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FACTORS AFFECTING METHANE PRODUCTION IN PEAT SOILS

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Two main factors control the rates of methane production in peat (*in senso* microbial formation of methane): the water table level and the chemical characteristics of the peat material. The water table restricts oxygen penetration into the peat because of the much slower diffusion of gases in water compared to gaseous phases. The oxygen distribution will govern the location of the strictly anaerobic, methanogenic bacteria in the peat profile. The degree of waterlogging will also influence the availability of the peat plant material for microbial decomposition, when it reaches the anaerobic zone. In waterlogged environments, the surface litter will quickly enter anoxic conditions. In such environments, high methane formation potentials are often found in the uppermost peat layers. Where the water table is positioned further down in the peat profile, a higher proportion of the easily degradable compounds are degraded under oxic conditions and therefore gone by the time the litter enters the anoxic layers. Lignified organic matter reaching the anaerobic zone will be little further degraded. This effect is most likely to be compounded if the nitrogen content of the litter is low. The net flux of methane from peat surfaces is highly dependent on the extent of microbial methane oxidation in the peat profile. Methane oxidizing bacteria need oxygen for the primary oxidation of methane and for their oxygen dependent respiration. The oxygen distribution, and hence the water table position, will therefore also affect the activity of the methanotrophic bacteria. Typically, highest methane oxidation activity is found around the most frequent position of the water table. At this level, high concentrations of methane meet oxygen diffusing down from the peat surface. Methane oxidation potentials in peat have been observed to correlate with the level of the water table, the concentration of methane just below this level, and in some sub-habitats, with the emissions of methane. Field studies have also shown that comparatively dry environments with fluctuating water table levels may act as sinks as well as sources for atmospheric methane. Some habitats show diurnal rhythms, with higher emissions during night. This is probably due to temperature limitation of the methanotrophic bacteria during the night.

Keywords: Carbon flow, methanogenic bacteria, methanotrophic bacteria, mire ecology

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INTRODUCTION

The term methane production in connection with peat and other anoxic environments in nature has been used to mean the actual microbial formation of methane (Williams & Crawford 1984, Yavitt et al. 1988, Conrad 1989). The term has also been used synonymously for the release of methane to the atmosphere (Clymo & Reddaway 1971, Svensson 1976, Svensson & Rosswall 1984). In the following, methane production will be addressed from these two points of view:

1. The microbiological conversion of organic matter (peat and peat forming litter) to methane.
2. The net production of methane resulting from the formation processes above and the microbiological oxidation of methane in peat. This production will give rise to methane concentrations in the peat profile, which in turn determine whether the actual peat will be a net sink or net source for atmospheric methane.

Biological methane production is the ultimate result of degradation of complex organic matter under anoxic conditions. The degradation proceeds as a concerted activity of different groups of anaerobic bacteria, each of which are interdependent. Methanogenic environments are found in anoxic habitats, where only terminal electron acceptor couples with redox potentials lower than approximately that of sulphate/sulphide are available. Despite this thermodynamical restriction, methane formation may occur simultanously with sulphate reduction under certain conditions (Lovley & Klug 1986). During methanogenic conditions methane is the terminal carrier of the electrons originating from the anoxic oxidation of organic material. Energy released during this oxidation is utilized for growth by the microorganisms involved in the degradation of organic matter. Thus methane is the anoxic counterpart to water during oxic degradation. There are some fundamental differences between the oxygen mediated routes and the anoxic methanogenic pathways for the decomposition of organic matter:

1. During the presence of oxygen one single microorganism species (bacterium or fungus) may completely degrade e.g. cellulose to carbon dioxide and water to achieve energy for growth.
2. Under methanogenic conditions at least three microorganisms (mostly bacteria) are needed: one hydrolytic and fermentative bacterium, one acetotrophic methanogen and one hydrogenotrophic methanogen.
3. Organic compounds formed in synthesis processes, where molecular oxygen take part in the reaction, will not be degraded under anoxic conditions (Zehnder & Svensson 1986), but very well so when molecular oxygen is available.

The fact that several groups of microorganisms are necessary for anoxic degradation of organic matter to methane, means that effects of general growth- or activity-regulating factors such as temperature, pH, nutrient availabillity, etc. may be more complex under anoxic conditions, since the different organisms involved may show different response spectra to different factors. Furthermore, since lignin formation is an oxygen requiring process the lignified compounds in the litter will resist anoxic degradation.

In many habitats, where methane formation occurs, some of the methane produced is released into the atmosphere, but part of it may be consumed by methane oxidizing microorganisms (Conrad 1989, Galchenko et al. 1989). The factors regulating the release or net production of methane in peat will therefore also influence the activity of the methanotrophic microorganisms. These include diffusion possibilities for methane and oxygen to reach and sustain methane oxidation, together with general factors such as nutrient availability, pH and temperature.

The purpose of this article is to put these general features and differences into perspective with peat decomposition resulting in methane formation, and to evaluate how the consumption of methane finally determines the direction of the methane exchange between peat and the atmosphere.

METHANE FORMATION

General requirements

For the biological formation of methane to take place, favourable conditions for methanogenic bacteria are needed. These include an anoxic environment and the presence of microorganisms capable of supplying the methanogenic bacteria with their restricted substrate menu, i.e. hydrolytic and fermentative as well as proton-reducing bacteria.

Anoxic conditions

Since methanogenic bacteria are extremely sensitive to oxygen when they are metabolically active, anoxic conditions are an absolute requirement for biological methane formation. Generally, anoxic conditions in terrestrial ecosystems are formed by a combination of high water content in the soil and the consumption of oxygen by chemoorganotrophic organisms, i.e. microorganisms and roots of higher plants. A high water content restricts oxygen distribution, since the diffusion constant for oxygen is much lower in the water phase than in the gaseous phase. The difference is about four orders of magnitude. Soils rich in organic matter are able to store more water and are also able to support higher activities of microorganisms as long as they are not too low in oxygen content. However, the quality of the organic matter, i.e. its availability for degradation, also plays an important role in the regulation of the activity of the microorganisms, and thus for their oxygen consumption.

The importance of the higher plant roots for the oxygen concentration in soils has been particularly stressed in investigations of soil denitrification and its regulation. Klemedtsson et al. (1987) showed that denitrification rates were directly correlated with the abundance of living roots. Higher abundance of roots also caused a shift towards nitrogen in the proportion of nitrous oxide and nitrogen as denitrification products. This was interpreted as being caused by the root exudation resulting in lower oxygen concentrations due to a high microbial oxygen consumption in the root vicinity. This would preferentially lead to nitrogen rather than nitrous oxide release.

The same general pattern for oxygen availability is certainly valid for peat soils. The position of the water table varies among peatland sites from just above the peat surface to 1 m below the surface. This means that, in some areas, oxic conditions may prevail only in a thin layer close to the surface whereas in other areas, the peat may be oxic to a considerable depth. That it is the distribution of oxygen that largely determines the distribution of methane production in peatlands is indicated by the correlation between most frequent position of the water table during the season and the depth of maximal methanogenic activity (Nigel Roulet, pers. comm.). Methanogenic activity is mostly positioned just below this level, i.e. the methanogenic bacteria will rarely be exposed to oxygen. If this is the case for all types of peatlands, the water table position should be the main factor determining the location of the main part of the methanogenic population. However, this pattern may be complicated by oxygen consumption, which will be regulated by the substrate (litter) quality and possible translocation of root exudates into the peat. The methane oxidizing bacteria may also be important contributors to the regulation of the oxygen content. Their activity is mostly concentrated at the position of the water table (Ingvar Sundh, unpubl. data). The whole picture is then affected by temperature, i.e. higher temperatures will give rise to increased oxygen consumption. In the day time, waterlogged peat surfaces may release oxygen due to the photosynthetic activity of mosses and algae, which may affect the anaerobic degradation and methanogenesis.

The methanogenic bacteria

Methanogens are a group of strictly anaerobic bacteria belonging to the Archeabacteria. As a group they are fairly specific in that they only utilize a limited number of substrates. However, they show a considerable diversity, both in morphology and subcellular composition. They are active over a wide range of environmental conditions: pH 3–11; alcalophiles have been isolated but no true acidophiles have so far been reported (Williams & Crawford 1985, Patel et al. 1990); temperatures from 2 to >100°C; extreme as well as "normal" thermophiles have been isolated, but so far no pure cultures of psychrophilic methanogens have been reported in the literature. According to prof. G. Zavarzin (pers. comm.), a psychrophilic methanogenic strain has been isolated in his laboratory. Evidence for the occurence of a psychrotrophic acetotrophic population of methanogens has been given by Svensson (1984). The most important substrates used by methanogens are acetate or hydrogen and carbon dioxide. Some methanogenic bacteria are also able to oxidize alcohols to supply hydrogen for the reduction of carbon dioxide and some are able to use different methylated compounds.

Because of their limited substrate menu, methanogens have to rely on other anaerobic bacteria which are able to degrade organic polymers and their building blocks into compounds that can be utilized by the methanogens. The non-methanogenic bacteria benefit from the methanogens and gain more energy from their conversion of organic material when forming hydrogen and acetate as their sole products, as compared to the formation of a variety of fermentation products (Zinder 1984).

Although we do not know the main pathways of methane production in peat, there is no reason to believe that the anoxic degradation of organic material in peat should not follow the general pattern established in other methanogenic systems (Goodwin & Zeikus 1987). Stimulation of methane formation in peat samples incubated in the presence of hydrogen has been observed (Svensson 1984, Williams & Crawford 1984, Yavitt &

Lang 1990), indicating the presence of hydrogenotrophic methanogens. However, Yavitt and Lang (1990) found no stimulation in samples from two of their sites. In other experiments in our laboratory, hydrogen was observed to inhibit methane formation from acetate in peat samples at temperatures below 25°C (Jan Lantsheer, pers. comm.). Williams and Crawford (1984) found that acetate additions rather inhibited than stimulated methane production in peat. The reason for this inhibition may have been the low pH, since acetate may take up protons enabling it to passively pass membranes and become toxic to organisms, including the methanogens. Contrary to this observation, Yavitt and Lang (1990) found that acetate amendment stimulated the methane production in samples from two of their sites. These authors, as well as Williams and Crawford (1984), observed an increased methane formation from some peats by adding glucose.

Enrichment cultures at different temperatures with peat samples from a tundra mire gave evidence for the occurrence of two populations of methane-forming bacteria with different temperature optima (Svensson 1984). Methanogenesis from acetate had an optimum at 20°C while hydrogen utilizing methanogens had their optimum at 28°C. Methane was also formed in parallel experiments with ethanol as the substrate. The ethanol was most likely converted to acetate and hydrogen prior to methane production, since activity peaks were found at the temperatures of the optima found. The low temperature in peat profiles, where methane formation takes place, may play an important role in regulating the flow of carbon and electrons to methane (cf. Conrad et al. 1987, 1989, Westerman et al. 1989).

Microorganisms utilizing other electron acceptors than carbon dioxide for anaerobic respiration have competitive advantages over methanogens (Westerman & Ahring 1986, 1987, Conrad 1989). Such compounds are nitrogen oxides (nitrate, nitrite and nitrous oxide) and sulphate. Occurrence of these compounds will therefore influence the activity and abundance of methanogens. In peatlands, these compounds are mainly available in the surface layers. This may result from precipitation in ombrotrophic peat systems or from contact with water in the surroundings (lakes, brooks and ground water) in minerotrophic systems. Most likely, these interfering electron acceptors will be utilized quickly, either assimilated as nutrients by plants or respired by microorganisms in the upper parts of the anoxic zones. The increased occurrence of nitrate and sulphate in precipitation may, in the long-term, affect the anoxic degradation pathways in peats and other freshwater wetlands.

Organic matter in peat as a source for methane formation

The organisms performing the primary attack on the dead organic material in peatlands will face the same situation as in any other ecosystem: their activity will, to a great extent, depend on the degradability of the organic matter. This means that the structure of the organic compounds is a crucial factor. Mature and thus often more lignified litter is more resistant to degradation. As mentioned above, molecular oxygen is necessary for the degradation of lignin. Therefore, any lignified material that ends up in waterlogged peat depleted of oxygen, will be highly resistant to decomposition.

The distance between the water table level and the soil surface is of great importance as a regulator for the quality of the substrate entering the anoxic zone. The duration of litter degradation under oxic conditions will be shorter in waterlogged habitats than in habitats with the water table positioned at greater depths in the peat profile. Therefore, the probability for the presence of "easily" degradable organic matter, when the litter enters the anoxic zone, is higher for the waterlogged situation compared with the case when the oxygenated zone is thicker. This is reflected in higher rates of methane production in peat samples from water saturated peat areas as compared to areas with drier top layers (Nilsson 1992). Characteristically, the highest rates of methane production are mostly found within 10 cm of the surface in waterlogged peat, indicating that the main part of the easily degradable substrate is used at these levels. The rates found in samples taken further down in the peat profile are often about an order of magnitude lower, and similar to production rates found in the anoxic zone of peat overlain by a substantial peat layer, which is influenced by oxygen (Nilsson 1992).

The importance of the chemical composition of the peat as a factor controlling the methane production has recently been discussed by Yavitt and Lang (1990), Nilsson (1992) and Valentine et al. (1993). The first authours found a significant correlation ($r = 0.74$) between the amount of none-lignin, acid soluble, compounds in peat and methane production rates in peat samples. Thus, lignified organic material does not seem to be the origin of substrates for the methanogenic population in peat. By using the total spectral signal from near-infra-red (NIR) spectroscopy on peat samples from different depths from several mire ecosystems, Nilsson (1992) was able to explain 50 to 85% of the variation in the methane production rates. The samples investigated originated from peat of different degrees of humification. His results clearly support the influence of the organic matter composition as a regulating factor.

Table 1 summarizes some of the data presented by Valentine et al. (1993). They studied the methane formation from peat samples collected at the main sites of the joint North American study of methane exchanges with the atmosphere at the Hudson Bay Lowland in Canada (Roulet et al. 1992). Their two extreme sites were chosen here to illustrate the importance of the peat composition on methane formation rates: the minerotrophic coastal fen, with a thin peat layer of recent origin, and the ombrotrophic bog area, which has developed over the last 4 000 years. The data have been recalculated by averaging their results from different depths. According to the arguments above, the bog peat should give rise to higher methane production rates than the fen, since the cellulose content is higher and the lignin fraction lower in the bog peat. However, the methane production measured by peat-sample incubations show more than one order of magnitude higher rates for the fen than for the bog. The authors claim that the difference in nitrogen content is a possible explanation for this difference, since the nitrogen content decreases relatively more than the lignin content. Indeed, the carbon to nitrogen ratio and the lignin to nitrogen ratio are substantially higher in the bog peat compared with the fen peat material. These ratios strongly indicate a much lower inclination to degradation of the bog peat compared with that of the fen (Valentine et al. 1993). Another factor, which may contribute to the difference observed, is the position of the water table. At the Coastal fen site the average position was at 14 and at the bog at 26 cm below the vegetation surface. Thus, in light of the discussion above concerning water table position and its effects on the substrate quality of the below ground peat, the influence of the water table position should not be neglected.

Table 1. Relative contents (% of dry matter) of major components of peat from two areas within Hudson Bay Lowland in Canada as averaged from data presented by Valentine et al. (1993).

	Coastal Fen (minerotrophic)	Kinosheo Lake (ombrotrophic bog)
Carbon	48	48
Lignin	40	21
Cellulose	20	36
Nitrogen	2.1	0.7
C:N	23	68
Lignin:N	19	51

The importance of the nutritional status of mire subhabitats in relation to methane formation has earlier been addressed by Svensson et al. (1975), Svensson (1976, 1983) and by Svensson and Rosswall (1984). Minerotrophic habitats characterized by a high input of nitrogen due to fixation of atmospheric nitrogen by cyanobacteria (corresponding to 90 kg N ha^{-1}) showed much higher methane emissions than similar sites with low nitrogen fixation. These habitats of high nitrogen fixation were also characterized by a much higher net primary production and lower peat accumulation rates than the ombrotrophic subhabitats (Svensson 1983, 1986).

In conclusion there is clear evidence that the peat organic matter composition is an important factor determining the methane production in peat. The composition of the plant material forming the peat is therefore important. The water table level interacts with this factor, since the distance between the peat surface and the water table largely determines to what extent "easily" degradable organic material will occur in the anoxic parts of the peat. The availability of inorganic nutrients is also influencing the degradation both during oxic and anoxic conditions.

METHANE OXIDATION

Biological oxidation of methane in fresh water systems seems to occur only in the presence of molecular oxygen (Conrad 1989). Since there are no reports showing considerable anoxic methanotrophic activity in peat soils, the same concept is probably also applicable to peats. In the metabolism of methanotrophic microorganisms oxygen serves two functions: 1) molecular oxygen is used in the primary oxidation of methane and 2) oxygen is the terminal electron acceptor of their energy metabolism. Therefore, the availability of oxygen and the primary substrate methane can be expected to be important in determining the distribution and activity of methane oxidizing organisms in natural environments. The extent of methane formation is therefore, at least in part, controlling the abundance, activity and location of methanotrophs in peat habitats. Ultimately, the balance between production and oxidation of methane in peat profiles governs the rate of methane exchange with the atmosphere. Methane oxidation as a regulator of methane emissions from peat was addressed by Svensson (1974), when he observed that incubations of peat samples with methane in the headspace showed methane consumption. The same type of results were reported by Williams (1980), and Harriss et al. (1982) presented the first observation of *in situ* methane consumption in peatlands. The importance of methane consumption was further discussed by Svensson (1976) and by Svensson and Rosswall (1984). The occurrence of this process in peatlands has later been more thoroughly discussed (Crill et al. 1988, Yavitt et al. 1988, Whalen & Reeburgh 1990, Whalen et al. 1991, Moore et al. 1992, Mikkelä et al. 1992). Sundh et al. (1992a) emphasized the importance of the methane supply, via methane production, for the occurrence and distribution of methanotrophic activity in peat profiles.

It is difficult to measure *in situ* rates of methane oxidation in peats and most studies so far have been made in the form of laboratory incubations. Whalen and Reeburgh (1990) used soil cores in their investigations of tundra soil methane oxidation, while Yavitt et al (1988) studied methane oxidation potentials in slurries of peat and water. Although not revealing actual *in situ* rates, this type of studies have provided a comprehensive concept for the occurrence of methane oxidation in soils, including peat.

Because of the big difference between gas diffusion constants in aqueous and in gas phases, the water content of a soil will determine the gas transport rates, of both oxygen and methane, to the methanotrophic bacteria. This means that the position of the water table level is very important not only for the methane formation in peat soils, but also for the rates of methane oxidation (Whalen & Reeburgh 1990). The methane oxidizing organisms will therefore, most likely, be concentrated to the seasonal mean position of the water table level, since the chances for a simultaneous supply of methane and oxygen will be maximal at this level. Evidence for this pattern in tundra and taiga soils have been given by Whalen and Reeburgh (1990) and Whalen et al. (1991).

In a treed bog in Canada, methane oxidation activity was found to peak at the peat level corresponding to the most frequent position of the water table during the season (Nigel Roulet, pers comm). Sundh et al. (1992a) observed a correlation (r = 0.81) between potential methane oxidation rates and the water table position at the time of sampling for untreed mire habitats. Treed habitats (pines) were not atypical in having water table levels deep in the peat profile, but despite this they gave rise to low potential methane oxidation rates. In the same data set a corresponding correlation (r = 0.78) was found between mean methane oxidation and the methane concentration 10 cm below the water table position (Ingvar Sundh, unpubl. data). This indicates a coupling between the methane production rate in the peat and the extent of methane oxidation. In other words, the rates of methane formation in the peat will influence the occurrence of methane oxidation. This pattern fits with the situation in the areas with pine trees, where both the pore water methane concentrations and the potential oxidation rates were low. The pine treed areas have more humified peat, probably as a result of a stimulation of the mineralization by the tree roots. Therefore, the peat in these areas, according to the coupling between substrate quality and methane formation, which was outlined above, should give rise to lower methane production rates. Experiments with anaerobic incubations of peat from the different peat habitats have resulted in lower methane formation rates in peat from the pine treed areas (Sundh et al. 1992b), which support the view outlined above.

One conclusion of the discussion above, is that waterlogged peat areas should exhibit higher rates of methane emission to the atmosphere than areas with an unsaturated top layer. The reason is that the methane formed in the waterlogged layers close to the surface will not have the same chance to be consumed by methane oxidizing organisms. A special type of waterlogged habitats, the mud-bottoms studied by Sundh et al. (1992a), deviated from the general pattern of low methane oxidation in water saturated areas. These sites showed comparatively high potential oxidation rates, while being the most potent habitats for methane emissions to the atmosphere. By excluding these two extreme habitats (pine tree areas and mud-bottoms) and regressing the mean potential methane oxidation of the different habitats with the mean emissions for the very same sampling days a correlation (r = 0.71) was found.

This implies that about 50% of the variability in methane realease rates of these sites may be explained by the methane oxidation capacity of the peat profile.

Mikkelä et al. (1992) sometimes observed diurnal fluctuations in methane emission rates from environments, where the water level position was well below the peat surface. Emissions were higher during the night than during daytime. These observations were from days when temperature decreased 7°C in the peat during the night at the position of the water table. During days when only small temperature differences over day and night were observed no considerable fluctuations in emissions were seen. The explanation given was that the quite large temperature difference caused an effect on the methane oxidizing bacteria, which are present close to the water table position. They were able to consume the methane formed during the warm daytime, but were restricted in activity during the cold night and thus allowing more methane to escape to the atmosphere. The temperature shift was much less deeper in the peat profile, where the methanogenic flora was mainly present.

SUMMARY AND CONCLUSIONS

The microbiological production of methane is affected by several direct and indirect factors. Many of these factors are mainly related to the distribution of oxygen in the top layers of the peat profiles. The water regime is the key factor, since the oxygen diffusion is several orders of magnitude slower in water as compared with the gaseous phase. The extent of oxic conditions in the upper layers also affects the availability of the litter for anoxic degradation to methane. This is a result of the much more rapid degradation of the organic matter in the oxic zone compared with the anoxic condition deeper in the peat profile. The water level also influences the net production of methane of peat, which form the basis for the emission of methane to the atmosphere. The methane oxidation by methanotrophic bacteria is also regulated by the oxygen diffusion (and also methane diffusion) to the peat levels, where these bacteria are located. Other factors such as temperature, pH and nutrient availability are important modulators of the rates of both methane production and consumption. At oxic conditions methane is not formed, and no methane oxidation under anoxic conditions has so far been reported for peatlands.

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