

Methane production and methane consumption: a review of processes underlying wetland methane fluxes

REINOUW SEGERS

Department of Theoretical Production Ecology, Wageningen Agricultural University, PO Box 430, 6700 AK Wageningen, The Netherlands, email: reinoud.segers@staff.tpe.wau.nl

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Abstract. Potential rates of both methane production and methane consumption vary over three orders of magnitude and their distribution is skew. These rates are weakly correlated with ecosystem type, incubation temperature, *in situ* aeration, latitude, depth and distance to oxic/anoxic interface. Anaerobic carbon mineralisation is a major control of methane production. The large range in anaerobic CH₄:CO₂ production rates indicate that a large part of the anaerobically mineralised carbon is used for reduction of electron acceptors, and, hence, is not available for methanogenesis. Consequently, cycling of electron acceptors needs to be studied to understand methane production. Methane and oxygen half saturation constants for methane oxidation vary about one order of magnitude. Potential methane oxidation seems to be correlated with methanotrophic biomass. Therefore, variation in potential methane oxidation could be related to site characteristics with a model of methanotrophic biomass.

Introduction

Methane contributes to the enhanced greenhouse effect. Wetlands, including rice paddies, contribute between 15 and 45% of global methane emissions (Prather et al. 1995). Methane emissions from wetlands show a large variation (Bartlett & Harris 1993) which can only partly be described by correlations with environmental variables (Moore & Knowles 1989; Moore & Roulet 1993; Dise et al. 1993; Hogan 1993; Whiting & Chanton 1993; Bubier et al. 1995a,b; Kettunen et al. 1996; Denier van der Gon & Neue 1995a). This limits the accuracy of estimates of both current and future global emissions, the latter being the result of possibly changed conditions due to a change climate or changed soil management. Insight in the underlying processes could improve this situation.

Methane fluxes from or to soils result from the interaction of several biological and physical processes in the soil (Hogan 1993; Schimel et al. 1993; Conrad 1989; Cicerone & Oremland 1988; Bouwman 1990; Wang et al. 1996); Methane production is a microbiological process, which is predominantly controlled by the absence of oxygen and the amount of easily

degradable action. Methane consumption is also a microbiological process. Major controls are soil oxygen and soil methane concentrations. Gas transport influences aeration and determines the rate of methane release from the soil. Gas transport occurs via the soil matrix and via the vegetation. In the first case it is controlled by soil water and in the second case it is sometimes influenced by weather conditions. The vegetation also influences the amount of easily degradable carbon. All these processes are affected by temperature, and thus by heat transport.

In the last decade, knowledge of methane production and methane consumption has increased considerably. This increased knowledge has been used to support the descriptive models mentioned above and to develop process models (Cao et al. 1995, 1996; Walter et al. 1996; Watson et al. 1997). However, these process models require fit procedures or intensive on site measurement of parameters which are as variable as methane fluxes, which limits their applicability for understanding and developing general relationships between methane fluxes and environmental variables. To improve the process models in this respect the knowledge of methane production and methane consumption is reviewed and it is investigated how this knowledge could be used to establish quantitative relations between the rates of both processes and environmental variables.

Two pathways are followed. Firstly, potential, laboratory rates, collected from a large number of studies, are related directly to environmental variables with statistical methods. Secondly, the process knowledge underlying these relations is summarised. Methane production and consumption are driven by organic matter mineralisation, soil aeration and heat transport. For understanding the relation between environmental variables and methane kinetics, these driving processes have to be understood as well. However, these processes are not reviewed here to limit the size of the paper.

Methane production

Methane production in soils can occur when organic matter is degraded anaerobically (Oremland 1988; Svensson & Sundh 1992; Conrad 1989). Several bacteria that degrade organic material via a complex food web are needed to perform this process. The final step is performed by methanogens, methane producing bacteria. Methanogenic bacteria can use a limited number of substrates, of which acetate and hydrogen are considered the most important ones in fresh water systems (Peters & Conrad 1996; Goodwin & Zeikus 1987; Lovley & Klug 1983; Yavitt & Lang 1990). Other substrates have never been shown to be responsible for more than 5% of the methane production. Acetate and hydrogen are formed by fermentation from hydrolysed organic

matter (Dolfing 1988). Alternative electron acceptors suppress methane production, which is most easily understood from thermodynamics (Zehnder & Stumm 1988).

Potential methane production correlated to environmental variables

Potential methane production, *PMP*, is the methane production by an anaerobically incubated soil sample. Rates of *PMP* have been determined in a large number of studies in various natural wetlands and rice paddies. Here, it is investigated whether general applicable relations emerge when all data are put together. To do so, the following assumptions were made: Zero rates in tables were assigned values equal to half of the detection limit, which was, when not specified, equal to half of the lowest value. Zero rates in graphs were assigned a value of 1/20 of the smallest unit. All rates were converted to volumetric units, because both the ultimate controls (primary production and oxygen influx) and the quantity to be explained (methane fluxes) are on an area basis, which is more closely related to volumetric rates than to gravimetric rates. Consequently, all rates which were originally expressed on a soil weight basis had to be multiplied with soil density. In case the soil density was not given, wet bulk densities of peat were 1 g cm^{-3} , dry bulk densities of peat varied between 0.04 and 0.11 g cm^{-3} , depending on depth and soil type (Minkinen & Laine 1996) and dry bulk densities of mineral soils were 1.5 g cm^{-3} (Koorevaar et al. 1983). For roots a dry bulk density of 0.08 g cm^{-3} was calculated, assuming a water content of 90% and a porosity of 20% (Crawford 1983). To improve future comparisons of rates in any unit it is recommended to measure bulk density and soil moisture contents in addition to the biogeochemical rates.

The distribution of *PMP* rates is skew and variation is large (Figure 1), as is for methane fluxes in the field (Bubier et al. 1995a,b; Dise et al. 1993; Panikov 1994). Typical *PMP* rates vary from 10^{-2} to $10^1 \mu\text{mol m}^{-3} \text{ s}^{-1}$. An exception are the very high values of around $10^3 \mu\text{mol m}^{-3} \text{ s}^{-1}$ found by Bachoon and Jones (1992). This may be attributed to their relatively high incubation temperature (30°C) and the high concentration of available organic matter, as they sampled only the upper 2 cm of subtropical minerotrophic wetland.

Evaluation of experimental methods

No standard procedure exists for measuring *PMP*, though the effect of the experimental procedure on measured rates could be large. Hall et al. (1996) observed that small periods of aerobiosis (5 min.) decreased *PMP* in peat soil samples 10 to 70%. Sorrell and Boon (1992) reported that rigorously mixing

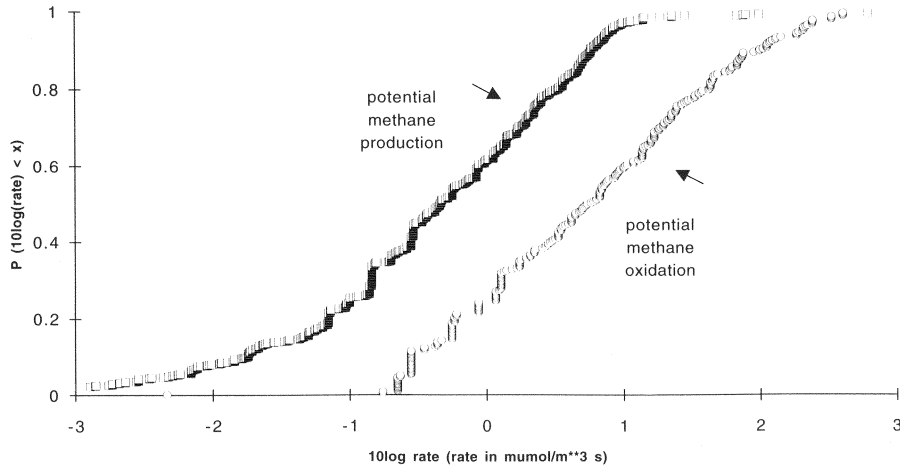


Figure 1. Accumulated probability density functions of $10\log$ of potential methane production and $10\log$ of potential methane oxidation. Methane production data are from 1046 samples (Amaral & Knowles 1994; Bahooon & Jones 1992; Bridgham & Richardson 1992; Chapman et al. 1996; Chin & Conrad 1995; Crozier & Delaune 1996; Crozier et al. 1995; Dunfield et al. 1993; Frenzel et al. 1992; King 1994; Krumholz et al. 1995; Magnusson 1993; Moore & Dalva 1993; Moore & Knowles 1990; Moore et al. 1994; Nedwell & Watson 1995; Rothfuss & Conrad 1993; Roulet et al. 1993; Rouse et al. 1995; Sass et al. 1990; Sundh et al. 1994; Valentine et al. 1994; Westermann 1993; Williams & Crawford 1984; Yavitt & Lang 1990; Yavitt et al. 1987; Yavitt et al. 1988). Methane oxidation data are from 328 samples (Amaral & Knowles 1994; Bender & Conrad 1994; Dunfield et al. 1993; Gerard & Chanton 1993; King 1990; King et al. 1990; King 1994; Krumholz et al. 1995; Moore & Knowles 1990; Nedwell & Watson 1995; Sundh et al. 1994; Yavitt et al. 1990a).

of a sediment decreased methane production by an order of magnitude. By contrast, Kengen and Stams (1995) found higher production of both methane and carbon dioxide in slurried samples compared to unslurried samples of a drained peat soil. Valentine et al. (1994) suggested that slurring could decrease methane production as a result of inhibition by a flush of fatty acid production. Kelly and Chynoweth (1980) could stimulate methane production in deep fresh water sediments (3–20 cm) by stirring. By contrast, in the top sediment (0–3 cm) they could not do so. So, the effect of measurement procedure of methane production is highly uncertain, which was also concluded by Sundh et al. (1994). Knowledge of the effect of sampling procedure on the process underlying methane production is needed to improve this situation. Recently, Dannenberg et al. (1997) made considerable progress in this area by showing that acetoclastic methanogens in paddy soils are seriously affected by stirring and moderately by gently shaking.

The effect of sampling procedures on the conclusion drawn in this paper may be limited by the large number (19) of used data sets. Due to the wide

variety in experimental methods it was not possible to investigate the effect of sampling procedures with statistical methods.

In situ aeration, ecosystem type and latitude

In situ aeration affects *PMP* significantly (Table 1a). Mean $^{10}\log(PMP)$ of samples from aerobic sites was more than one order of magnitude less than the mean $^{10}\log(PMP)$ of samples from anaerobic sites, probably caused by higher concentration of electron acceptors and/or lower concentrations of methanogenic biomass.

PMP in samples from oligotrophic natural wetlands is lower than methane production in samples from minerotrophic natural wetlands (Table 1a), possibly because of the lower amount of fresh organic material as a result of lower primary production. In contrast, Moore and Knowles (1990) did not find any correlation between trophic status of the soil and *PMP*. This difference can only partly be explained by the difference in units used, because also when the data of this paper are converted to the gravimetric units of Moore and Knowles (1990), *PMP* in oligotrophic wetlands is relatively low. *PMP* in soil samples from paddy soil is higher than *PMP* in samples from natural wetlands. The minus sign in the summary relation for the I_{pad} (Table 1) suggests, that this is caused by more anaerobic conditions, higher temperature, and lower latitude.

The relatively high *PMP* at lower latitudes (Table 1) can be explained the higher incubation temperatures and by the higher primary production (resulting in more easily degradable carbon).

Temperature

Incubation temperature could describe part of variation in the $^{10}\log PMP$ (Table 1). Q_{10} of all samples together was 4.1 (± 0.4). Alternatively, Q_{10} values have been determined in incubation experiments with temperature as single varying factor, resulting in a range from 1.5 to 28 (Table 2). To explain this large range Q_{10} , values of underlying processes are listed as well. Q_{10} of anaerobic C-mineralisation is between 1 and 4 and methanogenic bacteria have Q_{10} values up to 12, which is still not high enough to explain the highest end of the Q_{10} values for methane production. A possible explanation for the high Q_{10} values for methane production is the interaction of several processes: An increasing temperature increases rates of electron acceptor reduction, which results in lower electron acceptor concentrations which has an additional positive effect on methane production. This mechanism could explain the high Q_{10} values of Updegraff et al. (1995) and Tsutsuki and Ponnamperna (1987) in their long term (\geq several weeks) experiments in

Table 1a. Statistics of potential methane production (*PMP*). Data are the same as in Figure 1. *SEM* is the standard error of the mean and *SD* is the standard deviation. *Aerobic* samples were taken from ≥ 5 cm above the water table, *intermediate* samples from within 5 cm of the water table and *anaerobic* samples were taken from ≥ 5 cm below the water table. In submerged soils the aeration of the first cm was considered *intermediate*, deeper layers were considered *anaerobic*. Values with the same letter are not significantly different from each other ($p = 0.05$).

Qualitative variables	$^{10}\log(PMP)$ (PMP in $\mu\text{mol m}^{-3} \text{s}^{-1}$)			
	Mean	<i>SEM</i>	<i>SD</i>	<i>n</i>
<i>In situ aeration</i>				
Aerobic	-1.7 ^a	0.1	0.8	39
Intermediate	-0.42 ^b	0.06	1.0	268
Anaerobic	-0.42 ^b	0.04	1.1	621
<i>Ecosystem type</i>				
Minerotrophic natural wetlands	-0.47 ^a	0.05	1.2	657
Oligotrophic natural wetland	-0.91 ^b	0.06	0.8	176
Rice paddy	0.09 ^c	0.05	0.7	210

Table 1b. Linear regressions for potential methane production (*PMP*). T_{inc} is the incubation temperature ($^{\circ}\text{C}$), lat is the latitude ($^{\circ}\text{N}$) and $depth$ is the depth below the soil surface (cm). I_{oli} (oligotrophic) I_{pad} (paddy) and I_{aer} (aerobic) are dummy variables, used to combine qualitative and quantitative variables. $I_{\text{oli}} = 1$ if soil type is oligotrophic and $I_{\text{oli}} = 0$ for the other soil types, ect. Standard errors of coefficients are between brackets.

PMP in $\mu\text{mol m}^{-3} \text{s}^{-1}$	r_{adj}^2	<i>n</i>
$^{10}\log(PMP) = -1.8(0.1) + 0.069(0.005) \cdot T_{\text{inc}}$	0.16	973
$^{10}\log(PMP) = 1.3(0.1) - 0.040(0.003) \cdot lat$	0.20	1001
$^{10}\log(PMP) = -0.28(0.04) + 0.008(0.001) \cdot depth$	0.03	1042
$^{10}\log(PMP) = -0.2(0.2) + 0.069(0.006) \cdot T_{\text{inc}} -$ $0.026(0.003) \cdot lat - 0.39(0.08) \cdot I_{\text{oli}} - 0.7(0.1) \cdot I_{\text{pad}}$ $- 1.2(0.2) \cdot I_{\text{aer}} - 0.012(0.002) \cdot depth$	0.36	926

which methane production increased with time. However, for the shorter term experiments (a few days) of Dunfield et al. (1993) and Nedwell and Watson (1995) this explanation is not applicable as methane production was more or less constant over the incubation time (*Knowles pers. comm.*; *Watson pers. comm.*), indicating that depletion of an inhibiting electron acceptor did not occur during the incubation experiment.

Table 2. Temperature dependence of methane production and sub processes responsible for methane production.

Sample source, process or organism	Q_{10}
<i>Methane production, soil sample scale</i>	
Minerotrophic peat ^{4,5,6,13,15,19}	1.5–6.4
Oligotrophic peat ^{6,10,13,14,15}	2–28
Paddy ^{1,8,17}	2.1–16
<i>Methanogenesis of pure cultures</i>	
Acetotrophic ^{3,16,18,20}	2.9–9.0
Hydrogenotrophic ^{1,3}	1.3–12.3
Growth of <i>M. soehngenii</i> ^{16,20}	2.1
<i>Processes related to anaerobic carbon mineralisation</i>	
Anaerobic CO ₂ production in peat ^{6,14}	1.5
Total anaerobic C-mineralisation in paddy soil ¹⁷	0.9–1.8
Anaerobic hydrolysis of particulate organic matter ²	1.9
Acetate production from various substrates ¹¹	1.7–3.6

¹ Schütz et al. (1990), ² Imhoff and Fair (1956), ³ Westermann et al. (1989), ⁴ Westermann and Ahring (1987), ⁵ Westermann (1993), ⁶ Updegraff et al. (1995), ⁸ Sass et al. (1990), ¹⁰ Nedwell and Watson (1995), ¹¹ Kotsyurbenko et al. (1993), ¹³ Valentine et al. (1994), ¹⁴ Bridgham and Richardson (1992), ¹⁵ Dunfield et al. (1993), ¹⁶ Huser et al. (1982), ¹⁷ Tsutsuki and Ponnampuruma (1987), ¹⁸ Van den Berg et al. (1976), ¹⁹ Williams and Crawford (1984), ²⁰ Gujer and Zehnder (1983).

In summary, variation in reported Q_{10} values of methane production is large. This could be due to the anomalous temperature behaviour of the methanogens themselves and due to the interaction of the underlying processes.

pH

Most known methanogenic bacteria have their optimum pH at 7. However, anaerobic bacteria with lower optima have been isolated from acidic peats (Williams & Crawford 1985; Goodwin & Zeikus 1987). Mostly, increasing pH in incubated samples increases *PMP* (Dunfield et al. 1993; Yavitt et al. 1987; Valentine et al. 1994). A correlation between pH and *PMP* was found in most samples by Valentine et al. (1994), but not by Moore and Knowles (1990). Dunfield et al. (1993) observed that optimum pH was 0–2 units above field pH for peat samples from five different acidic sites. So, the adaptation to *in situ* pH of the microorganisms controlling methane production is variable.

Root-associated methane production

Roots can affect methane production both positively and negatively, because root oxygen transport suppresses methane production, whereas root decay and root exudation promote methane production. King (1994) reported methane production in roots and rhizomes of anaerobically incubated *Calamagrostis canadensis* and *Typha latifolia*, which were washed aerobically. The conversion time of photosynthesised ^{13}C to emitted methane was sometimes less than 1 day in a rice paddy (Minoda & Kimura 1994; Minoda et al. 1996). These two observations point at methane production inside, at, or near roots. Apparently, aeration of roots and rhizosphere is not complete, as follows also from the observation of organic acids within waterlogged plants (Ernst 1990), a root oxygen diffusion model of Armstrong and Beckett (1987) and rhizosphere oxygen measurements (Conlin & Crowder 1988; Flessa & Fischer 1992).

The relative contribution of root-associated methane production to methane emissions could be important in a rice paddies, as it varied between 4 and 52% in a case study of Minoda et al. (1996). Also in natural wetlands the contribution of root-associated methane production to methane emissions could be large, because removing above ground vegetation decreased methane emissions considerably (up to more than a factor 10) without a concurrent decrease of stored methane in the soil (Waddington et al. 1996; Whiting & Chanton 1992).

Inhibitory compounds

Under anaerobiosis, compounds can be formed that are toxic to plants (Drew & Lynch 1980) and possibly also to bacteria involved in methane production. Some volatile compounds may inhibit methanogenesis (Williams & Crawford 1984) and anaerobic carbon dioxide production (Magnusson 1993), as flushing with N_2 resulted in an increase in gas production in anaerobic incubation experiments. It is not known what kind compounds are involved and whether this effect is important under *in situ* conditions.

Fatty acids can inhibit anaerobic bacteria when its undissociated concentrations are too high (Wolin et al. 1969). Consequently, especially acid environments are sensitive for this inhibition. Fukuzaki et al. (1990) found that two methanogens had distinct optimum undissociated acetate concentrations (140 and 900 μM) for acetate consumption. Also in laboratory incubations experiments with acid soil samples, acetate inhibited methane production (Yavitt et al. 1987; Williams & Crawford 1984) and glucose decomposition (Kilham & Alexander 1984). By contrast, Van den Berg et al. (1976) obtained a methanogenic enrichment culture for a waste digester, in which

acetate uptake was independent of acetate concentration between 0.2 and 200 mM.

Also sulfide can inhibit methane production. Cappenberg (1975) found a total inhibition of methane formation at 0.1 mM, and no inhibition at 0.001 mM, but in methanogenic enrichment cultures from a waste digester there was no inhibition of methanogenesis below approximately 1 mM (VandenBerg 1976; Maillacheruvu & Parkin 1996).

Explanation of methane production via the underlying processes

Substrate, organic matter

Once anaerobiosis is established, organic substrate is considered as the major limiting factor for methane production; Firstly, both the addition of direct methanogenic substrates, like hydrogen or acetate, and the addition of indirect substrates, like glucose and leaf leachate, enhanced methane production in anaerobically incubated soil samples (Williams & Crawford 1984; Valentine et al. 1994; Amaral & Knowles 1994; Bachoon & Jones 1992). Yavitt and Lang (1990), however, did not find substrate limitation in some of their soil samples. Secondly, Denier van der Gon and Neue (1995a) found a positive correlation between methane emission and organic matter input at 11 rice paddy sites. Thirdly, Whiting and Chanton (1993) and Chanton et al. (1993) found a relation between carbon dioxide fixation and methane emission in flooded wetlands, though this could also be a consequence of a large vegetational transport capacity. Fourthly, root-associated methane production could contribute to methane emissions (see above). Fifthly, methane production measured in laboratory incubations of soil samples often decreases with depth, when taken from below the water table (Sundh et al. 1994; Williams & Crawford 1984; Yavitt et al. 1987), as does the availability of organic matter. Sixthly, the ^{14}C fraction of emitted methane was near the ^{14}C fraction of atmospheric carbon dioxide (Chanton et al. 1995), indicating that the methane was mainly derived from recently fixed carbon. And seventhly, often there is a correlation between organic matter quality parameters and methane production: (i) Crozier et al. (1995) found a good correlation between aerobic carbon dioxide production and anaerobic methane production in dried and fresh undisturbed peat cores. (ii) Yavitt and Lang (1990) found positive correlations with total organic matter and acid-soluble organic matter, though no correlations were found with dissolved organic matter and hot water-soluble organic matter and a negative correlation was found with acid-insoluble organic matter. (iii) Valentine et al. (1994) found positive correlations with carbohydrate content. Correlations with C:N and lignin:N content

Table 3. Comparison between rates of methane production, aerobic carbon dioxide production and anaerobic carbon dioxide production.

Sample source	aer CO ₂ / anaer CO ₂ mol:mol	anaer CO ₂ / anaer CH ₄ mol:mol
Oligotrophic peat	1.6–2.7 ¹	4–882 ^{1–4}
Minerotrophic peat	2.7 ¹	0.6–630 ^{1–7}
Paddy soil ¹⁰		1–594
Drained peat soil, 4 day incubation ⁸	4.8 ± 3.1	
<i>Sphagnum</i> ⁹	1.4 ^a	
Plant material in mineral soils ^{11(a),12,13}	2–8	
Various peat soils ¹⁴	2.5 (1–5)	

¹ Bridgham and Richardson (1992), ² Updegraff et al. (1995), ³ Yavitt et al. (1988), ⁴ Yavitt and Lang (1990), ⁵ Amaral and Knowles (1994), ⁶ Yavitt et al. (1987), ⁷ Schimel (1995), ⁸ Glenn et al. (1993), ⁹ Tenney and Waksman (1930), ¹⁰ Tsutsuki and Ponnampereuma (1987), ¹¹ Bhaumik and Clark (1947), ¹² Broadbent and Stojanovic (1952), ¹³ Parr and Reuszer (1959), ¹⁴ Moore and Dalva (1997); ^a anaerobiosis established by submergence.

were not consistent, however. (iv) Nilsson (1992) successfully correlated methane production to infrared spectra of peat samples, suggesting that the organic composition of the peat samples was a major determinant of methane production.

As organic substrate availability under anaerobic conditions is a major control of methane production it is worthwhile to summarise the information on anaerobic carbon mineralisation. In Table 3 various aerobic versus anaerobic mineralisation rates, measured as carbon dioxide production, are compared. Aerobic degradation rates are higher with a factor 1 to 8 with the average in the lower end of this range. Little is known about the causes of this variation, which limits the accuracy of soil carbon models with respect to anaerobic carbon mineralisation.

Microbial biomass

Limitation of methane production by microbial biomass occurs when microbial uptake capacity does not meet substrate supply. In principle, it can be a result of (i) periodical damage to bacteria due to poisoning or starvation, (ii) nutrient stress of the bacteria and (iii) an increase of substrate supply that is larger than the growth rate of the bacteria. Methanogenic bacteria are more likely to limit methane production than fermenting bacteria for several reasons. Firstly, their relative growth rate is relatively low (Pavlosthatís & Giraldo-Gomez 1991) and secondly, accumulation of substrates for ferment-

ing bacteria, like sugars, has never been observed, whereas accumulation of substrates for methanogenic bacteria, especially acetate, did occur at lower temperatures (Shannon & White 1996; Drake et al. 1996) and upon anaerobic incubation of non-wetland soils (Peters & Conrad 1996; Küsel & Drake 1995; Wagner et al. 1996).

Damage to a methanogenic population could be the result of aerobiosis, either directly by poisoning or indirect by C-starvation due to competition for substrates with aerobic microorganisms. If damage occurs during aerobiosis the methanogenic population needs time to recover when anaerobiosis returns, especially because relative growth rates of methanogenic bacteria are low, typically 0.4 d^{-1} at $35 \text{ }^\circ\text{C}$ (Pavlostathis & Giraldo-Gomez 1991). Shannon and White (1994) attributed the reduction of methane emission from a bog in the year following a dry year to this mechanism. By contrast, in rice paddies methane emission can develop quickly after inundation (Holzapfel-Pschorn & Seiler 1986), which can be explained by the good oxygen survival abilities of methanogenic bacteria in paddy soil (Mayer & Conrad 1990; Joulain et al. 1996). These differences in the onset of methane emission after aerobiosis can be explained by (i) differences in kind and concentration of electron acceptors that suppress production, which are formed during an aerobic period (Freeman et al. 1994), by (ii) differences in temperature causing differences in rates of electron acceptor reduction and differences in rates of bacterial growth and by (iii) differences in oxygen survival times of methanogenic bacteria, ranging from a few hours to several months (Kiener & Leisinger 1983; Fetzer et al. 1993; Huser et al. 1982; Huser 1981). The latter explanation is not so likely, as, from an ecological point of view, it is likely that methanogenic bacteria in sites with a fluctuating aeration have good oxygen survival characteristics.

N or P limitation for the methanogenic consortium does not seem to occur, as N or P additions generally do not stimulate methane production (Bridgham & Richardson 1992; Williams & Crawford 1984; Bachoon & Jones 1992). Additionally, Williams and Crawford (1984) found no reaction of methane production on the addition of yeast extract and vitamins in samples from an acid bog. Yavitt and Lang (1990) suggested that in rain water fed mires nickel could be limiting, as explanation why they could not enhance methane production by adding various substrates. For *Methanothrix concilii* optimum Ni^{2+} concentration was about $0.1 \text{ } \mu\text{M}$ (Patel et al. 1988). Apart from the concentration of Ni^{2+} also the form of Ni^{2+} (chelated or not) could be relevant (Nozoe & Yoshida 1992).

Flushes of substrate are not a likely cause of biomass limitation, because plant decay, which is the major source of labile organic matter, is a rather stable process. Even the application of organic material in agricultural ecosystems

is not a likely cause of biomass limitation, because normally it is managed in such a way that fatty acids do not accumulate, as they are toxic.

Electron acceptors

Alternative electron acceptors, like NO_3^- , Fe^{3+} , Mn^{4+} , SO_4^{2-} and possibly humic acids (Lovley et al. 1996) suppress methanogenesis, because reduction of alternative electron acceptors supplies more energy than methanogenesis (Zehnder & Stumm 1988). Three mechanisms, that could operate at the same time, could be responsible for this effect. Firstly, reduction of electron acceptors could reduce substrate concentrations to a value which is too low for methanogenesis (Achnich et al. 1995; Peters & Conrad 1996; Kristjansson et al. 1982; Schönheit et al. 1982). Secondly, the presence of electron acceptors could result in a redox potential which is too high for methanogenesis (Wang et al. 1993; Peters & Conrad 1996; Jakobsen et al. 1981). Thirdly, electron acceptors could be toxic for methanogens (Jakobsen et al. 1981).

The large range of anaerobic $\text{CO}_2:\text{CH}_4$ production rates (Table 3) indicate that reduction of terminal alternative electron acceptors uses a large and variable part of the anaerobically mineralised carbon, provided that no substantial accumulation of fermentation products occurs, which has never been observed in the $\text{CO}_2:\text{CH}_4$ measurements. Consequently, cycling of electron acceptors is probably a major process in controlling methane production.

Reduction of electron acceptors requires organic matter. Consequently, anaerobic carbon mineralisation influences methane production not only directly, but also indirectly, via the rate of electron acceptor depletion. A dynamic process model centered around this relation was developed by Segers & Kengen (*accepted by Soil Biol Biochem*).

Summary

The knowledge of the processes underlying methane production can be summarised in a simple equation (Segers & Leffelaar 1996):

$$MP = ICF, \quad (1)$$

where MP is the methane production rate, I is an aeration inhibition function, which is one under anaerobiosis and zero under aerobiosis, C is the anaerobic C-mineralisation rate and F is the fraction of the anaerobically mineralised C, which is transformed into methane. When PMP rates are considered I is equal to one. A basic assumption underlying equation (1) is that availability of organic matter is a major control of methane production. Variation in F

is caused by a varying contribution of the reduction of terminal electron acceptors. Therefore, to explain variation in F , cycling of electron acceptors should be considered.

Methane consumption

In contrast with methane production, methane consumption in wetlands is considered to be mainly performed mainly by a single class of microorganisms: a methanotroph (Cicerone & Oremland 1988; King 1992). Methane consumption is essential for understanding methane emission. Although the methods for determining *in situ* methane oxidation on the field scale are under debate (Denier van der Gon & Neue 1996; Frenzel & Bosse 1996; King 1996; Lombardi et al. 1997), it is likely that a large and a varying part (1–90%) of the produced methane could be consumed again, either in the oxic top layer or in the oxic rhizosphere (De Bont et al. 1978; Holzapfel Pschorn & Seiler 1986; Schütz et al. 1989; Sass et al. 1990; Fechner & Hemond 1992; Oremland & Culbertson 1992; Happell et al. 1993; Epp & Chanton 1993; Kelley et al. 1995; King 1996; Denier van der Gon & Neue 1996; Schipper & Reddy 1996; Lombardi et al. 1997). This large variation could be explained by knowledge of methane oxidation on the soil sample scale, which is reviewed below.

High affinity and low affinity methane oxidation

It is convenient to distinguish two kinds of methanotrophic activity: high affinity (low, atmospheric, methane concentrations) and low affinity (high methane concentrations). The essential difference is that growth and ammonium inhibition of high affinity activity is barely understood (Roslev et al. 1997; Gullede et al. 1997), while the basic kinetics of low affinity methane oxidation are relatively well established (King 1992). The transition point between high and low affinity oxidation is somewhere between 100 and 1000 ppmv methane (gas phase) (Bender & Conrad 1992, 1995; Nesbit & Breitenbeck 1992; Schnell & King 1995; King & Schnell 1994). When soil methane concentrations are in the range of high affinity methane oxidation, methane emission can only be relatively small for wetlands. A closer study of (high affinity) methane oxidation will not change that picture. Therefore, the peculiarities of high affinity methane oxidation are not considered in this article, which is restricted to wetlands.

Aerobic methane oxidation

Aerobic methane oxidation, *MO*, requires both oxygen and methane. So, in principle, both substrates could be limiting. The following double Monod expression describes this double substrate dependence:

$$MO = PMO \frac{[CH_4]}{[CH_4] + K_{m,CH_4}} \cdot \frac{[O_2]}{[O_2] + K_{m,O_2}}. \quad (2)$$

Potential methane oxidation, *PMO*, is typically between 0.1 and 100 $\mu\text{mol m}^{-3} \text{s}^{-1}$ (Figure 1). This is about one order of magnitude larger than *PMP*. K_{m,CH_4} and K_{m,O_2} vary about one order of magnitude (Table 4). In experiments with pure cultures the higher values for K_{m,CH_4} could have been too high, because in those experiments *MO* was determined as the oxygen uptake rate, while methane concentrations were assumed to be constant (Joergensen & Degn 1983). However, this reasoning does not hold for the experiments with peat soils, because in those cases K_{m,CH_4} values were determined by monitoring the decrease of methane concentration in the headspace above continuously stirred samples. Therefore, the large variation in K_m values may be an intrinsic property of methanotrophic bacteria.

There are two strategies to find predictive relations for *PMO*. Firstly, by using descriptive relations between *PMO* and soil environmental variables, like water table. Secondly, by using a model for methanotrophic biomass, because *PMO* appears, logically, to be correlated with methanotrophic biomass (Bender & Conrad 1994 and Sundh et al. 1995b).

Anaerobic methane oxidation

Thermodynamically, it is possible to oxidise methane anaerobically with the alternative electron acceptors that inhibit methane production. However, bacteria that perform this process have never been isolated. Nevertheless, for anaerobic methane oxidation by sulphate in marine systems fairly strong evidence is present (Cicerone & Oremland 1988; King 1992). In freshwater systems indications were obtained at sulphate concentrations from 0.5 mM, but not at concentrations below 0.2 mM (Panganiban 1979; Nedwell & Watson 1995; Yavitt et al. 1988). Panganiban (1979) could not find any anaerobic methane oxidation at any nitrate concentration. Ferrous iron (Miura et al. 1992) and sulphate (Murase & Kimura 1994b) may be involved in anaerobic methane oxidation in paddy soil (with about 1 mM sulphate and 2.5% of free iron), with an upper limit of about 4 $\mu\text{mol m}^{-3} \text{s}^{-1}$ (calculated from Miura et al. (1992) and Murase and Kimura (1994a,b)). This upper limit is of the same order of magnitude as typical rates of *PMO* in paddy rice (Table 5a).

Table 4. Half saturation constants for methane oxidation.

Organism or sample source	K_{m,CH_4} μM	K_{m,O_2} μM
<i>Wetlands soils</i>		
Fresh water sediment	2.2–3.7 ¹	
Sediment free roots	3–6 ²	
Natural peat soils	1–45 ^{3,4,6,7}	200 ^{a,7}
Agricultural peat	66.2 ⁴	37
Paddy soil	8 ^{8,a}	
<i>Other methanotrophic environments</i>		
Various methanotrophs	0.8–48 ^{9–15}	0.3–1.3 ^{11,12}
Deep lake sediments	4.1–10 ^{16,18}	20 ¹⁸ , <18 ¹⁷
Landfill soils	1.6–31.7 ^{19,20}	

¹ King (1990), ² King (1994), ³ Yavitt et al. (1988), ⁴ Megraw and Knowles (1987), ⁵ Dunfield et al. (1993), ⁶ Nedwell and Watson (1995), ⁷ Yavitt et al. (1990a), ⁸ Bender and Conrad (1992), ⁹ Linton and Buckee (1977), ¹⁰ Lamb and Garver (1980), ¹¹ Joergensen (1985), ¹² Nagai et al. (1973), ¹³ Harrison (1973), ¹⁴ O'Neill and Wilkinson (1977), ¹⁵ Ferenci et al. (1975), ¹⁶ Bucholz et al. (1995), ¹⁷ Frenzel et al. (1990), ¹⁸ Lidstrom and Somers (1984), ¹⁹ Kightley et al. (1995), ²⁰ Whalen et al. (1990). ^a upper limit, obtained in unshaken samples.

Table 5a. Statistics of potential methane oxidation (*PMO*). Data are the same as in Figure 2, but without the marl samples of King et al. (1990). Values with the same letter are not significantly different from each other ($p = 0.05$).

(Eco)system type	¹⁰ log(<i>PMO</i>) (<i>PMO</i> in $\mu mol m^{-3} s^{-1}$)			
	Mean	<i>SEM</i>	<i>SD</i>	<i>n</i>
Minerotrophic natural wetland	0.75 ^a	0.07	0.9	159
Oligotrophic natural wetland	0.74 ^a	0.11	1.0	77
Rice paddy	0.48 ^a	0.14	0.5	11
Roots of wetland plants	0.91 ^a	0.11	0.9	65

Concluding, anaerobic methane oxidation in freshwater systems could be possible from sulphate concentrations of about 1 mM, which is relatively high for natural freshwater wetlands. Also anaerobic methane oxidation by iron may occur, while very little is known about the other alternative electron acceptors. However, it has never been shown that anaerobic methane oxidation is relevant for the total soil methane budget in a freshwater system. In a case study of Murase and Kimura (1996) anaerobic methane oxidation in the subsoil of a rice paddy was below 5% of the methane emission during the

whole growth period. Therefore, and because little more is known, for the remaining part of this article anaerobic methane oxidation is not considered.

Potential methane oxidation correlated to environmental variables

Effects of experimental methods on potential methane oxidation

In contrast with *PMP*, there are no reports on large effects of experimental methods on *PMO*. The main precaution of experimentalists seems to be the avoidance of mass transfer limitation. This is necessary, because, when molecular diffusion is the only mass transfer process, the characteristic length scale is typically only 1 mm (calculated by $\sqrt{\frac{D_{\text{aq}}[\text{CH}_4]_{\text{aq}}}{MO}}$, assuming $MO = 10 \mu\text{mol m}^{-3} \text{ s}^{-1}$, $[\text{CH}_4]_{\text{aq}} = 10 \mu\text{M}$, and a diffusion constant, D_{aq} , of $2 \cdot 10^{-9} \text{ m}^2 \text{ s}^{-1}$). So, to avoid mass transfer limitation samples should be dry, shallow (<1 mm) or shaken.

To measure a true *PMO* the methane concentration in the soil solution should be above the half saturation constant. Taking a typical half saturation constant of $10 \mu\text{M}$, this implies that, at 15°C , the methane concentration in a head space with atmospheric pressure should be at least 6000 ppmv. Therefore, in this paper, *PMO* rates obtained below 2000 ppmv were not used and rates obtained between 2000 and 10,000 ppmv were only used when there was a linear decreased in methane concentration with time. It is recommended to use at least 10,000 ppmv in future determinations of *PMO*.

Distance to oxic/anoxic interface

Highest *PMO* is expected near oxic/anoxic interfaces, because substrates from the aerobic zone (oxygen) and the anaerobic zone (methane) are needed for this process. Indeed, all high values of *PMO* ($>50 \mu\text{mol m}^{-3} \text{ s}^{-1}$) were found within 25 cm of the anoxic/oxic interface (Figure 2). At the anoxic site of the aerobic/anaerobic interface potential rates are higher than at the oxic site. This reflects the better survival abilities of methanotrophs under anaerobic circumstances compared to aerobic circumstances (Roslev & King 1994, 1995). The negative correlation relation between *PMO* with (absolute) distance to water table was also found by Sundh et al. (1995a), Vecherskaya et al. (1993) and Moore and Dalva (1997) using their own data. However, the variation of *PMO* that can be described with distance to water table is limited (Table 5b).

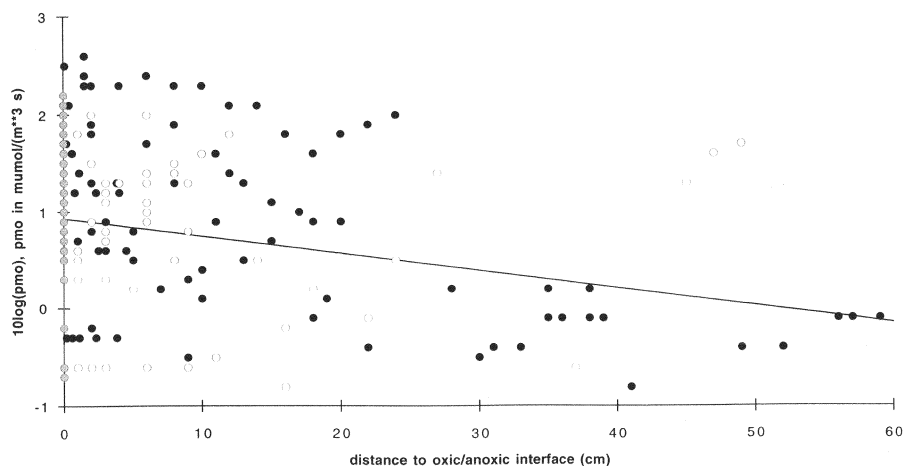


Figure 2. Potential methane oxidation rates as function of distance to oxic/anoxic interface. Data are the same as in Figure 1. For bulk soil samples it was assumed that water table resembled the oxic/anoxic interface. For roots it was assumed that the distance was zero. Open dots are samples from above the water table, black dots are samples from below the water table, grey dots are from the oxic/anoxic interface. The linear regression line is taken from Table 5b.

Table 5b. Linear regressions for potential methane oxidation (PMO) ($p < 0.01$). T_{inc} is the incubation temperature ($^{\circ}C$). $d_{ox/anox}$ is the distance (cm) to the nearest oxic/anoxic interface, which is the water table for non-root samples and zero for root samples. Standard errors of coefficients are between brackets.

PMO in $\mu\text{mol m}^{-3} \text{s}^{-1}$	r_{adj}^2	n
$^{10}\log(PMO) = 1.0(0.1) - 0.021(0.005) \cdot d_{ox/anox}$	0.07	252
$^{10}\log(PMO) = 0.1(0.2) + 0.032(0.008) \cdot T_{inc}$	0.05	312
$^{10}\log(PMO) = 0.4(0.2) - 0.022(0.005) \cdot d_{ox/anox} + 0.028(0.009) \cdot T_{inc}$	0.10	252

Seasonality and methane production

A seasonality of PMO has been observed by King (1990), Bucholz et al. (1995), Amaral and Knowles (1994) and King (1994). Highest PMO was observed in summer. In the study of King (1994) it seemed as if potential root-associated methane oxidation lagged ambient field temperature by about one month. This could indicate that methanotrophic activity is driven by methane availability, which is related to temperature dependent methane production. This was confirmed by Bucholz et al. (1990) who compared sediments of two fresh water sediment lakes. The lake with the higher sedimentation rate had a higher organic matter content, a higher methane concentration and a higher

methane oxidation potential. It could be hypothesized that high methane production rates would lead to high methane concentrations and also to high methane oxidation potentials. Moore et al. (1994) and Moore and Dalva (1997) measured *PMO* and *PMP* in more than 100 samples from several wetlands. They concluded that a high *PMP* resulted in a *PMO*. However, a high *PMO* did not necessarily go with a high *PMP*, which was suggested to be caused by methane diffusion from below the water table to zones above the water table with low production potentials. This asymmetric relation may also be caused by temporal inhibition of *PMP* due to the presence of electron acceptors or damage to the methanogenic population as a result of *in situ* aerobiosis.

Soil type, root-associated methane oxidation, pH, temperature and salinity

There is no difference between *PMO* at minerotrophic and ombrotrophic natural wetlands (Table 5a). At roots, *PMO* is relatively high, though the difference is not significant. This is reflected by the relatively high number of methanotrophic bacteria in rhizosphere soil (De Bont et al. 1978; Gilbert & Frenzel 1995). Root-associated methane oxidation depends on plant type and may be controlled by root oxygen release (Calhoun & King 1997). Gerard and Chanton (1993) found zero methane oxidation in stems and most rhizomes of several wetland plants. King et al. (1990) could not find methanotrophic activity in a subtropical marl sediment, in contrast with a peat sediment with a similar vegetation.

Dunfield et al. (1993) found that the pH optimum for *PMO* was 0–1 pH units above the *in situ* pH, which varied between 4 and 6. No trend between optimum pH and *PMO* was observed. So, pH does not seem to be a discriminating factor for methane oxidation at different sites.

Q_{10} of methane oxidation was around 2, when determined in experiments with temperature as single varying factor (Table 6). Lumping all incubation experiments of Figure 1 results in a similar value: 1.9 ± 0.4 .

In moderately saline soil, salt concentrations 40–80 mM (US Salinity Laboratory Staff 1954), methane oxidation is seriously reduced but not completely inhibited (Denier van der Gon & Neue 1995b and Kighthley et al. 1995). At high salinities (>9‰) methane oxidation was completely inhibited, despite the presence of ample methane and oxygen (Conrad et al. 1995).

Summary

Rates of *PMO* are skewly distributed and vary three orders of magnitude. Only a very limited part ($r^2 = 0.10$) of this variation can be described with well established variables: distance to average water table and incubation

Table 6. Temperature dependence of methane oxidation.

Sample source or organism	Q_{10}
Oligotrophic and minerotrophic peat ¹	1.4–2.1
Roots of <i>C. canadensis</i> ²	4.1 ^a
<i>M. rubra</i> ³	2.2 ^a
Landfill soil ⁴	1.9
Landfill soil, high affinity methane ⁵	2.3 ^a

¹ Dunfield et al. (1993), ² King (1994), ³ King and Adamsen (1992), ⁴ Whalen et al. (1990), ⁵ Boeckx and Van Cleemput (1996), ^a Calculated with $Q_{10}^{\frac{T - T_{ref}}{10}} = e^{-\frac{E_a}{RT}}$, where T is the temperature, T_{ref} is the reference temperature, E_a is the activation energy, R is the gas constant and $T = T_{ref} = 288$ K.

temperature (Table 5b). Possibly, the descriptive relations can be improved by adding correlations with methane and oxygen concentrations, time averaged over a certain period, possibly a month. In this way, seasonal variation and the good survival characteristics of methanotrophs are incorporated.

A methanotrophic biomass model to explain variation in potential methane oxidation

Correlations with soil environmental variable describe only a small part of the variation in PMO . Therefore, it is investigated to what extent a kinetic model for methanotrophic biomass can explain the variation in PMO . Coupled equations (2–5) represent the model:

$$PMO = Q_{mo} B_{mo} \quad (3)$$

$$Q_{mo} = (\mu_{mo,max} + D_{mo}) / Y_{mo} \quad (4)$$

$$\frac{dB_{mo}}{dt} = MO Y_{mo} - D_{mo} B_{mo} \quad (5)$$

Here, B_{mo} is the methanotrophic biomass, Q_{mo} is maximum methane oxidation rate per unit of biomass, Y_{mo} is the yield of biomass on methane, $\mu_{mo,max}$ is the maximum relative growth rate of methanotrophs and D_{mo} is the relative decay rate of methanotrophs. Equation (4) is used to relate Q_{mo} to variables that have been measured regularly. Reported estimated values for Y_{mo} vary between 0.02 and 0.8 C-biomass $(C-CH_4)^{-1}$ (Table 7). This range can be reduced to 0.15–0.67 C-biomass $(C-CH_4)^{-1}$, because (i) the highest

Table 7. Carbon partitioning of methane consumed by methanotrophs

Organism or sample source	Yield (Y_{mo}) C-biomass (C-CH ₄) ⁻¹	Extra cellular product
		C (C-CH ₄) ⁻¹
Drained peat	0.77 ^a	
Tundra soil	0.5 ^b	
Various methanotrophic bacteria ^{3,4,5,6,12}	0.19–0.67	0–0.48 ^c
<i>M. trichosporium OB3b</i> ¹	0.80 ^a	
<i>Mthyllococcus capsulatus</i> ⁷	CH ₄ limited	0 ^c
	O ₂ limited	0.7 ^c
Fresh water sediment ^{8,9}	0.15–0.61	
Landfill soil ⁵	0.69 ^b	
High affinity conditions ^{9,10,11}	0.02–0.6	

¹ Megraw and Knowles (1987), ² Vecherskaya (1993), ³ Nagai et al. (1973), ⁴ Nagai et al. (1973) from data of Sheehan and Johnson (1971), ⁵ Whalen et al. (1990), ⁶ Ivanova and Nesterov (1988), ⁷ Hardwood and Pirt (1972), ⁸ Buchholz et al. (1995), ⁹ Lidstrom and Somers (1984), ¹⁰ Yavitt et al. (1990a), ¹¹ Yavitt et al. (1990b), ¹² Linton and Drozd (1982), ^a calculated as CH₄ consumption – CO₂ production, ^b C in biomass + organic compounds, ^c calculated as CH₄ added – (CO₂ produced + C incorporated in biomass).

values were obtained by neglecting extra-cellular products and because (ii) the lowest values were obtained at low methane concentrations at which maintenance respiration would dominate over biomass growth. $\mu_{mo,max}$ is between 0.14 and 0.34 h⁻¹ at mesophilic temperatures (Linton & Vokes 1978; Lamb & Garver 1980; Linton & Drozd 1982).

Decay of biomass may be described with a maintenance coefficient, m_{mo} (Pirt 1975, p. 67):

$$D_{mo} = m_{mo}Y_{mo} \quad (6)$$

Taking m_{mo} and Y_{mo} from Nagai et al. (1973) and Sheehan and Johnson (1971), who measured these under optimal and suboptimal growth conditions, leads to $D_{mo} = 1 \text{ d}^{-1}$, which is substantially higher than the aerobic and anaerobic C-starvation rates of methanotrophs, which were about 0.1 d⁻¹ (Roslev & King 1994). Apparently, methanotrophs are able to decrease their maintenance requirements under conditions of C-starvation. So, the maintenance coefficient at (sub)optimal growth conditions cannot be used to describe the starvation of methanotrophs. A solution may be the introduction of an extra state variable, representing the physiological state of the microorganism (Panikov 1995, p. 203), in combination with experimental data of starvation kinetics of methanotrophs (King & Roslev 1994).

So, it is possible to model *PMO* via a model for methanotrophic biomass, although predictability of the model will be limited, because of a large variation in parameters which is hard to explain.

Concluding remarks

Like methane fluxes, rates of potential methane production (*PMP*) and potential methane oxidation (*PMO*) are skewly distributed and vary three orders of magnitude. In relating (potential) rates of methane production and methane consumption to environmental variables, like weather, soil and vegetation data, two lines were followed. Firstly, potential rates collected from a large number of studies were statistically analysed. 34% of the variation in the $^{10}\log$ of *PMP* and 10% of the variation in the $^{10}\log$ of *PMO* could be described with correlations with environmental variables. Secondly, the knowledge of the processes underlying methane production and oxidation was reviewed and summarised in explanatory models. For a quantitative evaluation of these models they need to be integrated in a framework that provides the dynamics of water, heat and gas transport, carbon and vegetation dynamics on a sufficiently small scale. Given the large unexplainable variation in the descriptive models it is worthwhile to do so, although expectations for predictive modelling should not be too high, as the variation in parameters of the process models is large. Anyhow, such an integrating effort would provide a lot of insight in the dynamic, non-linear, interactions between processes and in the causes of the large variations in methane fluxes.

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