Helsinki University of Technology

Systems Analysis Laboratory Research Reports E10, November 2002

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This report is available at
www.e-reports.sal.hut.fi/pdf/E10.pdf

Series E - Electronic Reports
www.e-reports.sal.hut.fi

ISBN 951-22-6234-7
ISSN 1456-5218

Title: Connecting methane fluxes to vegetation cover and water table fluctuations at microsite level: A modeling study

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Date: November 2002

Status: Systems Analysis Laboratory Research Reports E10 November 2002

Abstract:

The paper presents a process-based model describing methane flux dynamics in different microsites of boreal peatlands. The simulated fluxes matched well to measurements in all microsites without any parameter adjustment. The model emphasizes the importance of microsite characteristics, water table and vegetation cover for methane fluxes. Water level determines the moisture and oxygen profile in peat matrix and therefore affects methane production and oxidation rates in peat profile. Vascular plants provide methanogenesis with substrates, form a pathway for methane to liberate from peat to the atmosphere and enhance methane oxidation by transporting oxygen to water saturated peat. The model connects methane fluxes to the seasonal photosynthetic cycle of plants at the microsite level and hence dynamically combines the microbial processes in peat to changing environmental factors in the level of peatland ecosystem. Sensitivity analysis of the model reveals the importance of substrate supply to methane fluxes. In addition, the capability of the vascular plants to transport oxygen downwards has a large effect on model outcome. Lack of oxygen and methane keep methane oxidation at a low level in the model simulations and changes that compensate for these lacks have a remarkable decreasing effect on simulated flux. Dry periods decrease the simulated methane flux considerably, especially if the drought prevails long, threshold for a dramatic decrease lying between 4 and 6 weeks of drought. Increase in air temperature enchances methane flux especially if the effect of increased temperature on gross primary production is taken into account.

Keywords: boreal peatlands, microsites, vegetation cover, water table, photosynthetic carbon cycle, methane flux dynamics, process-based models

Connecting methane fluxes to vegetation cover and water table fluctuations at microsite level: A modeling study

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Abstract

The paper presents a process–based model describing methane flux dynamics in different microsites of boreal peatlands. The simulated fluxes matched well to measurements in all microsites without any parameter adjustment. The model emphasizes the importance of microsite characteristics, water table and vegetation cover for methane fluxes. Water level determines the moisture and oxygen profile in peat matrix and therefore affects methane production and oxidation rates in peat profile. Vascular plants provide methanogenesis with substrates, form a pathway for methane to liberate from peat to the atmosphere and enhance methane oxidation by transporting oxygen to water saturated peat. The model connects methane fluxes to the seasonal photosynthetic cycle of plants at the microsite level and hence dynamically combines the microbial processes in peat to changing environmental factors in the level of peatland ecosystem. Sensitivity analysis of the model reveals the importance of substrate supply to methane fluxes. In addition, the capability of the vascular plants to transport oxygen downwards has a large effect on model outcome. Lack of oxygen and methane keep methane oxidation at a low level in the model simulations and changes that compensate for these lacks have a remarkable decreasing effect on simulated flux. Dry periods decrease the simulated methane flux considerably, especially if the drought prevails long, threshold for a dramatic decrease lying between 4 and 6 weeks of drought. Increase in air temperature enchances methane flux especially if the effect of increased temperature on gross primary production is taken into account.

1 Introduction

Along with increasing concern of climate change, studies on carbon cycles have received much attention. Wetlands are important contributors to global carbon cycle as they sequester atmospheric carbon into peat but simultaneously emit trace gases, carbon dioxide and methane to atmosphere. In wetlands, dynamics of methane fluxes are affected by complex interactions between abiotic and biotic environmental factors and actual processes, methane production, methane oxidation and transport from peat to atmosphere.

This paper presents a process–based model that connects methane fluxes to site specific factors, water level and vegetation cover and describes the dynamic effects of water table fluctuations on

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methane flux patterns. In fact, process-based models for methane fluxes from natural wetlands have been presented before [*Arah and Stephen*, 1998; *Cao et al.*, 1996; *Granberg et al.*, 2001; *Grant*, 1998; *Potter*, 1997; *Segers and Leffelaar*, 2001a; 2001b; *Segers et al.*, 2001; *Walter and Heimann*, 2000; *Walter et al.*, 1996; 2001a; 2001b). The simplest models [*Cao et al.*, 1996; *Grant*, 1998; *Potter*, 1997] connect methane production directly to carbon cycling, especially to primary production without modeling the processes and transport within the soil while more detailed models [*Arah and Stephen*, 1998; *Granberg et al.* 2001, *Segers and Leffelaar*, 2001a; 2001b, *Segers et al.*, 2001; *Walter and Heimann*, 2000; *Walter et al.* 1996; 2001a; 2001b] consider also the processes in the soil profile. Nevertheless, the existing models do not explicitly describe the connection between the microsite vegetation, water table and methane fluxes. Furthermore, most of the models do not take into account the dynamic effects of changes in water table patterns on methane fluxes. Only the model in [*Segers and Leffelaar*, 2001a; 2001b, *Segers et al.*, 2001] present conceptual ideas how water table changes should be taken into account but the model predictions do not match very well to measurements. In contrast, the model presented here simulates methane fluxes from different microsites in accordance to measured data.

The connection to site specific factors is important as methane fluxes have been found to vary over an order of magnitude within a few meters distance [*Frenzel and Karofeld*, 2000; *Funk et al.*, 1994; *Kettunen et al.*, 2000; *Saarnio et al.*, 1997; *Svensson and Rosswall*, 1984; *van den Pol-van Dasselaar et al.*, 1999; *Waddington and Roulet*, 1996; *Wickland et al.*, 2001]. Average water table in the microsite has traditionally been seen as crucial factor for methane flux levels [*Funk et al.*, 1994; *Morrissey et al.*, 1993; *Saarnio et al.*, 1997; *Svensson and Rosswall*, 1984; *Waddington and Roulet*, 1996] but the water table definitely it is not the only one. The comparison of two intensively studied microsites [*Kettunen et al.*, 2000, this study] where both water tables and methane fluxes were continously monitored reveals that during June-July period water table was always lower in flark B than in lawn A (average difference of 4 cm) but methane emissions were almost twice as high from lawn A as from flark B. In fact, sedge cover has been found to be the most important single variable affecting methane flux in several recent studies [*Bellisario et al.*, 1999; *Bubier et al.*, 1995; *Granberg et al.*, 2001b; *Nilsson et al.*, 2001; *Schimel*, 1995; *Tuittila et al.*, 2000; *van den Pol-van Dasselaar et al.*, 1999]. Hence, it is surprising that none of the recent process–based models [*Arah and Stephen*, 1998; *Cao et al.*, 1996; *Granberg et al.*, 2001; *Grant*, 1998; *Potter*, 1997; *Segers and Leffelaar*, 2001a; 2001b; *Segers et al.*, 2001; *Walter and Heimann*, 2000; *Walter et al.* 1996; 2001a; 2001b] explicitly considers vegetation cover while the model presented in this paper connects the methane fluxes to vegetation cover.

Another aspect where the current model differs from the previous models is the way it describes the dynamic effects of water table fluctuations on methane fluxes. Water tables typically show both a seasonal pattern with lowest values during midsummer and short-term fluctuations due to occurrence or lack of rain showers. In future climate, precipitation and water table patterns are likely to change [*IPCC Climate Change*, 2001] and therefore, it is extremely important to model the relationship between the fluctuating water table and methane fluxes.

The paper begins by introducing the microsites and describing the basic assumptions on which the model is based, continue by validating the model simulations against the measured fluxes and finish by sensitivity analysis of the model outcome to model parameters and changes in environmental factors.

2 Materials and methods

2.1 Mire, microsites and measurements

The mire, microsites and measurements are described in detail in [*Kettunen et al.*, 2000] and here, only basic information is given. Methane fluxes, temperature and water tables were intensively measured over a summer season in six different microsites situated close to each other in a boreal low-sedge *Sphagnum papillosum* pine fen lagg of the mire complex Salmisuo situated in eastern Finland (62° 47' N, 30° 56 E'). The six microsites were selected to represent different moisture conditions and vegetation surfaces of the mire. The driest microsites in the mire were *Sphagnum fuscum* hummocks and the wettest microsites *S. balticum – S. majus* flarks while the dominant microsite type was *Eriophorum vaginatum – S. balticum* lawn. Better understanding of the microsite characteristics have resulted in more valid names for two microsites, as flark A in [*Kettunen et al.*, 2000] is now referred to as *Carex* lawn A, while lawn A [*Kettunen et al.*, 2000] is now called *Eriophorum* lawn A in order to differentiate it from the *Carex* lawn A. The names for other four microsites, hummocks A and B, lawn–low hummock B, and flark B, have remained unchanged.

2.1.1 Photosynthesis level in relation to microsite vegetation

To reconstruct the daily gross primary production of the vegetation community in the microsites of the fen, a multiplicative model described in detail in an earlier paper [*Kettunen*, 2000] was used

$$GPP(t) = a_1 T_0 ETI \frac{PAR}{PAR + k_1} \tag{1}$$

where PAR = photosynthetically active radiation, ETI = effective temperature sum index (summing temperatures exceeding + 5°C) = average temperature sum and T_0 = peat surface temperature. Hourly values for $GPP(t)$ were first calculated using hourly values for T_0 and PAR and daily values for ETI and hourly values were then integrated to get daily values for $GPP(t)$. In the study by *Kettunen* [2000] parameters a_1 and k_1 were estimated separately for each microsite class from measurements from the same Salmisuo mire during the same growing season. For details on the measurements, see [*Alm et al.*, 1997] and and for details on the modeling aspects, see [*Kettunen*, 2000].

Photosynthesis level differed among microsites [*Kettunen*, 2000]. As all microsites had a 100 % coverage of bottom layer vegetation, the level of photosynthesis depended on the coverage of field layer vegetation. The field layer covered only 2.5 % of the microsite surface in the flark B (Table 1) which had maximum photosynthesis rate of around 600 mg CO_2 m^{-2} h^{-1}. In dry microsites, the field layer coverage percent varied between 10 and 25 % and maximal photosyntesis rate ranged between 900 and 1400 mg CO_2 m^{-2} h^{-1}. The maximal photosynthesis rate was linearly related to field layer coverage percentage (r^2=0.94, p=0.001). Using this linear relationship, it was estimated that the field layer vegetation binds approximately 64 % of GPP in dry microsites and approximately 13 % of GPP in the flarks while the propotion of bottom layer sphagna in these microsite types is 36 % and 87 %, respectively.

As sphagna do not have roots, it is assumed that the carbon bound by the bottom layer vegetation remains in the topmost layer 0-5 cm. A proportion of the carbon bound by sphagna in the topmost layer is in principle available for methanogenesis in the model but due to availability of oxygen in the surface layer, the contribution of carbon from sphagna to methane fluxes remains

	Coverage (%) of different plant types			
	Non–transporting species	Transporting non–sedges	Sedges	Total field layer
C. lawn *A*	0.5	0.0	25.0	25.5
Flark *B*	0.0	0.0	2.6	2.6
E. lawn *A*	1.0	0.1	12.6	13.7
Lawn–low hummock *B*	11.5	7.5	0.5	19.5
Hummock *A*	11.7	10.0	1.0	22.7
Hummock *B*	15.5	0.0	1.0	16.5

Table 1: The coverage percentage of different plant groups (see text for details) and total field layer. Non-transporting species include *Andromeda polifolia*, *Chamaedaphne calyculata*, *Drosera rotundifolia*, *Empetrum nigrum*, *Ledum palustre*, *Vaccinium microcarpum* and *Vaccinium oxycoccus*, transporting non–sedges include *Rubus chamaemorus* and sedges include *Carex rostrata*, *Carex limosa*, *Carex pauciflora*, *Eriophorum vaginatum*, *Eriophorum angustifolium* and *Scheuchzeria palustris.* The vegetation cover in the microsites is presented in detail in *Kettunen et al.* [2000].

negligible.

Field layer vegetation, that is far more important in relation to methane flux dynamics, was divided to three different plant type categories in the model (Table 1). Non–transporting species, like *Potentilla sp.* were not assumed to transport methane upwards or oxygen downwards. The roots of these plants were assumed to be located mainly in the uppermost 0-15 cm [*King et al.* 1998; *Saarinen*, 1996]. The roots of transporting non–sedges, like *Rubus chamaemorus* were assumed to be located similarly as those of non–transporting species [*Wallén* 1986, 1992] but transporting non–sedges were assumed capable of transporting methane upwards and oxygen downwards. Sedges, like *Carex and* Eriophorum species, were assumed to have roots down to 2 meters as measured by *Saarinen* [1996] and to be capable of transporting methane upwards and oxygen downwards. A proportion of the carbon bound by field layer species is assumed to promote methanogenesis in the layers where the plants have their roots.

2.2 Modeling aspects

2.2.1 General

The model is a structural one-dimensional (peat depth) partial-differential equation model where chemical compounds (acetate, methane and oxygen) and peat microbes (methane producers and methane oxidizers) in peat profile act as state variables. The model uses daily values for photosynthetically active radiation PAR(t), peat temperature profile T(t,z) and water table WT(t) as forcing inputs and simulates the temporal evaluation of chemical compounds and peat microbes in peat profile and methane fluxes from the different microsites for the growing period from May till October with simulation step of one day. The moisture content in each layer is calculated according to the model by *Weiss et al.* [1998] and the dependence of diffusivity coeffient on moisture is treated similarly as in *Campbell* [1985] (see Fig. 4 in *Segers & Leffelaar* [2001b] for a graphical representation). Michaelis-Menten dynamics are used to describe dependence of process rates on substrate and oxygen concentrations and $Q10$ values to describe temperature dependence. In the computations, the partial-differential equations are transformed to ordinary differential equations by dividing the peat to 5 cm layers. Each layer is assumed to be homogenous in relation to concentrations of chemical compounds, microbial biomass, root biomass and physical circumstances. The model deals with concentrations i.e. mol of chemical compound or g of or bacterial biomass per volume unit (cubic meter). Model was written to a C++ program and solved numerically with the fourth order Runge–Kutta method with an adaptive step size as implemented by *Press et al.* [1988].

2.2.2 Model dynamics

In mathematical terms, the model (2)–(18) describes dynamics of the five state variables (Table 2), $Subs(z,t)$ = substrate for methanogenesis at depth z of peat profile on time t, $CH_4(z,t)$ = methane at depth z of peat profile on time t, $O_2(z,t)$ = oxygen at depth z of peat profile on time t, $Methanogens(z,t)$ = methane producers at depth z of peat profile on time t and $Methanotrophs(z,t)$ = methane oxidizers at depth z of peat profile on time t.

Dynamics for substrate concentration

$$\begin{aligned}\frac{\partial Subs(z,t)}{\partial t} &= SubsProd - SubsCons \\ &+ \frac{\partial^2}{\partial z^2}[D(z)Subs(z,t)] \end{aligned} \tag{2}$$

where

$$\begin{aligned} SubsProd &= [(f_{GPP}GPP(t) + f_{ETI}ETI(t)]\rho(z) \\ x & \ [1 - \frac{O_2(z,t)}{O_2(z,t) + kSubsProd_{O_2}}] \\ x & \ T(SubsProdQ10) \qquad (3) \\ SubsCons &= \frac{\mu_{Methanogens}}{Y_{Methanogens}} Methanogens(z,t) \\ x & \ \frac{Subs(z,t)}{Subs(z,t) + kCH_4Prod_{Subs}} \\ x & \ [1 - \frac{O_2(z,t)}{O_2(z,t) + kCH_4Prod_{O_2}}] \\ x & \ T(CH_4ProdQ10) \qquad (4) \end{aligned}$$

The concentration of substrate available for methanogenesis (equation 2) depends on substrate production rate *SubsProd* (equation 3) and substrate consumption rate *SubsCons* (equation 4) which both increase with increasing temperature with $T(x) = x^{\frac{T(z)-10}{10}}$ and, being anaerobic processes, decrease with increasing oxygen concentration. Substrate for methanogenesis is assumed to diffuse (last term in equation 2). Substrate consumption rate *SubsCons* also depends on substrate concentration and methane producing bacteria. Two types of easily degradable carbon are considered in equation (3), one proportional to gross primary production describing root exudation and the other proportional to the average temperature sum index (ETI index, see [*Alm et al.*, 1997; *Kettunen*, 2000] describing root litter decomposition and contribution of dying roots to methanogenesis.

Dynamics for methane concentration

$$\begin{aligned}\frac{\partial CH_4(z,t)}{\partial t} &= CH_4Prod - CH_4Oxid \\ &- CH_4PlantFlux + \frac{\partial^2}{\partial z^2}[D(z)CH_4(z,t)] \end{aligned} \tag{5}$$

where

$$\begin{aligned}
CH_4Prod &= \gamma_{CH_4Prod}(1 - Y_{Methanogens})SubsCons && (6)\\
CH_4Oxid &= \frac{\mu_{Methanotrophs}}{Y_{Methanotrophs}}Methanotrophs(z,t)\\
&x \; \frac{CH_4(z,t)}{CH_4(z,t) + kCH_4Oxid_{CH_4}}\\
&x \; \frac{O_2(z,t)}{O_2(z,t) + kCH_4Oxid_{O_2}}\\
&x \; T(CH_4OxidQ10) && (7)\\
CH_4PlantFlux &= PlantTrans\ \rho(z)[CH_4(z,t) - \bar{CH}_4] && (8)
\end{aligned}$$

Methane concentration (equation 5 depends on methane production rate CH_4Prod (equation 6) and methane oxidation rate CH_4Oxid (equation 7). Methane is assumed to diffuse (last term in equation 5) and to be transported by plants (equation 8) but ebullition is not taken into account. Methane production rate equals substrate consumption rate with stoichiometric and mass balance corrections (equation 6). Methane oxidation (equation 7) depends on methane concentration, methane oxidizers and increases with increasing temperature and oxygen concentration.

Dynamics for oxygen concentration

$$\begin{aligned}
\frac{\partial O_2(z,t)}{\partial t} &= +O_2PlantFlux - AerO_2Cons\\
&- \; CH_4O_2Cons + \frac{\partial^2}{\partial z^2}[D(z)O_2(z,t)] && (9)
\end{aligned}$$

where

$$\begin{aligned}
AerO_2Cons &= \gamma_{Aer}[(f_{GPP}GPP(t) + f_{ETI}ETI(t))\rho(z)\\
&x \; \frac{O_2(z,t)}{O_2(z,t) + kAer_{O_2}}T(AerDecomQ10) && (10)\\
CH_4O_2Cons &= \gamma_{CH_4Oxid}CH_4Oxid && (11)\\
O_2PlantFlux &= PlantTrans\ \rho(z)\\
&x \; [\bar{O}_2 - O_2(z,t) - PlantO_2Cons] && (12)
\end{aligned}$$

Oxygen (equation 9) is consumed by aerobic oxygen decomposition $AerO_2Cons$ (equation 10) and methane oxidation CH_4O_2Cons (equation 11). It is assumed that the part of easily available carbon $(f_{GPP}GPP(t) + f_{ETI}ETI(t))$ that is not used as substrate for methanogenesis is exposed to aerobic decomposition that consumes oxygen. Also diffusion (last term in equation 9) and transport of oxygen by plants (equation 12) affect oxygen concentration. The oxygen consumption of the plant ifself is accounted for in equation (12) while methane transport and oxidation within the plant are not explicitly modeled.

Dynamics for methane producers and oxidizers

$$\begin{aligned}
\frac{\partial Methanogens(z,t)}{\partial t} &= MethanogenGrowth - MethanogenDying && (13)\\
\frac{\partial Methanotrophs(z,t)}{\partial t} &= MethanotrophGrowth - MethanotrophDying && (14)
\end{aligned}$$

where

$$\begin{aligned}
MethanogenGrowth &= Y_{Methanogens} SubsCons &(15)\\
MethanotrophGrowth &= Y_{Methanotrophs} CH_4 Oxid &(16)\\
MethanogenDying &= \lambda_{Methanogens} Methanogens(z,t) &(17)\\
MethanotrophDying &= \lambda_{Methanotrophs} Methanotrophs(z,t) &(18)
\end{aligned}$$

Methane producers and methane oxidizers (equations 13 and 14) gain biomass when producing (equation 15) and oxidizing (equation 16) methane, respectively. Dying of methane producers $MethanogenDying$ and oxidizers $MethanotrophDying$ is assumed proportional to their biomass (equations 17 and 18). Bacteria are assumed to be fixed to peat particles which is supported by the work by *van den Pol-van Dasselaar and Oenema* [1999] who found highest methane production in largest peat particles.

2.2.3 Parameter values

The constants and parameters used in simulations are presented in Table 2 and Table 3, respectively. The data set, on which the current study is based, contains continuous measurements on environmental conditions and methane fluxes but only few and in most case indirect measurements on the actual processes taking place in peat profile and no data on substrate, methane or oxygen concentrations or microbial populations in peat profile at any time point. As different parameter combinations can result in essentially the same outcome i.e. similar methane flux pattern, it was not reasonable to carry out algorithmic paramater estimations. Hence, the current parameter values are not claimed to be truly optimal. Nevertheless, the literature provides information on the range of variation and order of magnitude of the parameter values. Furthermore, some parameters have a very limited effect on methane flux and are hence not very important to consider (see Sensitivity to model parameters). Concentrating on the parameters for which the model is most sensitive and comparing the predicted flux to measurements, a set of parameters given in Table 3 was selected. As the simulated methane fluxes from six different microsites are in accordance with the measured, accurate enough parameter values for simulating relevant methane flux patterns have apparently been found.

2.2.4 Initial states

The first model run used initial values of zero for substrate $S(z,0)$, methane $M(z,0)$ and oxygen $O(z,0)$ and non–zero values for methane producing and oxidizing bacteria. Simulations were then repeated starting from the state at the end of simulation for each microsite to achieve an equilibrium state. When equilibrium for each microsite was found, it was then used as initial state for the final simulation. In *Eriophorum* lawn A that is the dominant microsite type in the fen studied, initial substrate and oxygen concentrations at peat surface were 0.02 mM and 0.22 mM at the equilibrium state. Deeper in peat profile, both initial substrate and oxygen concentrations were close to zero. Initial methane concentrations increased from 0.00 mM to 0.28 mM at 1 m depth. At equilibrium, methane producers were present down to 25 cm (to a lesser extent down to 75 cm) and methane oxidizers between 5 and 10 cm.

Variable			Unit		Range
$Subs(z,t)$	=	Substrate	(mol substrate)	m^{-3}	0.00–0.36
$CH_4(z,t)$	=	Methane	(mol CH_4)	m^{-3}	0.00–0.29
$O_2(z,t)$	=	Oxygen	(mol O_2)	m^{-3}	0.00–0.30
$Methanogens(z,t)$	=	Methane producers	(g biomass)	m^{-3}	0.00–2.01
$Methanotrophs(z,t)$	=	Methane oxidizers	(g biomass)	m^{-3}	0.00–2.01

Constant	Value	
d_{water}	2.0×10^{-9}	$m^2\ s^{-1}$ [a1]
d_{air}	2.0×10^{-4}	$m^2\ s^{-1}$ [a2]
γ_{Aer}	2	mol O_2 (mol C)$^{-1}$ [b1]
γ_{CH_4Prod}	2	mol CH_4 (mol acetate)$^{-1}$ [b1]
γ_{CH_4Oxid}	2	mol O_2 (mol CH_4)$^{-1}$ [b1]
$\bar{CH}_4$	3.33×10^{-6}	mol CH_4 m^{-3} [c1]
$\bar{O}_2$	0.35	mol O_2 m^{-3} [c2]

Table 2: Model state variables and constants used in simulations. Range for state variables represents minimum and maximum values when simulating model (2)–(18) with parameters in Table 3 for the six microsites.

[a1] [*Hesslein*, 1980; *Jähne et al.*, 1987]

[a2] [*Jost*, 1952; *Marrero and Mason*, 1972]

[b1] stoichiometric

[c1] calculated at NTP conditions, $\bar{CH}_4 = \frac{\alpha_{CH_4} P Air_{CH_4}}{RT}$ where $\alpha_{CH_4} = 0.040$ m^3 gas m^{-3} H_2O, [e.g. *Segers*, 1998], P = pressure [Pa], Air_{CH_4} = air methane concentration = 2 ppm (V/V), R = 0.083143 J mol^{-1} K^{-1} and T = temperature [K]

[c2] calculated at NTP conditions, $\bar{O}_2 = \frac{\alpha_{O_2} P Air_{O_2}}{RT}$ where $\alpha_{O_2} = 0.036$ m^3 gas m^{-3} H_2O [e.g. *Segers*, 1998], P = pressure [Pa], Air_{O_2} = air oxygen concentration = 21 % (V/V), R = 0.083143 J mol^{-1} K^{-1} and T = temperature [K]

Parameter	Value		Range reported in literature		
f_{GPP}	0.10		0.01-0.60		[d1]
f_{ETI}	0.001 (0.002)	for flark B			
	0.003 (0.006)	for other microsites			[d2]
$kAer_{O_2}$= $kSubsProd_{O_2}$	0.01	mM	0.0002–0.040	mM	[e1]
$kCH_4Prod_{O_2}$	0.01	mM	0.0002-0.040	mM	[e2]
kCH_4Prod_{Subs}	0.005	mM	0.004–0.70	mM	[e3]
$kCH_4Oxid_{CH_4}$	0.005	mM	0.0005–0.141	mM	[e4]
$kCH_4Oxid_{O_2}$	0.01	mM	0.0003–0.200	mM	[e5]
$\lambda_{Methanotrophs}$	0.02	d^{-1}	0.01–0.79	d^{-1}	[f1]
$\lambda_{Methanogens}$	0.01	d^{-1}	0.01–0.79	d^{-1}	[f2]
$\mu_{Methanotrophs}$	0.24	d^{-1}	0.24–10.32	d^{-1}	[g1]
$\mu_{Methanogens}$	0.20	d^{-1}	0.03–2.88	d^{-1}	[g2]
$AerDecomQ10$= $SubsProdQ10$	2.0				[h1]
$CH_4ProdQ10$	4.0		1.5–28.0		[h2]
$CH_4OxidQ10$	2.0		1.4–4.1		[h3]
$PlantO_2Cons$	0.10	mM	0.05–0.10	mM	[i1]
$PlantTrans$	0.68	m d^{-1}	0.008 - 17.2	m d^{-1}	[d3]
$Y_{Methanotrophs}$	0.40	mol C (mol CH_4)$^{-1}$	0.10–0.80	mol C (mol CH_4)$^{-1}$	[j1]
$Y_{Methanogens}$	0.08	mol C (mol acetate)$^{-1}$	0.037–0.30	mol C (mol acetate)$^{-1}$	[j2]

Table 3: Parameter values for simulating the peat profile concentrations and methane fluxes from the microsites.

[d1] [*Boon and Mitchell*, 1995; *Chasar et al.*, 2000; *Dannenberg and Conrad*, 1999; *Granberg et al.*, 2001; *King and Reeburgh*, 2002; *Minoda et al.*, 1996; *Saarnio et al.*, 1998; *von den Pol-van Dasselaar and Oenema*, 1999]

[d2] f_{ETI} was adjusted so that the contribution of carbon from root decay was on average the same as that from root exudation over the period from the start of the growing season till Aug 14 when ETI index showed increasing trend which resulted in different value for flark B for which the photosynthesis level and root exudation were lower. During the period from Aug 14 till the end of the season the value of f_{ETI} was doubled to describe the increased substrate availability due to dying roots (see [*Sorrell et al.*, 1997]

[d3] [*Segers and Leffelaar*, 2001a; *Sigren et al.*, 1997]

[e1] [*Segers and Leffelaar*, 2001a]

[e2] [*James*, 1993; *Segers and Leffelaar*, 2001a]

[e3] [*Fukuzaki et al.*, 1990; *Huser et al.*, 1982; *James*, 1993; *Lovley and Klug*, 1986; *Panikov et al.*, 2000; *Segers and Kengen*, 1998]

[e4] [*Bender and Conrad*, 1992; *Bosse and Frenzel*, 2001; *Granberg et al.*, 2001; *James*, 1993; *Jones and Morita* 1983; *Lee et al.*, 1993; *Segers*, 1998; *Segers and Leffelaar*, 2001a; *van Bogedom et al.*, 2001a; 2001b; *Walter and Heimann*, 2000; *Walter et al.*, 1996; *Yavitt et al.*, 1990]

[e5] [*Bender and Conrad*, 1994; *Segers*, 1998; *Segers and Leffelaar*, 2001a; *van Bogedom et al.*, 2001a; 2001b; *Yavitt et al.*, 1990]

[f1] [*James*, 1993; *Kettunen et al.*, 1999; *Servais et al.*, 1985]

[f2] [*Havlik et al.*, 1986; *James*, 1993; *Kettunen et al.*, 1999; *Lee et al.*, 1993; *Lovley and Klug*, 1986; *Servais et al.*, 1985]

[g1] [*James*, 1993; *Jones and Morita*, 1983; *Spivak and Rokem*, 1994; *van Bogedom et al.*, 2001a; 2001b]

[g2] [*Havlik et al.*, 1986); *James*, 1993; *Lovley and Klug*, 1986; *Panikov et al.*, 2000; *Segers and Kengen*, 1998; *Servais et al.*, 1985; *Yang and Guo*, 1990]

[h1] [*Atlas and Barta*, 1987; *van Hulzen et al.*, 1999]

[h2] [*Fey and Contrad*, 2000; *Segers*, 1998; *Walter and Heimann*, 2000; *Walter et al.*, 1996; 2001a; *Worthy et al.*, 2000]

[h3] [*Segers*, 1998]

[i1] 0.5 mol O_2 (kg dw roots)$^{-1}$ d^{-1} x 0.2 (kg dw roots) that corresponds to ≈ 12 % sedge coverage [*Saarinen*, 1996; *Segers and Leffelaar*, 2001a]

[j1] [*James*, 1993; *Segers*, 1998; *Spivak and Rokem*, 1994]

[j2] [*Huser et al.*, 1982; *James*, 1993; *Grant*, 1998; *Lee et al.*, 1993; *Lovley and Klug*, 1986; *Yang and Guo*, 1990; *Segers and Kengen*, 1998; *Panikov et al.*, 2000]

2.2.5 Sensitivity analysis

The reference situation to which the changes in model parameters and environmental condition were compared was the simulation with parameters in Table 3 and environmental conditions of *Eriophorum* lawn *A* that is the dominant microsite type in the mire studied. The criterion to evaluate the magnitude of change was the percentage difference in cumulative methane flux between the changed and reference situation.

All parameters except $Q10$ values were increased and decreased two–fold and ten–fold to analyze the effects of the parameter over a wide range. For $Q10$ values, a ten–fold decrease would have resulted in non–reasonable parameter values below 1.0 meaning that reactions would occur faster in lower temperatureees and hence, only two–fold decrease and two–fold and ten–fold increase were considered. For many parameter values, a ten–fold decrease or increase from the reference value results in a value outside the range reported in literature (see Table 3) and if dramatic changes in model simulations occur due to these ten–fold changes in parameter values, it is possible to be operating outside the valid range of the model. On the other hand, those parameters that cause dramatic changes in model outcome with a ten–fold change cause remarkable changes in model outcome already with a two–fold change that remains within the literature range. In cases where the change in the cumulative methane flux due to a ten–fold increase/decrease was less than 5 % in absolute value, the corresponding two–fold increase/decrease that would have resulted in even lower percentage difference were not considered further.

Changes in hydrological conditions were first studied simulating the system with a constant water table of 0, 5, 10, 15, 20, 30 and 200 cm below peat surface. The effects of a constant change in water table were simulated using measured *Eriophorum* lawn *A* water table +5, -5, -10, -20, -30 and -200 cm. The sensitivity of the model to increase and decrease in precipitation, respectively, was tested using artificially constructed water tables. The period of increased or decreased precipitation (wet/dry period) was started between 0 and 20 weeks from the beginning of the growing season and the duration varied from 2 to 20 weeks. Till the start of the wet/dry period, water table was assumed to be at the same level as the measured water table in *Eriophorum* lawn *A*. During the wet/dry period, water table was assumed to increase/decrease by 0.5 cm per day (if during wet period water table was already at peat surface it was assumed to stay there). At the end of wet/dry period, water table was assumed to decrease/increase by 0.5 cm per day until it reached the level of measured water table in *Eriophorum* lawn *A* which it then followed till the end of the season.

Effects of ± 1 and ± 2 °C change in air temperature was studied calculating the peat profile temperature according to temperature diffusion equation similarly as described in [*Granberg et al.*, 1999]. In one set of simulation, gross primary production was not changed but in another set, it was updated according to equation (1).

Effects of changes in vegetation cover were analyzed increasing/decreasing two–fold and ten–fold the coverage percentage of the different plant types, namely non–transporting species, transporting non–sedges and sedges (see Table 1). In cases where the change in the cumulative methane flux due to a ten–fold increase/decrease in vegetation coverage % was less than 5 % in absolute value, the corresponding two–fold increase/decrease that would have resulted in even lower percentage difference were not considered further.

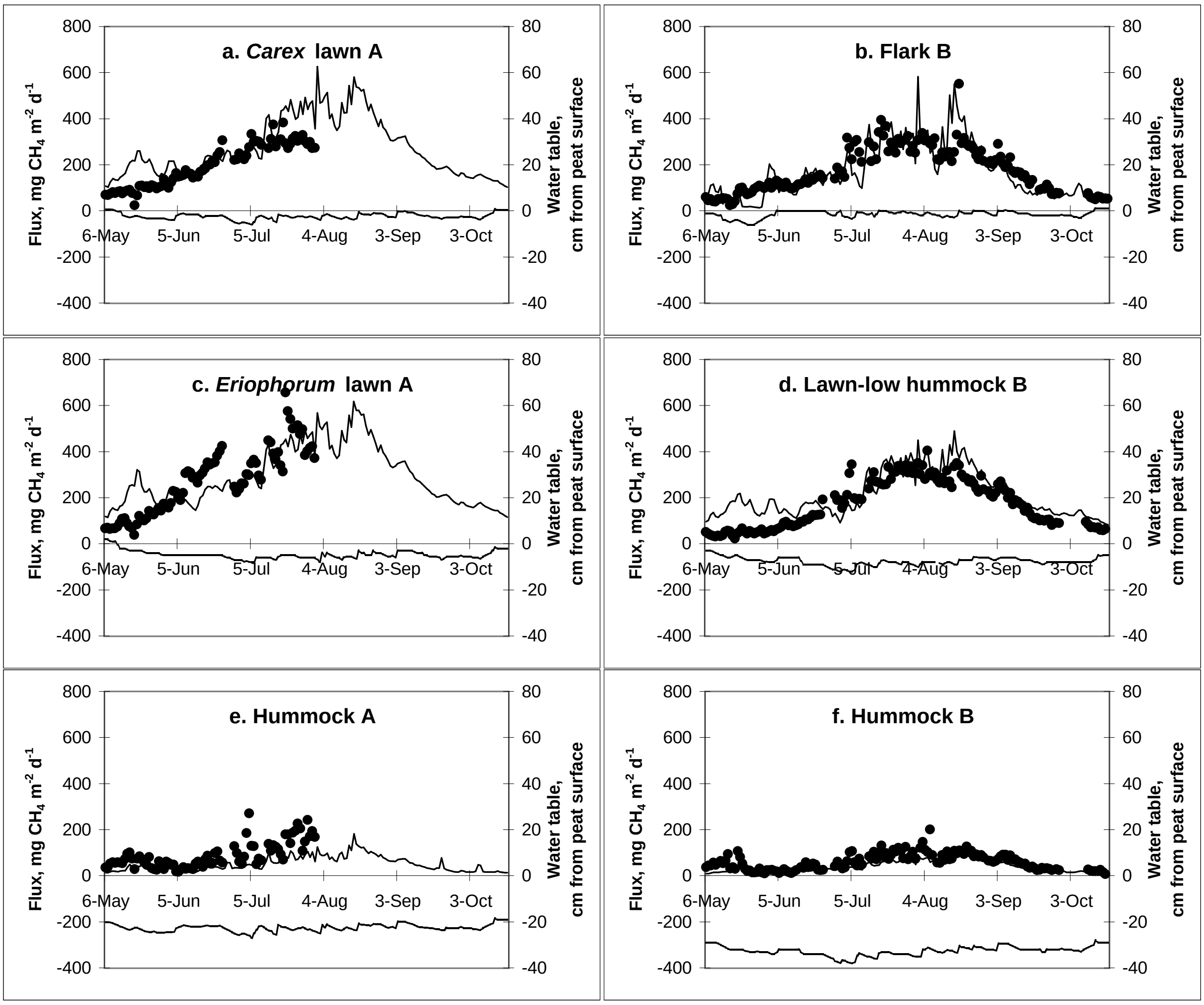

Figure 1: Simulated (solid line and left axis) and measured (circles and left axis) methane flux and measured water tables (solid line and right axis, negative values indicate that water table remains below peat surface) in a. *Carex* lawn *A* b. flark *B* c. *Eriophorum* lawn *A* d. lawn–low hummock *B* e. hummock *A* f. hummock *B*. For *Carex* lawn *A*, *Eriophorum* lawn *A* and hummock *A* data were available till the end of July.

3 Results

3.1 Model simulations for the six microsites

The simulated methane fluxes correspond relatively well to measured fluxes in all six microsites throughout the growing season (Figs. 1 and 2). The shape of the seasonal pattern is similar for all microsites, but methane flux levels are much lower from hummocks *A* (Fig. 1.e) and *B* (Fig. 1.f), lawn–low hummock *B* (Fig. 1.d) and flark *B* (Fig. 1.b) than from *Carex* lawn *A* (Fig. 1.a) and *Eriophorum* lawn *A* (Fig. 1.c). Water table varied in the surface layer 0–5 cm in *Carex* lawn *A* and flark *B* and in layer 5–10 cm in lawn–low hummock for most of the time while in *Eriophorum* lawn *A* it fluctuated around 5 cm below peat surface. In the dry microsites, hummock *A* and *B* water table varied between 20 and 25 cm and between 30 and 35 cm below peat surface, respectively.

Differences in methane fluxes result from differences in substrate, methane and oxygen concen-

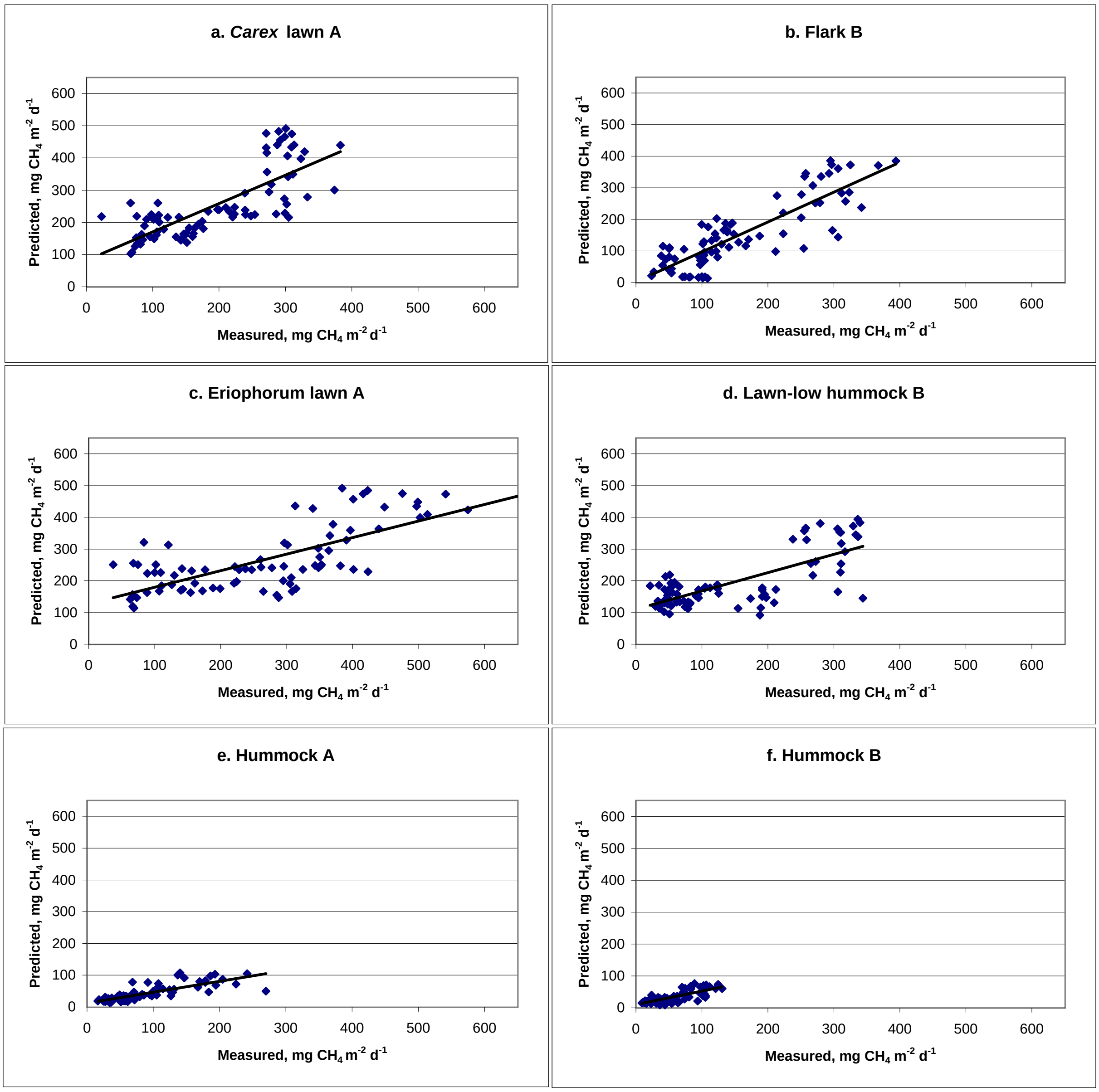

Figure 2: Simulated vs. measured methane flux in a. *Carex* lawn *A* b. flark *B* c. *Eriophorum* lawn *A* d. lawn–low hummock *B* e. hummock *A* f. hummock *B*.

trations and consequent differences in methane producing and methane oxidizing populations in peat profile. Figure 3 represents the temporal evaluation of the different variables in peat profile for *Eriophorum* lawn A that is the dominant microsite type in the mire studied while the average peat profiles of methane and oxygen concentrations and the biomass of methane producers for the different microsites are represented in Figure 4. Simulated substrate concentrations remain typically very low (below 0.001 mM) indicating that methane producers are able to use the substrate efficiently (layers 5–100 cm in Fig. 3.c). Only in the surface layer 0–5 cm of the wet microsites, *Carex* lawn A, *Eriophorum* lawn A and lawn–low hummock B, substrate concentrations sometimes peak following water table fluctuations (layer 0–5 cm shows peaks at both early and late season in Fig 3.c). According to model simulations, peat below water table is anoxic as oxygen concentrations typically stay below 0.001 mM (layers 5–100 cm in Fig. 3.d and Figs. 4.a–f). In the surface layer 0–5 cm of all microsites oxygen concentrations reach atmospheric equilibrium values (layer 0–5 cm in Fig. 3.d and Figs. 4.a–f) and in hummocks A and B also the layers 5–15 cm show non–zero oxygen concentrations that decrease with increasing distance to peat surface (Figs. 4.e–f). Simulated methane concentrations remain low (below 0.003 mM) above water table (layer 0–5 cm in Fig. 3.e and Figs. 4.a–f). At water table, simulated concentrations typically reach a value between 0.01 mM and 0.10 mM increasing with increasing peat depth (Fig. 3.e and Figs. 4.a–f). At flark B that has scarce field layer vegetation and low sedge coverage, methane concentrations stay below 0.05 mM thoughout the peat profile as there is very little carbon input to the peat profile by vascular plant roots (Fig. 4.b). In lawn–low hummock B and hummocks A and B, where shrub coverage is higher than in flark B, but sedge coverage still remains low methane concentrations in deep peat level between 0.10 and 0.15 mM (Figs. 4.d–f. In *Carex* lawn A and *Eriophorum* lawn A, methane concentration at 1 m reaches 0.30 mM (Figs. 3.e and 4.c).

All six microsites support methanogenic populations at some depth (Figs. 3.a and 4.a–f). In deep layers, lack of substrate prevents the existence of stable population, especially in those microsites where sedge cover is low (flark B, hummocks A and B and lawn–low hummock B). In surface layer of dry microsites, high oxygen concentration limits the survival of methanogens. At flark B that has scarce field layer vegetation, methanogenic population of 2.0 (g biomass) m^{-3} (that corresponds to $\approx 2 \times 10^7$ cells (g wet peat)$^{-1}$ if a single cell volume of 0.1 $\mu\mathrm{m}^3$ is assumed) lives in surface layer 0–5 cm, while layers 5-30 cm support much smaller populations (Fig. 4.b). At hummocks, methane producers live in layers 10–30 cm below peat surface with maximum population in layer 10–15 cm at hummock A and in layer 15–20 cm at hummock B in accordance with the difference in water table level between these microsites (Figs. 4.e–f). Lawn–low hummock B supports a large methanogenic population in layer 5–10 cm and a downwards decreasing population between 10 and 25 cm below peat surface (Fig. 4.d). *Carex* lawn A and *Eriophorum* lawn A support high methanogenic population between 5 and 25 cm below peat surface and relatively high population also in surface layer and layer from 25 to 30 cm (Figs. 3.a, 4.a and 4.c). Also deepest layers show non–zero methanogenic populations reflecting the contribution of sedge roots in providing substrate for methanogenesis.

Extremely wet growing season apparently did not favour methane oxidation as stable population of methane oxidizers only existed at single depth in four of the microsites, while hummock B and lawn–low hummock B did not support stable methane oxidizing population at all. In flark B, methane oxidizers existed in large number (3.1 g biomass m^{-3}) at surface layer 0-5 cm below peat surface. *Carex* lawn A and *Eriophorum* lawn A supported methane oxidizing population of 0.59 and 0.36 (g biomass) m^{-3}, respectively, at layer 5–10 cm below peat surface (Fig. 3.b). Hummock A supported a small population of 0.004 (g biomass) m^{-3} at layer 5–10 cm below peat surface.

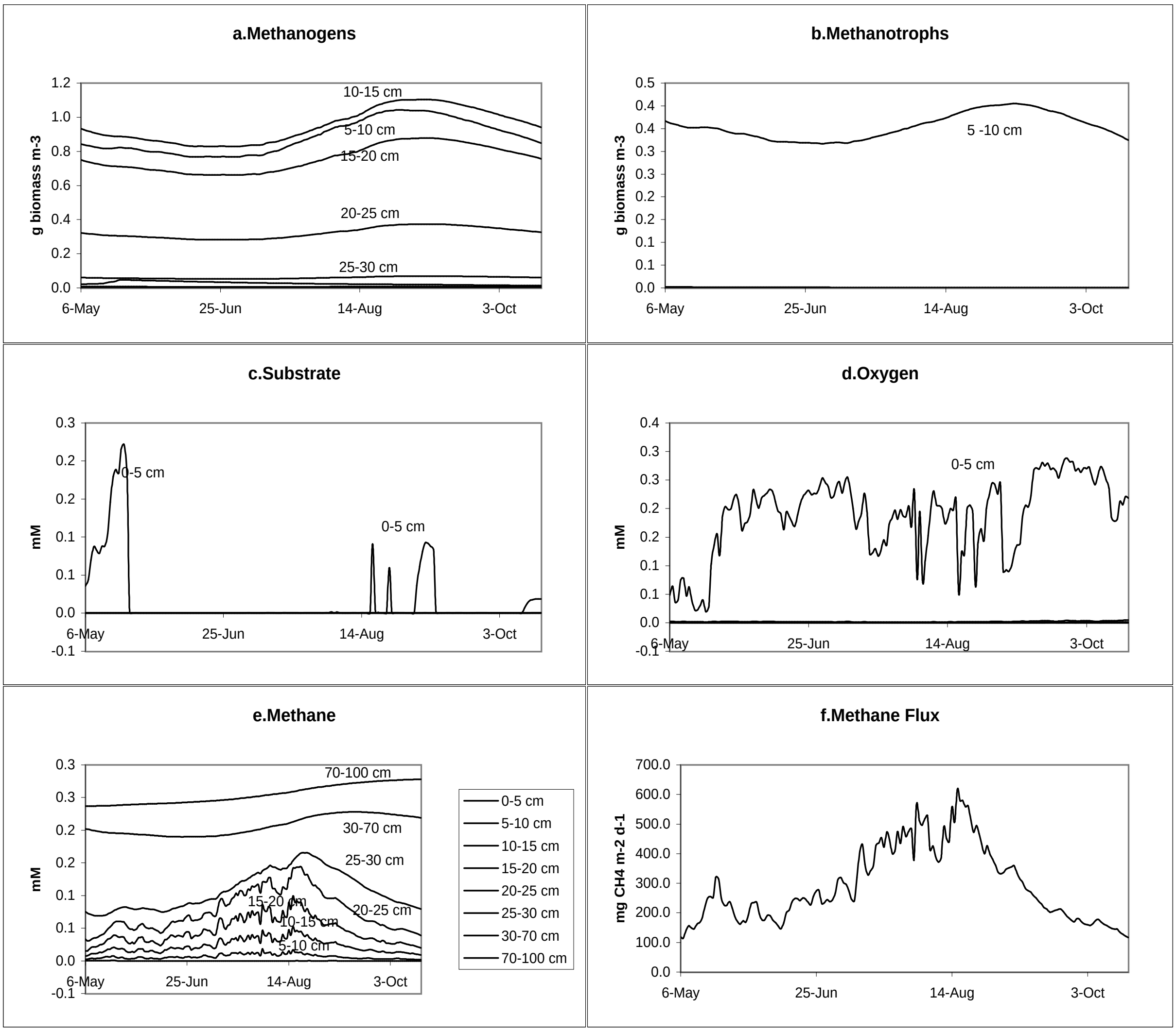

Figure 3: Simulated a. biomass of methane producers, b. biomass of methane oxidizers, c. substrate concentration, d. oxygen concentration and e. methane concentration in peat profile and f. methane flux from *Eriophorum* lawn *A*. The labels indicate layers as centimeters below peat surfaces. For clarity, only average values for layers 30-70 cm and 70-100 cm below peat surface are shown. Biomass of methane producers and oxidizers, substrate and oxygen concentration do not show concentration gradient between 30-70 cm and 70-100 cm, but methane concentrations increase downwards between 30-70 cm. In a, biomass of methane producers at layers 0–5, 30–70 and 70–100 cm below peat surface, in b, biomass of methane oxidizers at layers 0–5, 10–15, 15–20, 20–25, 30–70 and 70–100 cm below peat surface, in c, substrate concentrations at layers 5–10, 10–15, 15–20, 20–25, 30–70 and 70–100 cm below peat surface, in d, oxygen concentration at layers 5–10, 10–15, 15–20, 20–25, 30–70 and 70–100 cm below peat surface and in e, methane concentration at layers 0–5 and 5–10 cm below peat surface remain practically at zero level.

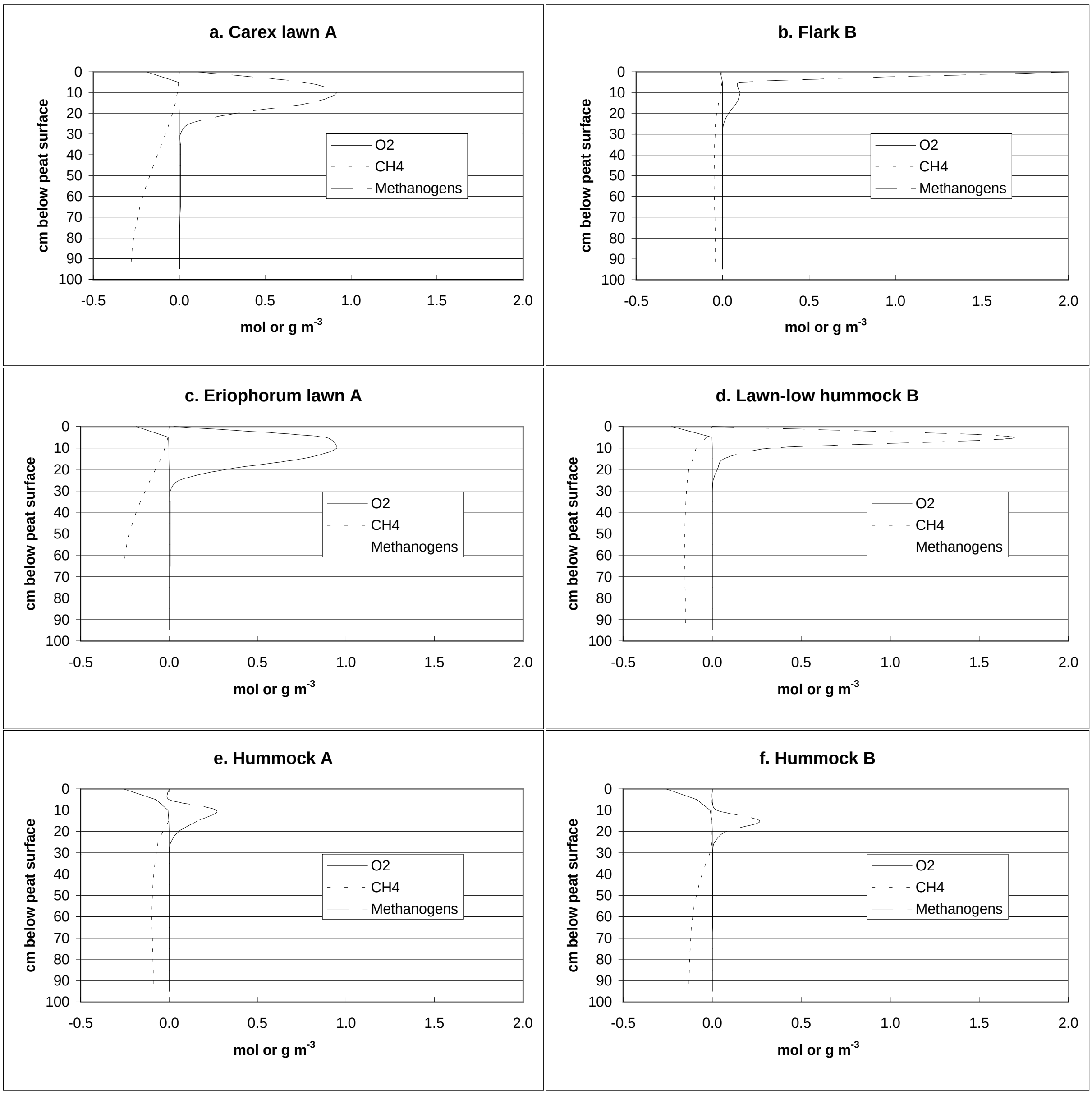

Figure 4: Average profile for oxygen and methane concentrations and methanogenic biomass in a. *Carex* lawn *A* b. flark *B* c. *Eriophorum* lawn *A* d. lawn–low hummock *B* e. hummock *A* f. hummock *B*.

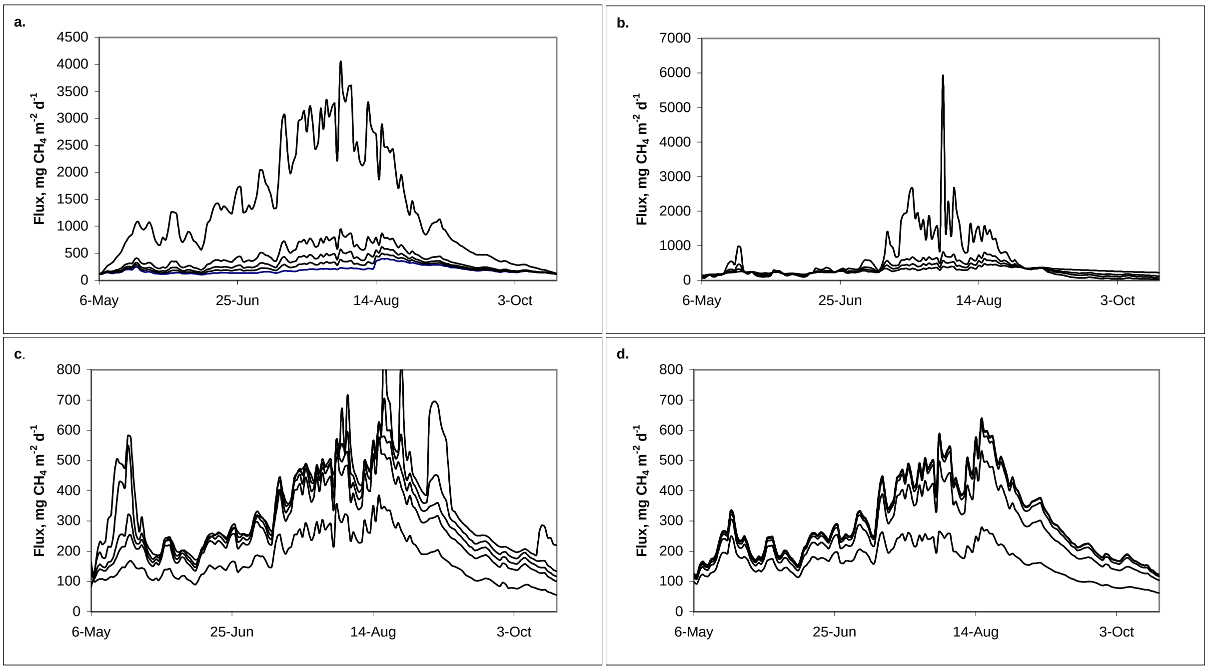

Figure 5: Simulated methane flux from *Eriophorum* lawn A with ten/two–fold increase/decrease in parameter values to which the model is very sensitive a. f_{GPP}: from lowest to highest curve $\frac{1}{10}$ x f_{GPP}, $\frac{1}{2}$ x f_{GPP}, f_{GPP}, 2 x f_{GPP}, 10 x f_{GPP} b. $AerDecomQ10 = SubsProdQ10$: from lowest to highest curve $\frac{1}{2}$ x $AerDecomQ10$, $AerDecomQ10$, 2 x $AerDecomQ10$, 10 x $AerDecomQ10$ c. $PlantTrans$ from lowest to highest curve 10 x $PlantTrans$, 2 x $PlantTrans$, $PlantTrans$, $\frac{1}{2}$ x $PlantTrans$, $\frac{1}{10}$ x $PlantTrans$ d. $\mu_{Methanotrophs}$ from lowest to highest curve 10 x $\mu_{Methanotrophs}$, 2 x $\mu_{Methanotrophs}$, $\mu_{Methanotrophs}$, $\frac{1}{2}$ x $\mu_{Methanotrophs}$, $\frac{1}{10}$ x $\mu_{Methanotrophs}$. Note differences in vertical axis scale between a, b and c and d.

3.2 Sensitivity to model parameters

Substrate availability turned out be the most important control for methane production in *Eriophorum* lawn A (Table 4 and Fig. 5.a). Methane flux increases/decreases remarkably with an increase/decrease in the parameters f_{GPP} and f_{ETI} related to substrate supply. It is interesting to note that also population of methane oxidizers increase with increasing substrate supply, but the increase in methanogenic population is larger and dominates the effects of increase in substrate supply. With a ten–fold decrease in f_{ETI}, the microsite is no longer able to support a stabile methane producer population. The effect of ten–fold decrease in f_{GPP} on methanogens is less dramatic as decaying roots in late season give enough substrate to keep the population stable. The reason for an increase in methane fluxes with an increase $SubsProdQ10$ also lies in the substrate supply, as higher $SubsProdQ10$ increases the substrate supply during the mid–season when both temperature and photosynthesis levels are at maximum (Table 4 and Fig. 5.b). Methane production is so strictly substrate limited, that the parameters related to conversion from acetate to methane and population dynamics of methane producing bacteria (i.e. $CH_4ProdQ10$, kCH_4Prod_{Subs}, $kCH_4Prod_{O_2}$, $Y_{Methanogens}$, $\mu_{Methanogens}$, $\lambda_{Methanogens}$) have only small effect on simulated methane flux (Table 4).

Parameter	ten–fold decrease	two–fold decrease	two-fold increase	ten–fold increase
f_{GPP}	-35	-20	+39	+361
f_{ETI}	-52	-29	+58	+537
$kAer_{O_2} = kSubsProd_{O_2}$	+5	+4	-9	-30
$kCH_4Prod_{O_2}$	-1			+2
kCH_4Prod_{Subs}	+0			-0
$kCH_4Oxid_{CH_4}$	-12	-4		+4
$kCH_4Oxid_{O_2}$	-30	-9		+4
$\lambda_{Methanotrophs}$	-9	-4		+5
$\lambda_{Methanogens}$	+0			-2
$\mu_{Methanotrophs}$	+4		-12	-43
$\mu_{Methanogens}$	-1			+3
$CH_4ProdQ10$		-0		+1
$CH_4OxidQ10$		+0	-1	-6
$AerDecomQ10 = SubsProdQ10$		-4	+10	+97
$PlantO_2Cons$	-1			+4
$PlantTrans$	+22	+10	-9	-41
$Y_{Methanotrophs}$	-13	-3		+4
$Y_{Methanogens}$	+1			-1

Table 4: Percentage difference in cumulative methane flux between simulation with a change in one parameter and the reference case with parameters values presented in Table 3 and *Eriohorum* lawn A vegetation and water table. The simulations with non–reasonable $Q10$ values below 1.0 that would have resulted from a ten–fold decrease in $Q10$ values are not reported. If the ten–fold change resulted in a change smaller than 5 % in absolute value, the corresponding two–fold change is not reported.

Another important factor affecting methane flux is connected to oxygen dynamics as a ten–fold increase/decrease in the capability of the plant to transport gases $PlantTrans$ results in an increase/decrease in oxygen concentrations in peat profile decreasing/increasing production and consequently, methane flux (Table 4 and Fig. 5.c). The capability of the plant to transport oxygen downwards dominates the dynamics so that plant oxygen consumption $PlantO_2Cons$ has only very limited effect on the methane flux.

The contribution of methane oxidation remains generally very low as lack of oxygen and, to certain extent, lack of methane, limits methane oxidation rates. So any change in parameter set that compensates the lack of oxygen results in an increase in oxidation and a decrease in flux (Table 4). Increased growth rate $\mu_{Methanotrophs}$ directly affects the survival of methane oxidizers (Fig. 5.d), similarly as decreased mortality $\lambda_{Methanotrophs}$, even though the effect of the latter one to the flux remains much weaker. Decrease in $kCH_4Oxid_{O_2}$ implies that the rate of oxidation in a given oxygen concentration is higher decreasing the flux. Decrease in $kCH_4Oxid_{CH_4}$ that implies that the rate of oxidation in a given methane concentration is higher results in similar but weaker effect as oxygen limits oxidation rates more than methane. Methane oxidation apparently is not temperature limited as the effect of changes in $CH_4OxidQ10$ remain low. The effects of changes in $Y_{Methanotrophs}$ and $kAer_{O_2} = kSubsProd_{O_2}$ are quite complex. A change in $kAer_{O_2} = kSubsProd_{O_2}$ affects more aerobic decomposition than methane production so that an increase in $kAer_{O_2} = kSubsProd_{O_2}$ results in a decrease in aerobic decomposition inducing a higher oxygen concentration hence decreasing the flux. A decrease in $Y_{Methanotrophs}$ increases oxygen concentrations and hence, shifts the balance from methane oxidation to aerobic decomposition which consumes substrate for methane production and decreases the flux somewhat.

3.3 Sensitivity to changes in environmental conditions

The water table in *Eriophorum* lawn *A* remains quite constant at about 5 cm below peat surface during the growing season. Hence, it is not surprising that a constant water table at 5 cm results in almost the same cumulative methane flux than the actual water table (Table 5). If the water table stayed at peat surface throughout the season, methane flux would increase by ≈ 20 %. Results in Table 5 emphasize the importance of the uppermost 15 cm as decrease in water table from peat surface to 15 cm below peat surface decrease methane flux by ≈ 50 % while further decrease from 15 cm to 30 cm changes the flux from -49 % of the reference to -57 % of the reference (i.e. with 8 % unit).

As actual water table remained close to peat surface, the simulated effects of wet periods were not very dramatic (Table 6). Actually, the longer the wet period prevailed, the closer the methane flux came to the situation where water table remained at the peat surface throughout the growing season (the + 18 % increase in Table 5 with wt=0 cm).

The dry periods affected methane fluxes more than wet periods (Table 7 and Fig. 6.a). The methane flux from a simulation with a two–week dry period was not much different from the reference case. Nevertheless, a dry period of four weeks already induced a clear drop in methane flux but after the end of the dry period methane flux soon recovered to the reference level. The reason for the fast recovery lies in the fact that methane producers had not declined severily during the dry period. When the duration of the dry period increased from four weeks to six weeks, methanogens declined much more and the recovery in the methane flux took much longer a time. After a dry period of more than eight weeks, the methanogens decreased to so low a level that the flux did not recover during the remaining growing season.

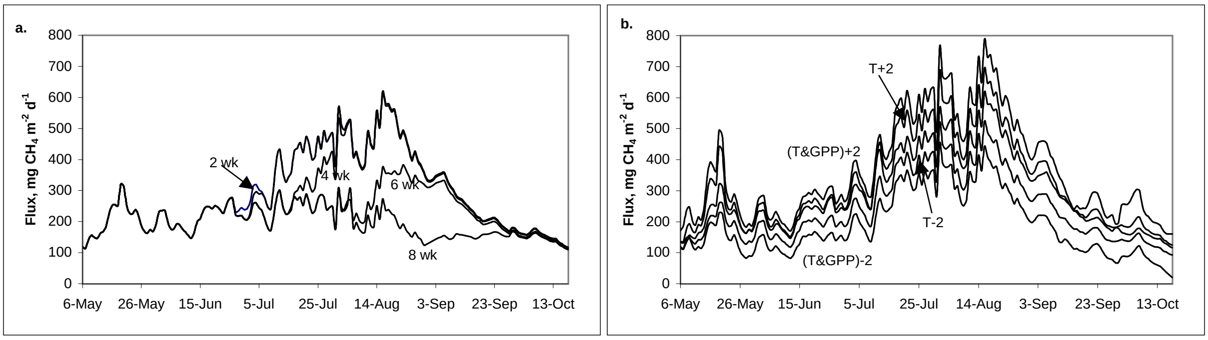

Figure 6: Simulated methane flux from *Eriophorum* lawn *A* when a. duration of wet period starting on June 17th increases from 0 to 8 weeks b. air temperature is increased by ±2 °C and GPP is either updated according to equation (1) ((T&GPP)-2 and (T&GPP)+2) or remains non–changed (T-2 and T+2.

An increase/decrease in air temperature results in consequent increase/decrease in methane flux even in the case when the effect of temperature on gross primary production in the microsite is not taken into account (Table 8). However, when gross primary production is recalculated to correspond to the new air temperature which results in higher amount of substrate for methane production, the order of change increases again emphasizing the fact that substrate availability limits the methane production in the current situation.

A decrease in sedge cover implies a clear decrease in methane flux. The reason for the small decrease in methane flux after an increase in sedge cover is due to the enchanced oxygen supply to deep peat layers when more sedges are present. In practise, a less than 10 % decrease in methane flux would probably lack notice. Still, the fact that *Carex* lawn *A* shows lower overall methane flux than *Eriophorum* lawn *A* even though the sedge cover is higher in *Carex* lawn *A* than in *Eriophorum* lawn *A* supports the idea that methane fluxes do not automatically increase with increasing sedge cover. The effect of a change in coverage % of either non–transporting species or transporting non–sedges is negligible which may be partly explained by the fact that the coverage of these species in *Eriophorum* lawn *A* is originally very small (Table 8). If the coverage of the transporting non–sedges in the basic case were at the same range as that of sedges, the response to a decrease and an increase in the coverage of transporting non–sedges would be similar but actually even stronger than the response to a decrease and an increase in the coverage of sedges.

c	-200	-30	-20	-15	-10	-5	0	+5
wt=c	-75	-59	-51	-34	-12	-0	+18	+18
wt+c	-76	-60	-57	-49	-31	-11	±0	+18

Table 5: Percentage difference in cumulative methane flux between simulation with constant water table or water table with a constant difference to the measured water table and the reference case with parameter values presented in Table 3 and *Eriohorum* lawn *A* vegetation and water table.

	Duration of wet period										
Start of wet period	2	4	6	8	10	12	14	16	18	20	22
06-May (week 00)	+0	+1	+2	+3	+8	+14	+16	+17	+18	+18	+18
20-May (week 02)	+1	+1	+3	+8	+13	+16	+17	+18	+18	+18	
03-Jun (week 04)	+1	+2	+7	+12	+15	+16	+16	+17	+17		
17-Jun (week 06)	+1	+6	+11	+14	+15	+15	+16	+16			
01-Jul (week 08)	+4	+9	+13	+14	+14	+14	+14				
15-Jul (week 10)	+3	+7	+8	+8	+9	+9					
29-Jul (week 12)	+2	+2	+3	+3	+3						
12-Aug (week 14)	+0	+1	+1	+1							
26-Aug (week 16)	+0	+0	+0								
09-Sep (week 18)	+0	+0									
23-Sep (week 20)	+0										

Table 6: Percentage difference in cumulative methane flux between simulation with higher water table for the wet period and the reference case with parameters values presented in Table 3 and *Eriohorum* lawn *A* vegetation and water table. Wet period was extended as far as possible till the end of the growing season but the later the wet period started the shorter time was available before the growing season ended and therefore, the values in lower triangle are not presented.

	Duration of dry period										
Start of dry period	2	4	6	8	10	12	14	16	18	20	22
06-May (week 00)	-0	-1	-4	-15	-31	-44	-53	-56	-59	-59	-59
20-May (week 02)	-0	-3	-12	-28	-41	-49	-53	-55	-57	-57	
03-Jun (week 04)	-1	-5	-18	-33	-42	-48	-51	-53	-54		
17-Jun (week 06)	-0	-7	-21	-33	-40	-43	-45	-47			
01-Jul (week 08)	-2	-12	-25	-33	-37	-39	-40				
15-Jul (week 10)	-1	-10	-18	-24	-25	-27					
29-Jul (week 12)	-5	-12	-18	-20	-20						
12-Aug (week 14)	-2	-7	-10	-11							
26-Aug (week 16)	-1	-4	-6								
09-Sep (week 18)	-0	-2									
23-Sep (week 20)	-1										

Table 7: Percentage difference in cumulative methane flux between simulation with lower water table for the dry period and the reference case with parameters values presented in Table 3 and *Eriohorum* lawn *A* vegetation and water table. Dry period was extended as far as possible till the end of the growing season but the later the dry period started the shorter time was available before the growing season ended and therefore, the values in lower triangle are not presented.

ΔT_{air}	-2 °C	-1 °C	+1 °C	+2 °C
No change in GPP	-17	-11	+3	+11
Change in GPP	-36	-22	+8	+26
	ten–fold decrease	two–fold decrease	two-fold increase	ten–fold increase
Coverage % of non-transporting species	+1		-1	-6
Coverage % of transporting non–sedges	+0			-1
Coverage % of sedges	-53	-36	-8	-7

Table 8: Percentage difference in cumulative methane flux between simulation with a change in air T either with (according to equation (1)) or without a change in gross primary production or simulation with a change in coverage percentage of different plant types (see Table 1) and the reference case with parameters values presented in Table 3 and *Eriohorum* lawn *A* vegetation and water table. If the ten–fold change in coverage % resulted in a change smaller than 5 % in absolute value, the corresponding two–fold change is not reported

4 Discussion

4.1 Model simulations in relation to literature data

The simulated substrate concentrations match well to measured acetate concentrations [*Avery et al.*, 1999; *Dannenberg and Conrad*, 1999; *Fey and Conrad*, 2000; *Sigren et al.*, 1997]. Both *Avery et al.* [1999] and *Sigren et al.* [1997] report early season peaks in acetate concentrations that resemble the simulated peaks in two of the microsites.

The simulation results support the idea that the water table roughly determines the boundary between oxic and anoxic peat [*King et al.*, 1990; *Nedwell and Watson*, 1995]). The critical limit of 0.02 mM below which methane oxidizers are able to compete with heterotrophs according to the modeling study by *van Bogedom et al.*, [2001b] is not exceeded in the model simulations except at the very surface layers indicating that methanotrophs would be able to outcompete heterotrophs in current conditions.

The measured peat methane concentrations [*Bosse and Frenzel*, 2001; *Chasar et al.*, 2000; *Crill et al.*, 1988; *Fechner and Hemond*, 1992; *Frenzel and Karofeld*, 2000; *King et al.*, 1990; *Lilley et al.*, 1988; *Moore et al.*, 1990; *Shannon and White*, 1994; *Shurpali et al.*, 1993; *Svensson and Rosswall*, 1984; *Thomas et al.*, 1996; *van der Nat and Middelburg*, 1998; *Whiting and Chanton*, 1992; *Windsor et al.*, 1992; *Yavitt et al.*, 1990] stay below 1.0 mol m^{-3}, being low above water table and increasing with increasing depth below water table in accordance to simulation results in the current paper.

Assuming a single cell volume of 0.1 μm^3, the simulated biomass of methane procuders ranged from less than 10^4 cells (g wet peat)$^{-1}$ in deep layers to maximal population of 3 x 10^6 cells (g wet peat)$^{-1}$ in hummocks *A* and *B* and further to maximal population of 1-2 x 10^7 cells (g wet peat)$^{-1}$ in flark *B*, *Carex* lawn *A*, lawn–low hummock *B* and *Eriophorum* lawn *A*. The simulated range match well with the estimates presented in literature of the amount of methane producers in per cm^{-3} when bulk density of 0.10 (g dry weight) cm^3 is used to convert the counts (g dry weight)$^{-1}$ to counts cm^{-3} [*Bodelier et al.*, 2000; *Boon et al.*, 1996; *Mayer and Conrad*, 1990; *Schütz et al.*, 1989; *van Bogedom et al.*, 2001b; *Williams and Crawford*, 1984].

The simulated populations of methane oxidizers that range from clearly less than 10^3 cells (g wet peat)$^{-1}$ in most cases to maximum value of 4 x 10^4 cells (g wet peat)$^{-1}$ for hummock *A*, 3–6 x 10^6 cells (g wet peat)$^{-1}$ for *Eriophorum* lawn *A* and *Carex* lawn *A* and 3 x 10^7 cells (g wet peat)$^{-1}$ flark *B* are somewhat smaller than the estimates presented in literature for the amount of methane oxidizers [*Bender and Conrad*, 1994; *Gilbert and Frenzel*, 1995; *Happell et al.*, 1993; *King*, 1994] indicating that the methane oxidation level is low in the microsites.

Estimates of the methane fraction that becomes reoxidated before it reaches atmosphere vary from 0 to 100 % [*Fechner and Hammond*, 1992; *Frenzel and Karofeld*, 2000; *King et al.*, 1990; *Moosavi and Crill*, 1998; *Sass et al.*, 1992; *Schütz et al.*, 1989; *Yavitt et al.*, 1988; 1990]. In five of the six microsites, methane oxidation remains at very low level according to the model simulations, as only 3 % and 6 % of the methane produced is oxidized before reaching the atmosphere in *Eriophorum* lawn *A* and *Carex* lawn *A*, respectively and in hummocks *A* and *B* and lawn–low hummock *B* the proportion is even smaller. In the flark *B* where the field layer vegetation was very scarce and most of the photosynthetic carbon cycles in the very surface layer where oxygen concentration was high enough to support oxidation, almost half of the produced methane was oxidized. The low oxidation is in accordance with *Bellisario et al.* [1999] who do not consider methane oxidation to be an important control of methane flux in northern wetlands. One explanation for the low oxidation rate is the relative high abundance of *Eriophorum* species in the majority of the microsites. In volumetric terms, large proportion of peat belong to the rhizosphere of *Eriophorum* where methane oxidation apparently does not take place [*Chanton et al.*, 1992; *Frenzel and Rudolph*, 1998; *Kelker and Chanton*, 1997; *King et al.*, 1990] and is not accounted for in the model. *Frenzel and Rudolph* [1998] present a hypothesis that type and quality of root exudates differ between plants species that do not support plant–associated methane oxidation and plants that support plant–associated methane oxidation which then would explain the observed difference in methane oxidation rates.

4.2 Transport pathways

It is a well known fact that there are three possible pathways for methane to be liberated from peat to atmosphere: diffusion, ebullition and passage through plants. However, literature also provides a lot of evidence that whenever vascular plants are present, bubbling is rare and flux via plants clearly dominates over diffusive flux in wetlands [*Chanton and Dacey*, 1991; *Morrissey and Livingston*, 1992; *Whiting and Chanton*, 1992; *Schimel*, 1995; *van der Nat et al.*, 1998; *Frenzel and Karofeld*, 2000]. Furthermore, the chamber method used to measure the methane fluxes dealt with in this paper is appropriate for measuring the plant flux and diffusive flux as bubbles result in a non-linear increase in the chamber headspace methane concentration [*Silvola et al.*, 1992; *Kettunen et al.*, 2000]. In fact, measurements where a non-linear increase in the headspace methane concentration was detected ($r^2 \leq 0.90$) were rejected from the data used in *Kettunen et al.*, [2000] and in the current paper. Such cases occurred only very rarely (only few percents of the measurements were rejected due to a non-linear increase in headspace methane concentration), in accordance with the literature information where well over 90 % of the flux from vegetated surfaces was plant mediated [*Chanton and Dacey*, 1991; *Morrissey and Livingston*, 1992; *Whiting and Chanton*, 1992]. As ebullition in the six microsites over the growing season was extremely rare and the data actually do not cover the rare situations where ebullition might have occurred, ebullitive pathway is not included to the model as it is not relevant in vegetated surfaces. If the model predictions were applied to non-vegetated surfaces, ebullition could be included to the model. Nevertheless, also the substrate supply for methane production differs between vegetated and non–vegetated surfaces as in non–vegetated surfaces, root exudation and root litter decay, that are assumed to be the relevant substrate sources in the current vegetated surfaces, would not be important. Hence, in order to predict methane fluxes from non–vegetated surfaces, both substrate supply and tranport pathways should be reconsidered.

4.3 Substrate for methanogenesis

Carbon in peat matrix is very resistant to decomposition in the water saturated conditions. Therefore, the contribution of peat carbon to methane fluxes remains small [*Kuder and Kruge*, 2001]. On the contrary, vegetation can promote methanogenesis in the form of root exudates and easily decomposable litter [*Rovira*, 1969].

A statistical relationship between photosynthesis and methane flux was first suggested by *Whiting et al.* [1991] and further developed in [*Whiting and Chanton*, 1993]. Recent work with stable and radioisotopes have demonstrated that in fact, photosynthetic carbon is rapidly, within the first day after fixation in photosynthetis, converted to methane both in rice paddies [*Dannenberg and Conrad*, 1999] and natural wetlands [*King and Reeburgh*, 2002; *Megonigal et al.*, 1996]. In some cases the recent photosynthates were found to be the predominant substrate for methane production [*Chasar et al.*, 2000; *Minoda et al.*, 1996; *von den Pol-van Dasselaar and Oenema*, 1998] while in others, their contribution was considered much lower [*Dannenberg and Conrad*, 1999; *King and Reeburgh*, 2002; *Minoda et al.*, 1996]. The large range of estimates can be easily explained as allocation of carbon to above– and below–ground parts of the plants and to exudation is known to be affected by plant species, plant age, tillering stage, root damage, light intensity, soil temperature, soil water stress, nutrient availability/deficiency and soil microorganisms [*Kummerow and Ellis*, 1984; *Rovira*, 1969; *Shaver and Cutler*, 1979]. For simplicity, the effects of these control variables on exudation are not taken into account, but a constant proportion f_{GPP} of gross primary production is assumed to promote methanogenesis.

If the substrate production was assumed directly proportional to gross primary production only, the simulated fluxes would remain much lower than measured during late season when the average daily temperature sum (ETI index, see [*Alm et al.*, 1997; *Kettunen*, 2000] has reached its maximum and starts to decline. Hence, another term describing the carbon supplied for methanogenesis from dying plant roots and root litter was included. As results from rice paddies [*Schütz et al.*, 1989; *Wang et al.*, 1990] and from wetlands [*Kettunen et al.*, 1999; *Saarnio et al.*, 1997; *Sorrell et al.*, 1997;) indicate that during late season, the contribution of dying plant roots and root litter to methane fluxes increase, the value of the parameter f_{ETI}, that is related to decomposition of dying roots and root litter, was doubled during the late season i.e. after the ETI index reached its maximum.

Another relevant question in relation to substrate supply is the contribution of acetate dissimilation (acetate pathway) versus bicarbonate reduction (hydrogen pathway) to methane fluxes. It is known that at low temperatures (between 10 and 15 ° C), acetate pathway was found to contribute 85–90 % of methane produced and the contribution of hydrogen pathway then increased with increasing temperature [*Avery et al.*, 1999; *Fey and Conrad*, 2000]. Furthermore, in vegetated sites, where plants provide the peat profiles with fresh organic matter acetate pathway dominates over hydrogen pathway (see [*Bellisalio et al.*, 1999; *Chasar et al.*, 2000; *Popp et al.* 1999]). As temperature in these six vegetated microsites remains below 15 ° C throughout the growing season and as recent studies using carbon isotope methods [*Avery et al.*, 1999; *Bellisario et al.*, 1999; *Chanton et al.*, 1995; *Chasar et al.*, 2000; *Popp et al.*, 1999] have observed that acetate pathway dominates during summer time in northern peatlands, the model presented in this paper describes only one substrate type that represents acetate.

Still, as the model presented in this paper turned out to be extremely sensitive to changes in substrate supply, the capability of the model to simulate methane fluxes in some future environmental conditions, where e.g. hydrogen pathway would become more important, might be improved if the different types of substrates, the controls of substrate supply and the interactions between environmental factors and the involved processes were modeled appropriately. Nevertheless, the current knowledge on these controls and interactions remains quite limited and probably, more basic research would be needed before a more complex model describing these processes could be constructed.

4.4 Oxygen concentrations and population dynamics of microbes in peat profile in relation to changes in environmental conditions

Oxygen concentration in vertical peat profile depends on water table position and peat moisture profile [*Weiss et al.*, 1998]. Hence, oxygen concentration in water saturated peat could be assumed constantly so low that it is not rate limiting to anaerobic processes, like methane production and in unsaturated peat constantly so high that it is not rate limiting to aerobic processes, like methane oxidation. With these assumptions, a model where methane production takes place in certain zone below water table and methane oxidation in another zone around water table can be constructed without describing oxygen dynamics [*Granberg et al.*, 2001; *Walter and Heimann*, 2000; *Walter et al.*, 1996; 2001a; 2001b]. Furthermore, if conditions in peat profile are assumed so stable that populations of methane producing and oxidizing microorganisms remain practically constant, the model can be further simplified by leaving out the population dynamics of these microbes [*Granberg et al.*, 2001; *Segers and Leffelaar*, 2001a; 2001b; *Segers et al.*, 2001; *Walter and Heimann*, 2000; *Walter et al.*, 1996; 2001a; 2001b].

As the number of studies reporting oxygen concentrations or methane producing and oxidizing microbes in peat is extremely limited, it is not easy to evualute the validness of the assumption of stable methane producing and oxidizing zones. Rice field data indicate that as long as the soil remains water saturated and other environmental conditions in paddy soil do not change, the populations of methane producing [*Bosse and Frenzel*, 1998; *Mayer and Conrad*, 1990; *Sass et al.*, 1990; *Schütz et al.*, 1989] and methane oxidizing microbes [*Bosse and Frenzel*, 1998; *Gilbert and Frenzel*, 1995] do not show considerable seasonal dynamics. However, changes in environmental conditions, like substrate supply, nutritional status or water table position are observed to result in fluctuations in microbe populations [*Bodelier et al.*, 2000; *Eller and Frenzel*, 2001; *King*, 1994; *van Bogedom et al.*, 2001b]. Of course, conditions are different in rice paddies than in pristine wetlands and the methodological difficulties in quantifying microbes in environmental samples make the interpretation of these results even more difficult. Nevertheless, it seems that models assuming stable methane producing and oxidizing zones capture relevant factors affecting methane fluxes as long as water table and other environmental conditions remain constant but apparently fail to correctly predict the consequences of changes in substrate supply or water table fluctuations.

As methane producers and methane oxidizers live in an environment where water table typically shows both short-term fluctuations and a seasonal pattern it is natural that they are able to survive periods of unsaturation and nutritional starvation [*Huser et al.*, 1982; *Kettunen et al.*, 1999; *Mayer and Conrad*, 1990; *Roslev and King*, 1994]. The models that deal with stable methane production and oxidation zones [*Granberg et al.*, 2001; *Walter and Heimann*, 2000; *Walter et al.* 1996; 2001a; 2001b] do not take into account any dynamic effects of water table fluctuations on methane production, methane oxidation and consequent methane flux. *Segers and Kengen* [1998], *Segers and Leffelaar* [2001a; 2001b] and *Segers et al.* [2001] model the effect of unsaturation using a concept of alternative electron acceptors that remain in reduced form and do not affect methane fluxes as long as the environment is water saturated. According to their assumptions, during a dry period with a lowering water table and consequent unsaturation, alternative electron acceptors become re-oxidized very rapidly, during the first day of unsaturation. A rise in water table induces the reduction of alternative electron acceptors that prevents methane formation by substrate competition until all alternative electron acceptors are reduced which typically takes from one week to one month. As it is not possible to measure the concentrations of either reduced or oxidized form of alternative electron acceptors, the lag in methane production is the most important argument in favour of models taking alternative electron acceptor cycle account. However, no lag was observed in methane production when peat samples that had been unsaturated from two days to several weeks were measured for methane production potential in laboratory conditions but a constant methane production rate prevailed during the first 10 days of incubation (data presented in [*Kettunen et al.*, 1999]. Therefore, the alternative electron acceptor cycle most likely is not relevant in the control of methane production in northern mires. Furthermore, in Segers' model, a drop in water table for a single day results in as long a lag before methane fluxes recover than a dry period of several weeks. Our previous data [*Kettunen et al.*, 1999], however, support the hypothesis that the lenght of the period of unsaturation controls the recovery of methane fluxes after an increase in water level. Hence, the effects of water table fluctuations are modeled describing the oxygen dynamics and the population dynamics of methane producing and oxidizing bacteria. In the model presented in this paper, methane producers and oxidizers decline less during short period of unsaturation than during a longer dry period resulting in faster recovery of methane fluxes after a short drop in water level. Hence, a simulated dry period to two weeks had only limited effect on methane flux pattern, while the effect of a simulated dry period of 4 weeks started to decrease methane flux and when the duration of the simulated dry period was further increased, the methane flux pattern never recovered to the reference level due to the severe decline in methane producing population. The most crucial model parameters in defining the characteristic times of the system, e.g. how much a dry period of a certain lenght affects the microbial populations are the death and to some extent, growth rates of methane producers and oxidizers.

In contrast to previous models, the model presented in this paper simulates the oxygen concentrations and bacterial populations in the peat profiles. Even though data from these variables are currently lacking, the capability of the model presented in this paper to produce reasonable estimates of the oxygen concentrations prevailing in peat profile and the zones where microbes grow in different situations indicates that the relevant interactions are correctly described in the model and thereby increases the reliability of the model. Furthermore, it is possible to validate the model presented in this paper against measurements if peat oxygen concentrations and microbes are measured in the future. With an experimental setup where methane fluxes and processes involved were measured in situations where water table rises after dry periods of different lenghts and remains high for periods of different lenghts, it is also possible to estimate the growth and death rates. This kind of a setup with fluctuating water levels would also be needed to truly validate the conceptual ideas to deal with water table fluctuations presented in this paper.

4.5 Effects of hydrological changes and increased temperature in the future climate

The most recent estimate [*IPCC Climate Change*, 2001] for the temperature increase in north-east Europe, where most of the European boreal zone belongs to, is +0.4 °C per decade implying that in 50 years the average air temperature would increase by +2 °C. Even though an increase in overall precipitation of +2 % per decade in anticipated for northern Europe [*IPCC Climate Change*, 2001], it is also considered very likely that frequencies and intensities of summer heat-waves will also increase resulting in longer dry periods in the future [*IPCC Climate Change*, 2001]. The effects of simultaneous increase in precipitation and increased likelihood for drought periods on water table patterns in northern peatlands are hard to anticipate, especially if one considers the complex interactions in hydrological and thermal cycles. It is also interesting to note that the summer season during which the methane fluxes and environmental conditions were measured was very wet and warm so the fluxes in during this summer with an extreme climate may already represent average future conditions.

As it still remains somewhat uncertain how much and even to which direction climate will change generally in northern latitudes and particularly in regional scale in the regions rich in mires, a wide variety of cases was covered in the simulations analyzing the effects of changes in environmental conditions. Simulations studied the effects of drier and wetter conditions and an increase and a decrease in air temperature, either with or without a change in gross primary production.

As already discussed in previous section 4.4, hydrological changes had a remarkable effect on methane fluxes even if everything else remained the same. As the current season already had high water tables, the effects of simulated wet periods remained smaller than those of simulated drought periods.

The model simulations support the previously suggested idea that substrate availability limits the temperature effects with complex interactions [*Bergman et al.*, 1998; *Granberg et al.*, 2001; *Westermann*, 1993] and do not provide evidence for the hypothesis that methane production in high latitudes is temperature limited [*Sorrell et al.*, 1997]. In addition to direct enchancement of process rates via Q10 values, increase in temperature might shift carbon allocation from shoots to roots promoting root litter and root exudation [*Kummerow and Ellis*, 1984] that would result in an increase in methane flux. Increased air temperature might also increase gross primary production as photosynthesis in northern conditions is temperature limited. *Verville et al.* [1998] actually observed that the increasing effect of increase in temperature to methane flux was due to increase in gross primary production.

5 Conclusion and future challenges

The current model describes methane flux dynamics in different microsites of a boreal peatland. As the current data cover one summer season, validation of model predictions to multiannual dataset would be most interesting future topic. The differences in methane fluxes result solely from site specific factors, vegetation cover and water table in the microsites and no parameter adjustment between different microsites, that is applied quite often even in process–based models [e.g. *Walter and Heimann*, 2000; *Walter et al.*, 1996], is needed. Current study emphasizes the importance of vegetation cover and water table pattern to methane fluxes. The extreme sensitivity of the model to changes in substrate availability provides future research with challenges as the model might be improved if the controls for plant related substrate supply and the complex interactions between environmental factors and the processes involved were understood more deeply. In the concept of climate change, increases in air temperature and carbon dioxide levels would, according to the model simulations, result in remarkable increases in methane fluxes if they enhanced gross primary production and substrate supply for methanogenesis. Even more dramatic changes in methane flux may occur if the vegetation experiences structural changes due to increases in carbon dioxide and/or changes in thermal and hydrological conditions. Another aspect that affects methane fluxes further complicating the interactions is the availability of nutrients that is also an interesting topic for future work. Even if vegetation and gross primary production remained the same, simulations suggest that drought periods would decrease the methane fluxes remarkably if the duration of drought exceeded 6 weeks due to dynamic effects of a decline in the methanogenic population. In the future, an experimental setup with flux measurements under a period of fluctuating water tables could be carried out to validate the charateristic times proposed by the current simulations. The simulations also suggest that any change that would enhance methane oxidation would result in a considerable decrease in methane flux. Overall, the current study provides a lot of information on the relative importance of changes in environmental controls or model parameters that can be used when considering the dynamics of methane fluxes in current and future conditions.

Acknowledgments

The author wishes to thank Prof. Veijo Kaitala, University of Jyvskylä Docent Hannu Rita, University of Helsinki, Docent Harri Vasander, University of Helsinki, other colleagues and the two anonymous reviewers for valuable comments.

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