using a generalised model for photosynthesis in C3 plants (Haxeltine and Prentice, 1996). Intercepted PAR is calculated from the leaf area index (LAI) and incident PAR flux. LAI is calculated so as to optimize NPP subject to the constraint that NPP must be sufficient to maintain the given LAI. Whole plant respiration costs are assumed to be 50% of total photosynthesis. For wetlands, soil water was assumed to be always adequate to satisfy evaporative demand and therefore not limiting to photosynthesis.

2.2. Respiration

Heterotrophic respiration (HR) is calculated from the following expression (Lloyd and Taylor, 1994):

$$HR = \beta \exp^{308.56(1/56.02 - 1/(T - 227.13))},$$

where T is soil temperature. β implicitly includes both the amount of decomposable carbon and the respiration rate of that carbon at a reference temperature. β was estimated iteratively such that the steady state constraint condition was satisfied.

To account for carbon storage in peat monthly respiration values were adjusted by subtracting monthly carbon storage values. Gorham (1991) estimates long-term rates of carbon accumulation in undisturbed northern peatlands to be 23–29 g C/m²/yr. However, given indications of a recent change in the carbon balance of some high northern wetland and tundra areas (Oechel et al., 1993) we estimate a somewhat more conservative mean annual carbon storage figure of 10 g C/m²/yr. This figure is not out of range of reported and calculated ranges from Canadian (Ovenden, 1990) and Eurasian (Botch et al., 1995) peatlands. It should be noted here that the carbon storage rates of these different studies are not directly comparable. For example, the estimates of Gorham (1991)

refers to average accumulation rates over thousands of years while the data presented by Oechel et al. (1993) represents short term studies of changes in the seasonal carbon balance. In any case the model is fairly insensitive to variations in the carbon storage value (varying the annual storage between 10 and 20 g C/m² only results in a 3% change in HR). Monthly carbon storage was calculated by distributing the total carbon storage through the year in proportion to monthly NPP. Thus, annual NEP is subject to the constraint that

$$\begin{aligned} \text{NEP} &= \sum_1^{12} [(\text{NPP})_{\text{month}} - (\text{HR})_{\text{month}}] \\ &= 10 \text{ g C m}^{-2} \text{ yr}^{-1}. \end{aligned}$$

This method eliminates the need to explicitly define specific decay rates, which can differ among peat types (Hogg, 1993), and also the need to estimate the total decomposable carbon content.

2.3. CH₄ flux

The Matthews and Fung (1992) digital wetland database was used to identify the coverage of wetlands north of 50°N. The area of wetland in each 1° grid cell was calculated as the total area of a grid cell multiplied by the percent inundation as given by Matthews and Fung (1992).

CH₄ emissions per unit area of non-forested wetlands and wet tundra were estimated as 3 ± 2% of heterotrophic respiration. This range covers estimates from studies in which NPP and/or respiration and CH₄ emission were simultaneously measured (Table 1). Applying this ratio to forested wetlands will most likely result in an overestimation of the total emissions since forested wetlands per se has a lower CH₄ flux to respiration ratio

than that of non-forested environments (Roulet et al., 1994). However, the forested wetland categories of Matthews and Fung (1987) encompasses significant areas of non-forested wetlands e.g. in Finland (categorised entirely as forested) where high emission rates have been found in several open bog environments (Alm and Martikainen, pers. comm. 1995). The available data from forested bogs suggests a CH₄ flux to respiration ratio of less than half that of open wetlands but given the high producing open bogs present within forested wetland categories we assume the forested wetland CH₄ flux to respiration ratio as having a mean of 1.5%.

The estimated CH₄ emission was multiplied by the area of wetland in each grid cell. Finally, the monthly values were summed to return total annual emissions per grid cell per year.

3. Results and discussion

3.1. NPP

Measured annual NPP shows a considerable range among sites (Fig. 1), from 100 to more than 500 g C/m²/yr (Bradbury and Grace, 1983; Potter et al., 1993; Klinger et al., 1994). All modelled NPP figures for northern wetlands fall within this range. The model furthermore reproduces variation of NPP with latitude and continentality, e.g., the contrast between Toolik Lake, Alaska, and Abisko, Sweden, both at 68°N. Colder summer temperatures and shorter growing seasons in Alaska causes a lower simulated annual NPP.

3.2. Respiration and methane flux

Fig. 2 illustrates the relationship between measured and modelled soil respiration at nine wet

Table 1. Ratios of C_{CH₄} flux to total carbon flux as found in different studies.

Relationship	%	Source	Ref
C _{CH₄} /C _{resp}	1–4.5	field study in Britain	Clymo and Reddaway (1971)
C _{CH₄} /C _{resp}	1.8	field study in Sweden	Svensson (1980)
C _{CH₄} /C _{NPP}	2–7	literature study	Aselmann and Crutzen (1989)
C _{CH₄} /C _{NPP}	<2	field study in HBL, Canada	Klinger et al. (1994)
C _{CH₄} /C _{NPP}	3.4	modelling study	Cao et al. (1996)
C _{CH₄} /C _{resp}	2.7–4.7	field study in Siberia	Christensen et al. (1995 and unpub.).

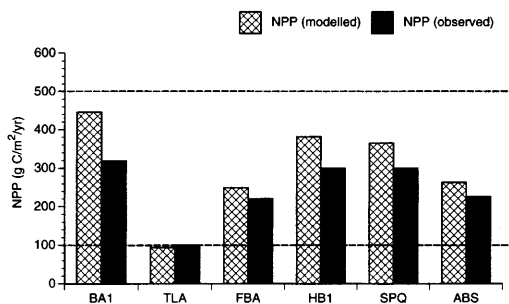


Fig. 1. Modelled and observed annual NPP figures from northern wetland sites. The range of NPP in northern wetlands is indicated by the dashed lines (Bradbury and Grace, 1983). BA1: Bethel, Alaska, 61°N, 162°W (Whiting et al., 1992). TLA: Toolik Lake, Alaska, 68°N, 149°W (Shaver & Chapin, 1991). FBA: Fairbanks, Alaska, 64°N, 145°W (Lieth and Whittaker, 1975). HB1: Hudson Bay Lowlands, 51°N, 81°W (Whiting, 1994; Klinger et al., 1994). SPQ: Schefferville, Quebec, 55°N, 66°W (same as HB1). ABS: Abisko, Sweden, 68°N, 20°W (Lieth and Whittaker, 1975).

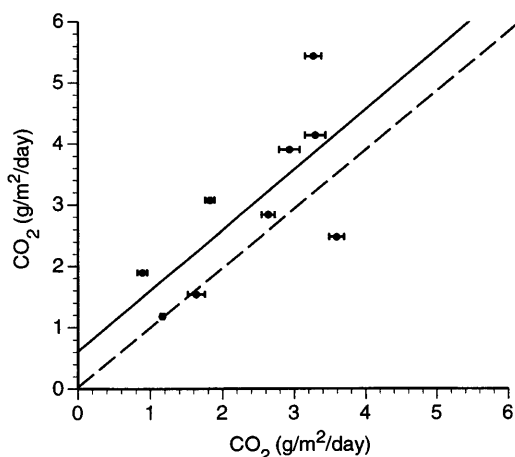


Fig. 2. Scatter diagram of measured (x-axis) and modelled (y-axis) summer (July–August) soil respiration rates across a range of wet tundra sites in northern Eurasia (Christensen et al., unpublished data, see Christensen et al., 1995 for site descriptions). The error bars along the x-axis are the standard error of mean in the observations ($n=10$). The solid line is a linear regression ($r=0.77$, $p<0.05$, $n=9$) and the dashed line indicate equality between modelled and measured respiration.

tundra sites across Siberia. The model reproduces the scale and variation in peak season respiration across a range of sites with reasonable accuracy. The model has a slight (non-significant) tendency

to overestimate respiration in the far north. Relatively high methane fluxes in the far north have been consistently reported in the literature (Sebacher et al., 1986; Whalen and Reeburgh, 1990; Morrissey and Livingston, 1992; Christensen, 1993; Christensen et al., 1995). On the contrary, relatively low fluxes were consistently found in some boreal peatlands at low latitudes (Roulet et al., 1994). However, due to shorter growing seasons in the far north and possible higher winter emissions in the south (Dise, 1992), those differences may be smaller when comparing annual fluxes rather than peak season emissions.

When comparing annual methane fluxes across study sites at different latitudes the modelled results are found to be within range of most observed emissions (linear regression: $r=0.54$, $p<0.1$, Fig. 3). The exception is the North Slope (TLA) site where fluxes previously have been found to have a somewhat higher flux than the average for comparable environments in Siberia (Christensen et al., 1995).

Whiting and Chanton (1993) showed a geographic correlation between NEP and methane emissions from wetlands. Whiting and Chanton based their comparison on field measurements of net CO_2 and methane fluxes at particular sites and times. Although this approach seems to work

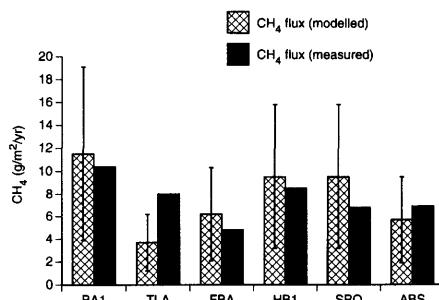


Fig. 3. Modelled and measured annual methane emission estimates at various northern wetland sites. The error bars on modelled bars represent the range given the CH_4/CO_2 ratio. BA1: Bethel, Alaska, 61°N, 162°W (Bartlett et al., 1992; Fan et al., 1992). TLA: Toolik Lake, Alaska, 68°N, 149°W (Christensen, 1993). FBA: Fairbanks, Alaska, 64°N, 145°W (Whalen and Reeburgh, 1992). HB1: Hudson Bay Lowlands, 51°N, 81°W (Moore et al., 1994; Roulet et al., 1994). SPQ: Schefferville, Quebec, 55°N, 66°W (Moore et al., 1990). ABS: Abisko, Sweden, 68°N, 20°W (Svensson and Roswall, 1984).

for the chosen sites and times it face problems when applied to seasonal cycles. Seasonal methane emission studies in high latitudes have generally shown peak emissions in late summer, typically August (Svensson, 1980; Whalen and Reeburgh, 1992; Christensen, 1993; Klinger et al., 1994; Moore et al., 1994). On the contrary, the highest rates of NEP in northern wetlands are normally found in early summer turning towards zero or negative rates in August–September (Potter et al., 1993; Whiting, 1994). Fig. 4 shows seasonal variations in methane flux as produced by our model all of which are roughly in accordance with field data.

Christensen (1993) showed that increasing methane emissions through the season at a wet tundra site were correlated with the number of growing degree days above 0°C through the season. The integrated effect of soil temperatures, thaw depth and soil moisture were found to be a sufficient basis for modelling seasonal fluctuations in methane flux from tundra (Christensen and Cox, 1995a; 1995b). The seasonal cycle of methane emission from a temperate peatland has also been modelled successfully as a relatively simple function of soil temperature and moisture (Frolking and Crill, 1994). These results indicate that methane emissions are strongly constrained by climatically controlled below-ground conditions. We therefore propose that soil respiration is a more appropriate index of methane emission than NPP or NEP since CH₄ emission is directly

related to the anaerobic fraction of heterotrophic respiration of soil organic matter and subsequently the oxidising heterotrophic processes in the upper soil horizon. Soil respiration and NPP are closely coupled on an annual time scale, however, and modelling NPP is an essential step in modelling respiration.

The CO₂/CH₄ ratio used in the model does not explicitly depend on changing moisture conditions. This is somewhat unrealistic. In reality the ratio varies with water table fluctuations, both seasonally and interannually. However, the present model was not designed to mechanistically model the response of wetland emissions to a changing climate as other models have done (e.g. Christensen and Cox, 1995a). For the present purpose it was more appropriate to assume constant wetland soil moisture conditions on a multi-year time scale. The simulated seasonal cycles (Fig. 4) are therefore to be regarded as standardised and we would expect there to be some variation around these cycles related to climatic variability, especially variations in the water balance.

3.3. Winter fluxes

There is accumulating evidence from field and laboratory surveys that soil respiration at sub-zero temperatures shows significant rates of CO₂ evolution (Zimov et al., 1993; Clein and Schimel,

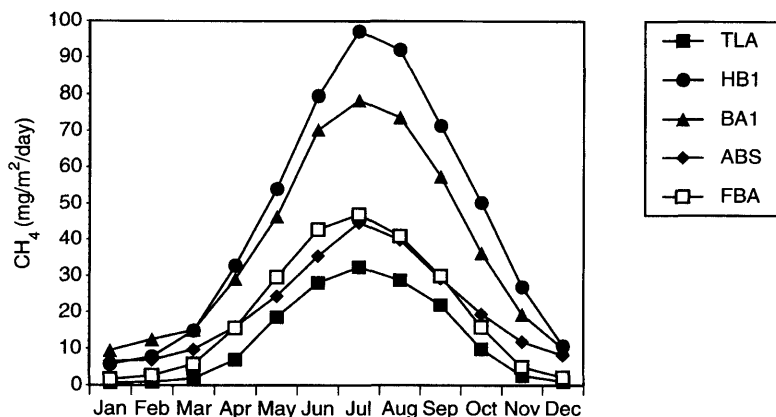


Fig. 4. Seasonal variations in mean net methane flux at a number of northern wetland sites as produced by the model. See Fig. 3 for site codes.

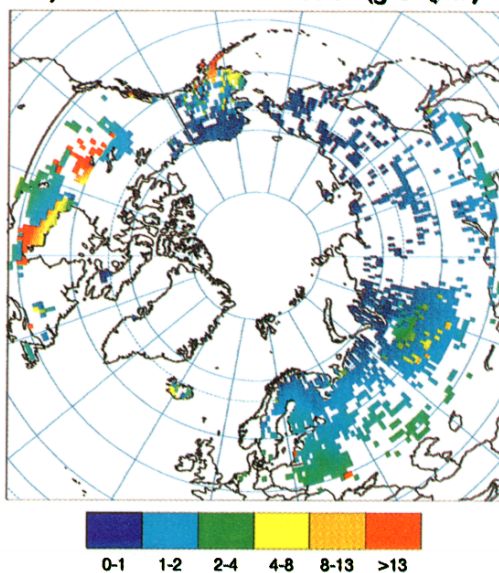
1995; Martikainen et al., 1995; Nykänen et al., 1995) and CH_4 emission (Dise, 1992; Martikainen et al., 1995; Nykänen et al., 1995) in northern wetland and tundra environments. The available information is scattered and more data are needed before model descriptions of the processes can be reliably tested (Clein and Schimel, 1995; Fan et al., 1995). Nevertheless, the available data seem to be in line with our model prediction to the effect that up to 45% of the total annual respiration may take place during the nongrowing season (months with no NPP, Fig. 5). Clein and Schimel (1995) estimated that up to 30% of the annual respiration in moist tundra communities may happen during winter. Similar ratios were found in interannual flux studies of Finnish peatlands (Martikainen et al., 1995; Nykänen et al., 1995). Oechel et al. (pers. comm., 1995) have found winter respiration to constitute up to 50–75% of the annual total in wet tundra habitats at Point Barrow, Alaska. Our model seem therefore to represent a realistic picture of seasonal variations in soil respiration.

3.4. Comparison of global estimates

Fig. 5 shows the geographical distribution of global methane emissions from northern wetlands according to our model using the Matthews and Fung (1987; 1992) global wetland dataset. Fig. 5 illustrates four main wetland regions: The lowlands of boreal Europe and Scandinavia, the Western Siberian Plain, the Alaskan wetland areas and the wetlands in central Canada, in particular the Hudson Bay Lowlands. The most widespread non-forested wetlands are those in Canada and western Siberia. Most of Alaska and many northern regions in Eurasia are shown to have relatively high emissions on a per square meter basis (Fig. 5a), but when extrapolated the regional fluxes to the atmosphere are lower (Fig. 5b). This phenomenon reflects a smaller percentage inundated area in these grid cells.

An estimate of the emission from all the Matthews and Fung (1987) categories of northern wetlands is seen in Fig. 5. The total global figure derived by this approach (with the same range as given previously for the CO_2/CH_4 ratio) amounts to $20 \pm 13 \text{ Tg CH}_4/\text{yr}$. Non-forested wetlands and tundra alone contribute $8.7 \pm 5.8 \text{ Tg CH}_4/\text{yr}$ to this modelled total.

a) Annual Methane Emission ($\text{g CH}_4/\text{m}^2$)



b) Annual Methane Emission ($\text{kg CH}_4/\text{grid cell}$)

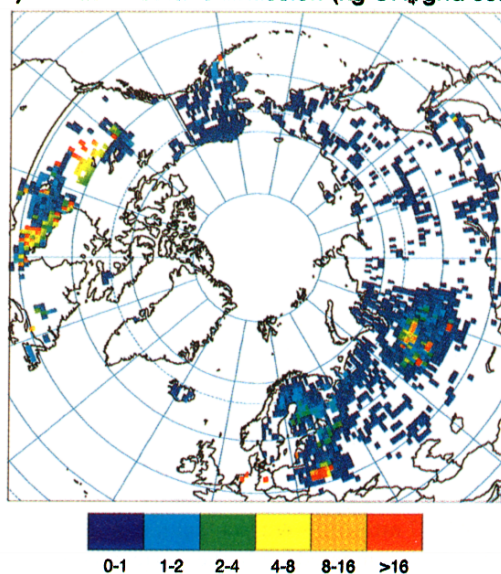


Fig. 5. Global methane emission from northern wetlands (above 50°N) as defined by Matthews and Fung (1992) and weighted by our model. Fig. 5a shows emission per square meter of wetlands within the respective grids. Fig. 5b shows the modelled total emissions per grid cell.

Aselmann and Crutzen (1989) estimated CH₄ emissions from global wetlands. Aselmann and Crutzen did not separate forested and non-forested wetlands and they used their own geographical dataset, which differs from Matthews and Fung's (see discussion in Aselman and Crutzen, 1989), so our estimates are not directly comparable to theirs. However, they linked NPP rates of 100–700 g C/m²/yr for northern wetlands (similar to those produced by our model) to methane emission by a C_{CH₄}/C_{resp} ratio of 2–7%. Using an approach quite similar to ours, they estimated northern wetland emission at 25 Tg/yr. This is within the range that we estimate.

Cao et al. (1996) used a process based model to estimate global CH₄ emissions from natural wetlands. This model estimates CH₄ emissions based on the substrate limitations on methanogenesis imposed by primary production and soil decomposition rates and the subsequent oxidation processes. The calculated net primary production rates are similar to those produced by our model, and the calculated mean proportion of NPP that is returned to the atmosphere as methane is 3.4%. Cao et al. (1996) estimates total northern wetland emission of 21.8 Tg/yr, i.e. very similar to our result. They used the TEM model (Raich et al., 1991; Mcguire et al., 1992) to produce NPP estimates and assumed, as we have, that wetland soils are constantly saturated. Since we also used the same geographical dataset (Matthews and Fung, 1987) the similarity in the results ultimately reflects agreement between the simulated NPP produced by TEM and BIOME 2. However, the simpler approach taken in the present paper seems sufficient for producing a well founded global estimate.

It thus appears that the global estimates of net CH₄ flux from northern wetlands obtained by process-oriented modelling approaches are consistently lower than the original Matthews and Fung (1987) estimate (the authors acknowledge their 1987 estimate were too high), and also somewhat low compared with the current consensus IPCC (1995) estimate of around 35 Tg CH₄/yr for northern wetland emissions. The IPCC estimate is based on reviews of the available field data (with a high North American bias) (Bartlett and Harriss, 1993; Reeburgh et al., 1994), but also on the, to date, most comprehensive inverse modelling

studies of the global methane cycle (Fung et al., 1991; Taylor et al., 1991). In addition, another recent inverse modelling study of the global atmospheric methane cycle does not suggest any lower emissions from northern wetlands (Hein et al., in preparation). The fact that we estimate lower global northern wetland emissions may therefore not necessarily reflect a smaller total atmospheric input from the northern wetland regions. Rather, it could indicate that the flux patterns may not be fully captured by averaged emission calculations alone. Localised high emissions (which are difficult to model) may influence the global signal. Some wetlands in West Siberia have been found to have extremely high emissions, beyond any relationships with environmental or biotic factors found elsewhere (Panikov et al., 1995). Wetland regions in Eurasia may therefore hold a key to understanding the apparent discrepancies between "bottom-up" and "top-down" CH₄ emission estimates.

In conclusion, using a process-oriented ecosystem source model, we estimate global northern wetland and tundra CH₄ emissions to be 20 ± 13 Tg CH₄/yr. This is lower than the current consensus estimate of 35 Tg CH₄/yr. The model is based on an observed proportionality between aerobic heterotrophic respiration and methane emission in wetland environments, with the NPP and respiration source figures being well in accordance with established data from northern wetlands. If CH₄ emissions from these environments are greater than our estimate the reason might lie in large but regionally localised emissions, which at present seems difficult to account for in models.

4. Acknowledgements

This work was made possible through a European Commission Post Doctoral Fellowship under the Human Capital and Mobility Programme to TRC. Financial support was also provided by the Swedish Natural Sciences Research Council (NFR). The work contributes to the core research of the IGBP core project on Global Change and Terrestrial Ecosystems (GCTE). We thank three anonymous reviewers for constructive comments.

REFERENCES

- Aselmann, I. and Crutzen, P.J. 1989. Global distributions of natural freshwater wetlands and rice paddies, their net primary productivity, seasonality and possible methane emissions. *Journal of Atmospheric Chemistry* **8**, 307–358.
- Bartlett, K.B., Crill, P., Sass, R.C., Harriss, R.S. and Dise, N.B. 1992. Methane emissions from tundra environments in the Yukon-Kuskokwim Delta, Alaska. *Journal of Geophysical Research* **97D**, 16645–16660.
- Bartlett, K.B. and Harriss, R.C. 1993. Review and assessment of methane emissions from wetlands, *Chemosphere* **26**, 261–320.
- 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 Biogeochemical Cycles* **9**, 37–46.
- Bradbury I.K. and Grace, J. 1983. Primary production in wetlands. In: *Ecosystems of the world 4a, mires: swamp, bog, fen and moor, general studies* (ed. Gore, A.J.P.) Elsevier, Oxford.
- Bubier, J.L. and Moore, T.R. 1994. An ecological perspective on methane emissions from northern wetlands. *Trends in Ecology and Evolution* **9**, 460–464.
- Cao, M., Marshall, S. and Gregson, K. 1996. Global carbon exchange and methane emissions from natural wetlands: Application of a process-based model. *Journal of Geophysical Research*, in press.
- Chanton, J.P. and Whiting, G.J. 1995. Trace gas exchange in freshwater and coastal marine environments: ebullition and transport by plants. In: *Biogenic trace gases: measuring emissions from soil and water* (eds. Matson, P.A. and Harriss, G.J.) Blackwell Science, London.
- Christensen, T.R. 1993. Methane emission from Arctic tundra. *Biogeochemistry* **21**, 117–139.
- Christensen, T.R. 1994. *Exchange of radiatively active trace gases in tundra environments, with particular attention to methane*, Ph.D. Thesis. University of Cambridge.
- Christensen, T.R. and Cox, P. 1995a. Response of methane emission from arctic tundra to climatic change: results from a model simulation. *Tellus* **47B**, 301–310.
- Christensen, T.R. and Cox, P. 1995b. Modelling response of methane emission from arctic tundra to climatic change: an overview of relevant controlling factors. In: *Global change and Arctic terrestrial ecosystems. Ecosystems research report 10* (ed. Callaghan, T.V.). European Commission, Luxemburg, pp. 296–304.
- Christensen, T.R., Jonasson, S., Callaghan, T.V. and Havström, M. 1995. Spatial variation in high latitude methane flux along a transect across Siberian and European tundra environments. *Journal of Geophysical Research* **100D**, 21035–21045.
- Clein, J.S. and Schimel, J.P. 1995. Microbial activity of tundra and taiga soils at sub-zero temperatures. *Soil Biology and Biochemistry* **27**, 1231–1234.
- Clymo, R.S. and Reddaway E.J.F. 1971. Productivity of Sphagnum (bog-moss) and peat accumulation. *Hydrobiologia* **12**, 181–192.
- Dise, N.B. 1992. Winter fluxes of methane from Minnesota peatlands. *Biogeochemistry* **17**, 71–83.
- Dlugokencky, E.J., Masarie, K.A., Lang, P.M., Tans, P.P., Steele, L.P. and Nisbet, E.G. 1994. A dramatic decrease in the growth rate of atmospheric methane in the northern hemisphere during 1992. *Geophysical Research Letters* **19**, 2313–2316.
- Fan, S.M., Wofsy S.C., Bakwin P.S., Jacob, D.J., Anderson, S.M., Keibian, P.L., McManus, J.B., Kolb, C.E. and Fitzjarrald, D.R. 1992. Micrometeorological measurements of CH₄ and CO₂ exchange between the atmosphere and subarctic tundra. *Journal of Geophysical Research* **97D**, 16627–16644.
- Fan, S.M., Goulden, M.L., Munger, J.W., Daube, B.C., Bakwin, P.S., Wofsy, S.C., Amthor, J.S., Fitzjarrald, D.R., Moore, K.E. and Moore, T.R. 1995. Environmental controls on the photosynthesis and respiration of a boreal lichen woodland: a growing season of whole-ecosystem exchange measurements by eddy correlation. *Oecologia* **102**, 443–452.
- Frolking, S., and Crill, P. 1994. Climate controls on temporal variability of methane flux from a poor fen in southeastern New Hampshire: measurement and modeling. *Global Biogeochemical Cycles* **8**, 385–397.
- Fung, I., John, J., Lerner, J., Matthews, E., Prather, M., Steele, L.P. and Fraser, P.J. 1991. Three-dimensional model synthesis of the Global methane cycle. *Journal of Geophysical Research* **96D**, 13033–13065.
- Gorham, E. 1991. Northern peatlands: role in the carbon cycle and probable responses to climatic warming. *Ecological Applications* **1**, 182–195.
- Haxeltine, A., Prentice, I.C. and Cresswell, I.D. 1996. A coupled carbon and water flux model to predict vegetation structure. *Journal of Vegetation Science*, in press.
- Haxeltine, A. and Prentice, I.C. 1996. A general model for the light/use efficiency of primary production. *Functional Ecology*, in press.
- Hogg, E.H. 1993. Decay potential of hummock and hollow Sphagnum peats at different depths in a Swedish raised bog. *Oikos* **66**, 269–278.
- IPCC 1990. *Climate change. The Intergovernmental Panel on Climate Change (IPCC) Scientific Assessment*. Cambridge University Press, Cambridge.
- IPCC 1992. *Climate change 1992. The supplementary report to The IPCC Scientific Assessment*. Cambridge University Press, Cambridge.
- IPCC (Intergovernmental Panel on Climate Change) 1995. *Climate Change 1994, Radiative forcing of climate change and an evaluation of the IPCC IS92 emission scenarios*. Cambridge University Press, Cambridge.
- Klinger, L.F., Zimmerman, 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. *Journal of Geophysical Research* **99D**, 1469–1494.
- Lieth, H. and Wittaker, R.H. 1975. *Primary productivity of the biosphere*. Springer, Berlin.
- Lloyd, J. and Taylor, J.A. 1994. On the temperature dependency of soil respiration. *Functional Ecology* **8**, 315–323.
- Martikainen, P.J., Nykänen, H., Alm, J. and Silvola, J. 1995. Changes in fluxes of carbon dioxide, methane and nitrous oxide due to forest drainage of mire sites of different trophic. *Plant and Soil* **168–169**, 571–577.
- Matthews, E. and Fung, I. 1987. Methane emission from natural wetlands: global distribution, area, and environmental characteristics of sources. *Global Biogeochemical Cycles* **1**, 61–86.
- Matthews, E. and Fung, I. 1992. Global data bases on distribution, characteristics and methane emission of natural wetlands. Digital raster data on a 1-degree geographic (lat/long) 180 × 360 grid. In: *Global ecosystems database version 1.0: Disc A*. NOAA National Geophysical Data Center, Boulder.
- Mcguire, A.D., Melillo, J.M., Toyle, L.A., Kicklighter, D.W., Grace, A.L., Moore III, B. and Vorosmarty, C.J. 1992. Interactions between carbon and nitrogen dynamics in estimating net primary productivity for potential vegetation in North America. *Global Biogeochemical Cycles* **6**, 101–124.
- Moore, T.R., Roulet, N. and Knowles, R. 1990. Spatial and temporal variations of methane flux from subarctic/northern boreal fens. *Global Biogeochemical Cycles* **4**, 29–46.
- Moore, T.R., Heyes, A. and Roulet, N.T. 1994. Methane emissions from wetlands, southern Hudson Bay lowland. *Journal of Geophysical Research* **99D**, 1455–1467.
- Morrissey, L.A. and Livingston, G.P. 1992. Methane Emission from Alaska Arctic Tundra: An Assessment of Local Spatial Variability. *Journal of Geophysical Research* **97D**, 16661–16670.
- Morrissey, L.A., Zobel, D.B. and Livingston, G.P. 1993. Significance of stomatal controls on methane release from *Carex*-dominated wetlands. *Chemosphere* **26**, 339–355.
- Nilsson, M. and Bohlin, E. 1993. Methane and carbon dioxide concentrations in bogs and fens—with special reference to the effects of the botanical composition of the peat. *Journal of Ecology* **81**, 615–625.
- Nykänen, H., Alm, J., Lång, K., Silvola, J. and Martikainen, P.J. 1995. Emission of CH₄, N₂O and CO₂ from a virgin fen and a fen drained for grassland in Finland. *Journal of Biogeography* **22**, 1149–1155.
- Oechel, W.C., Hastings, S.T., Vourlitis, G., Jenkins, M., Riechers, G. and Grulke, N. 1993. Recent change of Arctic tundra ecosystems from a net carbon dioxide sink to a source. *Nature* **361**, 520–523.
- Ovenden, L. 1990. Peat accumulation in northern wetlands. *Quaternary Research* **33**, 377–386.
- Panikov, N.S., Sizova, M.V., Zelenev, V.V., Machov, G.A., Naumov, A.V. and Gadzhiev, I.M. 1995. Methane and carbon dioxide emission from several vasyugan wetlands: spatial and temporal flux variations. *Ecological Chemistry* **4**, 13–23.
- Potter, C.S., Randerson, J.T., Field, C.B., Matson, P.A., Vitousek, P.M., Mooney, H.A. and Kloster, S.A. 1993. Terrestrial ecosystem production: a process model based on global satellite and surface data. *Global Biogeochemical Cycles* **7**, 811–841.
- Prentice, I.C., Sykes, S.T. and Cramer, W. 1993. A simulation model for the transient effects of climate change on forest landscapes. *Ecological Modelling* **65**, 51–70.
- Raich, J.W., Rastetter, E.B., Melillo, J.M., Kicklighter, D.W., Steudler, P.A., Peterson, B.J., Grace, A.L., Moore III, B. and Vorosmarty, C.J. 1991. Potential net primary productivity in South America: application of a global model. *Ecological Applications* **1**, 399–429.
- Reeburgh, W.S., Roulet, N.T. and Svensson, B. 1994. Terrestrial biosphere-atmosphere exchange in high latitudes. In: *Global atmospheric-biospheric chemistry* (ed. R.G. Prinn). Plenum Press, New York.
- Roulet, N.T., Jano, A., Kelly, C.A., Klinger, L., Moore, T.R., Protz, R., Ritter, J.A. and Rouse, W.R. 1994. Role of the Hudson Bay lowland as a source of atmospheric methane. *Journal of Geophysical Research* **99D**, 1439–1454.
- Schimel, J.P. 1995. Plant transport and methane production as controls on methane flux from arctic wet meadow tundra. *Biogeochemistry* **28**, 183–200.
- Schütz, H., Holzapfel-Pschorn, A., Conrad, R., Rennenberg, H. and Seiler, W. 1989. A 3-year continuous record on the influence of daytime, season, and fertilizer treatment on methane emission rates from an Italian rice paddy. *Journal of Geophysical Research* **94D**, 16405–16416.
- Sebacher, D.I., Harriss, R.C., Bartlett, K.B., Sebacher, S.M. and Grice, S.S. 1986. Atmospheric methane sources: Alaskan tundra bogs, an alpine fen, and a subarctic boreal marsh. *Tellus* **38B**, 1–10.
- Shaver, G.R. and Chapin, F.S. 1991. Production: biomass relationships and element cycling in contrasting Arctic vegetation types. *Ecological Monographs* **61**, 1–31.
- Svensson, B.H. 1980. Carbon dioxide and methane fluxes from the ombrotrophic parts of a subarctic mire. In: *Ecology of a subarctic mire*. (ed. M. Sonesson), Swedish Natural Science Research Council, Stockholm.
- Svensson, B.H. and Roswall, T. 1984. In situ methane production from acid peat in plant communities with different moisture regimes in a subarctic mire. *Oikos* **43**, 341–50.
- Svensson, B.H. and Sundh, I. 1992. Factors affecting methane production in peat soils. *Suo*, **43**, 183–190.
- Taylor, J.A., Brasseur, G.P., Zimmerman, P.R. and Cicerone, R.J. 1991. A study of the sources and sinks of methane and methyl chloroform using a global three-dimensional langrangian tropospheric tracer transport model. *Journal of Geophysical Research* **96D**, 3013–3044.
- Valentine, D.W., Holland, E.A. and Schimel, D.S. 1994. Ecosystem and physiological controls over methane

- production in northern wetlands. *Journal of Geophysical Research* **99D**, 1563–1571.
- VEMAP members, 1995. Vegetation/ecosystem modeling and analysis project: comparing biogeography and biogeochemistry models in a continental-scale study of terrestrial ecosystem responses to climate change and CO₂ doubling. *Global Biogeochemical Cycles* **9**, 407–437.
- Wahlen, M. 1993. The global methane cycle. *Annual Review of Earth and Planetary Science* **21**, 407–426.
- Whalen, S.C. and Reeburgh, W.S. 1990. A methane flux transect along the Trans-Alaska Pipeline Haul Road. *Tellus* **42B**, 237–249.
- Whalen, S.C. and Reeburgh, W.S. 1992. Interannual variations in tundra methane emissions: A four-year time-series at fixed sites. *Global Biogeochemical Cycles* **6**, 139–159.
- Whiting, G.J. and Chanton, J.P. 1992. Plant-dependent CH₄ emission in a subarctic Canadian fen. *Global Biogeochemical Cycles* **6**, 225–231.
- Whiting, G.J. and Chanton, J.P. 1993. Primary production control of methane emission from wetlands. *Nature* **364**, 794–795.
- Whiting, G.J., Bartlett, D.S., Fan, S., Bakwin, P.S. and Wofsy, S.C. 1992. Biosphere/atmosphere CO₂ exchange in tundra ecosystems: community characteristics and relationships with multispectral surface reflectance. *Journal of Geophysical Research* **97D**, 16,671–16,680.
- Whiting, G.J. 1994. CO₂ exchange in the Hudson Bay lowlands: community characteristics and multispectral reflectance properties. *Journal of Geophysical Research* **99D**, 1519–1528.
- Zimov, S.A., Zimova, G.M., Daviodov, S.P., Daviodova, A.I., Voropaev, Y.V., Voropaeva, Z.V., Prosiannikov, S.F. and Prosiannikova, O.V. 1993. Winter biotic activity and production of CO₂ in siberian soils: a factor in the greenhouse effect. *Journal of Geophysical Research* **98D**, 5017–5023.