Rising methane emissions in response to climate change in Northern Eurasia during the 21st century

Xudong Zhu¹, Qianlai Zhuang^{1,2}, Min Chen¹, Andrey Sirin³, Jerry Melillo⁴, David Kicklighter⁴, Andrei Sokolov⁵ and Lulu Song⁶

- ¹ Department of Earth and Atmospheric Sciences, Purdue University, West Lafayette, IN, USA
- ² Department of Agronomy, Purdue University, West Lafayette, IN, USA
- ³ Laboratory of Peatland Forestry and Amelioration, Institute of Forest Science, Russian Academy of Sciences, Uspenskoye, Moscow Oblast, Russia
- ⁴ The Ecosystems Center, Marine Biological Laboratory, Woods Hole, MA, USA
- Department of Earth, Atmospheric, and Planetary Sciences, Massachusetts Institute of Technology, Cambridge, MA, USA
- ⁶ Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences, Beijing, People's Republic of China

E-mail: zhu123@purdue.edu

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Abstract

We used a biogeochemistry model, the Terrestrial Ecosystem Model (TEM), to examine the methane (CH₄) exchanges between terrestrial ecosystems and the atmosphere in Northern Eurasia from 1971 to 2100. Multiple model simulations using various wetland extent datasets and climate change scenarios were conducted to assess the uncertainty of CH₄ fluxes, including emissions and consumption. On the basis of these simulations we estimate the current net emissions in the region to be 20–24 Tg CH₄ yr⁻¹ (1 Tg = 10^{12} g), two-thirds of which are emitted during the summer. In response to climate change over the 21st century, the annual CH₄ emissions in the region are projected to increase at a rate of $0.06 \text{ Tg CH}_4 \text{ yr}^{-1}$, which is an order of magnitude greater than that of annual CH₄ consumption. Further, the annual net CH₄ emissions are projected to increase by 6-51% under various wetland extent datasets and climate scenarios by the end of the 21st century, relative to present conditions. Spatial patterns of net CH₄ emissions were determined by wetland extent. Net CH₄ emissions were dominated by wetlands within boreal forests, grasslands and wet tundra areas in the region. Correlation analyses indicated that water table depth and soil temperature were the two most important environmental controls on both CH₄ emissions and consumption in the region. Our uncertainty analyses indicated that the uncertainty in wetland extent had a larger effect on future CH₄ emissions than the uncertainty in future climate. This study suggests that better characterization of the spatial distribution and the natural diversity of wetlands should be a research priority for quantifying CH₄ fluxes in this region.

Keywords: methane, wetlands, Terrestrial Ecosystem Model, Northern Eurasia

S Online supplementary data available from stacks.iop.org/ERL/6/045211/mmedia

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1. Introduction

Next to carbon dioxide (CO₂), methane (CH₄) is the most important greenhouse gas contributing to global climate change. While CO₂ has been responsible for a majority of the increases in radiative forcing, the steep rate of increase in atmospheric CH₄ is also of great concern because it is 25 times more effective on a per unit mass basis than CO₂ in absorbing long-wave radiation on a 100 yr time scale (IPCC 2007). The contribution of CH₄ to radiative forcing from pre-industrial to present time is estimated to be about 20% of that from all greenhouse gases (Le Mer and Roger 2001). Atmospheric CH₄ has a wide variety of natural and anthropogenic sources, and the most important natural sources are wetlands (Bartlett and Harriss 1993, Wuebbles and Hayhoe 2002). The total global CH₄ source is relatively well constrained from atmospheric observations, but the strength and trends of the contributing sources are considerably less known due to high spatial and temporal variability (IPCC 2007).

Net methane emissions from terrestrial ecosystems are determined by two different microbial processes: methanogenesis, which produces methane, and methanotrophy, which consumes methane. Methanogenesis occurs under anaerobic conditions such as typically found in wetlands and depends mainly on soil organic matter and vegetation. In contrast, methanotrophy occurs in aerobic soils or aerated surface waters and is strongly controlled by availability of oxygen. Both processes are influenced by water table depth, soil temperature and pH (Walter and Heimann 2000, MacDonald *et al* 1998).

Northern Eurasia accounts for 60% of the terrestrial land cover north of 40°N and contains vast areas of wetlands, especially peatlands, which contain a large amount of organic carbon and are often underlain by continuous and discontinuous permafrost (NEESPI 2004). Compared with low latitudes, the region, especially its northern areas, has been experiencing more dramatic environmental changes, including increasing temperatures, melting of permafrost, changes in precipitation and prolonged growing seasons (Fedorov 1996, Romanovsky *et al* 2000, IPCC 2007). These changes in climate, plant, soil thermal and hydrological conditions have resulted in changes in the magnitude and timing of CH₄ emissions and consumption (e.g., Friborg *et al* 1997, West and Schmidt 1998, Zimov *et al* 2006).

To quantify CH₄ fluxes at regional and global levels, many large-spatial-scale biogeochemical models have been developed to estimate current and future CH₄ exchanges between terrestrial ecosystems and the atmosphere (Cao *et al* 1996, Christensen *et al* 1996, Walter *et al* 2001). Large uncertainties exist in the regional and global CH₄ budgets from these model studies. Cao *et al* (1996) estimated global CH₄ emissions to be 145 Tg CH₄ yr⁻¹ (1 Tg = 10¹² g), of which 24 Tg CH₄ yr⁻¹ was from natural wetlands. Christensen *et al* (1996) gave a CH₄ flux of 20 Tg CH₄ yr⁻¹ from northern wetlands (>50°N). Walter *et al* (2001) put the estimate of global annual CH₄ emissions from wetlands to be 260 Tg CH₄ yr⁻¹, of which 25% originated from wetlands north of 30°N. One uncertainty in regional and global CH₄ budgets arises from uncertainty in the extent of wetlands, for it

is difficult to characterize inundated areas and their dynamics in a broad range of environmental conditions. For instance, a recent model study conducted by Petrescu *et al* (2010) put the estimate of current CH₄ emissions from circum-arctic wetlands (<5 °C for mean annual air temperature) in a broad range (between 38 and 157 Tg CH₄ yr⁻¹) based on multiple existing or modeled wetland extent datasets. Uncertainty in future climate is another source of uncertainty for estimates of future CH₄ exchanges between terrestrial ecosystems and the atmosphere. This climate uncertainty among estimates from global climate models is largely the result of different assumptions about effective climate sensitivity of the earth system, the strength of aerosol forcing, and the rate at which heat is mixed into the deep ocean (Meehl *et al* 2007).

To date, there is a lack of comprehensive estimates of CH₄ fluxes for Northern Eurasia that consider both emissions and consumption of CH₄ within different wetland types. Furthermore, little information is currently available about how regional CH₄ dynamics in Northern Eurasia will respond to transient changes in future climate. Here, we apply a process-based biogeochemistry model to examine how uncertainty in wetland extent and future climate influence projected CH₄ fluxes between terrestrial ecosystems and the atmosphere in Northern Eurasia over the 21st century.

2. Methods

2.1. Overview

In this study, we conducted simulations of CH_4 fluxes in Northern Eurasia during 1971–2100 with the Terrestrial Ecosystem Model (TEM, (Zhuang *et al* 2004)) based on three wetland extent datasets and six future climate scenarios. First, we examined the responses of CH_4 fluxes simulated by TEM with three wetland extent datasets to both historical and six future climate scenarios. Then, we assessed the spatial distribution and temporal variability of CH_4 fluxes among different simulations in both the historical period and the future. Finally, we identified the key controls on CH_4 dynamics for both emission and consumption with correlation analyses.

2.2. Model and data

The biogeochemistry model TEM explicitly simulates the processes of CH₄ production (methanogenesis) and CH₄ oxidation (methanotrophy), as well as the transport of the gas between the soil and the atmosphere (Zhuang *et al* 2004). The net CH₄ emissions from soils to the atmosphere are the total of the CH₄ fluxes at the soil/water–atmosphere boundary via different transport pathways (see supplementary material for detailed model description available at stacks.iop.org/ERL/6/045211/mmedia). To make spatially and temporally explicit estimates of CH₄ fluxes over Northern Eurasia with TEM, we used data of climate, wetland extent, vegetation type, soils, elevation and atmospheric CO₂ from a variety of sources. Detailed descriptions of data and processing methods are provided as supplementary material (available at stacks.iop. org/ERL/6/045211/mmedia).

2.3. Simulation protocol

TEM was applied to simulate both CH_4 emissions and consumption from both wetland and upland ecosystems in Northern Eurasia from 1971 to 2100 at a $0.5^{\circ} \times 0.5^{\circ}$ spatial resolution. Both wetland and upland ecosystems may occur in each grid cell. The ecosystem-specific CH_4 flux estimates were then area-weighted for each grid cell, as defined by the corresponding wetland extent datasets. We defined the regional net CH_4 emissions as the difference between CH_4 emissions from wetland ecosystems and CH_4 consumption in upland ecosystems. The model parameterization and validation were conducted in a previous study (Zhuang $et\ al\ 2004$), and the same parameter sets were used in this study.

In order to assess the estimate uncertainty of CH₄ emissions and consumption over Northern Eurasia, associated with wetland extent and climate change, we conducted three sets of simulations with TEM based on three wetland extent datasets: WET1 (Matthews and Fung 1987), WET2 (Lehner and Döll 2004), and WET3 (Papa et al 2010) (see supplementary material for explanations of each dataset available at stacks.iop.org/ERL/6/045211/mmedia). the historical period (1971-2000), each set of simulations contained one model run driven by historical climate data. For the future period (2001–100), each set of simulations was driven by one of six climate change scenarios developed by Sokolov et al (2005) that represented high and median climate responses to anthropogenic emissions based on either a 'business-as-usual' scenario or a level 1 stabilization scenario. See supplementary material (available at stacks.iop.org/ERL/ 6/045211/mmedia) for more details of climate scenarios.

2.4. Statistical analysis

We used the Mann–Kendall trend analysis method (Hamed and Ramachandra Rao 1998) to check the trend of the time-series data. Pearson's correlation coefficient was used to calculate the correlation coefficients between environmental factors and CH₄ fluxes. All the statistical analyses were conducted in MATLAB (The MathWorks, Inc., MA, USA).

3. Results and discussion

3.1. Spatial distribution of CH₄ fluxes

The net CH₄ emissions, the difference between emissions and consumption, showed substantial spatial variation over Northern Eurasia, with different spatial patterns visible among the three simulations with WET1, WET2 and WET3 (figure 1). During the 1990s, some ecosystems acted as a source of atmospheric CH₄, contributing up to 10 g CH₄ m⁻² yr⁻¹, and some dry ecosystems consumed up to 2 g CH₄ m⁻² yr⁻¹. A major source of atmospheric CH₄ was found in western Siberia where wetland ecosystems were identified in all three wetland extent datasets; strong sinks of atmospheric CH₄ were found mainly in the western and southern parts of Northern Eurasia, while other areas acted as weak sinks of atmospheric CH₄. During the 2090s, the magnitude of net CH₄ emissions

is projected to increase for each of the simulations with an unchanged general spatial pattern (figure 1).

Northern Eurasia as a whole acted as a CH₄ source of 21 ± 2.5 Tg CH₄ yr⁻¹ during the 1990s. This source was represented by net CH₄ emissions, which were the difference between the CH₄ emissions at 26 ± 2.4 Tg CH₄ yr⁻¹, and the CH₄ consumption at 5 ± 0.1 Tg CH₄ yr⁻¹ over the total area of 28.87 million km². The three sets of simulations gave different magnitudes of CH4 emissions and consumption due to the differences in the spatial distribution of wetland extent in the various datasets (figure S3, table S2 (available at stacks.iop.org/ERL/6/045211/mmedia)). Our estimates of net CH₄ emissions in Northern Eurasia were comparable to those modeled in previous studies (18–33 Tg CH₄ yr⁻¹, Anisimov 2007, Denisov et al 2010). The source of CH₄ emissions was dominated by wetlands within boreal forests, grasslands and wet tundra areas in the region. Among all ecosystem types, boreal forest accounted for the largest amount of CH4 fluxes in both emissions (9 \pm 3.7 Tg CH₄ yr⁻¹, figure 2(a)) and consumption (2 \pm 0.1 Tg CH₄ yr⁻¹, figure 2(b)) because of its vast wetland areas (table S2 available at stacks.iop.org/ERL/6/ 045211/mmedia).

On a per unit area basis, there were significant differences in variation patterns across ecosystems both in CH₄ emissions and consumption, compared with those for the regional total fluxes. For CH₄ emissions, the magnitude varied from 20 \pm 0.9 mg CH₄ m⁻² d⁻¹ in alpine tundra to 198 \pm 68.3 mg CH₄ m⁻² d⁻¹ in xeric woodlands, with a mean of 93 \pm 14.6 mg CH₄ m⁻² d⁻¹ for all ecosystem types (figure 2(c)). For CH₄ consumption, the magnitude varied from 0.3 \pm 0.0 mg CH₄ m⁻² d⁻¹ in alpine tundra to 0.7 \pm 0.0 mg CH₄ m⁻² d⁻¹ in temperate coniferous forests and xeric shrublands, with a mean of 0.6 \pm 0.0 mg CH₄ m⁻² d⁻¹ for all ecosystem types (figure 2(d)). Overall, ecosystems located in the warmer southern and western regions had higher CH₄ fluxes than the colder northern regions (figure S2a available at stacks.iop.org/ERL/6/045211/mmedia).

Apart from the different magnitudes of CH₄ fluxes per unit area across ecosystems, discrepancies were found among the three simulations although model parameters and climate inputs for a specific ecosystem were the same during the 1990s. These discrepancies were caused by different spatial distributions of wetland extent for each dataset: the spatial overlay of wetland distribution and vegetation types for the three simulations presented different spatial patterns for wetland types ('wetland-vegetation' combination), which gave different averaged climate conditions, affecting averaged CH₄ fluxes for a specific wetland type. For example, wetlands within xeric shrublands, which presented very different spatial patterns among the three wetland extent datasets (figure S3 available at stacks.iop.org/ERL/6/045211/mmedia), showed large differences in CH₄ emissions among the three simulations (figure 2(c)). In general, it seemed the differences in wetland extent in the warmer southern ecosystems had more influence on CH₄ emissions than in the colder northern ecosystems, which implied that it was more important to get accurate wetland extent data for modeling CH₄ emissions in warmer southern ecosystems in this region.

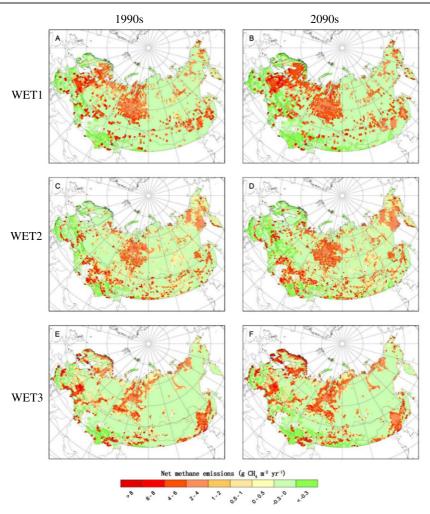


Figure 1. Spatial patterns of simulated annual net methane emissions with three wetland extent datasets across Northern Eurasia during the 1990s and the 2090s. For the 2090s, the simulated net methane emissions from future climate scenarios are averaged. Positive values indicate net release of methane to the atmosphere and negative values indicate net consumption of atmospheric methane by soils. Distribution of wetlands represented by the three datasets are compared in figure S3 (available at stacks.iop.org/ERL/6/045211/mmedia).

We compared our simulated daily CH₄ emissions and consumption against site measurements in Northern Eurasia for recent years. We found that, for tundra ecosystems, the mean modeled estimates of net methane emissions during the growing season (60 mg $CH_4\ m^{-2}\ d^{-1}$) were within the range of measurements (4–195 mg CH₄ m⁻² d⁻¹, Heyer et al 2002). For boreal forest ecosystems, the mean estimates of net methane emissions during the growing season (60-228 mg CH₄ m⁻² d⁻¹) were well within the range of measured values (21–233 mg CH₄ m $^{-2}$ d $^{-1}$ (Takeuchi *et al* 2003); 124 and 209 mg CH₄ m $^{-2}$ d $^{-1}$ -median for eutrophic and oligotrophic wetlands, respectively (Glagolev et al 2008). However, for grassland ecosystems, the mean modeled estimates of net methane emissions during the growing season (230 mg CH₄ m⁻² d⁻¹) was higher than the observed rates from 73 to 166 mg CH₄ m⁻² d⁻¹ (Tsuyuzaki *et al* 2001). The mean modeled estimates of net methane consumption during the growing season $(0.6-1.4 \text{ mg CH}_4 \text{ m}^{-2} \text{ d}^{-1})$ was at the low end of the observed rates, from 0.3 to 5.3 mg CH₄ m⁻² d⁻¹ (Gal'chenko *et al* 2001), while the simulated annual consumption (0.12–0.27 g CH₄ m⁻² yr⁻¹)

was above the high end of the range of measurements (0.04–0.12 g CH_4 m⁻² yr⁻¹, Flessa *et al* 2008).

3.2. Temporal variations of CH₄ fluxes

The annual CH₄ fluxes over Northern Eurasia exhibited a significant interannual variability from 1971 to 2100 (figure 3). In all three sets of simulations, CH₄ emissions increased much more rapidly than consumption in both the historical period and the future. For CH₄ emissions, there were notable differences among the three sets of simulations during the historical period. The WET1 simulation gave an obviously higher flux of annual CH4 emissions (~29 Tg CH₄ yr⁻¹ during the 1990s) than the other two simulations (\sim 25 Tg CH₄ yr⁻¹ during the 1990s). From 1971 to 2100, the annual CH₄ emissions for all the three sets of simulations showed significant increasing trends at the rates of $0.056\pm0.027\,\mathrm{Tg}\,\mathrm{CH_4}\,\mathrm{yr^{-1}}$ for the WET1 simulations, $0.055\pm$ $0.025\,\mathrm{Tg}\,\mathrm{CH_4}\,\mathrm{yr^{-1}}$ for WET2, and $0.059\pm0.033\,\mathrm{Tg}\,\mathrm{CH_4}\,\mathrm{yr^{-1}}$ for WET3. For CH₄ consumption, the three sets of simulations gave similar results during the historical period, while the

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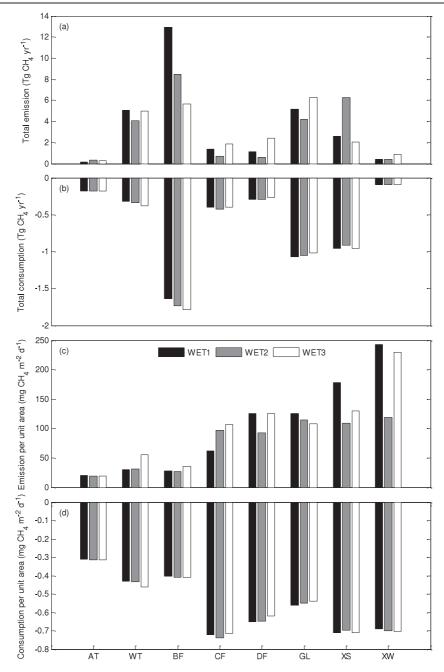


Figure 2. Methane emissions from different ecosystems in Northern Eurasia during the 1990s. Ecosystem types: alpine tundra (AT), wet tundra (WT), boreal forests (BF), temperate coniferous forests (CF), temperate deciduous forests (DF), grasslands (GL), xeric shrublands (XS), xeric woodlands (XW).

magnitudes grew increasingly different in the future under different climatic scenarios. The long-term increasing rate of annual CH_4 consumption for the three sets of simulations was $0.006 \pm 0.003~Tg~CH_4~yr^{-1}$.

Our simulations projected that the annual net CH₄ emissions will increase by 6–51% under various wetland extent datasets and future climate scenarios by the end of the 21st century in comparison with the present conditions. The annual net CH₄ emissions increased from 23 Tg CH₄ yr⁻¹ in the 1970s to 29 \pm 2.6 Tg CH₄ yr⁻¹ in the 2090s in the WET1 simulation, from 19 to 25 \pm 2.6 Tg CH₄ yr⁻¹ in WET2, and from 19 to 25 \pm 3.7 Tg CH₄ yr⁻¹ in WET3 (table 1). The averaged

25% increase of net methane emissions in this century in our multiple model simulations was within the same range as other studies. For example, Anisimov (2007) reported a 15–25% increase by the middle of this century, and an increase of 30% and more by 2080 for most fragile and methane 'rich' Arctic zone. After comparing estimated annual net CH₄ emissions from the three sets of simulations, we found the differences in CH₄ emissions between WE1 and WET2/WET3 simulations to be comparable with the differences we found between changing climate scenarios. Taking one standard error as the measure of uncertainty, the estimate uncertainty of CH₄ emissions from wetland extent (>2 Tg CH₄ yr⁻¹) was greater

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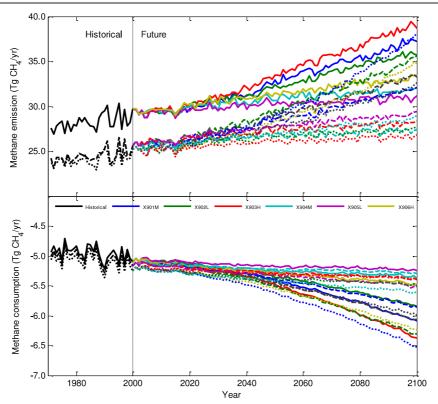


Figure 3. Interannual variations in annual methane emission (a) and consumption (b) over Northern Eurasia, using three wetland extent datasets (WET1—solid line; WET2—broken line; WET3—dotted line) and six climate change scenarios.

Table 1. Temporal variation in annual net emissions of CH_4 ($Tg CH_4 yr^{-1}$) (averaged for future climate scenarios) over Northern Eurasia using three wetland extent datasets.

	1970s	2000s	2030s	2060s	2090s
WET1	22.85	24.35 ± 0.08	25.59 ± 0.49	27.27 ± 1.64	28.84 ± 2.64
WET2	19.15	20.78 ± 0.11	21.97 ± 0.44	23.40 ± 1.41	24.99 ± 2.59
WET3	18.73	20.08 ± 0.12	21.19 ± 0.41	22.81 ± 1.64	25.08 ± 3.66

Table 2. Pearson correlations between annual methane emissions/consumption and environmental variables over Northern Eurasia in the historical period (1971–2000).

Variable	Soil temperature	Annual precipitation	Annual mean soil moisture	Water table depth	NPP
Consumption	0.89^{a}	0.53 ^a	-0.08	0.98^{a}	0.34
Emissions	0.79^{a}	0.45 ^b	0.06	0.80^{a}	0.50 ^a

^a P < 0.01. ^b P < 0.05.

than the uncertainty from climate scenarios except for the very end of the 21st century (table 1, figure 3).

The temporal dynamics of CH_4 fluxes showed substantial seasonal variation for the three sets of simulations, with weak fluxes in the winter and strong fluxes in the summer (figure 4). The monthly CH_4 emissions over the region were quite different in magnitude, particularly for peak fluxes (figure 4(a)), while monthly CH_4 consumption had only small differences (figure 4(b)). The monthly CH_4 emissions were one order of magnitude greater than that of CH_4 consumption. Net CH_4 emissions had a maximum monthly CH_4 source of 5.0 Tg CH_4 mon⁻¹ in July (averaged for all simulations). Summer (May, June and July) was responsible for two-thirds of the annual net CH_4 emissions.

3.3. Impact of environmental factors on CH₄ fluxes

To identify the key controls on CH_4 fluxes in Northern Eurasia, we examined correlations between environmental factors and CH_4 fluxes. Correlation analyses were performed between regional total CH_4 fluxes (emissions and consumption) and regional averaged environmental factors over all of Northern Eurasia. Our analysis indicated that increases in water table depth, soil temperature and labile carbon availability associated with climate change were the major factors that caused an increase in CH_4 emissions on an annual basis (table 2). Specifically, methane emissions were strongly correlated (N=30 years, P<0.01) with water table depth (r=0.80), soil temperature (r=0.79),

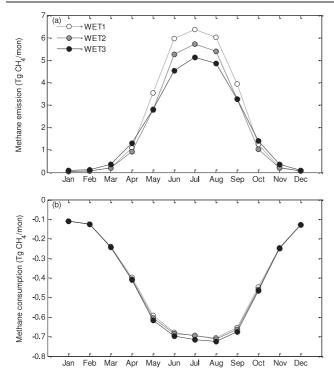


Figure 4. Seasonal dynamics of averaged monthly fluxes of CH₄ emission (a) and consumption (b) during the 1990s.

and NPP (r=0.50). The significant influences of soil temperature (figure 5(b)) and labile carbon availability (figure 5(e)) on methane emissions (figure 3(a)) were consistent with the conclusion that soil temperature and labile carbon availability were key factors in determining methanogenesis (e.g., Christensen *et al* 2003, Bellisario *et al* 1999).

For CH₄ consumption in Northern Eurasia, our analysis indicated that annual CH₄ consumption was strongly related to water table depth, soil temperature and precipitation (table 2). The lowering of the water table due to increases in soil temperature (figure 5(b)) and evapotranspiration resulted in an increase in CH₄ consumption (figure 3(b)). A negative trend in annual mean soil moisture (figure 5(c)) was noticeable, while precipitation tended to increase (figure 5(a)) over our projected study period, suggesting that any potential rise in the water table caused by additional precipitation was more than counteracted by the drop in the water table due to the increase in soil temperature. The correlation between water table depth and CH₄ consumption was consistent with field experiments (e.g., Nykänen et al 1998, Heikkinen et al 2002). The importance of soil temperature to the consumption rate was also consistent with the laboratory studies of Whalen and Reeburgh (1996) for soils with high CH₄ concentrations.

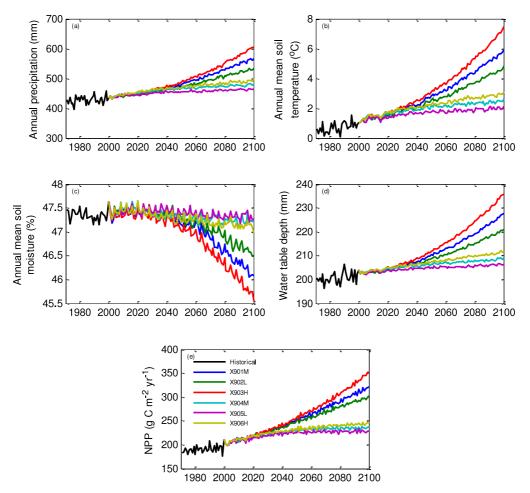


Figure 5. Interannual variations from 1971 to 2100 in (a) annual precipitation and simulated annual mean (b) soil temperature of the top 20 cm soil, (c) soil moisture of the top 20 cm soil, (d) water table depth and (e) net primary production (NPP).

4. Conclusions and future work

The CH₄ fluxes including emissions and consumption in Northern Eurasia were estimated with TEM for the period 1971–2100. Current net CH₄ emissions were estimated to be 20–24 Tg CH₄ yr⁻¹, and the magnitude is projected to increase by 6-51% under various wetland extent datasets and future climate scenarios by the end of the 21st century. Sources of CH₄ emissions were dominated by wetlands within boreal forests, grasslands and wet tundra areas in the region, and spatial patterns of emissions were determined by wetland extent. Water table depth and soil temperature were the two most important environmental controls on both CH₄ emissions and consumption in this region. Our uncertainty analyses indicated the uncertainty in wetland extent had a larger effect on future terrestrial CH₄ emissions than the uncertainty in future climate. This highlighted the importance of accurate wetland extent on modeling CH₄ dynamics at the regional scale.

One of the uncertainties in regional estimates of CH₄ arises from the uncertainty of the model parameterization derived from limited field measurements. Another source of uncertainty is the high variability of wetland extent data, which determines the magnitude of CH₄ fluxes. All three wetland extent datasets we used in the simulations represent the extraction of the global datasets, which are not aimed directly at Northern Eurasia, and do not consider specific conditions of wetlands distribution and diversity in the region, which means that they could seriously underestimate the real extent of wetland areas in the region (see Global Peatland Database www.imcg.net, Minayeva et al 2009, Vompersky et al 2005). A large part of wetlands may not be detected by satellite sensors, and more efforts are required to develop more accurate wetlands distribution data for the region. In addition, a number of additional factors should be considered in future analyses. One is consideration of the effects of the deep carbon substrate for methane production (Sirin et al 1998). Second, humaninduced disturbances can both inhibit (e.g., drainage) and enhance (e.g., ditching, damming) CH₄ fluxes from wetlands (Sirin and Laine 2008, Chistotin et al 2006, Glagolev et al 2008), but these effects were not considered in our study. Large areas of wetlands in Europe, central and western parts of European Russia, southern regions of West Siberia and some in the Far East have been disturbed by human activities. To improve future assessment of CH₄ dynamics in this region, research priorities should be directed at better characterizing the spatial distribution and natural diversity of wetlands in the region, associated with human- and climate-induced land use and land cover changes, as well as more detailed and precise descriptions of CH₄ cycling in these biogeochemically complex and spatially uneven ecosystems.

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