Global carbon exchange and methane emissions from natural wetlands: Application of a process-based model

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Abstract. Wetlands are one of the most important sources of atmospheric methane (CH_{4}) , but the strength of this source is still highly uncertain. To improve estimates of CH_4 emission at the regional and global scales and predict future variation requires a process-based model integrating the controls of climatic and edaphic factors and complex biological processes over CH_4 flux rates. This study used a methane emission model based on the hypothesis that plant primary production and soil organic matter decomposition act to control the supply of substrate needed by methanogens; the rate of substrate supply and environmental factors, in turn, control the rate of CH_4 production, and the balance between CH_4 production and methanotrophic oxidation determines the rate of CH_4 emission into the atmosphere. Coupled to data sets for climate, vegetation, soil, and wetland distribution, the model was used to calculate spatial and seasonal distributions of CH_4 emissions at a resolution of 1° latitude \times 1° longitude. The calculated net primary production (NPP) of wetlands ranged from 45 g C m⁻² yr⁻¹ for northern bogs to 820 g C m⁻² yr⁻¹ for tropical swamps. CH₄ emission rates from individual gridcells ranged from 0.0 to 661 mg CH₄ m⁻² d⁻¹, with a mean of 40 mg CH₄ $m^{-2} d^{-1}$ for northern wetland, 150 mg CH₄ $m^{-2} d^{-1}$ for temperate wetland, and 199 mg CH₄ m⁻² d⁻¹ for tropical wetland. Total CH₄ emission was 92 Tg yr⁻¹. Sensitivity analysis showed that the response of CH₄ emission to climate change depends upon the combined effects of soil carbon storage, rate of decomposition, soil moisture and activity of methanogens.

Introduction

The concentration of atmospheric CH₄ has increased during the last 200 years [*Pearman et al.*, 1986; *Steele et al.*, 1992], and accounts for approximately 15% of anthropogenic greenhouse effects [*Rodhe*, 1990]. Wetland is one of the most important terrestrial sources of CH₄ because of its anaerobic conditions, high organic matter content, and large area. It is currently estimated that wetlands account for 20% to 30% of the total annual emission of CH₄ to the atmosphere [*Intergovernmental Panel on Climate Change* (IPCC), 1990; *Fung et al.*, 1991]. Accurate quantification of this source strength and its spatial and seasonal variation across the globe must play an important role in predicting the trend in atmospheric CH₄ concentration and its impact on climate.

There have been several attempts to use measured rates of emission from wetlands to arrive at estimates for the global total CH_4 emission from wetlands. Early studies suggested that tropical wetlands were the main source of atmospheric CH_4 ; *Seiler and Conrad* [1987] reported that total emission was 47 Tg yr⁻¹, of which 38 Tg yr⁻¹ was released from

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tropical wetlands. However, field measurements in the 1980s revealed that northern tundra and peatlands also made a major contribution to the global source strength. Matthews and Fung [1987] generated a global distribution of wetlands from wetland vegetation types, pond soils, and land inundation data. Using this data set and CH₄ flux rates measured in the early 1980s, these authors estimated that the annual emission of CH₄ from natural wetlands was 111.1 Tg, and that northern wetlands contributed 60% of this total emission. Aselmann and Crutzen [1989] developed a different data set for wetland distribution and CH₄ flux rates. Their estimate of annual CH₄ emission was in the range 40 to 160 Tg. Bartlett and Harris [1993] recently reviewed the published measurements of CH₄ flux rates from wetlands globally, and using averaged CH₄ fluxes for various wetland types, they calculated the total CH₄ emission to be 109 Tg yr⁻¹. Considerable uncertainty exists in the estimates of CH_4 emissions at both the regional and global scales since, although there has been a large increase in the number of CH₄ flux rate measurements, their spatial coverage is still poor, and most of the measurements were made over less than 1 m^2 and over periods of only a few months. Few studies have records spanning more than 1 year, or a spatial scale of hundreds of square kilometers. It seems unlikely that the extrapolation of CH4 rates from point measurements to the regional or global scale can yield a reliable estimate of current CH_4 emissions. Moreover, climate change and modifications to hydrological conditions and vegetation patterns are occurring within wetlands [*Maxwell*, 1992; *Bliss* and Matveyeva, 1992], and there is a need to predict the resulting variations in CH_4 emissions. Existing methodologies are unable to address these concerns.

The rate of CH_4 emission is a reflection of the complex interaction between the processes of plant primary production, soil organic carbon decomposition, methanogenesis, and methanotrophic oxidation. Improvement in estimates of CH_4 emissions under different climatic regimes requires the development of a process-based model to link environmental factors and biological processes with CH_4 emission rates.

This study concerns the development of such a CH_4 emission model for natural wetlands, based on substrate supply by plant primary production and organic matter decomposition, regulation of methanogenesis by temperature and soil moisture, and the balance between CH_4 production and oxidation. The model was used to estimate spatial and seasonal variations in CH_4 emissions from natural wetlands at the global scale.

The Methane Emission Model

Emission of CH_4 is the final step in the mineralization of organic matter in anaerobic ecosystems and represents a part of the cycling of carbon within the plant-soil-atmosphere system. Plant primary production is the ultimate source of substrate for CH_4 production. A positive relationship

between CH_4 emission and plant primary production or net CO_2 exchange rates has been reported by *Whiting and Chanton* [1993] and by *Sass et al.* [1990]. Plant biomass entering the soil must first be depolymerized and fermented by a variety of microbial organisms into low molecular weight substances, which are then transformed to CH_4 by methanogens [*Jones et al.*, 1987]. The potential rate of CH_4 production is a function of the amount and decomposability of soil organic matter in the soil [*Svensson*, 1983; *Valentine et al.*, 1994], and a linear relationship between CH_4 production and readily decomposable carbon in the soil has also been reported [*Yagi and Minami*, 1990].

With a given supply of substrate, CH_4 production depends on the control over methanogenesis by environmental factors, such as temperature [Westermann, 1993; Dunfield et al., 1993] and soil moisture [Moore and Knowles, 1989]. The CH₄ produced passes through the oxic-anoxic boundary before entering the atmosphere. During that passage, it is subject to oxidation by methanotrophic bacteria, where 40% to 95% of the CH₄ produced may be consumed by methanotrophs in the soil [King et al., 1990; Pulliam, 1993]. Thus the rate of CH₄ production should be constrained by availability of substrate, arising from plant primary production and organic matter decomposition, and regulated by environmental factors. The balance between production and oxidation of CH4 determines the rate of emission into the atmosphere. The wetland methane emission model (WMEM) was developed using these hypotheses as a basis (Figure 1).



Figure 1. Schematic representation of the wetland methane emission model (WMEM). The bold lines represent mass (carbon and water) exchanges, while the fine lines represent interactions between different factors. Four carbon compartments are used in the model: carbon in living vegetation (VEGC), carbon in the soil (SOIC), decomposed carbon (DCPC), and carbon in the form of CH₄ (CH4C). The carbon flows between these compartments are represented by LITD (total carbon deposition into the soil arising from vegetation), SOMD (decomposition of organic carbon in the soil), MPR (methane production), MOR (methane oxidation), and MER (methane emission into the atmosphere). EPT is evapotranspiration.

The WMEM is a compartmental model in which four carbon compartments were used: carbon in living vegetation (VEGC), carbon in the soil (SOIC), decomposed carbon (DCPC), and carbon in the form of CH_4 (CH4C). The carbon fluxes between these pools were assumed to be controlled by the size of donor pools, by specific parameters related to characteristics of the pool involved, and by environmental factors, e.g., solar radiation, temperature, and soil moisture (see Figure 1). The rates of change of the size of each of these pools were calculated from

$$\frac{d\text{VEGC}}{\Delta t} = \text{GPP}_{t} - \text{RES}_{t} - \text{LITD}_{t}$$
(1)

$$\frac{d\text{SOIC}}{\Delta t} = \text{LITD}_{1} - \text{SOMD}_{1}$$
(2)

$$\frac{d\text{DCPC}}{\Delta t} = \text{SOMD}_{t} - \text{MPR}_{t} - \text{OCR}_{t}$$
(3)

$$\frac{dCH4C}{\Delta t} = MPR_{t} - MOR_{t}$$
 (4)

where GPP is gross primary production (g C m⁻² month⁻¹), RES is plant autotrophic respiration (g C m⁻² month⁻¹), LITD is the rate of carbon deposition into the soil arising from vegetation (g C m⁻² month⁻¹), both above and below ground, SOMD is the decomposition rate of organic carbon in the soil (g C m⁻² month⁻¹), MPR is the rate of CH₄ formation (g C m⁻² month⁻¹), OCR is the rate (g C m⁻² month⁻¹) at which carbon is released in the form of other gaseous carbon products, such as CO₂, and MOR is the CH₄ oxidation rate (g C m⁻² month⁻¹). The time step (Δt) over which calculations were performed was 1 month.

Net Primary Production and Organic Carbon Decomposition

Net primary production (GPP-RES), deposition of litter carbon into the soil (LITD), and organic carbon decomposition (SOMD) were calculated following the Terrestrial Ecosystem Model, which is described in detail by *Raich et al.* [1991] and *McGuire et al.* [1992]. In the case of inundated wetland, it was assumed that the soil is always saturated.

Methane Production

The suitability of the soil environment for methanogens affects the proportion of decomposed carbon transformed to CH_4 . Moore and Knowles [1989] reported that the molar ratio of CH_4 to CO_2 emissions from wetlands increases exponentially with water table height. Yavitt et al. [1987] and Tsutsuki and Ponnamperuma [1987] suggested that this ratio is also a function of temperature. Field observations have demonstrated that the hydrological regime is the

primary factor associated with the variation of CH_4 emissions [*Torn and Chapin*, 1993] because it defines the anaerobic conditions and low redox potentials which are essential for methanogenesis. *Dise* [1991] and *Torn and Chapin* [1993] found that water table position and temperature together could explain from 75% to 90% of the variability in CH_4 fluxes, and in the present model they were considered to be the major environmental factors regulating the production of CH_4 . Thus the rate of CH_4 production (MPR) was described by

$$MPR_{t} = SOMD_{t} P_{o} f(WTP) f(TEM)$$
(5)

where P_o is the proportion of the decomposed organic carbon transformed to CH₄ under optimal conditions of temperature and soil water status for methanogens and the functions f(WTP) and f(TEM) represent proportional CH₄ production factors for soil water table position (WTP) and temperature (TEM) under suboptimal conditions respectively.

Usually, 3-25% of decomposed organic carbon is transformed to CH₄ [*Moore and Knowles*, 1990; *Yavitt et al.* 1987], but this proportion can be as high as 40-60% in an ideal environment for methanogens. *Yavitt et al.* [1987] reported approximately equimolar production of CH₄ and CO₂ in anaerobic peatlands at high temperature (19°C). *Tsutsuki and Ponnamperuma* [1987] found that CH₄-C accounted for 0.41 to 0.52 of the total decomposed carbon (CH₄-C + CO₂-C), with a mean of 0.47, which was used as the value for P_0 in the present model.

 CH_4 flux increases logarithmically with increasing water table height [*Moore and Knowles*, 1989; *Christensen*, 1993], and this positive relationship may be maintained until a 10cm depth of water above the soil surface is reached [*Sebacher et al.*, 1986]. For inundated wetlands, we used an empirical relationship reported by *Roulet et al.* [1992]. The effect of water table position was modelled as a multiplier acting upon potential CH_4 production, with the maximum value of 1.0 when the water table was 10 cm or more above the soil surface, and a smaller value at lower water table positions:

$$f(SWP) = 0.383 \ e^{0.096SWP}$$
(6)

where SWP (cm) is water table position, relative to the soil surface. The method by which SWP was calculated for noninundated wetlands is shown in the appendix. In the calculations for the inundated wetlands, the soil was considered to be saturated, so that moisture had no effect on CH_4 production.

The observed effect of temperature, represented by a Q_{10} value (the rate of change in CH₄ flux due to a 10°C change in temperature), falls within a broad range, from 1.2 to 16 [Westermann, 1993; Dunfield et al., 1993]. This high degree of uncertainty may be caused by the influence of other factors for example, substrate availability for methanogens [Whiting and Chanton, 1993; Conrad et al., 1987], since temperature also influences plant growth and organic matter decomposition. Laboratory studies have shown that methanogenesis has a Q_{10} value of 1.2-3.5 [Conrad, 1989;

Kelly and Chynoweth, 1981]. By assuming a Q_{10} value of 2.0, which is generally used for biochemical processes, and 30°C as the optimal temperature for most methanogens [Dunfield et al., 1993; Neue and Scharpenseel, 1984], the influence of temperature, f(TEM), was represented by

$$f(\text{TEM}) = \frac{e^{0.0693\text{TEM}}}{7.996}$$
(7)

where TEM is the temperature (°C).

In the model, CH_4 was produced only during thaw/wet seasons, which were defined following *Fung et al.* [1991]. For a location that experiences temperature above freezing throughout the year, the wet season was considered to be the period over which monthly precipitation exceeded monthly potential evapotranspiration. The thaw season was assumed to begin when monthly mean temperature exceeded 5°C and to end when monthly mean temperature fell below 0°C.

Methane Oxidation and Emission

CH4 oxidation occurs above the water table and in the rhizosphere, where O_2 is likely to be available. It has been reported that from 55% to 85% of the CH₄ diffusing to the soil surface may be oxidized [Happell et al., 1993]. In plant-free paddylands, CH₄ oxidization may consume 65% of the CH₄ production [Holzapfel-Pschorn et al., 1986], and in the seedling stage of rice growth, when rhizospheric oxidation is not significant, the proportion of the CH₄ oxidized varied from 44% to 59% [Schütz et al., 1989]. The delivery of O_2 to the rhizosphere by plants may stimulate the oxidation of CH₄. Positive relationships between CH₄ oxidation and live root density have been reported [Gerard and Chanton, 1993; Smits et al., 1990]. The root O₂ supply and thus the oxidative power, should increase with plant growth [Albera, 1953]. Schütz et al. [1989] found that the proportion of CH₄ being oxidized increased from about 50% in the early stage to 95% in the late stage of rice growth. It seems therefore that rhizospheric CH₄ oxidation is correlated with plant physiological activity. In line with the above analysis, it was assumed that 60% of the CH₄ produced in the anoxic zone was oxidized at the soil-water surface, that oxidation in the rhizosphere increased with the rate of plant physiological activity, and that together they might consume up to 90% of the CH₄ produced. Thus, using gross primary production (GPP) to represent physiological activity, the rate of CH₄ oxidation (MOR) in inundated wetlands was calculated from

$$MOR_{t} = MPR_{t} \left[0.60 + 0.30 \frac{GPP_{t}}{GPP_{max}} \right]$$
(8)

where GPP_{max} is the maximum GPP occurring during any month.

When the wetland soil is not inundated, the process of oxidation becomes more complicated. There should be more oxidation of CH_4 , but the rate depends on the soil water content, water table position, O_2 and CH_4 diffusion within

the soil profile, and the pathways taken by CH_4 transport from the soil into the atmosphere [Whalen and Reeburgh, 1988; Chanton and Dacey, 1991]. The effect of any of these processes is uncertain, and in the present study it was assumed that 90% of CH_4 produced in any month was oxidized in noninundated wetlands [Fechner and Hemond, 1992].

Finally, the rate of CH_4 emission into the atmosphere (MER) was calculated as the difference between CH_4 production and oxidation:

$$MER_{t} = MPR_{t} - MOR_{t}$$
(9)

Application of the Model

Natural wetlands are distributed globally from polar to tropical regions, and exist in diverse climatic, vegetation, and soil types. Thus the important environmental characteristics determining the rate of CH_4 emission exhibit heterogeneity in both space and time. To assess rates of methane emission globally with the WMEM, it was necessary to develop a georeferenced database containing all of the independent variables needed to run the model. The database contained information on the location, area, soil, vegetation, and climate of global wetlands. This information was organized within a Geographical Information System (GIS) at a resolution of 0.5° latitude $\times 0.5^\circ$ longitude.

The International Institute of Applied System Analysis (IIASA) terrestrial climate data set [Leemans and Cramer, 1991] was used to provide information on temperature, precipitation, and cloudiness. The climatic data represent long-term monthly mean values at the 0.5° latitude $\times 0.5^{\circ}$ longitude spatial resolution. The global solar radiation and photosynthetically active radiation needed to calculate plant photosynthesis were estimated from the data on cloudiness following the method used by *Raich et al.* [1991].

The data on wetland location, area, and vegetation information were derived from Matthews and Fung [1987]. They defined natural wetlands by integrating the data of vegetation, soil, and land inundation. This resulted in a total global wetland area of 5.3 \times 10⁹ km², occupying 3233 1° latitude \times 1° longitude grid cells. In order to maintain the resolution of the climate data set, we extrapolated the wetland data to a resolution of half a degree. The area of wetlands calculated by Matthews and Fung [1987] was for inundated soils only, but moist/dry tundra is also believed to be an important source of atmospheric CH₄. The area of moist/dry tundra can be estimated by subtracting the area of wet tundra (unforested bogs, $0.884 \times 10^{12} \text{ m}^2$) from the global area of tundra, 7.34×10^{12} m² [Matthews, 1983]. The distribution of moist/dry tundra was considered to be associated proportionally with those of inundated wetlands. Soil data for wetlands were derived from the digitized Food and Agriculture Organization (FAO) map [Zobler, 1986]. The initial-state values for various vegetation types defined by Melillo et al. [1993] and McGuire et al. [1992] in their global ecosystem model were used in model calculations.

The WMEM was run for each of the wetland cells until a year-to-year equilibrium was reached. The equilibrium was considered to have been attained when the flux of net primary production, litter deposition, and organic matter decomposition differed annually by less than $1 \text{ g C m}^{-2} \text{ yr}^{-1}$.

In *Matthews and Fung's* [1987] wetland data set, wetlands were classified into five types: forested bog, nonforested bog, forested swamp, nonforested swamp, and alluvial formation. In the present study, three regional categories of wetlands were also used in the analysis of model results: northern, temperate, and tropical wetland. The northern wetland was defined to be north of 50°N, the temperate wetland was in the regions from 20°N to 50°N and to the south of 30°S, and the tropical wetland was between 20°N and 30°S.

Results and Discussion

Net Primary Productivity and Carbon Exchange

The annual NPP of wetlands calculated with the present model ranged from 0 to 1500 g C m⁻² yr⁻¹ (Plate 1). For the individual vegetation categories, the mean values varied from 45 g C m⁻² yr⁻¹ for arctic bogs to 820 g C m⁻² yr⁻¹ for tropical swamps. Generally, this spatial distribution of NPP was consistent with other estimates. Miller et al. [1983] reported that the NPP of various arctic ecosystems ranged from 19 to 450 g C m^{-2} yr⁻¹, and that the average value was 130 g C m⁻² yr⁻¹ for tundra and 226 g C m⁻² yr⁻¹ for boreal forests. Bartsch and Moore [1985] estimated that NPP was from 50 to 150 g C m⁻² yr⁻¹ in the subarctic region and from 100 to 200 g C m⁻² yr⁻¹ for boreal bogs. The global ecosystem model predicted a mean NPP of 120 g C m⁻² yr⁻¹ for wet/moist tundra, 173 g C m⁻² yr⁻¹ for boreal woodland, and 238 g C m⁻² yr⁻¹ for boreal forest [Melillo et al., 1993]. Various field studies have shown that the NPP of marshes and swamps in Northern American and Europe is in the range from 400 to 1000 g C m⁻² yr⁻¹ [McNaughton, 1966; Van der Valk and Bliss, 1971; Baradziej, 1974]. Melillo et al.'s [1993] results for temperate forests ranged from 335 to 741 g C m⁻² yr⁻¹. Few field data are available for the NPP of tropical wetland. Our results in this region were somewhat lower, but close to, the estimates of Warnant et al. [1994] for tropical woodlands and rain forests, which ranged from 711 to 925 g C m⁻² yr⁻¹.

The calculated NPP of temperate and tropical wetlands was balanced by the rate of soil organic carbon decomposition (SOMD), but the northern wetland showed an excess of NPP over SOMD, resulting in accumulation of soil organic carbon (Table 1). Rates of accumulation were in the range 5 to 60 g C m⁻² yr⁻¹, with a mean of 33 g C m⁻² yr⁻¹. This was in agreement with the results of *Miller et al.* [1983], who reported that from 10 to 40 g C m⁻² yr⁻¹ was accumulated in arctic tundra and boreal forests.

The proportion of SOMD transformed to CH_4 -C annually varied from 2.0% to 40.5% (Table 1), with a mean of 14.2% over all wetlands. Of the CH_4 produced, from 70% to 80% was oxidized to CO_2 by methanotrophs; the remainder was emitted into the atmosphere. The proportion

of NPP-C that was decomposed as CH₄ and released into the atmosphere was 2.3% in northern wetland, 4.2% in temperate wetland, and 4.8% in tropical wetland. These estimates are in line with the results of other studies: *Aselmann and Crutzen* [1989] calculated that the ratio of CH₄-C emission to NPP-C of wetlands was from 2% to 7%, and data from simultaneous carbon exchange and CH₄ emission measurement showed that this ratio was 5.5% [*Sebacher et al.*, 1986], 1.0-14.0% [*Moore and Knowles* 1990], or 2.3% [*Whiting and Chanton*, 1992]. *Pulliam* [1993] reported that 10% of the decomposed carbon was transformed to CH₄, of which 52% was oxidized and 48% emitted into the atmosphere.

Spatial Variation in CH₄ Flux

The spatial variation in CH₄ emission rates from inundated wetlands, calculated with the WMEM, is presented in Plate 1. The CH₄ fluxes within individual grid cells ranged from 0.0 to 118.8 g CH₄ m⁻² yr⁻¹. The mean rate estimates for the five wetland types ranged from 3.6 g CH₄ m⁻² yr⁻¹ for nonforested bogs to 38.2 g CH₄ m⁻² yr⁻¹ for forested swamps (Table 2). CH₄ fluxes varied widely, even within the same climatic-ecological zone and for a single wetland type. However, they generally increased from the arctic to the tropical region. The latitudinal distribution of CH₄ fluxes showed an increase from the north to south, but a decrease beyond 30°S. In terms of wetland type, swamps showed a much higher CH₄ emission rate than bogs; forested wetlands emitted more CH₄ than nonforested (Table 2).

The high variability in CH₄ emission rate is a reflection of the spatial heterogeneity in climate, vegetation, and soil, and their complex interactions. The distribution of CH₄ flux rate along the latitudinal axis was related to temperature, but more closely to NPP and SOMD (Figure 2). CH₄ emission rates were typically high in the tropics, where temperature, NPP, and SOMD are all high. In temperate wetland, NPP and SOMD were not necessarily lower than those in tropical wetland, but CH₄ emission rates were lower because of the lower temperature; 87% of bogs were located to the north of 50°N, while 83% of swamps were within the tropical zone. The mean temperature over the CH_4 production season in bogs was 9.7°C, while in swamps it was 23.8°C, and this temperature difference, through its effect on MPR, was largely responsible for the large difference in the calculated CH₄ emission rates between bogs and swamps. The NPP of forested bogs was almost the same as that of nonforested bogs, but the mean temperature and SOMD was higher, giving rise to increased CH₄ fluxes (Table 1). Similarly, the CH₄ emission rate from forested swamp was higher than that from nonforested because of the higher temperature, NPP, and SOMD

A comparison between the results calculated with WMEM and measured CH_4 emission rates reported in the literature is given in Table 3. In northern wetland, CH_4 emission rates calculated with the model were about 2-4 times lower than estimates generated from field measurements, but close to the results of field investigations performed at the regional scale (Table 3). In the Yukon-Kuskokwim Delta, Alaska



Plate 1. Net primary productivity and methane emission rates for natural wetlands calculated with the model.

Table 1. Mean Net Primary Productivity (NPP), Rate of Decomposition (SOMD), and Carbon Transformation in the Process of CH_4 Emission Calculated with the Wetland Methane Emission Model

Latitude	NPP g C m ⁻² y ⁻¹	SOMD g C m ⁻² y ⁻¹	RMED	RMEE
80-70°N	183	66	0.06	0.01
70-60°N	172	138	0.12	0.03
60-50°N	243	218	0.16	0.04
50-40°N	413	421	0.22	0.06
40-30°N	618	620	0.16	0.04
30-20°N	615	613	0.25	0.07
20-10°N	461	465	0.28	0.08
10-0°N	599	604	0.24	0.06
0-10°S	667	675	0.25	0.06
10-20°S	555	548	0.26	0.06
20-30°S	668	667	0.29	0.07
30-40°S	709	696	0.21	0.05
40-50°S	622	597	0.12	0.03

RMED is the proportion of the decomposed organic carbon being transformed into CH_4 in methaneogenesis. RMEE is the proportion of the NPP-C being released into the atmsophere as CH_4 .

(61°5'N, 162°92'W), Fan et al. [1992] measured regional CH₄ fluxes ranging from 25 to 30 mg CH₄ m⁻² d⁻¹, using eddy correlation techniques with both tower and aircraft. The mean CH₄ emission rate calculated with our model for gridcells at 61°N was 25.7 (9.5-85.8) mg CH₄ m⁻² d⁻¹. *Moore et al.* [1990] estimated CH₄ fluxes from a large area (130 km²) in Schefferville of Canada (54°N, 66°W). The CH₄ flux rates estimated for various wetland types ranged from 7.5 to 71.9 mg CH₄ m⁻² d⁻¹, and the average flux from the whole area was 56.3 mg CH₄ m⁻² d⁻¹. Our estimates for

gridcells at 54°N ranged from 27.4 to 134.7 mg CH₄ m⁻² d⁻¹, with a mean of 59.4 mg CH₄ m⁻² d⁻¹. The lower CH₄ emission rates obtained in this study, compared with "point" measurements, may arise because point measurements give the flux rates from specific sites at a scale of 1 m² or less, but those from the model represented the mean over 50-1500 km²; *Fan et al.* [1992] and *Bartlett et al.* [1992] showed that the CH₄ flux rate from enclosure measurements was higher than that from tower and aircraft measurements in the same area.

In temperate and tropical wetlands, our results were in the same range as reported in field measurements. However, the mean CH_4 emission rate from temperate wetland calculated with the model appeared higher than that suggested by field experiments. Using data from field campaigns, *Bartlett and Harriss* [1993] calculated that the average CH_4 flux from temperate swamps was lower than those from arctic tundra and boreal forest (Table 3). The temperature, NPP, and SOMD in temperate wetland are much higher than those in northern wetland, and the CH_4 emission rate would therefore be expected to be higher.

For moist/dry tundra, the calculated CH₄ emission rates varied from 0.0 to 55.0 mg CH₄ m⁻² d⁻¹. This was lower than that of the inundated wetlands at the same location by a factor of 5 to 10. The mean rates at various latitudes ranged from 1.0 mg CH₄ m⁻² d⁻¹ to 13.0 mg CH₄ m⁻² d⁻¹. The average CH₄ emission rate from all moist/dry tundra was 8.5 mg CH₄ m⁻² d⁻¹. This rate was in line with the results of most field measurements. A recent review of 14 field experiments by *Bartlett and Harriss* [1993] showed CH₄ fluxes from moist/dry tundra varied from 0.6 to 29 mg CH₄ m⁻² d⁻¹, with a mean of 7.0 mg CH₄ m⁻² d⁻¹.

Seasonal Variations in CH₄ Emission

Figure 3 illustrates the seasonal pattern in CH_4 emission rate for different wetlands. For northern wetland, CH_4 emissions in winter were insignificant, while those in

 Table 2. Methane Emission Rates of Various Wetland Types, Calculated Using the Wetland Methane

 Emission Model

	Rates of CH ₄ Emission, mg CH ₄ m ⁻² d ⁻¹						- m - 1
Latitude	Forested Bogs	Non forested Bogs	Forested Swamps	Non forested Swamps	Alluvials	Mean	Emission, Tg yr ⁻¹
80-70°N	18.0	12.2	6.9	0.0	0.0	12.1	0.3
70-60°N	35.7	22.4		29.6		31.6	10.8
60-50°N	57.3	30.6	87.8	103.5		51.2	10.7
50-40°N	90.8	35.8	177.5	164.4		120.5	7.4
40-30°N	168.2		126.4	125.5	122.5	143.5	3.2
30-20°N	119.4		242.5	318.7	334.5	235.1	3.6
20-10°N			239.7	170.8		1 9 2.7	8.2
10-0°N	206.6	161.2	203.9	150.4	195.7	182.1	10.2
0-10°S	205.5		205.9	152.3	200.9	198.5	14.2
10-20°S			221.3	164.5	154.5	184.3	8.2
20-30°S			206.3	318.3		249.8	10.8
30-40°S			145.1	213.3		180.5	3.1
40-50°S			89.1			89.1	0.1



Figure 2. Latitudinal distributions of temperature (°C), net primary productivity (NPP, g C m² yr⁻¹), and methane emission (10⁻¹ g CH₄ m⁻² yr⁻¹). The temperature shown is the mean temperature in the methane production season.

summer averaged from 40 to 60 mg CH₄ m⁻² d⁻¹. In temperate wetland, CH₄ emission rates in summer ranged from 100 to 400 mg CH₄ m⁻² d⁻¹, while in the other seasons the rate varied from 20 to 150 mg CH₄ m⁻² d⁻¹. These seasonal variations were closely correlated with changes in

temperature, NPP, and SOMD. Tropical wetland showed a different seasonal pattern in CH_4 emission. Because CH_4 production ceased during the dry season, the shift between dry and wet seasons played an important role in determining the seasonal variation in CH_4 fluxes. To the north of the

	CH ₄ Emission Rates From Field Measurements, mg CH ₄ m ⁻² d ⁻¹		Calculated CH ₄ Emission Rates with the Present Model, mg CH ₄ m ⁻² d ⁻¹	
	Range	Mean ^a	Range	Mean
Northern wetland				39.7
Wet tundra	20-150 ^b (25-85) ^d	96	6.4-50.6	
Boreal	30-200° (19-50) ^d	87	12.1-132.6	
Temperate wetland				149.6
Bogs	20-300°	135	50.6-278.2	
Forested swamps	10-250 ^f	75	35.4-301.4	
Nonforested swamps	5-150 ^g	70	12.3-286.1	
Tropical wetland				199.0
Forested swamps	75-350 ^h	165	127.9-360.3	
Nonforested swamps	30-390 ^h	233	120.3-474.7	

Table 3. A Comparison Between the Calculated CH₄ Emission Rates With the Model and Values Reported in the Literature, Derived From Field Measurements

* Bartlett and Harriss [1993]

^b Sebacher et al. 1986; Whalen and Reeburgh [1990], Bartlett et al. [1992], and Morrissey and Livingston; [1992].

^c Crill et al. [1988]; Vitt et al. [1990]; and Moore and Knowles 1989).

^d rates obtained at regional scale [Bartlett et al., 1992; Fan et al., 1992; Whalen and Reeburgh, 1992; Christensen, 1993].

^c Yavitt et al. [1990]; Routlet et al. [1992a]; and Harriss et al. [1985].

^t Harriss and Sebacher [1981], and Wilson et al. [1989].

⁸ Barber et al. [1988], Burke et al. [1988]; Harriss et al. [1988].

^h Bartlett et al. [1990], Devol et al. [1988, 1990]; Tathy et al. [1992], Keller [1990].



🗕 Northern 🚽 Temperate 📥 Tropical

Figure 3. Seasonal variations in methane emission rates (mg CH_4 m⁻² d⁻¹) in the northern, temperate, and tropical wetland.

equator, the rainy season was generally from May to October, when the mean CH₄ flux rates ranged from 150.0 to 300.0 mg CH₄ m⁻² d⁻¹, but in dry months, CH₄ flux rates were 50-120 mg CH₄ m⁻² d⁻¹. The highest CH₄ flux rates occurred in May or June. To the south of the equator, the high temperature and rainy seasons occur between October and March. Accordingly, high CH₄ emission rates, of 150-300 mg CH₄ m⁻² d⁻¹, appeared in these seasons. In contrast, the average CH₄ flux rate in other seasons was only 10-100 mg CH₄ m⁻² d⁻¹.

Field experiments have also shown a significant seasonal variation in CH_4 flux rates. Whalen and Reeburgh [1992] reported that CH_4 flux rates increased by 4 orders of magnitude from winter to midsummer in their 4-year observations in tundra. In northern and temperate wetland, seasonal variation was found to be driven largely by temperature [Bartlett et al., 1992], soil moisture [Moore et al., 1994; Roulet et al., 1992], or both [Moore and Knowles,

1990; Christensen, 1993], while in tropical wetland, it may arise from the transition between wet and dry seasons. In the Amazon floodplain, Devol et al. [1990] observed that the average CH_4 flux during the period of low water level was about one third of that for the period of high water levels.

Total CH₄ Emission Into the Atmosphere

Globally, total CH₄ emission from natural wetlands was estimated to be 92 Tg yr⁻¹, of which inundated wetland and moist/dry tundra emitted 85 Tg and 7 Tg, respectively. The latitudinal distribution of fluxes from the various wetland types is presented in Figure 4. The large fluctuations in CH_4 emission shown in this figure represent the combined variations in flux and wetland area along the latitude axis. High peaks appeared in both northern and tropical wetlands. In northern wetland, CH₄ flux rates were low, but the area of wetland was large. The inundated wetland covers 2.7 \times 10^{12} m², accounting for 53% of the total area globally, and there is $6.46 \times 10^{12} \text{ m}^2$ moist/dry tundra. Northern wetland emitted 16.7 Tg yr⁻¹, and moist/dry tundra emitted 6.6 Tg yr¹; together they contributed 25% to the global emission. The mean CH₄ flux rate from temperate wetland was much higher than that of the northern wetland, but the area, 5.8 \times 10^{11} m², is smaller. Its total emission was 17.2 Tg yr⁻¹. The CH₄ emission from tropical wetland was 51.4 Tg yr⁻¹, accounting for 56% of the global emission. Although the area of tropical wetland was less than that of northern wetland, the mean CH_4 flux rate was much higher. CH_4 emissions from different wetland types are shown in Table 3.

The calculated total CH₄ emission from moist/dry tundra was close to the estimates of from 4.0 Tg yr⁻¹ to 4.8 Tg yr⁻¹ [*Bartlett and Harriss*, 1993; *Bartlett et al.*, 1992; *Fung et al.*, 1991], but it is much smaller than the result of



Figure 4. Latitudinal distribution of total annual methane emissions from various wetland types, predicted with the WMEM.



Figure 5. Seasonal variation in methane emission from wetlands predicted with the WMEM.

Christensen [1993], 12.1-22.9 Tg yr⁻¹. According to his field measurements, Christensen assumed the mean CH_4 flux was 25 mg CH_4 m⁻² d⁻¹, which is twice the rate used in this study. However, more recently, Christensen et al. [1995]

have measured CH_4 fluxes in Siberia and the European Arctic to discover that fluxes there are considerably less than those in Alaska. The Alaskan values have previously been assumed to apply throughout the northern hemisphere, and so overestimates of the total flux are to be expected.

Seasonal variation in total CH_4 emission is illustrated in Figure 5. The global emission of CH_4 in July (12 Tg) was about twice as large as in January or December. In northern wetland, CH_4 emissions in summer (June-August) accounted for more than 70% of the annual emission, while almost no CH_4 was released in winter. In temperate wetland, summer emission still dominated (47%), but there was some CH_4 emitted in winter (12%). In tropical wetland, most CH_4 was emitted during the wet season; only 28% of the CH_4 was released in the dry season.

Our results are compared with other estimates of the global CH_4 emission in Figure 6. Matthews and Fung [1987] used the limited database of CH_4 fluxes then available for northern wetland to estimate global emissions. The CH_4 flux rate used for bogs was about 2 times higher than for swamps and 7 times higher than for alluvial formations.



Figure 6. Comparisons between the CH₄ emissions calculated with the WMEM and published estimates: (a) total CH₄ emissions (Tg yr⁻¹), (b) mean CH₄ emission rates (mg CH₄ m⁻² d⁻¹).

Consequently, northern wetland was estimated to contribute as much as 58.6% of the total CH_4 emission, while the tropical wetland only contributed 28.4%. It seems that the role of northern wetland was overestimated. Aselmann and Crutzen [1989] classified wetlands into bog, fen, swamp, marsh, floodplain, and shallow lake, and gave each of them a CH₄ flux rate and an active CH₄ producing period. As the flux rates given to swamps, marshes, and floodplains were higher and the periods of CH_4 production were longer, they estimated that tropical wetland accounted for 55% of the total CH₄ emission, while the northern and temperate wetlands contributed 31% and 14%, respectively. By reviewing recent field measurements of CH₄ emission rates, Bartlett and Harriss [1993] defined CH₄ flux rates for various wetland types in different regions, and calculated that northern, temperate, and tropical wetlands contributed 28.9%, 8.5%, and 62.6%, respectively, to the total global CH_4 emission. The total CH_4 emission estimated using the WMEM was within the range of existing estimates, and the contributions of the three latitudinal regions were quite similar to the results of Aselmann and Crutzen [1989] and Bartlett and Harriss [1993], although the estimate for temperate wetland appeared somewhat high.

Sensitivity Analysis

Sensitivity to Model Parameters

Temperature and the position of the soil water table are important factors modulating CH_4 production, but the reported quantitative relationships vary between different studies and are rather uncertain. Therefore the consequences of using different relationships in the model were studied.

In the present model, a Q_{10} value of 2 was used to define the direct influence of temperature on methanogenesis, but it may range from 1.2 to 3.5 [Conrad et al., 1987; Kelly and Chynoweth, 1981]. Thus different temperature relationships with Q_{10} values of 1.5, 2.5, and 3.0 (Figure 7a) were used in the model to show the effect on CH₄ emissions. Compared to the results presented above, a Q_{10} value of 1.5 gave an increase in the rate of CH₄ emission, while values of 2.5 and 3.0 led to a reduction. The scale of the changes was large in northern and temperate wetlands (30% to 100%), and small in tropical wetland (10-30%) (Figure 7b). As Figure 7a shows, the larger the Q_{10} value, the larger the reduction in CH4 production rate with decreasing temperature; the lower the temperature, the larger the difference between CH₄ production rates with different Q_{10} values. The estimate of total CH₄ emission from inundated wetlands with a Q_{10} of 1.5 was 108.4 Tg yr⁻¹, while those with Q_{10} of 2.5 and 3.0 were 73 Tg yr⁻¹ and 65 Tg yr⁻¹, respectively. Thus using different (reasonable) temperature relationships for methanogenesis might cause variations in the resulting total CH_4 emission of from -24% to 27%.

Various relationships between water table position and CH_4 emission have been reported [Vourlitis et al., 1993; Moore and Knowles, 1989]. Linear and exponential functions (Figure 8) were tested in the model to calculate CH_4 emissions from moist/dry tundra, where the effects of soil



Figure 7. Sensitivity analysis. (a) The relationships between temperature and the rate of methanogenesis with different Q_{10} values. The relationship with $Q_{10} = 2.0$ was used in the present model. (b) The change in CH₄ emissions with different temperature relationships, relative to the results of the present model.

water table position on CH_4 production were considered. The linear relationship was obtained by assuming that the proportional CH_4 production factor is 0.0 when the water table position is 30 cm below soil surface and increased linearly with the increase in soil water table height to 10 cm above the soil surface. The exponential relationship was derived from the data of *Moore and Knowles* [1989]. The calculated CH_4 emissions with these two relationships were higher by 9.5% and 20.7%, respectively, than the estimates predicted by the present model.

Response to Changes in Climatic Conditions

General circulation model (GCM) projections indicate that, with a doubling of the current concentration of atmospheric CO₂, an average annual global warming of from 1.9 to 5.2° C [Lashof and Ahuja, 1990] and a global annual precipitation increase of 15% may occur [Boer et al., 1990]. The temperature and precipitation change not only affects methanogenesis directly, but also the equilibrium of carbon exchange in wetland ecosystems. The analysis described



Figure 8. The three relationships between soil water table position and methanogenesis used in the sensitivity analysis.

below was performed to test the sensitivity of the model, and it is not intended that the results be interpreted as a realistic prediction of future trends.

For inundated wetlands, the sensitivity to temperature increase across the range from 1°C to 4°C was studied based on the assumption that soil water conditions remained unchanged (Figure 9). In northern wetland, mean NPP, soil carbon storage (SOMC), SOMD, and annual CH₄ emission rates (YMER) all increased. In temperate wetland, the positive effect on NPP, SOMD, and YMER remained, although the increase was smaller than that in northern wetland, and a negative effect on SOMC was observed. This was due to a larger increase in the rate of decomposition relative to the rate of carbon input into the soil from vegetation. In tropical wetland, CH₄ emission was still enhanced, but SOMC, NPP, and SOMD declined with increased temperature. The decrease in NPP was caused by an excess of plant respiration over the rate of photosynthesis. The low rate of increase in carbon input into the soil compared with the increase in the rate of decomposition resulted in a decrease of soil carbon storage, which in turn, reduced the rate of decomposition. It was no surprise that northern wetland showed a larger and more positive response to temperature increase. Increased temperature would improve conditions for plant growth and microbial activity and so enhance the rate of carbon exchange and CH4 emission. In the case of a 2°C increase, the CH₄ emission rate was increased by 36% for northern wetland, 29% for temperate wetland, and 12% for tropical wetland. The total CH4 emission from all inundated wetlands could be increased by 19%.

For moist/dry tundra, the responses both to temperature and precipitation changes were studied. When temperature was increased by between 1°C and 5°C, both NPP and SOMD were enhanced; soil carbon storage and methane emission were increased with the 1°C and 2°C temperature increases but decreased with a greater temperature increase (Figure 10). Temperature increase can, on one hand, stimulate CH₄ production by increasing carbon substrate supply and the activity of methanogens but, on the other hand, may attenuate CH₄ production by lowering the soil water table as a result of increased evapotranspiration. The balance between these effects determines the change in CH₄ emission. At constant temperature, increasing precipitation of between 5% and 15% caused increases in SOMC, NPP, SOMD, and YMER. For example, when precipitation was increased by 10%, SOMC was increased by 6.8%, NPP and SOMD were increased by 5.8% and 11.8%, respectively, and YMER was enhanced by 35%.



Figure 9. Changes in net primary productivity (NPP), soil organic carbon decomposition (SOMD), soil organic carbon storage (SOMC), and yearly methane emission (YMER) in inundated wetlands arising from temperature increase (°C), relative to the values obtained under current conditions.



Figure 10. Changes in net primary productivity (NPP), soil organic carbon decomposition (SOMD), soil organic carbon storage (SOMC), and yearly methane emission (YMER) of moist/dry tundra arising from increased temperature (°C), relative to the values obtained under current conditions.

Conclusion and Discussion

The present study represents the first published attempt to develop and use a process-based model to estimate spatial and seasonal variations in CH_4 emissions from natural wetlands at the global scale. The CH_4 emission rates calculated using the model for various wetland types were in the same range as those suggested by field measurements reported in the literature. The total CH_4 emission, 92 Tg yr⁻¹, is in the middle of the existing range of estimates: higher than the results of *Aselmann and Crutzen* [1989], but lower than others [*Matthews and Fung*, 1987; *Bartlett et al.*, 1990; *Fung et al.*, 1991; *Bartlett and Harriss*, 1993]. Sensitivity analysis showed that the response of CH_4 emission to climate change depends upon the combined effects of soil carbon storage, rate of decomposition, soil moisture, and activity of methanogens.

The present model still contains some uncertainties. It is clear that the model is sensitive to the values of the parameters describing the response of CH_4 production rate to water table position and temperature. However, the relationships between CH_4 production and soil water table position and temperature reported in the literature vary widely and are uncertain [Svensson and Rosswall, 1984; Sebacher et al., 1985]. Even if these parameter values could be determined reliably, the scale at which the model must operate imposes the need for a "smoothing" of the true spatial and temporal heterogeneity in soil moisture and temperature values.

The model's treatment of CH_4 oxidation provides an example of an aspect of the carbon flux that is poorly understood. The availability of O_2 in the soil may be a chief factor controlling the oxidation rate. It is related to soil moisture, O_2 diffusion through the soil-water body or plant aerenchymous system, and competition for O_2 by other processes [King et al., 1990; Gerard and Chanton, 1993]. Plants may enhance CH_4 oxidation by providing O_2 to methanotrophs associated with the rhizosphere, but the

arenchymous system of plants can also serve as an effective pathway for the transport of CH_4 from the soil to the atmosphere. Thus the presence of plants may also reduce the exposure of CH_4 to potential oxidation [Whalen and Reeburgh, 1988]. In addition, environmental factors, such as temperature and pH, also influence CH_4 oxidation [Dunfield et al., 1993], but these processes and relationships are also poorly understood. Hence the treatment of this important process within the current model is entirely empirical and rather crude.

Further improvements to the model depend on an improvement in the understanding of important processes and relationships involved. For progress to be made in this area, the focus of field studies should move away from flux measurement per se, toward investigation of the mechanistic processes and quantitative relationships concerning the impact of environmental factors on CH₄ production and oxidation in soil. Methanotrophic oxidation especially warrants further research. Since oxidation consumes much of the CH₄ produced, it is probably a major determinant of the magnitude of CH_4 emissions into the atmosphere. The results of the present study were compared with estimates based on measurements made over a small spatial scale. Further validation with more data at the regional scale would allow development of the model and a more reliable parameterization.

As with any model, the result of the WMEM depends on the quality of the data used to drive it. The spatial resolution of soil, vegetation, and wetland, and the temporal resolution of the climate were limiting factors. Data on the seasonal variation in wetland area and soil water table position with fine spatial resolution are not currently available, but these are important factors in determining CH₄ emissions. While the development of a more detailed database for soil, vegetation, and climate is in progress, remote-sensing imagery may also provide useful information on vegetation phenology, seasonal variations in soil temperature and moisture, river water level, and wetland area. When the present model is coupled to these databases, its ability to simulate and interpret the global patterns of CH₄ emissions should be greatly enhanced. Nevertheless, the "realistic" results obtained from the model demonstrate the ability to simulate CH₄ emissions within the framework of climatevegetation-soil interactions at the global scale. This represents a major step forward in the quantification of CH₄ emission from global wetlands, and when linked with scenarios of climate and land utilization change, the model will provide a basis for prediction of future CH_4 emissions.

Appendix Calculation of Soil Moisture and Water Table Position for Dry/Moist Tundra

Monthly variations in soil moisture and water table position in the moist/dry tundra were simulated with a simple one-dimensional (vertical) model as follows.

For the moist/dry tundra, water inputs would be simply precipitation and snowmelt. According to *Aber and Federer* [1992], a constant fraction of precipitation (IFRA) was considered to be intercepted and evaporated before entering into the soil (12%). The remaining precipitation was divided between snow and rain. The partition was calculated as

SNFC = 0.0 TEM₁
$$\ge$$
 5°C
SNFC = $\left(\frac{\text{TEM}_{1} - 2}{-7}\right)$ 2°C < TEM₁ < 5°C (10)
SNFC = 1.0 TEM < 2°C

where SNFC is the fraction of the precipitation (PRCP, cm) as snow. TEM is monthly mean temperature (°C).

Snowmelt (SNME) (cm) was given as

SNME =
$$4.5$$
TEM, TEM, > 1° C (11)

Total water input into the soil was

WATI = PRCP
$$(1 - IFRA - SNFC) + SNME$$
 (12)

In *Frolking and Crill's* [1994] model, soil water evapotranspiration (AEP) was given as

$$AEP = PE \qquad Z_w < Z_f$$

$$AEP = \left[\frac{PE(Z_w - Z_m)}{Z_f - Z_m}\right] \qquad Z_w \ge Z_f$$
(13)

where PE is the potential evapotranspiration calculated with the *Thornthwaite* [1948] equation. Z_w is water table depth, Z_y is the water table depth at which evaporation begins to fall from PE (8 cm), and Z_m is the maximum water table depth (30 cm). For temperatures below zero, AE was set to zero. Water was allowed to pool over the soil surface to 10 cm, and any water input above this maximum pool was assumed to be lost as runoff (RUNF).

The change of soil water content (SWC) (cm) was

$$\frac{dSWC}{dt} = WATI - AE - RUNF$$
(14)

On the basis of *Frolking and Crill's* [1994] study in northern wetlands, the soil moisture (relative to the saturation content) above water table (unsaturated zone) was calculated as

$$SW(Z) = a + bZ \tag{15}$$

where Z is the depth within the soil profile (cm). Below the water table SW is 1.0. Following *Frolking and Crill* [1994], the parameters a and b were taken as 0.05 and 0.022, respectively. The total water content of the soil profile to depth Z_m would then be

$$W_t = \int_0^{Z_m} \text{SAT SW}(Z) \ dZ \tag{16}$$

where SAT is the volumetric water content at the saturation point. Equation (16) can be integrated and inverted to give a quadratic function for the water table depth as a function of total water content, SWC. After the water balance for each time step was solved, the water table depth was calculated from this quadratic equation, and the water content of the unsaturated zone was determined from (16).

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