A process-based, climate-sensitive model to derive methane emissions from natural wetlands: Application to five wetland sites, sensitivity to model parameters, and climate

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Abstract. Methane emissions from natural wetlands constitute the largest methane source at present and depend highly on the climate. In order to investigate the response of methane emissions from natural wetlands to climate variations, a one-dimensional process-based climate-sensitive model to derive methane emissions from natural wetlands is developed. In the model the processes leading to methane emission are simulated within a one-dimensional soil column and the three different transport mechanisms, diffusion, plant-mediated transport, and ebullition, are modeled explicitly. The model forcing consists of daily values of soil temperature, water table, and net primary productivity, and at permafrost sites the thaw depth is included. The methane model is tested using observational data obtained at five wetland sites located in North America, Europe, and Central America, representing a large variety of environmental conditions. It can be shown that in most cases seasonal variations in methane emissions can be explained by the combined effect of changes in soil temperature and the position of the water table. Our results also show that a process-based approach is needed because there is no simple relationship between these controlling factors and methane emissions that applies to a variety of wetland sites. The sensitivity of the model to the choice of key model parameters is tested and further sensitivity tests are performed to demonstrate how methane emissions from wetlands respond to longer-term climate variations.

1. Introduction

Methane is one of the important greenhouse gases, contributing about 22% to the greenhouse effect at present [*Lelieveld et al.*, 1998]. Its atmospheric concentration has increased by a factor of 2.5 since the onset of industrialization and is now 1720 ppbv. Since methane has a large radiative effect, one unit mass of CH_4 has 21 times the radiative effect of one unit mass of CO_2, changes in the atmospheric methane concentration affect the temperature on Earth [*Houghton*, 1996]. Natural wetlands are the largest methane source at present, contributing about 40% to the total methane emissions and form a significant nonanthropogenic methane source [*Hein et al.*, 1997]. Furthermore, unlike most other methane sources, methane emissions from natural wetlands depend highly on the climate being influenced by temperature as well as by wetness.

The emission of methane from natural wetlands is a result of biological and physical processes taking place in the soil: methane production by methanogenic bacteria under anaerobic conditions,

methane oxidation by methanotrophic bacteria under aerobic conditions, and transport of methane to the atmosphere [e.g. *Conrad*, 1989]. Numerous studies have been carried out to investigate which factors control these processes. It has been shown that the most dominant determinants are the following.

1. The position of the water table because it determines the extent of the anoxic soil zone, where methane is produced, and the oxic soil zone, where methane is oxidized [e.g. *Bartlett and Harriss*, 1993; *Bubier et al.*, 1995; *Dise et al.*, 1993; *Fowler et al.*, 1995; *Funk et al.*, 1994; *Moore and Roulet*, 1993; *Morrissey and Livingston*, 1992; *Sebacher et al.*, 1986].

2. The soil temperature, since it influences the rates at which microbiological processes such as degradation of organic matter (i.e., the production of substrate for methanogenesis), methane production, and methane oxidation occur [e.g. *Baker-Blocker et al.*, 1977; *Bartlett and Harriss*, 1993; *Bubier et al.*, 1995; *Christensen et al.*, 1995; *Crill et al.*, 1988; *Dise et al.*, 1993; *Fowler et al.*, 1995; *Frolking and Crill*, 1994; *Kettunen and Kaitala*, 1996; *Morrissey and Livingston*, 1992; *Whalen and Reeburgh*, 1992].

3. The availability and quality of suitable substrate for methane production. Several authors observed a correlation between factors indicating substrate availability, such as the net primary productivity (NPP), the net ecosystem production (NEP), or the amount of biomass and methane production. Others observed enhanced methane emission after addition of substrate to the soil or from sites with a higher substrate quality [e.g. *Bridgham and*

Richardson, 1992; *Klinger et al.*, 1994; *Morrissey and Livingston*, 1992; *Valentine et al.*, 1994; *Whiting et al.*, 1991; *Whiting and Chanton*, 1992; *Whiting and Chanton*, 1993].

4. The pathways by which methane is transported to the atmosphere can be crucial for determining the fraction of produced methane that is emitted into the atmosphere. Transport can proceed by molecular diffusion, ebullition, and transport through the stems of vascular plants [*Conrad*, 1989]. Depending on the prevailing soil conditions, the occurrence of one or more of those mechanisms can significantly alter the amount of emitted methane: Ebullition can bring methane much faster to the water table than diffusion and thus increase methane emission [*Bartlett et al.*, 1990; *Boon and Sorrell*, 1995; *Devol et al.*, 1990; *Wassmann et al.*, 1992]. Plant-mediated transport can enhance methane emission through bypassing the often existing oxic top soil layer and thereby avoiding methane oxidation there [*Bartlett et al.*, 1992; *Boon and Sorrell*, 1995; *Bubier et al.*, 1995; *Chanton et al.*, 1992a; *Chanton and Dacey*, 1991; *Dacey and Klug*, 1979; *Happell et al.*, 1993; *Holzapfel-Pschorn et al.*, 1986; *Morrissey and Livingston*, 1992; *Schimel*, 1995; *Shannon et al.*, 1996; *Shannon and White*, 1994; *Torn and Chapin III*, 1993; *Waddington et al.*, 1996; *Whiting and Chanton*, 1992; *Yavitt and Knapp*, 1995]. However, atmospheric oxygen can be conducted by vascular plants down to the rooting zone. Therefore, in water saturated soils covered by vascular plants, a small oxic zone establishes around the root tips leading to methane consumption there [*Gerard and Chanton*, 1993; *Holzapfel-Pschorn et al.*, 1986; *Schipper and Reddy*, 1996; *Schütz et al.*, 1989].

These controlling factors are not independent of each other; for example, higher temperatures can lead to lower water table levels due to enhanced evapotranspiration. Thus higher temperatures will lead only to higher methane emissions, if the soil stays water saturated. For example *Roulet et al.* [1992] found that temperature explained the variances in methane emissions as long as the soil was water saturated, but as soon as the water table decreased below the soil surface, methane emissions were determined by the position of the water table. *Valentine et al.* [1994] observed that the temperature dependence of methane production increased with increasing amount and quality of substrate at sites that were substrate limited. Hence the controlling factors are not independent of each other, and their relative importance depends on the conditions present in the wetland. Therefore different factors are determining at different times and sites. Thus the results of these studies are site-specific and depend on the situations prevailing during the measurements.

Some of the authors cited above have also developed simple models to predict methane emissions from a wetland site. These models are based on observed empirical relationships between the factors controlling methane emissions and methane fluxes and, as discussed above, are not capable of simulating methane emissions from other wetland sites and under conditions different from those on which the models are based. Besides the model described and used in this article, there are two models in the literature using a more process-based approach, one by *Cao et al.* [1996] and one by *Potter* [1997]. *Cao et al.* [1996] simulate the carbon dynamics in the soil and derive the methane production rate as a function of the amount of decomposed organic carbon, the position of the water table, and the temperature. Methane emission rates are calculated as the difference between methane production and oxidation rates. The model is applied on the global scale, but it has not

been tested against data from any wetland site. The model by *Potter* [1997] is based on an ecosystem cycling model and simulates methane production rates from a microbial production ratio of CO_2-to-CH_4 that changes as a function of the water table depth. The three different transport mechanisms are modeled as simple functions of methane production, water table, and ecosystem type. However, the model when tested against data from one field site does not reproduce observations very well.

The objective of the present work is to provide a model that can be applied to simulating methane emissions from different wetland types in various regions as a function of the prevailing climate. The idea is to have a tool that can be used to study climate-dependent variations of methane emissions from natural wetlands on a larger scale (e.g., global scale) as it has already been done to investigate interannual variations of methane emissions from natural wetlands under present-day climatic conditions [*Walter*, 1998]. Therefore the model used here is a more process-based, climate-sensitive model than others. In the remainder of this paper we give an extended description of a slightly modified version of the methane emission model briefly described by *Walter et al.* [1996] and show the results of tests of the model against data from five different test sites located in North America, Europe, and Central America, representing a large variety of environmental conditions. In addition, we present the results of sensitivity studies of the model and demonstrate how methane emissions from natural wetlands might change under possible climatic conditions in the future.

2. Model Description

Since the processes leading to methane emission from wetlands occur in the soil, the following model structure is chosen (Figure 1): A one-dimensional soil column is divided into 1 cm thick parallel layers. The position of the water table is assumed to be the boundary between the anoxic and the oxic soil zone. Methane is produced in the layers below the water table. The methane production rate is calculated as a function of the soil temperature and the NPP, which is assumed to be a measure for substrate availability. In the layers above the water table, methane is consumed. The methane oxidation rate is calculated using the Michaelis-Menten equation. Oxidation is also a function of the soil temperature. Three different transport mechanisms are modeled explicitly: (1) molecular diffusion through the water or air filled soil pores and the standing water, if the water table is above the soil surface, (2) transport by ebullition from the depth where bubbles are formed up to the water table, and (3) transport through plants from soil layers above the rooting depth directly up to the atmosphere. Transport of gas due to moving water table is not considered. The model forcing consists of daily values of the position of the water table, the soil temperature profile, and the NPP. The model output is methane fluxes to the atmosphere and methane concentration profiles in the soil, both obtained on a daily basis by numerically solving the one-dimensional continuity equation within the entire soil/water column:

$$\frac{\partial}{\partial t}C_{CH_4}(t, z) = -\frac{\partial}{\partial z}F_{diff}(t, z) + Q_{ebull}(t, z) + Q_{plant}(t, z) + \quad (1)$$

$$R_{prod}(t, z) + R_{oxid}(t, z)$$

where $C_{CH_4}(t, z)$ is the methane concentration at time t and depth z, $F_{diff}(t,z)$ is the diffusive flux of methane through the soil,
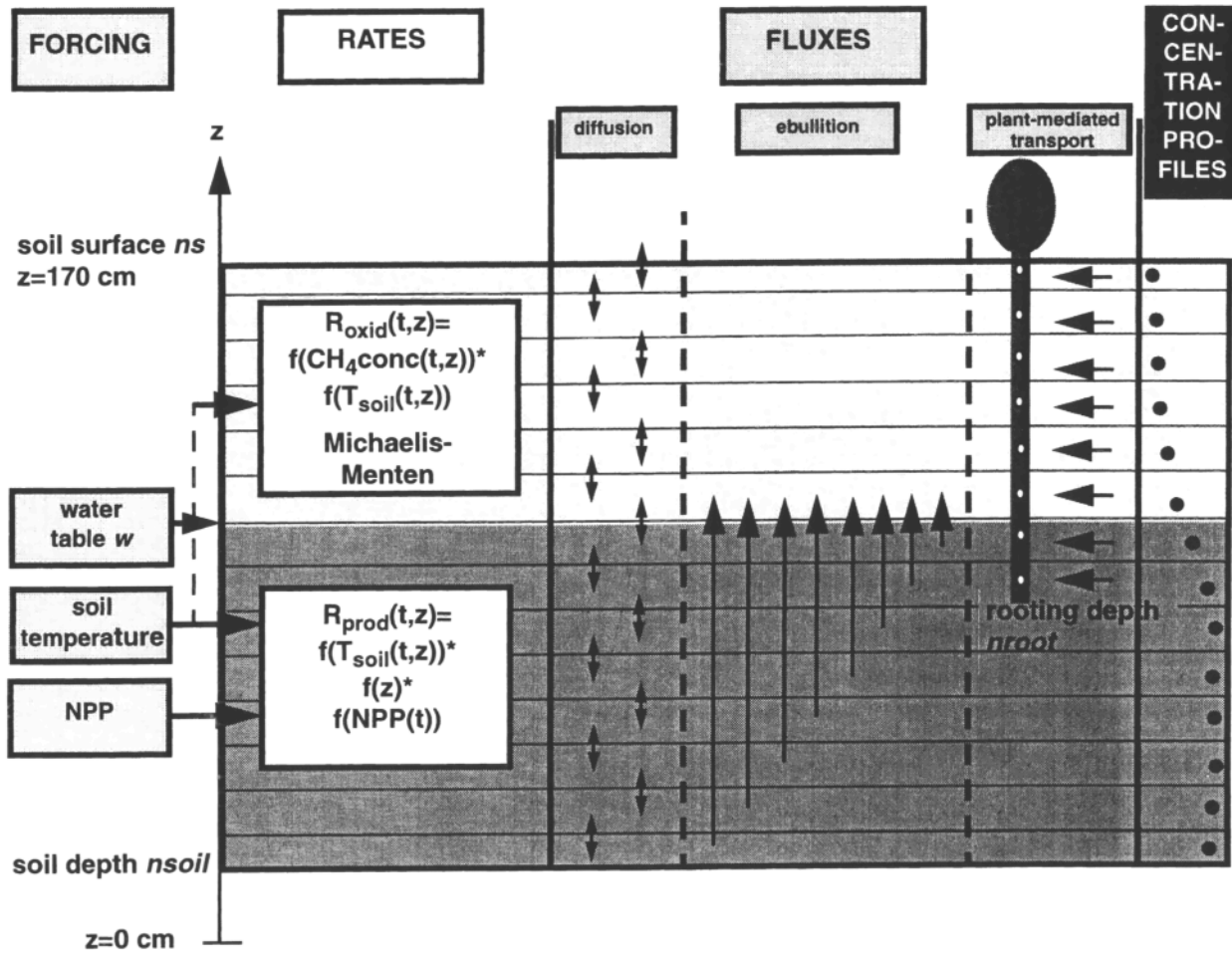
Figure 1. Schematic representation of the model structure. The one-dimensional soil column is divided into 1 cm thick parallel layers. The forcing consists of daily records of the water table, the soil temperature, and the NPP. Methane production occurs in the soil zone between the soil depth nsoil and the water table w, which can be either below or above the soil surface ns. The methane production rate $R_{prod}(t,z)$ is a function of the soil temperature $T_{soil}(t,z)$ and the NPP, which is taken as a measure for substrate availability. Methane oxidation is confined to the soil layers between the water table and the soil surface. The methane oxidation rate $R_{oxid}(t,z)$ follows Michaelis-Menten kinetics and is a function of the soil temperature $T_{soil}(t,z)$. Transport proceeds by (1) molecular diffusion through the soil pores, (2) ebullition, which is the formation of gas bubbles in the water saturated layers and their ascent to the water table, and (3) plant-mediated transport from layers above the rooting depth nroot to the atmosphere. The model calculates methane fluxes to the atmosphere and methane concentration profiles in the soil on a daily basis.

$Q_{ebull}(t,z)$ and $Q_{plant}(t,z)$ represent sinks due to ebullition and plant-mediated transport, respectively. $R_{prod}(t,z)$ is the methane production rate, while $R_{oxid}(t,z)$ denotes the methane oxidation rate In the following, each of the terms will be described in detail.

2.1. Methane Production Rate R_{prod}

Methane production is calculated in all soil layers below the water table. There are two factors controlling the rate of methanogenesis (1) the availability and quality of suitable substrate which originates mainly from root exudates, dead fine roots, and the input of plant litter and (2) temperature [e.g. *Conrad*, 1989; *Heyer*, 1990] We consider only fresh organic matter to be suitable substrate for methanogenesis [e.g. *Chanton et al.*, 1995; *Bridgham and Richardson*, 1992]. Hence, the availability of substrate is assumed to be connected with NPP, which is used as a measure for

the production of fresh organic carbon in soil. Its variation with time $f_{in}(t)$ has been parameterized in the following way: It is calculated as a function of the variation of the NPP with time, $f_{NPP}(t)$, which is derived from the simulated NPP(t) of the global terrestrial carbon cycle model Biosphere-Energy Transfer and Hydrology (BETHY) [*Knorr*, 1997] (appendix A). Thus the variation of substrate availability with time t, $f_{in}(t)$, is parameterized as

$$f_{in}(t) = 1 + \frac{f_{NPP}(t)}{NPP_{max}}, \qquad (2)$$

where NPP_{max} denotes the annual maximum value of the NPP (g C m^{-2} month^{-1}); that is, only relative changes in the NPP with time are considered. It is assumed that the seasonality of the NPP is essentially the same for wetland and nonwetland ecosystems Therefore this seasonality has been taken from calculations with the BETHY model, which calculate NPP for a mixture of vegeta-

tion types derived from the vegetation map of *Wilson and Henderson-Sellers* [1985], with wetlands as one possibility. This particular type is distinguished by an absence of water stress, while values for photosynthetic capacity are assumed to be the same as those for C3 grasses [*Beerling and Quick*, 1995]. The availability of potential substrate for methanogenesis also decreases with increasing soil depth z, because the sources of fresh organic material are located either at the soil surface or in the upper soil layers. There are several studies where methane production potentials in the soil have been measured [*Roulet et al.*, 1993; *Valentine et al.*, 1994; *Saarnio et al.*, 1997; *Kettunen et al.*, 1999]. The vertical pattern of methane production potentials is assumed to be linked with substrate availability [*Valentine et al.*, 1994]. In addition, it depends on vegetation. Under saturated conditions most of the observed profiles show an exponential decrease of methane production potentials with depth, whereby most of the production occurs in the upper 50 cm of the soil, and below 100 cm, methane production becomes insignificant. Therefore, in vegetated soils, it is assumed that the availability of substrate $f_{org}(z)$ is constant throughout the rooting zone because fresh litter and probably also root exudates represent a major source of substrate. Below the rooting depth, $f_{org}(z)$ decreases exponentially with depth z reaching a value of about 10% at 20 cm and almost 0 at 50 cm below the rooting depth:

$$f_{org}(z) = \begin{cases} 1 & nroot \le z \le ns \\ e^{(-|z - nroot|)/(10cm)} & nsoil \le z < nroot \end{cases}, \quad (3)$$

nroot denotes the rooting depth, ns denotes the soil surface, and nsoil denotes the soil depth, i.e., the lower boundary of the active layer. In unvegetated soils the vertical distribution of substrate $f_{org}(z)$ is assumed to decrease exponentially from the soil surface to the lowest soil layer. Here, $f_{org}(z)$ has been chosen in a way that at 50 cm below the soil surface $f_{org}(z)$ is about 10% of the value at the soil surface and becomes insignificant below 100 cm soil depth:

$$f_{org}(z) = 0.857 \ e^{(-|z - ns|)/(20cm)} \quad nsoil \le z \le ns \quad . \quad (4)$$

Possible methane production from soil layers deeper than 50 cm below the rooting depth (Equation (3)) or 100 cm soil depth (Equation (4)) is neglected in the model because it is assumed to be very small. This might lead to slightly underestimating total methane production from wetlands with peat layers deeper than 1 m, particularly in winter when soil temperatures are higher in deeper soil layers. Using information on the depth of peat layers in different wetlands, if available, could help to improve this in the future. The variation of the methane production rate with temperature is formulated in the following way. A Q_{10} dependence is chosen using a Q_{10} value of 6 lying within the range of observed Q_{10} values ranging from 1.7 to 16 [*Dunfield et al.*, 1993; *Valentine et al.*, 1994; *Westermann*, 1993]. It is assumed that this temperature function includes both the temperature dependence of the production of substrate for methanogenesis and that of methane production. The temperature function describes the response to the seasonal variation of the soil temperature T(t,z) at time t and depth z relative to the annual mean soil temperature T_{mean} at the site. Consequently, the methane production rate $R_{prod}(t,z)$ at time t and depth z is described as

$$R_{prod}(t, z) = R_0 \ f_{org}(z) \ f_{in}(t) \ f(T) \ Q_{10}^{\frac{T(t, z) - T_{mean}}{10}} \quad . \quad (5)$$

R_0 is a constant rate factor expressed in units of $\mu M \ h^{-1}$ (1M=1mol L^{-1}). It is a measure for the absolute substrate availability and quality (since $f_{in}(t)$ and $f_{org}(z)$ describe only relative changes in the substrate availability with time and depth). Since in the model these quantities are not simulated explicitly, the parameter R_0 is a tuning parameter which has to be adjusted to each data set; that is, the value of R_0 is chosen to get the correct amplitude of simulated methane emissions. As shown in section 4.1, it only changes the amplitude but not the pattern of the modeled methane emissions. The function f(T) is a step function being 1 if T(t,z) is above 0°C, and 0 all other times. This is equivalent to the assumption that there is no methane production at subzero temperatures. There are a few studies that report winter methane emissions [*Dise*, 1992; *Melloh and Crill*, 1996], and at least one study that reports methane production at temperatures down to -5°C [*Clein and Schimel*, 1995], but it seems that methane production at subzero temperatures is small. In some of these studies it is also suggested that part of the methane emitted in winter is methane produced already in summer and stored in the soil. Furthermore, there are several studies showing that methane emissions during the wintertime are significantly lower than during the growing season [e.g. *Whalen and Reeburgh*, 1992; *Shannon and White*, 1994].

The chemical conditions in the soil can also affect methanogenesis [e.g. *Conrad*, 1989]. For example, pH conditions can be important. In addition, methanogenesis requires the absence of competing electron acceptors like sulfate (SO_4^{2-}), nitrate (NO_3^-), or ironIII (Fe^{3+}) and a redox potential below -200 mV. In addition, the availability of nutrients can enhance the productivity [*Schlesinger*, 1991]. These effects are not taken into account in the model. The potential effect of a disadvantageous pH and the availability of nutrients on methane production rates is included in the parameter R_0. Concerning the effect of competing electron acceptors and the redox potential on methane production, it is assumed in the model that the timescale, on which such effects are inhibiting methane production, is small compared to the timescale of the model, being 1 day.

2.2. Methane Oxidation Rate R_{oxid}

Methane oxidation is calculated in all soil layers above the water table. The methane oxidation rate $R_{oxid}(t,z)$ at time t and depth z is assumed to follow Michaelis-Menten kinetics [*Bender and Conrad*, 1992]. In addition, it depends on the soil temperature with observed Q_{10} values lying in the range between 1.4 and 2.1 [*Dunfield et al.*, 1993; *Knoblauch*, 1994]. In the model, Q_{10} for oxidation has been chosen to be 2. Thus $R_{oxid}(t,z)$ is calculated from

$$R_{oxid}(t, z) = \frac{V_{max} \ C_{CH4}(t, z)}{K_m + C_{CH4}(t, z)} \ Q_{10}^{\frac{T(t, z) - T_{mean}}{10}} \quad , \quad (6)$$

where K_m and V_{max} are the Michaelis-Menten coefficients. $C_{CH4}(t,z)$ denotes the methane concentration (μM) at time t and depth z, whereas T_{mean} is the annual mean soil temperature (°C). The observed values for K_m lie between 1 and 5 μM [*Dunfield et al.*, 1993; *Knoblauch*, 1994], while V_{max} has been found to cover the range of about 5-50 $\mu M \ h^{-1}$ [*Dunfield et al.*, 1993; *Knoblauch*, 1994; *Krumholz et al.*, 1995; *Moore and Dalva*, 1997; *Sundh et al.*, 1994; *Watson et al.*, 1997]. In the model, K_m and V_{max} have been set to 5 μM and 20 $\mu M \ h^{-1}$, respectively. During the tests of

the model against data sets from various wetlands, it turned out that a V_{max} value of 20 μM h^{-1} cannot be used at all sites. Therefore, at sites where a value of 20 μM h^{-1} does not yield satisfactory results, we choose another value for V_{max}; the resulting values lying in the range from 3 to 45 μM h^{-1}. In the model, methane oxidation occurs only in the unsaturated soil layers. It has been observed that in ecosystems with a water table being several decimeters above the soil surface, there can be, due to turbulent diffusion, enough oxygen in the standing water column to make methane oxidation possible (D.W. Valentine, personal communication, 1997; W.S. Reeburgh, personal communication, 1997). Since it is not known if this effect is of general importance in different wetland types, it has not been incorporated into the model.

2.3. Diffusion F_{diff}

The diffusive flux $F_{diff}(t,z)$ is calculated using Fick's first law:

$$F_{diff}(t, z) = -D_{CH4}(z) \frac{\partial}{\partial z} C_{CH4}(t, z), \qquad (7)$$

where $D_{CH4}(z)$ is the diffusion coefficient of methane at depth z and $C_{CH4}(t,z)$ is the methane concentration at time t and depth z. Since in the soil diffusion occurs only through the soil pores, the diffusion coefficient is obtained from

$$D_{CH4}(z) = D_i \ 0.66 \ f_{coarse}, \qquad (8)$$

which is the so-called Penman relation [Hillel, 1982], using a tortuosity coefficient, which has been set to 0.66, suggesting that the distance covered by diffusion is about two-thirds of the length of the real average path. In the unsaturated soil layers, D_i is the diffusion coefficient of methane in bulk air, which is 0.2 cm^2 s^{-1} [D'Ans and Lax, 1967], while in the water-saturated soil layers $D_i = 10^{-4}$ 0.2 cm^2 s^{-1} [Scheffer and Schachtschabel, 1982]. The factor f_{coarse} denotes the relative volume of the coarse pores; that is, we assume that diffusion proceeds mainly through the large pores. To solve the diffusion equation, the Crank-Nicolson scheme [Press et al., 1992] is used. The methane concentration values are defined in the middle of each layer, whereas the diffusion coefficients are defined at the layer boundaries. The following boundary conditions are chosen:

$$\frac{\partial}{\partial z} C_{CH4}(t, z = nsoil) = 0 \qquad (9)$$

at the lower boundary nsoil and

$$C_{CH4}(t, z = u + 4cm) = C_{atm} \qquad (10)$$

at the upper boundary u, which is either the water table w(t) (if w(t)>ns) or the soil surface ns. C_{atm} is the atmospheric methane concentration of 0.076 μM. At the water-air interface the methane concentrations in both phases are assumed to be in equilibrium. Hence their ratio is specified by the Bunsen solubility coefficient.

2.4. Ebullition Q_{ebull}

As soon as the methane concentration in a layer exceeds a certain threshold concentration C_{thresh}, bubbles are formed. Since there is usually enough condensation nuclei in the soil and owing to the occurrence of other gases such as nitrogen (N$_2$), C_{tresh} usually is significantly lower than the saturation concentration (which is 1875 μM at 10°C [Kaltofen et al., 1975]). In vegetated soils, for example, the concentration of N$_2$ was reported to be higher than in

unvegetated soils [Chanton and Dacey, 1991]. Thus, according to Chanton and Dacey [1991], Shannon et al. [1996], and Holzapfel-Pschorn et al. [1986], we assume that C_{tresh} is lower at vegetated sites than at unvegetated sites. In the model it is assumed that bubble formation occurs at methane concentrations between 500 and 1000 μM at totally vegetated and unvegetated soils, respectively, being equivalent to a mixing ratio of 27-53% of methane in the bubble (at 10°C). Thus the threshold concentration for bubble formation is calculated from

$$C_{thresh} = C_{min} \left(1 + \frac{P_{unveg}}{100}\right), \qquad (11)$$

where C_{min} is the concentration at which bubble formation occurs, if the site is totally vegetated (500 μM) and P_{unveg} is the percentage of unvegetated, bare soil. In order to determine the flux $F_{ebull}(t)$ of methane reaching the water table w(t) at time t in the form of gas bubbles, the rate $Q_{ebull}(t,z)$ at which methane in the form of bubbles is removed from depth z is calculated:

$$Q_{ebull}(t, z) = -k_e \ f(C_{CH4}) \ (C_{CH4}(t, z) - C_{thresh}), \qquad (12)$$

where k_e is a rate constant of the unit 1 h^{-1} and $f(C_{CH4})$ is a step function taking the value 1, if the methane concentration $C_{CH4}(t,z)$ is greater than C_{thresh}, and 0 otherwise. In the layers above the water table, $Q_{ebull}(t,z)$ is 0. Bubbles are assumed to reach the water table within one model time step being 1 hour. This assumption is supported by the fact that wetland soils are generally very porous, the relative pore volume being often greater than 90% [Scheffer and Schachtschabel, 1982], and the finding that the velocity of bubbles ascending in pure water lies in the order of 1-10 cm s^{-1} [e.g. Shafer and Zare, 1991]. Thus the ebullitive flux $F_{ebull}(t)$ is obtained by integrating $Q_{ebull}(t,z)$ over the whole water saturated zone:

$$F_{ebull}(t) = \int_{nsoil}^{w(t)} Q_{ebull}(t, z) dz, \qquad (13)$$

where nsoil is the lower boundary of the active layer and w(t) is the water table. If the water table is at or above the soil surface, $F_{ebull}(t)$ contributes directly to the methane flux into the atmosphere. Otherwise, the amount of methane rising to the water table in the form of bubbles is added to the methane concentration in the lowest unsaturated soil layer. While the effect of subzero temperatures on methane production is accounted for in the model (Equation (5)), the soil frost state does not affect diffusion (Equation (7)) or ebullition (Equation (13)). However, winter methane production is very low in the model, so that considering a further inhibiting effect on winter methane flux is not expected to have a significant effect on model results.

2.5. Plant-Mediated Transport Q_{plant}

The occurrence of vascular plants provides an effective mechanism by which methane can be transported to the atmosphere [e.g. Chanton et al., 1992a; Schimel, 1995; Shannon et al., 1996]. Moreover, oxygen can be conducted down to the roots this way establishing a small aerobic region in the rhizosphere [Gerard and Chanton, 1993; Holzapfel-Pschorn et al., 1986; Schipper and Reddy, 1996; Schütz et al., 1989]. The results from several studies of plant-mediated transport suggest that the main emission pathway is by molecular diffusion or effusion through the plant stems [Chanton et al., 1992a; Chanton et al., 1992b; Happell et al., 1993; Nouchi and Mariko, 1993; Shannon et al., 1996]. Conse-

quently, the flux of methane through plants is assumed to be proportional to the concentration gradient between the soil and the atmosphere, and since the atmospheric methane concentration is very small compared to soil methane concentrations, the plant-mediated flux is proportional to the methane concentration in the soil. *Nouchi and Mariko* [1993] found a linear relationship between methane emission rates through plants and pore water methane concentrations. Hence the rate $Q_{plant}(t,z)$ at which methane is removed by plants from depth z at time t is calculated from

$$Q_{plant}(t, z) = -k_p \, T_{veg} \, f_{root}(z) \, f_{grow}(t) \, C_{CH4}(t, z), \quad (14)$$

where k_p is a rate constant of the unit 0.01 h^{-1} and T_{veg} is a factor describing the quality of plant-mediated transport at a site, depending on the density of plant stands and the plant types. The range of T_{veg} (0-15) was derived from studies where information on vegetation and/or the fraction of plant mediated transport was available, and both methane emissions and methane concentration profiles in the soil were observed, as it was the case at sites 1 and 2 [*Shannon and White*, 1994; *Shannon et al.*, 1996; *Dise*, 1993]. At sites where the predominant plant types and their capability of conducting gas are known, T_{veg} is derived from that knowledge. Otherwise, we consider shrubs not contributing to plant-mediated transport and trees being poor, and grasses and sedges being good gas transporters [*Walter*, 1998]. The function $f_{root}(z)$ represents the vertical distribution of roots in the soil. It is assumed to decrease with depth, and for the sake of simplicity, we choose a linear relationship between root biomass and soil depth z:

$$f_{root}(z) = 2 \, \frac{z - nroot}{ns - nroot} \qquad nroot \le z \le ns, \quad (15)$$

where nroot denotes the rooting depth and ns denotes the soil surface. Below the rooting depth nroot, $f_{root}(z)$ is 0. The ability of plants to conduct gas is considered to vary with the growing state of the plants. This assumption agrees well with observations by *Schütz et al.* [1989], who found that the fraction of methane transported through rice plants increases with the growing maturity of the plants. In the model we use the leaf area index (LAI) as a measure for the growing state $f_{grow}(t)$ of the plants (appendix B). Since methane entering the roots of plants has to pass through the small oxic zone around the root tips, a certain fraction P_{ox} of methane is oxidized. There are a few studies examinig rhizospheric oxidation: *Schipper and Reddy* [1996] determined the fraction of methane consumed by rhizospheric oxidation using two different methods and found values of 65±24 and 79±20 %. *Schütz et al.* [1989] observed that about 90% of the methane produced was oxidized in cases when plant-mediated transport was the main (97%) emission pathway, while *Gerard and Chanton* [1993] obtained values for rhizospheric oxidation between 39 and 98%. Taking into consideration the high variability of observed values, we set P_{ox} to 50%. Finally, the methane flux due to plant-mediated transport $F_{plant}(t,z)$ is calculated from

$$F_{plant}(t) = \int_{nroot}^{ns} (Q_{plant}(t, z) \, (1 - P_{ox})) dz, \quad (16)$$

where ns and nroot are the soil surface and the rooting depth, respectively.

2.6. Total Methane Emission F_{tot}

The total methane emission $F_{tot}(t)$ is calculated by adding all the fluxes from the different transport mechanisms: the diffusive flux $F_{diff}(t,z=u)$ at the soil/water-atmosphere boundary u, the flux due to plant-mediated transport $F_{plant}(t,z)$, and the ebullitive flux $F_{ebull}(t,z)$. The latter contributes only to the total flux $F_{tot}(t)$, if the water table is at or above the soil surface. Hence $F_{tot}(t)$ is obtained from

$$F_{tot}(t) = F_{diff}(t, z = u) + F_{ebull}(t) + F_{plant}(t). \quad (17)$$

As mentioned in section 1, this model differs slightly from the model used by *Walter et al.* [1996]. While in the earlier version, substrate availability $f_{org}(z)$ was constant to a depth of 80 cm below ground and 0 below that depth, an exponential relationship has been chosen now (Equations (3) and (4)) because it seems to be more realistic (J. Harden, personal communication, 1997) and [*Roulet et al.*, 1993; *Valentine et al.*, 1994; *Saarnio et al.*, 1997; *Kettunen et al.*, 1999]. In the current version the methane oxidation rate $R_{oxid}(t,z)$ (Equation (6)) is considered to be temperature dependent [*Dunfield et al.*, 1993; *Knoblauch*, 1994], which was not the case in the earlier version. The threshold concentration for bubble formation C_{thresh} (Equation (11)) is now a function of the fraction of unvegetated, bare soil P_{unveg} [*Chanton and Dacey*, 1991, *Shannon et al.*, 1996, *Holzapfel-Pschorn et al.*, 1986], while it was considered to be constant (500 μM) earlier. In the earlier version of the model it was assumed that a certain fraction of rising gas bubbles are trapped in soil and released only if the water table falls below the depth where they are located or the pore space filled by gas bubbles exceeds a certain limit. Now equilibrium between trapped and released gas bubbles is assumed at any time, so that all gas bubbles formed at a time are immediately transported to the water table (Equation (13)). While in the earlier version of the model, the growing state $f_{grow}(t)$ of plants was derived from an empirically defined function, it is now calculated from the LAI [*Dickinson et al.;* 1993] (Equation (14) and appendix B). None of these changes has lead to a significant change in the model results at site 1 where the earlier version was tested. However, these changes were made to get more realistic model results, in particular at sites which are drier than site 1 or where plant-mediated transport is less dominant.

3. Results and Discussion

The methane model is tested against observational data from 15 microsites within six wetlands located in North America, Europe, and Central America [*Walter*, 1998]. The observation periods range from 1 season up to 3 years. Here we discuss results from five microsites within five wetlands, and the data sets used in this study are summarized in Table 1. At each site, methane emissions were measured about 2-4 times per month, and at two sites (1, 2) also methane concentration profiles in the soil were obtained 1-2 times per month. At all sites except site 5 the position of the water table and the soil temperature at different soil depths were observed at least at the same frequency as methane emissions. Since at site 5 the forcing data were not observed, a hydrologic model [*Walter*, 1998] in combination with the European Center/Hamburg 4 (ECHAM4) model [*Roeckner et al.*, 1996] is used to run the methane model there. The daily forcing required by the methane model is obtained by a linear interpolation of the observed input data. The NPP is obtained from the BETHY model [*Knorr*, 1997] for that 1° by 1° grid box in which the wetland is located. The parameters soil depth nsoil, rooting depth nroot, and the quality of plant-mediated transport T_{veg} are chosen based on

Table 1. Data Sets Used to Test the Model

	1	2	3	4	5
Site	Michigan	Minnesota	Finland	Alaska	Panama
Location	42°N, 84°W	47°N, 93°W	63°N, 31°E	65°N, 148°W	9°N, 80°W
Wetland Type	ombrotrophic bog	poor fen	oligotrophic pine fen	Arctic tundra	swamp
Dominant Vegetation	*Sphagnum, Scheuch-zeria palustris*	*Sphagnum, Carex, Scheuchzeria palustris*	*Sphagnum, Eriopho-rum vaginatum*	*Sphagnum*	*Raphia taedigera* (palm)
T_{mean}, °C	12	6.5	3.5	0	27
Reference	*Shannon and White* [1994]	*Dise* [1993]	*Saarnio et al.* [1997]	*Whalen and Ree-burgh* [1992]	*Keller* [1990]

Description of location, wetland type, dominant vegetation, annual mean temperature T_{mean} and references of the data sets used to test the model.

information about the specific wetland site given by the investigators. The parameter V_{max} is set to 20 µM h^{-1} in most cases but is adjusted to the data set in situations where a value of 20 µM h^{-1} does not yield optimal results. The values of V_{max} used in this study range from 3 to 45 µM h^{-1}. It is not clear what causes these differences in methane oxidation rates. Possible candidates are the chemical conditions in soil such as pH or different populations of methanotrophs having temperature optima which are not optimal for the respective sites. Another reason could be that soil texture and/or soil moisture in the unsaturated soil (i.e., the fraction of soil volume where oxidation can occur) is different. The parameter R_0 is adjusted to the data set in each case. The values for R_0 obtained lie between 0.3 and 0.6 at the high-latitude sites and 2.8 at the tropical site. R_0 varies, as mentioned above, as a function of substrate quantity and quality and the chemical conditions in soil such as redox potential, pH, and the presence of competing electron acceptors. Until now, there is no method to predict R_0 for different sites, owing to both lack of sufficient data on the study sites and, at least in part, knowledge about the quantitative relationship between all important environmental parameters and R_0. However, as more data become available, a model like that one proposed by *Valentine et al.* [1994] and *Holland* [unpublished] could

Table 2. Site-Specific Model Parameters at the Five Test Sites

Site	R_0	V_{max}, µM h^{-1}	ns-nsoil, cm	ns-nroot, cm	T_{veg}
1	0.60	45	80	50	15
2	0.30	20	80	40	4
3	0.34	20	70	30	12
4	0.30	3	thaw depth	0	0
5	2.80	20	128	74	9

Model parameters used at the five test sites presented in this article: R_0 (tuning parameter), V_{max} (maximum methane oxidation rate), ns-nsoil (soil depth below soil surface), ns-nroot (rooting depth below soil surface), and T_{veg} (quality of plant-mediated transport) (see model description).
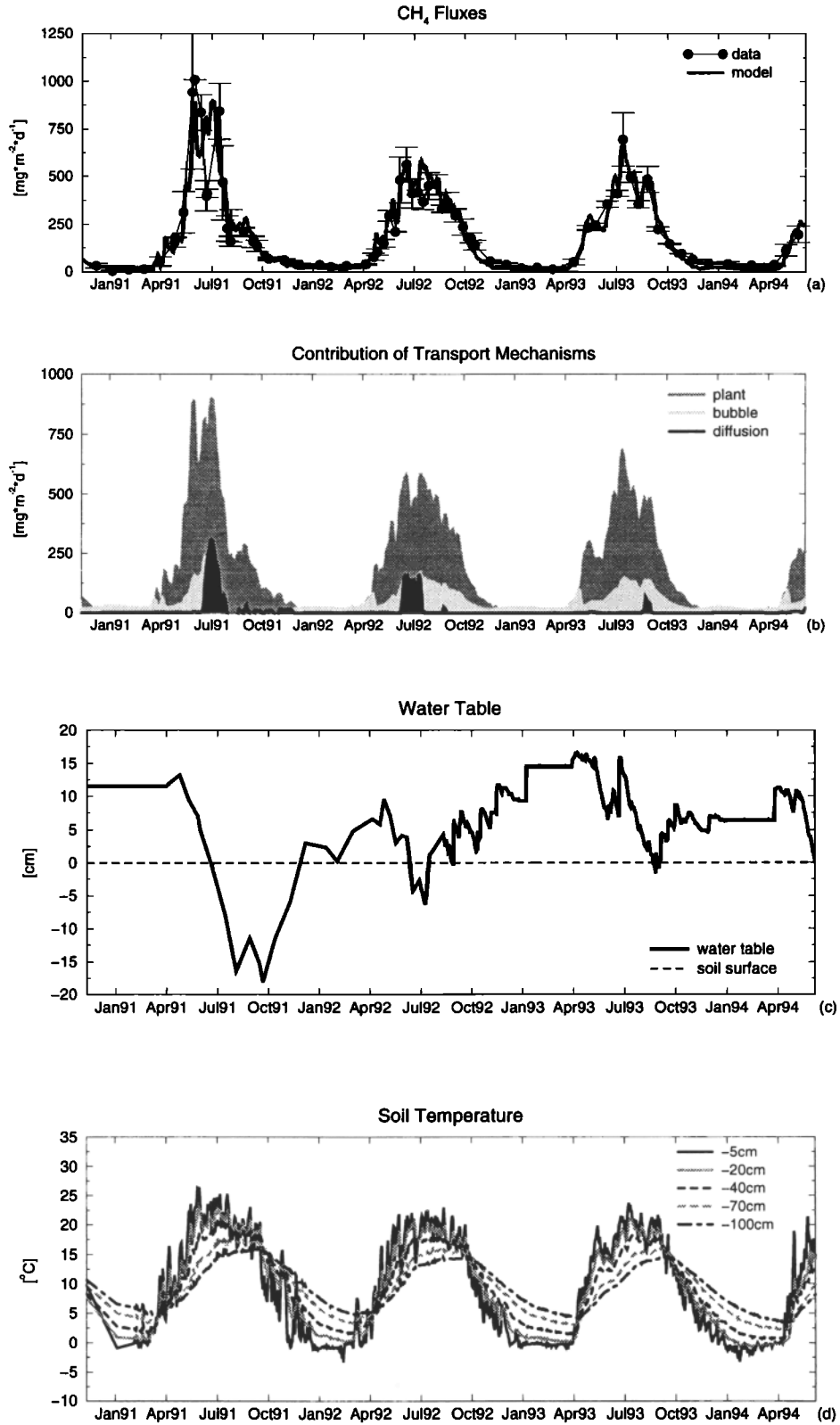
be used to predict R_0 for different sites. For a global application, *Walter* [1998] used a simple method to derive R_0 for different regions as a function of annual mean temperature and total annual NPP. In this article, results of five tests from one station at sites 1-5 are shown. Table 2 lists the parameters used at the five test sites.

3.1. Site 1: Michigan

Figure 2 shows the results of a test of the model at site 1 using data by *Shannon and White* [1994]. The forcing data are plotted in the lower part, Figure 2c shows the observed position of the water table relative to the soil surface, and Figure 2d shows the observed soil temperatures at different soil depths. In Figure 2a the comparison between simulated and observed (the average of 3 chamber measurements ±1 standard deviation error bars) methane emissions is shown. When the water table is above the soil surface, the patterns of observed as well as simulated methane emissions are dominated by changes in the soil temperature. This applies to both day-to-day and interannual variations of methane emissions. For example, methane emissions are higher in 1991 than in the two following years because of slightly higher soil temperatures in 1991. As soon as the water table falls below the soil surface, this connection between methane emission and soil temperature is no longer evident. In this situation, methane diffusing through the soil pores is partly oxidized in the unsaturated soil layers. In addition, rising bubbles cannot reach the soil surface anymore and only the deeper roots extend into the water saturated soil zone where high methane concentrations prevail. The consequence of a long period with the water table being below the soil surface can be seen in 1991 when methane emissions drop to smaller values of about 200 mg m^{-2} d^{-1} already in August even though the soil temperature is still high at that time. The reason for this is that the water table stays at depths of about 15 cm below ground since July 1991. In 1992 and 1993 this drop of methane emissions occurs much later in the year, attributable to wetter conditions. In Figure 2b the simulated relative contributions of the three different transport mechanisms diffusion, ebullition, and plant-mediated transport are depicted. At sites covered by vascular plants, as it is the case at site 1, plant-mediated transport plays an important role during the growing season. *Shannon et al.* [1996] observed in plant enclosure experiments that 64-90% of the net methane flux

Figure 2. For site 1, (a) comparison between modeled (thick line) and measured (dots with +/- 1 standard deviation error bars) methane emissions; (b) modeled contributions of the three transport mechanisms, diffusion (black), ebullition (light grey), and plant-mediated transport (dark grey); (c) forcing, observed position of the water table; and (d) forcing, observed soil temperature at different soil depths (observational data from *Shannon and White* [1994]).

was emitted through *Scheuchzeria palustris*. The model results are in good agreement with this finding (Figure 2b). Ebullition occurs only at times when the water table is above the soil surface. Diffusion plays only a role if the water table is below the soil surface. For example, immediately after the fall of the water table below the soil surface in June 1991, diffusion increases considerably because the diffusion coefficient increases by a factor of 10^4 as soon as the soil becomes unsaturated and methane concentrations are still high in the uppermost layers. After a period of about 15 days, emission by diffusion declines again owing to oxidation in the unsaturated zone. *Moore and Roulet* [1993] observed a similar pattern: increased fluxes with falling water table to 20 cm depth within 10 days, followed by decreased fluxes as the water table continues to fall further.

Figure 3 shows a comparison between simulated and observed methane concentration profiles for the period between January 1992 and January 1993. The observations and model results show the same seasonal pattern: higher methane concentrations in the winter and spring and decreased methane concentrations in the summer and autumn. The reason for this is that during the growing season a large fraction of methane is removed from the soil by plants. However, in the model, removal of methane from the soil by plants seems to start too early (May 16 and June 4). This probably happens because in the model the time plants need to develop is underestimated. At the beginning of the winter, the concentrations increase faster in the data than in the model (November 14, December 13, and January 9) again because the simulation of the seasonal variation of the growing stage of the plants seems to fail in late autumn. However, these discrepancies occur only at times when the production rate is relatively low and thus affect simulated methane emissions only slightly.

3.2. Site 2: Minnesota

Figure 4 shows the results of a model-data comparison performed at site 2 with data from *Dise* [1993]. As in section 3.1, in the lower part, the observed forcing data which are the position of the water table (Figure 4b) and the soil temperature (Figure 4c) are plotted. In Figure 4a the comparison between observed and simulated methane emissions is shown. Here the agreement seems to be not as good as at site 1 which can be partly explained by the fact that at site 1 the model results are compared to an average of three measurements, which clearly differ from each other at some times (see ±1 standard deviation error bars in Figure 2a), whereas at site 2 only one chamber was used. In addition to that, other factors affecting methane production and emission such as the chemical conditions in the soil, which are not considered in the model (see above), could be important at some times. Generally, simulated methane emissions respond in a similar way to changes in the soil temperature and the position of the water table as at site 1. Further tests of the model conducted at four other microsites within this wetland where vegetation and soil temperatures were similar, but the position of the water table is in one case much lower (-40 to -50 cm belowground) yield similar results [*Walter*, 1998].

3.3. Site 3: Finland

In Figure 5 the results of a comparison between modeled and observed methane emissions from two microsites (flark (minerotrophic hollow) and low hummock) of a Finnish wetland
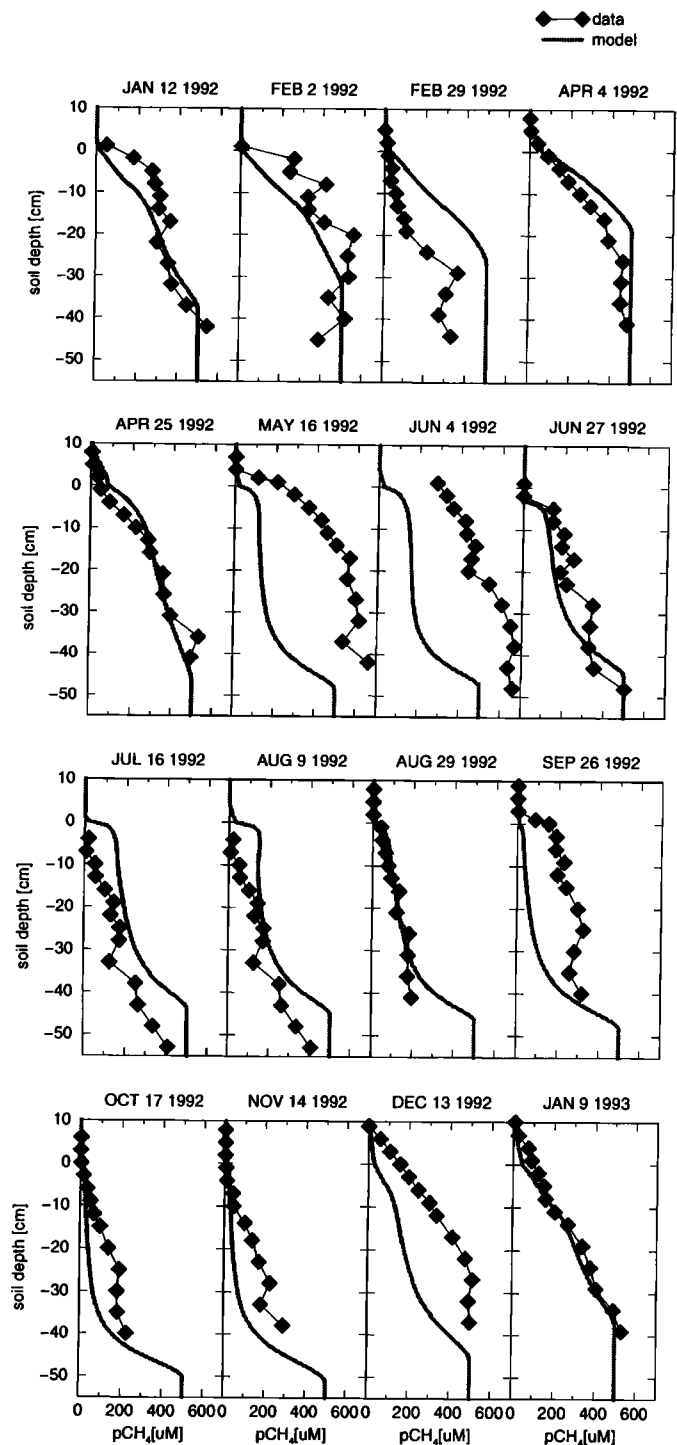

Figure 3. For site 1, comparison between modeled (thick line) and observed (squares) methane concentrations in the soil (observational data from *Shannon and White* [1994]).

[*Saarnio et al.*, 1997] are shown. We focus on intrasite variations within the same wetland based on differences in the position of the water table. The same values for R_0, V_{max}, nsoil, nroot, and T_{veg} [*Alm et al.*, 1997] for description of vegetation] are used at the two microsites. In addition, the soil temperatures as shown in Fig-
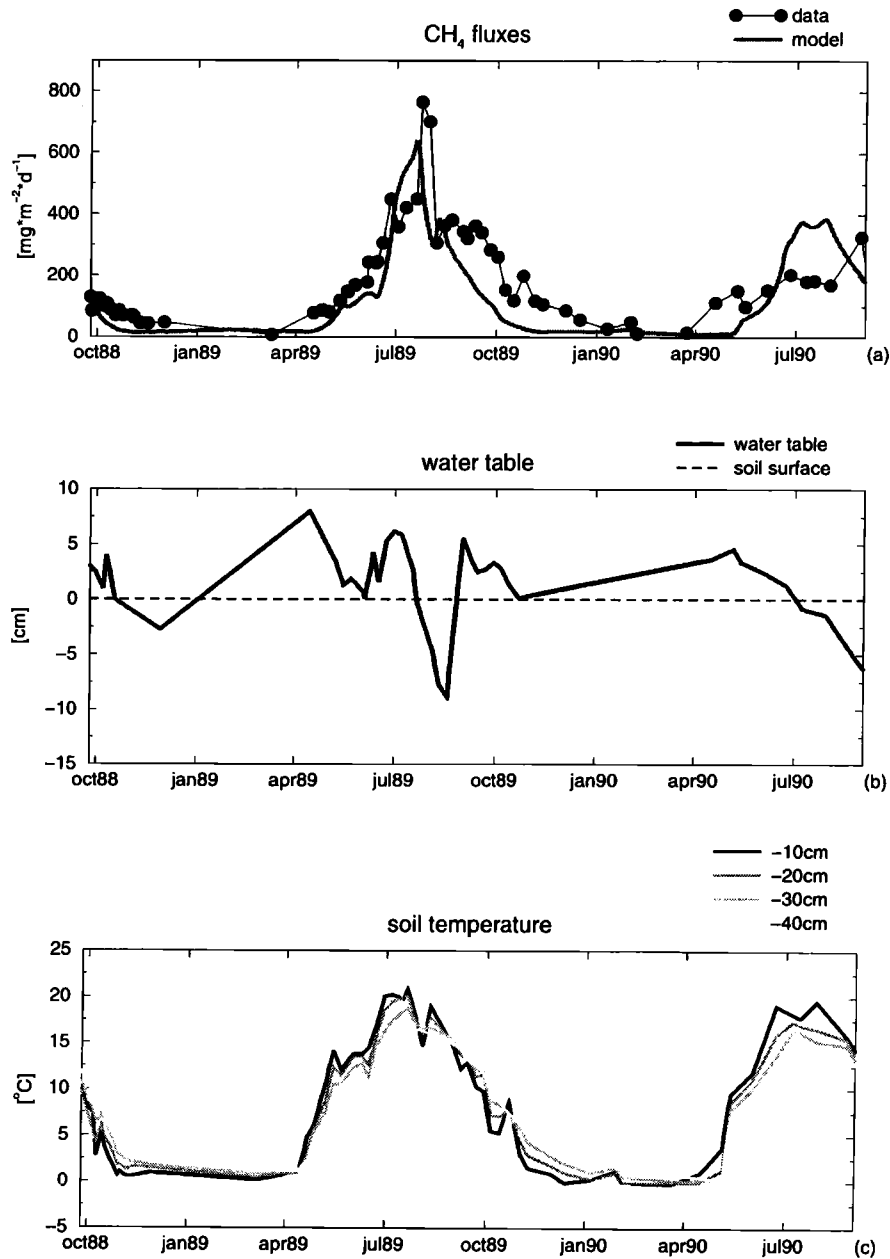
Figure 4. For site 2, (a) comparison between modeled (thick line) and measured (dots) methane emissions; (b) forcing, observed position of the water table; and (c) forcing, observed soil temperature at different soil depths (observational data from *Dise* [1993]).

ure 5c are the same at both microsites. Hence the differences in simulated methane emissions between these two microsites are attributed to differences in the positions of the water table only. The low hummock is elevated by about 15 cm relative to the flark. Figure 5b shows the positions of the water table at the low hummock and the flark. The modeled and observed methane emissions from these two microsites are plotted in Figure 5a (the grey areas are averages of the fluxes from all the collars of the two microsites ±1 standard deviation). The methane emissions from the flark are considerably higher than those from the low hummock because there is less oxidation due to the higher water table level at the flark site. This effect can be seen both in the observations and the

model results. At the flark, simulated methane emissions begin too early (Figure 5a). The modeled fluxes follow directly the changes in the soil temperature (Figure 5c) whereas in the observations there is a time lag between the soil temperature and methane emissions. The reason for this time lag could be that before methane production can start, appropriate soil conditions for methanogenesis must be established and suitable substrate for methanogenesis must be produced. This is not taken into account in the model. Another reason could be that at these microsites, the deeper soil layers contribute more to methane production than the upper ones, possibly owing to better substrate availability and/or quality. This would cause modeled methane emissions to follow the soil tem-
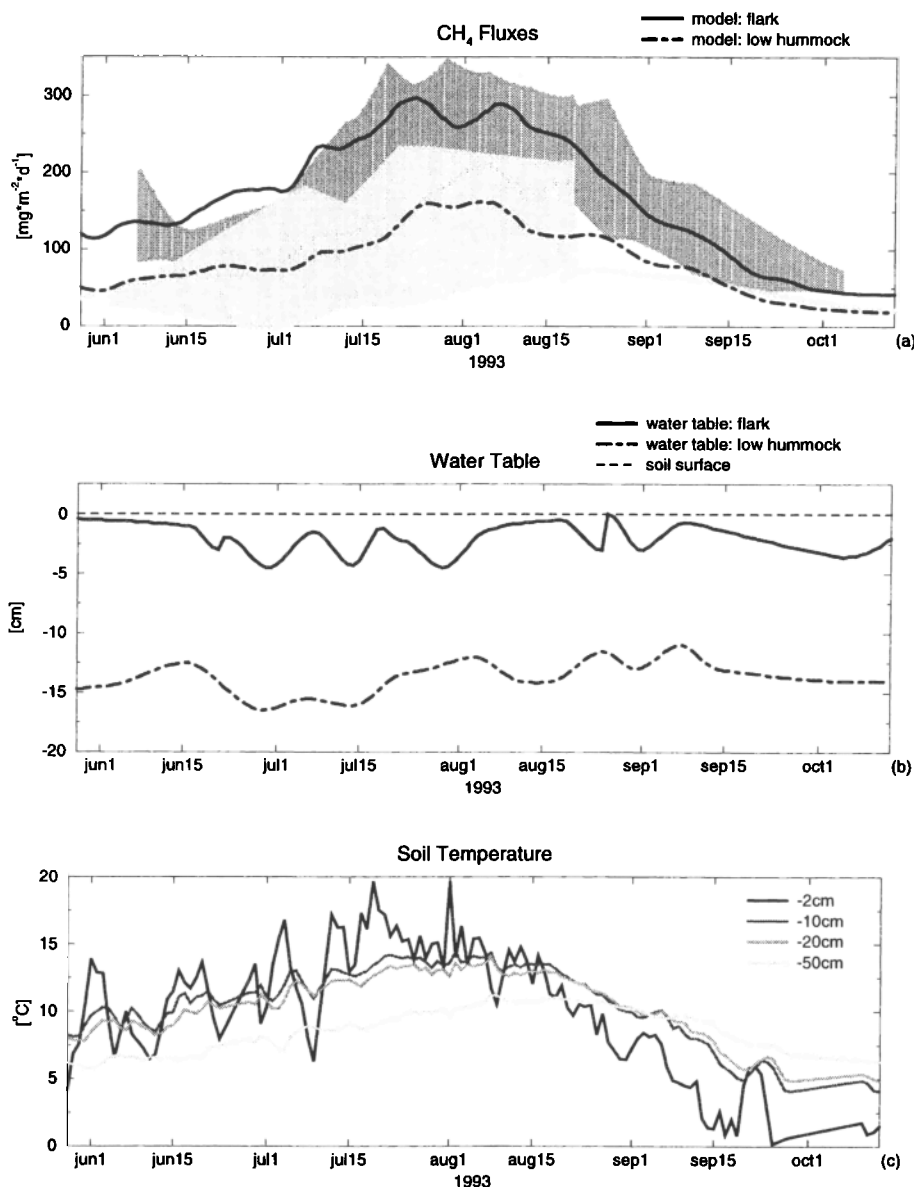
Figure 5. For site 3, comparison of methane emissions from two microsites. (a) Modeled fluxes from the flark (solid line) and the low hummock (dot-dashed line); the shaded areas are the areas between the average of all measurements from the respective microsite +/- 1 standard deviation, flark (dark grey) and low hummock (light grey). (b) Forcing, observed positions of the water table at the flark (solid line) and the low hummock (dot-dashed line) relative to the soil surface (dashed line). (c) Forcing, observed soil temperature at different soil depths (the same at both microsites) (observational data from *Saarnio et al.* [1997]).

perature of deeper soil layers which lags behind the temperature of the upper soil layers. This effect, however, is only seen at the two microsites of the Finnish wetland. The model is also tested at two further sites within this wetland with similar water table patterns and vegetation (one site has a deeper rooting depth) [*Walter*, 1998]. The results obtained there are similar to the ones presented here

3.4. Site 4: Alaska

A further test is performed with data from an Alaskan Arctic tundra site which is underlain by permafrost [*Whalen and Reeburgh*, 1992] In Figures 6b and 6c the observed forcing data water

table, thaw depth, and soil temperature are plotted. Since the three chamber measurements at the black hole microsites (called BH1-3) differ much, we plot the obtained fluxes from each chamber as well as the average of these measurements to compare them with the simulated fluxes (Figure 6a). The vegetation consists of *Sphagnum* mosses, and there are no vascular plants which means that plant-mediated transport does not occur and hence $T_{veg}=0$ (Table 2). During the summer the soil starts to thaw, and the maximum depth of thaw is about 60 cm belowground, attained in autumn An increasing thaw depth means that the production zone is being enlarged with time. Therefore simulated methane emissions are of the same magnitude in September as in August even though both the soil temperature and the water table levels are lower in Sep-
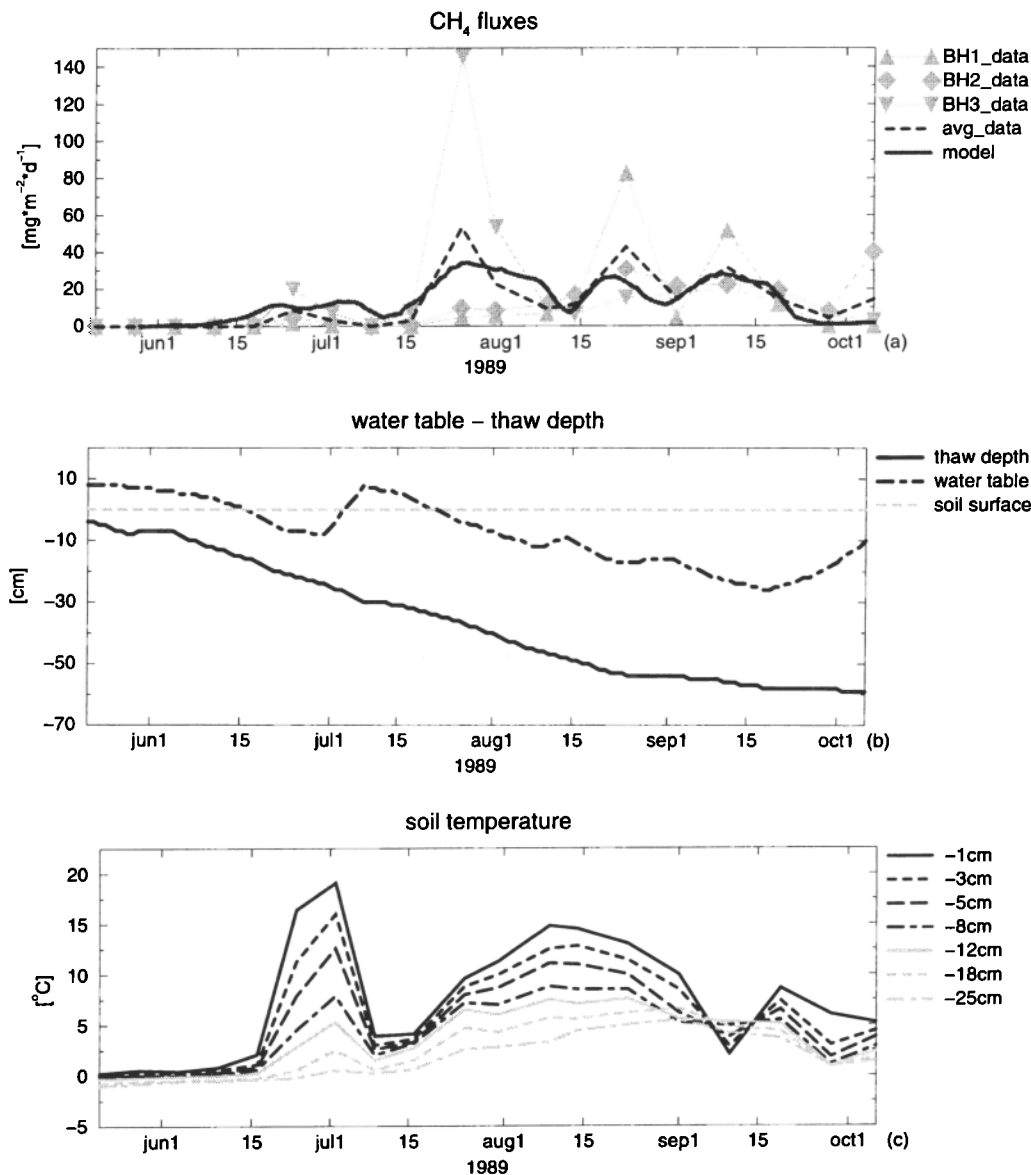
Figure 6. For site 4, comparison between modeled (thick line) and measured (the triangles and the square are observations from three stations within the "Black Holes" site, the dashed line marks the average of those three measurements) methane emissions. (b) Forcing, observed thaw depth (soild line) and water table (dot-dashed line). (c) Forcing, observed soil temperature at different soil depths (observational data from *Whalen and Reeburgh* [1992]).

tember. Here V_{max}, which describes the maximum methane oxidation rate in the unsaturated soil zone, has been set to only 3 µM h^{-1} as opposed to values of 20 µM h^{-1} at most other sites (Table 2) Because of that low V_{max} value, the effect of a declining water table on methane emission is smaller than at the Finnish wetland site discussed in section 3.3. One could speculate what the reason for this low V_{max} value might be. For example, the oxidation potential of the methanotrophic bacteria could be lower at that site, or the soil moisture content in the soil layers above the water table could be higher (the soil moisture in the unsaturated zone is not taken into account in the model). However, the V_{max} value chosen here is still close to observed values for V_{max} lying in the range between 5 and 50 µM h^{-1} [*Dunfield et al*, 1993; *Knoblauch*, 1994, *Krumholz et al*, 1995, *Moore and Dalva*, 1997, *Sundh et*

al., 1994; *Watson et al.*, 1997]. Data from two other microsites of this wetland are used to test the model [*Walter*, 1998]. There again three chambers were used at each microsite, and soil temperature and thaw depth show a similar behavior as at the microsite shown here. However, water table levels go down to -40 cm, and one microsite is vegetated. Again, the results from the three chambers differ considerably and agreement between simulated and observed methane emissions is worse than at the other test sites.

3.5. Site 5: Panama

As a last example, a test against data from a tropical wetland in Central Panama [*Keller*, 1990] is discussed At this site, methane emissions were measured, but neither the soil temperature nor the
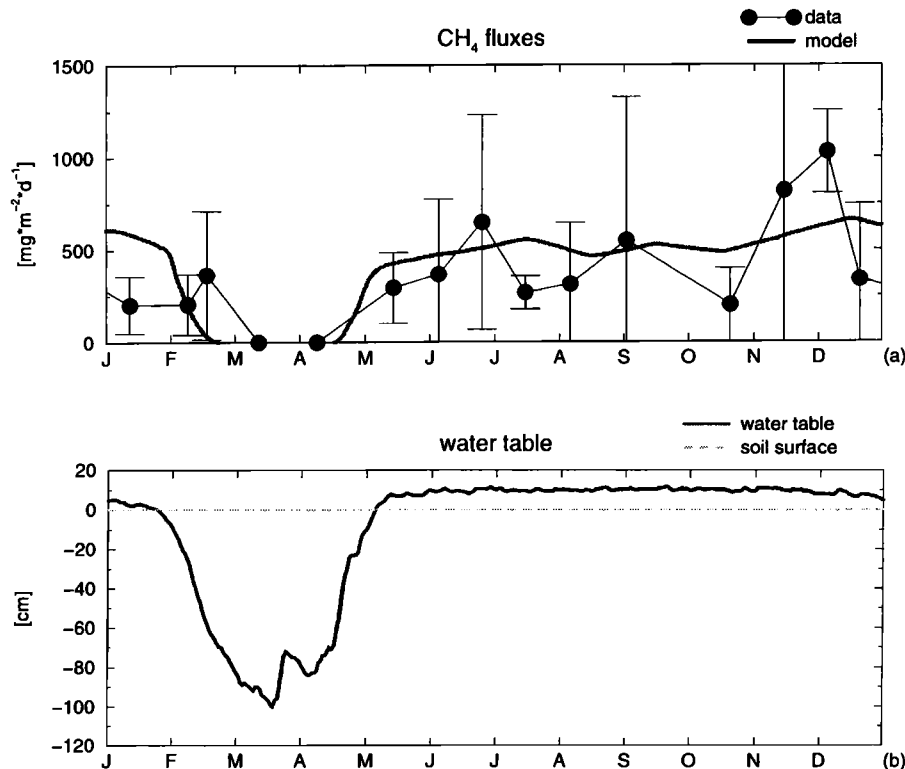
Figure 7. For site 5, (a) comparison between modeled (thick line) and measured (dots with +/- 1 standard deviation error bars) methane emissions and (b) forcing, position of the water table relative to the soil surface as calculated with the hydrologic model forced by the ECHAM4 model (see text) (observational data from *Keller* [1990]).

water table was observed. This site is characterized by a 4-month dry season between February and May. According to M. Keller (personal communication, 1997), the water table rarely exceeded +30 cm during the wet season and was below 50 cm below ground during the dry season, and the soil temperature was nearly constant over the whole year. In order to obtain input data for the methane model for this test, the output of a climatological run of the ECHAM4 model [*Roeckner et al.*, 1996] in T106 (T106-truncation corresponds to 1.1° by 1.1°) is used. The soil temperature at different soil depths is calculated by the ECHAM4 model, and the water table levels are calculated by a hydrologic model [*Walter*, 1998] driven by climate data from the same run of the ECHAM4 model. Since the necessary model parameters (Table 2) are not known for this site the values from global data sets of these parameters which have been established for a global application of the methane model [*Walter*, 1998] are used. In Figure 7b the water table calculated by the hydrologic model forced by the ECHAM4 model is plotted. The soil temperature is almost constant throughout the year (not shown). This is consistent with the information by M. Keller (personal communication, 1997) (see above). Figure 7a shows the comparison between the simulated and the observed methane emissions. The latter are averages of seven stations plotted with ±1 standard deviation error bars. The most striking point is that the modeled as well as the observed methane emissions are zero or even negative during the dry season, attributable to the decline of the water table to depths of about 80-100 cm belowground, causing the development of a large oxic zone where methane is consumed. This data set is the only tropical data set where

methane emissions were measured over a period of at least one season that has been available to us until now. Since it is possible that in tropical wetlands processes are dominant which are not yet included in the model, additional data sets from tropical wetlands are needed, in order to further improve and test the model. This is particulary important because tropical wetlands are a very large methane source [e.g., *Hein et al.*, 1997].

3.6. Relationship Between Climate Input and Methane Emissions

The time series used above to test the model show that the pattern of methane emissions at most high-latitude sites (1-3) is mainly controlled by soil temperature as long as the water table is above the soil surface. If the water table is below the soil surface and does not vary much, like at site 3 (Figure 5, hummock), the pattern of methane emissions is again mainly driven by changes in soil temperature, but the amplitude is influenced by the water table depth. However, as soon as the water table fluctuates around the soil surface, as for example at site 1, this connection between soil temperature and methane flux no longer applies. As it is shown in Figure 2 and discussed in section 3.1, methane emissions increase in the first about 15 days after a fall of the water table below the soil surface. This behavior is also reflected in Figure 8 which shows the connection between simulated methane emissions and soil temperature and water table at site 1. Figure 8 shows that there is a positive connection between soil temperature and simulated methane emissions. However, in the temperature range
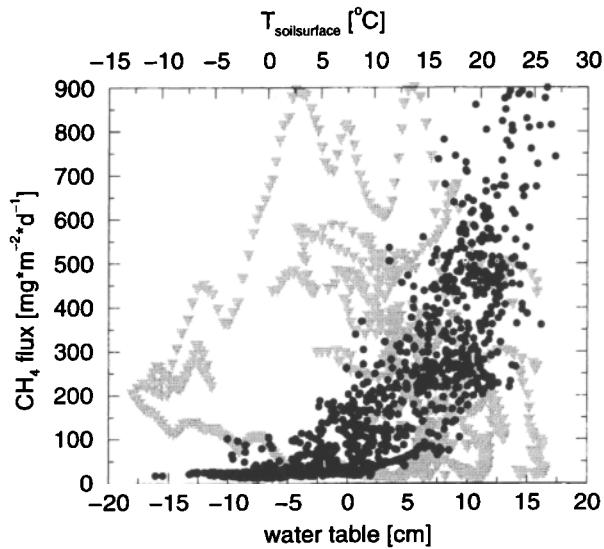
Figure 8. For site 1, the relationship between input data and simulated CH_4 emissions and the connection between the soil temperature T_{soil} at the soil surface (black dots) and the position of the water table (grey triangles) and simulated CH_4 emissions.

between 15° and 20°C, for example, simulated methane emissions range between 50 and 900 mg m^{-2} d^{-1}. Figure 8 also shows that there is no connection between water table and simulated methane emissions at site 1. The highest methane emissions occur when the water table is 5 cm above or 5 cm below the soil surface. When the water table is 13 or 17 cm belowground, methane fluxes can be as high as 450 and 250 mg m^{-2} d^{-1}, respectively. This agrees well with the results of *Shannon and White* [1994] who calculated the correlation between soil temperature and water table and observed methane fluxes at that site. At the Arctic tundra site (site 4) the connection between the environmental parameters soil temperature, water table and thaw depth, and simulated methane emissions looks different (Figure 9). There is no obvious connection
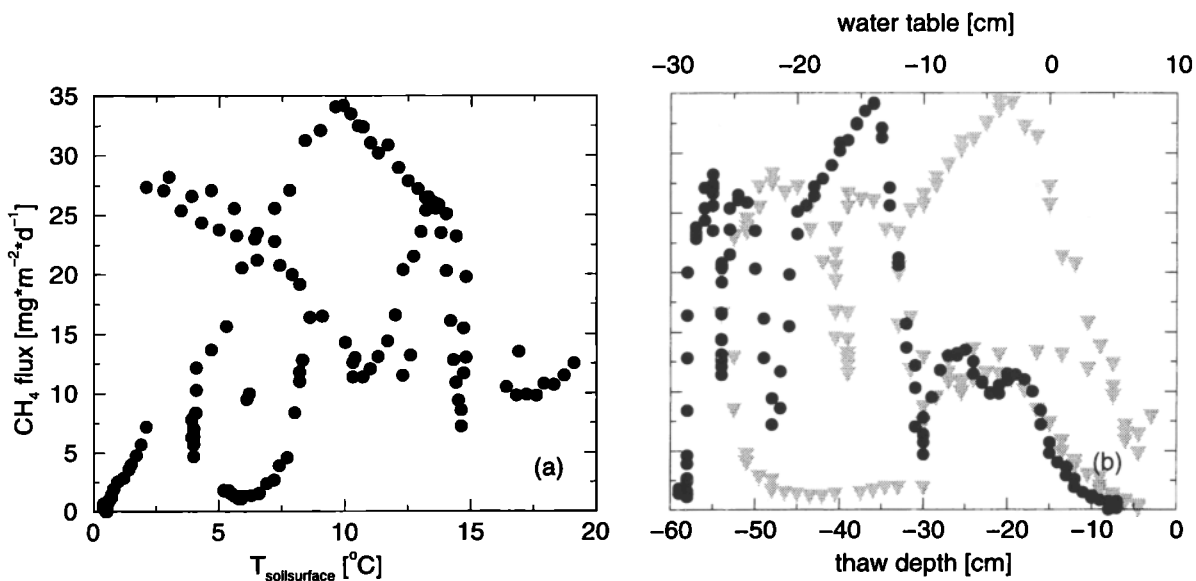
between soil temperature and simulated methane emissions (Figure 9a), and the same applies to the connection between water table depth and simulated methane emissions (Figure 9b). However, simulated methane fluxes are higher at lower thaw depths (Figure 9b), i.e., when a larger part of the soil is thawed. *Whalen and Reeburgh* [1992] found that methane emissions from all stations investigated at that Arctic tundra site correlated best with "centimeter-degrees," being defined as the absolute value of the product of thaw depth and mean soil temperature to permafrost. At the tropical test site (site 5) the temperature does not vary much, and from Figure 7 it is clear that there is a connection between the position of the water table and simulated methane emissions. These results show that in most cases, simple relationships between environmental parameters and methane fluxes do not even apply at one particular site. They differ from site to site and hence a relationship between climate input and methane emissions found at one site cannot be applied to other sites and other conditions. This means that if one wants to model methane emissions from different wetlands and under varying environmental conditions, a more process-based approach is needed.

4. Sensitivity Tests

4.1. Sensitivity to Model Parameters

The sensitivity of the model to the choice of the parameters listed in Table 2 is tested at site 1. The only other site-specific model parameter not listed in Table 2 is the relative volume of coarse pores f_{coarse}, which has been set to 0.5 at all sites except site 5, where it has been derived from a global data set used for the global model run as discussed by *Walter* [1998]. This data set gives a f_{coarse} value of 0.22 for the tropical site 5 and also f_{coarse} values around 0.5 for the regions where sites 1-4 are located The model is only sensitive to the choice of f_{coarse} at sites where diffusion is the dominant transport mechanism. This is only the case at site 4, which is unvegetated and where the water table is below the soil surface most of the time. A sensitivity test carried out at site 4 shows that a change in f_{coarse} of +0.1/-0.1 leads to a 12 5%
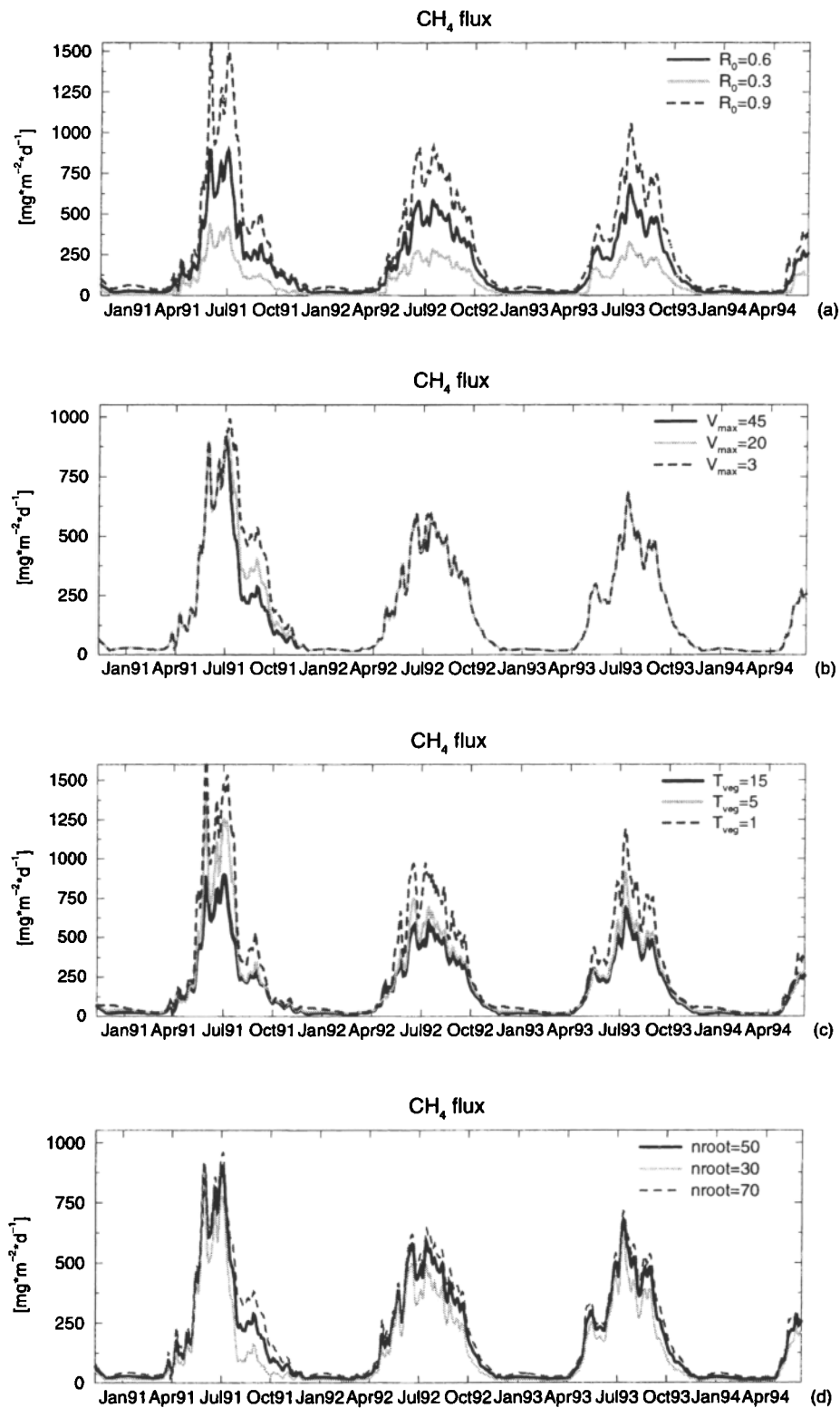

Figure 9. For site 4, the relationship between input data and simulated CH_4 emissions. (a) Connection between the soil temperature T_{soil} at the soil surface and simulated CH_4 emissions (b) Connection between the position of the water table (grey triangles) and the thaw depth (black dots) and simulated CH_4 emissions

Figure 10. Sensitivity to R_0, V_{max}, T_{veg}, and nroot tested at site1. (a) Simulated CH_4 emissions using three different values for R_0, namely 0.6 (soild line), 0.3 (grey line) and 0.9 (dashed line). (b) Simulated CH_4 emissions using three different values for V_{max}, namely 45 μM h^{-1} (soild line), 20 μM h^{-1} (grey line), and 3 μM h^{-1} (dashed line). (c) Simulated CH_4 emissions using three different values for T_{veg}, namely 15 (solid line), 5 (grey line), and 1 (dashed line). (d) Simulated CH_4 emissions using three different values for nroot, namely 50 cm (solid line), 30 cm (grey line) and 70 cm (dashed line)

increase/decrease in simulated methane emissions at that site (not shown). Differences in the soil depth nsoil only rarely affect simulated methane emissions (provided nsoil<nroot; not shown) because below the rooting depth the availability of substrate for methane production decreases exponentially (Equation (3)). In Figure 10 the results of the sensitivity tests with R_0, V_{max}, T_{veg}, and nroot are shown. The results of the test with R_0 (Equation (5)), which is adjusted to each data set, show that R_0 influences the amplitude of simulated methane emissions but not the pattern (Figure 10a). The choice of the parameter V_{max} changes the model results only in situations when the water table is below the soil surface (Figure 10b). In this situation a lower V_{max} leads to higher methane emissions because of lower methane oxidation rates (Equation (6)). The parameter T_{veg} influences not only the fraction of methane which is transported through plants but also the amount of methane that is oxidized in the rhizosphere (Equation (14)). Its influence on simulated methane emissions depends on the water table level. If the water table is above the soil surface, a higher T_{veg} leads to lower methane emissions (Figure 10c) because, in this case, less methane is transported by ebullition and more through plants. Therefore more methane is oxidized in the rhizosphere. This agrees well with observations by *Holzapfel-Pschorn et al.* [1986] who found that there was more ebullition at unvegetated sites than at vegetated ones and that a larger fraction of produced methane was emitted from unvegetated sites, if the water table was above the soil surface. If the water table is below the soil surface, diffusion is high in the first month after the fall of the water table below the soil surface (Figure 2b). Since a lower T_{veg} leads to higher diffusion rates because less methane is removed from the soil in this case (Figure 11), a lower T_{veg} leads to higher methane emissions in the first month after the water table fell below the soil surface. In situations where the water table is below the soil surface for a longer period of time, a higher T_{veg} leads to higher methane emissions because then a huge fraction of methane diffusing through the oxic soil layer is oxidized and methane transported through plants bypasses this oxic layer [*Walter*, 1998]. In Figure 11 the effect of T_{veg} on the simulated soil methane concentration is shown. It is clear that higher T_{veg} values lead to lower soil methane concentrations because more methane is removed from the soil by plants. This agrees well with observations that the soil methane concentration is higher at unvegetated sites than at vegetated sites [*Chanton and Dacey*, 1991]. The rooting depth nroot is the soil depth down to which plants can extract methane from the soil (Equation (16)). Furthermore, nroot affects the vertical distribution of substrate in the soil (Equation (3)). Throughout the root zone, substrate availability is constant, then it decreases exponentially. In the model the combined effect of an enlarged production zone and more plant-mediated transport and hence more rhizospheric oxidation is almost balanced, if the water table is above the soil surface (Figure 10d). However, if the water table falls below the soil surface transforming the soil above the water table from a production into a consumption zone, the enlargement of the zone with high productivity (higher nroot) shows a pronounced effect on simulated methane emissions.

4.2. Sensitivity to Changes in the Input Data (Climate Forcing)

The effect of changes in the soil temperature and water table on simulated methane emissions is shown in Figure 12. The effect of the water table being raised or lowered by 10 cm (Figure 12b) on simulated methane emissions is plotted in Figure 12a. As long as
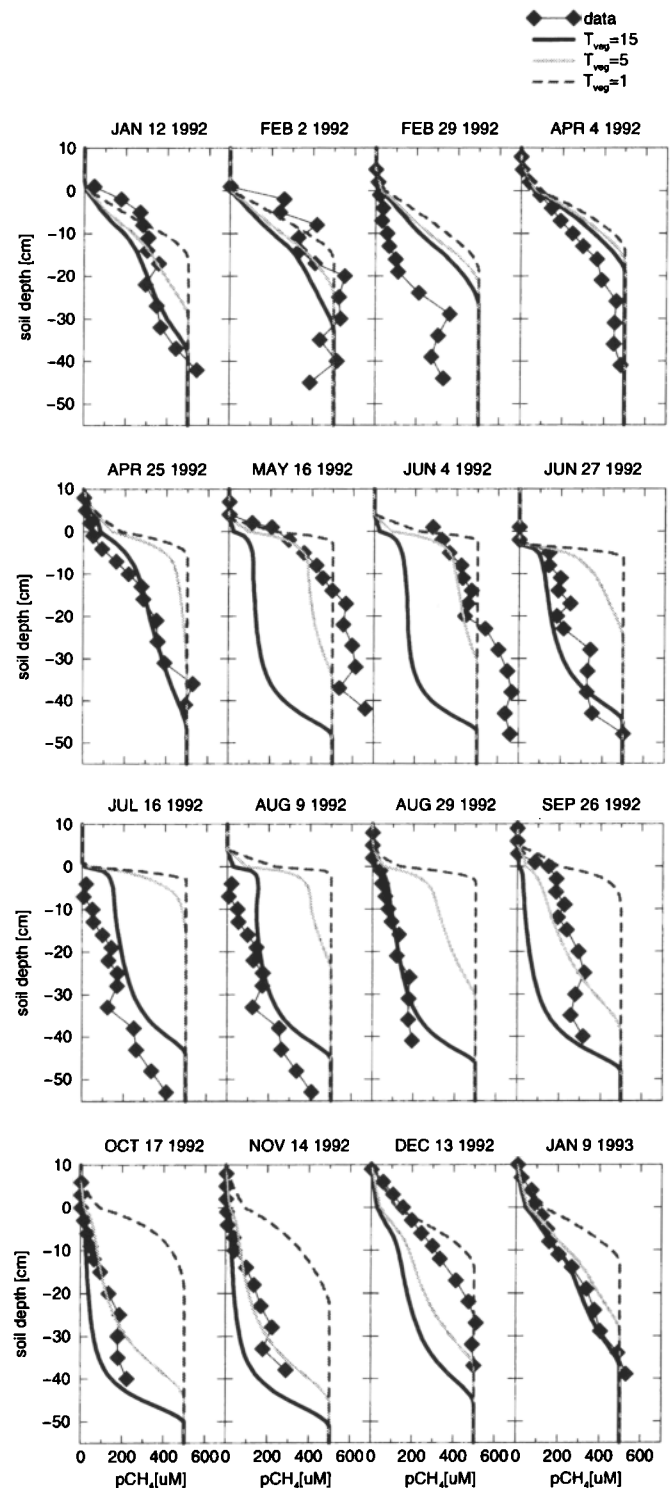

Figure 11. Sensitivity to T_{veg} tested at site 1. Simulated CH_4 concentration profiles in the soil using three different values for T_{veg}, namely $T_{veg}=15$ (solid lines), $T_{veg}=5$ (grey lines), and $T_{veg}=1$ (dashed lines) and comparison with observations (squares).

the water table is above the soil surface, the height of the water table does not change simulated methane emissions If the water table is below the soil surface, methane emissions decrease with decreasing water table Therefore the effect of a climatic change
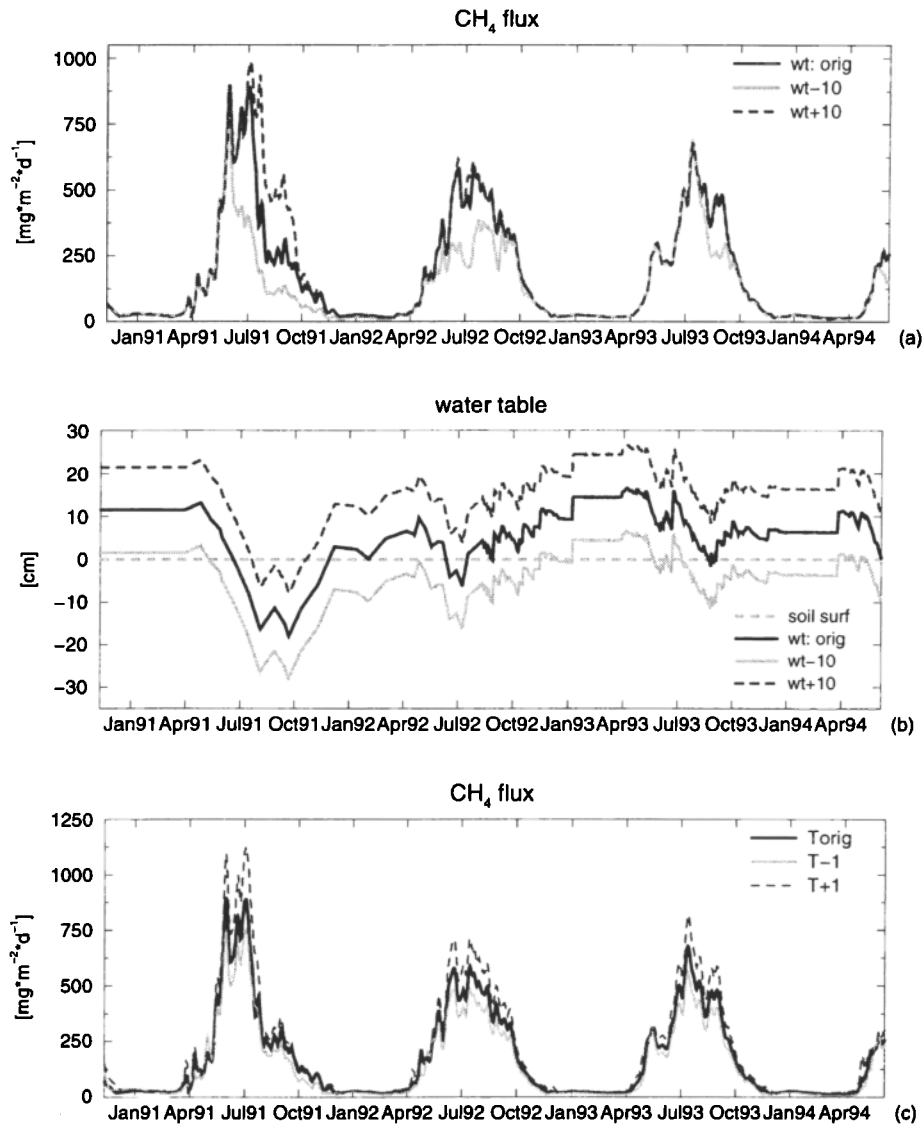
Figure 12. Sensitivity to forcing data for (a and b) water table and (c) soil temperature tested at site 1. (a) Simulated CH_4 emissions using the original water table (solid line), a by 10 cm lowered water table (grey line), and by 10 cm raised water table (dashed line). (b) Forcing, different water table levels relative to the soil surface (grey, dashed line) used to test the sensitivity of the model to the water table. Original water table (black, solid line), by 10 cm lowered water table (grey, soild line), by 10 cm raised water table (black, dashed line). (c) Simulated CH_4 emissions using the original soil temperature (solid line), by 1°C lowered water table (grey line) and by 1° raised water table (dashed line).

leading to a shift in the position of the water table at a given site depends on the conditions prevailing at that site. If the site is relatively dry like in 1991, a shift in the position of the water table is very pronounced (Table 3), whereas if the site is relatively wet as in 1993, the same shift in the water table changes methane emissions much less. A uniform change in the soil temperature by ±1° C leads to a regular shift in the amplitude of simulated methane emissions which does not depend on the position of the water table (Figure 12c). In summer, when soil temperature is higher, absolute changes in simulated methane emissions due to a ±1° C change in soil temperature are larger than in winter (see also Figure 8) A uniform increase in the soil temperature of 1°C leads to an increase in simulated methane emissions of about 21% at that site in all 3 years (Table 3), whereas a uniform decrease in the soil

temperature of 1°C reduces methane emissions by about 17% Sensitivity tests with a ±1° C change performed at sites 2-5 yield similar results (not shown). In all cases a ±1° C soil temperature change leads to a regular shift in the amplitude of simulated methane emissions, which increase by 19-23% if the soil temperature is 1°C higher and decrease by 17-21% if the soil temperature is 1°C lower. Thus a ±1° C change in the soil temperature leads to a change of the order of ±20 % in simulated methane emissions, independent of the environmental conditions prevailing in the wetland. Further sensitivity tests conducted at site 1 but using a by 10 or 20 cm lower water table and in one case also a T_{veg} of 0 (no vegetation/plant-mediated transport) show similar results. Changes in temperature mainly affect methane production and oxidation rates (Equations (5) and (6)) Methane production

Table 3. Sensitivity of Simulated CH_4 Fluxes to Climate Forcing

Run	1991	1992	1993
T+1°C	+20.5%	+20.7%	+20.5%
T-1°C	-16.6%	-17.0%	-17.1%
wt+10 cm	+25.3%	+1.4%	0.0%
wt-10 cm	-36.6%	-20.6%	-10.8%
control	78.2 g m⁻² yr⁻¹	70.4 g m⁻² yr⁻¹	65.5 g m⁻² yr⁻¹

Results of the sensitivity tests to the input data at site 1. In runs T+1°C/T-1°C the soil temperature was uniformly increased/decreased by 1°C in all soil layers throughout the whole simulation period (rows 1 and 2). In runs wt+10 cm/wt-10 cm the position of the water table was uniformly increased/decreased by 10 cm throughout the whole simulation period (see Figure 12) (rows 3 and 4). Simulated annual methane emissions for the years 1991-1993 (g CH_4 m⁻² yr⁻¹) (row 5).

depends much stronger on temperature (Q_{10}=6) than methane oxidation (Q_{10}=2), which explains why this result is obtained at all sites. The same sensitivity test (a ±1° C soil temperature change) performed with this model on a global scale shows the same result [*Walter*, 1998]. However, it is worth noting that the effect of temperature changes on the position of the water table (through evapotranspiration) is not considered in this sensitivity test. In addition, climatic changes always have irregular spatial and temporal patterns in more than one climate variable. In order to predict changes in methane emissions from natural wetlands due to climatic changes on longer timescales, it will be necessary to consider also the effects of changes in other factors such as vegetation, NPP, and the global wetland distribution. However, these sensitivity studies demonstrate that methane emissions from natural wetlands could considerably be affected by possible climatic changes in the future.

5. Summary and Conclusion

In this study we presented a model to simulate the processes leading to methane emission within a one-dimensional soil column as a function of climate. The model differs from all other models in the literature in the way that transport is parameterized. Two opposing processes operate in soil, namely methane production in the anoxic soil zone and methane consumption in the oxic soil zone. Therefore transport, which occurs by diffusion, ebullition, and through plants, plays an important role in determining the fraction of produced methane that is emitted into the atmosphere. Moreover, the different transport mechanisms influence the velocity at which methane is transported to the atmosphere. For climate forcing variables, soil temperature, water table, and thaw depth (which had been observed at four sites and were simulated at one site) as well as model derived NPP were used. Site-specific model parameters are soil depth nsoil, rooting depth nroot, the relative volume of the coarse pores f_{coarse}, the quality of plant-mediated transport T_{veg}, and in some cases the maximum methane oxidation rate V_{max}. The chemical properties (including substrate availability and quality for methanogenesis) of the soil and their influence on methane production are not modeled explic-

itly but are included in the parameter R_0 which has been adjusted to each data set. In order to apply the model to other sites without tuning R_0 or to larger (regional or global) scales, a method must be developed to derive R_0 from biogeochemical, biogeographical, and climatic variables. In the future a process-based model to simulate the production of substrate for methanogenesis as a function of the soil conditions and the climate could also be used to replace the tuning parameter R_0. The occurrence of turbulent diffusion in the standing water and its effect on transport and reoxidation of methane could be important at tropical sites in particular. However, since the data sets used in this study showed no evidence that this process is of general importance, it has not been included in the model.

In this article results of tests of the model against observational data from five different wetland sites located in North America, northern Europe, and Central America, representing a large variety of environmental conditions, are presented. The observational periods range from one season to several years. One site is underlain by permafrost and undergoes a seasonal freeze thaw cycle, while one site is located in the tropics where there is a dry/wet-seasonal cycle. At one site, simulated methane concentration profiles in the soil were compared with observed vertical concentration profiles which reflect the vertical distribution of methane production, methane oxidation, and removal of methane by the different transport mechanisms. Hence, methane concentration profiles constitute an additional constraint to the model. We investigated the climate-induced variations of simulated methane emissions at the test sites and conclude that this model can be applied to different wetlands under various conditions and can also be applied to the global scale. The relationship between the input data (soil temperature, water table, and thaw depth at the permafrost site) and simulated methane emissions was examined. Simple relationships between the input data and simulated methane emissions do not, in general, apply at single sites, and they differ from site to site. This means that a more process-based approach is needed in order to simulate climate-induced variations of methane emissions from different wetland sites. Sensitivity tests of the model to the choice of model parameters were performed. The tuning parameter R_0 (in the methane production rate equation) changes the amplitude but not the pattern of simulated methane emissions. The choice of the parameter V_{max} (in the methane oxidation rate equation) alters simulated methane emissions in situations when the water table is below the soil surface. The response to different choices of the parameter T_{veg} (quality of plant-mediated transport) depends on if the water table is above or below the soil surface and in the latter case for how long. In addition, the sensitivity of the model to uniform changes in the input data (soil temperature and water table) was tested. The response of a uniform change in the soil temperature of ±1° C is of the order of a ±20 % change in methane emissions, independent of the environmental conditions prevailing in the wetland. However, the response of the model to uniform changes in the water table of ±10 cm depends highly on the prevailing hydrologic conditions in the soil. In a relatively dry year an increase in the water table of 10 cm can enhance simulated methane emissions by as much as 25%, whereas in a wet year, there can be no change at all. Similarly, a decrease in the water table of 10 cm affects simulated methane emissions much more in a relatively dry year (in this study 37% less methane is emitted) than in wetter years. These numbers suggest that possible climate change in the future could considerably

affect methane emissions from natural wetlands. However, in order to assess the change in methane emissions due to future possible climate change, a more realistic scenario simulation should be carried out. It should use simulated future climate as input data and include possible substrate limitation, changes in wetland areas, and melting of permafrost. The latter is included in the model via the soil temperature, since the soil layers where the soil temperature is below 0°C are considered to be frozen.

Further studies and data sets are necessary to further improve the model and test it more thoroughly. For example, only one data set from tropical wetlands was available to us. Since tropical wetlands are a very important methane source, we propose that in the future emphasis should be placed on long-term studies of methane emissions from tropical wetlands. In addition, it would be advantageous to test the model with a data set consisting not only of time series of the input and output data of the model (as it was the case in this study) but also of quantities calculated in the model such as methane production rate, methane oxidation rate, and the fraction of methane transported by the different transport mechanisms. No such data set is currently available, and the development of such a data set is therefore a priority to enable a more thorough testing of this model.

Appendix A: Calculation of $f_{NPP}(t)$

The function $f_{NPP}(t)$ is derived from the variation of the NPP with time, NPP(t), as calculated by the Biosphere-Energy Transfer and Hydrology (BETHY) model [*Knorr*, 1997]. The BETHY model is a process-based model describing the water balance on vegetated surfaces and bare soils and the CO_2 balance in vegetation and soils. It uses remote sensing data and calculates the NPP on a $0.5°$ by $0.5°$ grid with monthly time steps. The model output from the BETHY model is linearly interpolated to get daily NPP(t) values. NPP(t) is used as a measure for the variation of substrate availability with time. Since part of the substrate is degraded from organic matter incorporated into the soil from dying plants in autumn, we presume that in regions with a change between growing and nongrowing seasons, i.e., where the growing season lasts for 3-9 months, the substrate availability increases again in autumn. We define the duration of the growing season as the time span when the soil temperature at 50 cm depth belowground is above 5°C.

In regions where the growing season is shorter than 3 months or longer than 9 months, $f_{NPP}(t)$ is

$$f_{NPP}(t) = NPP(t) \qquad \text{at any time,} \qquad (18)$$

whereas in regions with a growing season lasting 3 to 9 months, $f_{NPP}(t)$ is obtained from

$$f_{NPP}(t) = \begin{array}{ll} NPP(t) & grs \\ NPP_{last} + \dfrac{NPP_{max} - NPP_{last}}{0.5\ t_{nongrow}}\ t & 1.\text{half non-grs} \\ NPP_{max} - \left(\dfrac{NPP_{max} - NPP_{first}}{0.5\ t_{nongrow}}\ t\right) & 2.\text{half non-grs} \end{array} \qquad (19)$$

Here $t_{nongrow}$ is the duration of the nongrowing season in days and NPP_{last} and NPP_{first} denote the NPP(t) values of the last and first day of the growing season, respectively, and grs stands for "growing season."

Appendix B: Calculation of $f_{grow}(t)$

The function $f_{grow}(t)$ describing the growing state of the plants is assumed to be a function of the LAI and is calculated according to *Dickinson et al.* [1993]. We define a mean LAI depending on the daily mean temperature at 50 cm depth below ground $T_{50}=T(t,z=120\ cm)$ and hence calculate $f_{grow}(t)$ from

$$f_{grow}(t) = \begin{array}{ll} \Lambda_{min} & T_{50} < T_{gr} \\ \Lambda_{min} + \Lambda\left(1 - \left(\dfrac{T_{mat} - T_{50}}{T_{mat} - T_{gr}}\right)^2\right) & T_{gr} \le T_{50} \le T_{mat} \\ \Lambda_{max} & T_{mat} < T_{50} \end{array} \qquad (20)$$

where Λ_{min} and Λ have been chosen to be 0 and 4, respectively, and $\Lambda_{max}=\Lambda_{min}+\Lambda$. T_{gr} is the temperature at which plants start to grow. In regions where the annual mean soil temperature is below 5°C, T_{gr} has been set to 2°C and elsewhere to 7°C. This distinction has been made because in cold regions plants start to grow at lower temperatures than in temperate and warm regions. The same is valid for the temperature at which they reach maturity, T_{mat}, which has been set to $T_{mat}=T_{gr}+10°C$.

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