



# Methane production and oxidation potentials in relation to water table fluctuations in two boreal mires

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## Abstract

We studied the response of methane production and oxidation potentials in a minerotrophic and an ombrotrophic mire to water table fluctuations. In profiles where water table had not varied, the water-saturated layers showed significant potentials while the unsaturated layers did not. The production potentials in the saturated layers below water level ranged from 0.1 to 2.4  $\mu\text{g CH}_4 \text{ h}^{-1} (\text{g d.w.})^{-1}$  and oxidation potentials (first order reaction rate constants) between  $-0.010$  and  $-0.120 \text{ h}^{-1} (\text{g d.w.})^{-1}$ . In profiles with constant water level, the maximal production potential occurred 20 cm and maximal oxidation potential 10 cm below water level. When water table varied only a little, production potentials slightly increased towards the autumn. After a water level draw-down, in the profiles from the dry microsites, production and oxidation potentials were detected in layers that had been unsaturated up to 6 weeks. The maximal oxidation zone was shifted downwards during low water periods. In a wet microsite, a 2 week period of unsaturation eliminated the production potentials and decreased the oxidation potentials. After a rise in the water level, the potentials were reactivated more rapidly in the wet than in the dry microsites. © 1999 Elsevier Science Ltd. All rights reserved.

## 1. Introduction

The dynamic balance between methane production and oxidation rates in peat profile and the transport rate from peat to atmosphere control methane fluxes from wetlands (Bubier and Moore, 1994). The fluxes show high spatial and temporal variations (Moore et al., 1990; Whalen and Reeburgh, 1992; Dise, 1993) that can to some extent be related to variations in environmental factors, like temperature or the water level (Moore and Knowles, 1989; Moore et al. 1990, 1994; Whalen and Reeburgh, 1992; Christensen, 1993; Moore and Roulet, 1993; Roulet et al., 1993; Kettunen

et al., 1996; Kettunen et al., unpublished data). However, as the interactions are complex, all variation frequencies in methane fluxes cannot be captured correlating the flux with any single environmental factor (Whalen and Reeburgh, 1992; Christensen, 1993; Kettunen et al., 1996; Kettunen et al., unpublished data). Methane production and oxidation rates depend on substrate availability, presence of alternative electron acceptors that compete for substrate with methanogenesis, oxygen availability which is connected to peat moisture conditions, temperature and the activity of methane-producing and methane-oxidizing bacteria in the peat matrix. Methane-producing bacteria require anoxic conditions (Sundh et al., 1994) and a suitable carbon source: acetate or carbon dioxide and molecular hydrogen (Valentine et al., 1994). The oxygen concentration in peat decreases downwards while the new

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carbon which can be quickly metabolized in anaerobic fermentation processes to a suitable form for methanogenesis is mainly supplied to uppermost layers where plant roots can survive (Schütz et al., 1991; Schimel, 1995). In fact, maximal methane production has been observed at about 20 cm below the water table (Sundh et al., 1994). As methane oxidation requires methane as substrate and oxic conditions, a population of methane-oxidizers develops where methane and oxygen overlap in the peat profile (Sundh et al., 1995). Changes in both substrate availability and oxygen concentration during the growing season affect the population dynamics of methanogenic and methanotrophic bacteria (Svensson and Rosswall, 1984; Whiting and Chanton, 1993) and are reflected in the net flux of methane.

The water table in mires typically shows a seasonal pattern with lowest water levels during the period of high evaporation in midsummer. In addition, there are short-term fluctuations in water table due to rain showers. Previous studies on production and oxidation potentials (Yavitt et al., 1988, 1990; Moore and Knowles, 1990; Bubier et al., 1993; Dunfield et al., 1993; Moore et al., 1994; Sundh et al., 1994; Valentine et al., 1994; Nedwell and Watson, 1995; Segers, 1998) do not consider the seasonal pattern of water table nor analyze the effects of water table fluctuations on methane production and oxidation potentials. The response of the potentials to fluctuations in water table is, however, an important question as the potentials give information on the activity of the microbial populations and hence, the response of methane-producing and -oxidizing microbes to altered water level can be analyzed using production and oxidation potentials. As drought periods have been anticipated to become more frequent in future climates (IPCC Climate change, 1995), it is important to know how the methanogenic and methanotrophic bacteria survive periods of low water level (unsaturation) to predict the lag in the reactivation of methane production and oxidation after a rise in the water level which crucially affects the methane flux dynamics in wetlands.

We used laboratory measurements of methane production and oxidation potentials from two Finnish mires to analyze the response of potentials to both falls and rises in water level. The mires represent two different patterns in methane emissions due to differences in nutritional status and also the seasonal water table pattern differed among the mires.

## 2. Materials and methods

### 2.1. Sites and sampling

Peat samples for measurements of methane pro-

duction and oxidation potentials were collected at two Finnish virgin mires during two summer seasons. Low-sedge *Sphagnum papillosum* pine fen situated at the margin area of the mire complex of Salmisuo (62°47'N, 30°56'E) in eastern Finland reflects minerotrophic conditions while treeless *Sphagnum fuscum* bog in the mire complex of Ahvensalo (65°51'N, 30°53'E) represents ombrotrophic conditions. The microsites within the mires were selected to represent different moisture conditions with different vegetation. The dry microsites were *Sphagnum fuscum* hummocks and *Eriophorum vaginatum*–*S. balticum* lawns both at the fen and at the bog. The wet microsites at the fen were *S. balticum*–*S. majus* flarks and those at the bog *S. balticum*–*S. lindbergii* hollows. The vegetation in the microsites is described in detail by Saarnio et al. (1997) for the fen and by Alm et al. (1999) for the bog.

Peat profiles from the peat surface down to 45–100 cm were sampled 3–5 times during the growing season from the different microsites at the fen in 1993 and at the bog in 1994. Each 5 cm layer of the peat profile from each microsite at each peat collection time was divided into three samples for the laboratory analyses. After the peat collection, 15 ml peat samples were inserted to 100 ml infusion bottles with rubber stoppers, 30 ml of distilled water was added and the flasks were flushed with 99.96% nitrogen to obtain anoxic conditions for methane production measurements. In methane oxidation measurements, 30 ml samples were disjoined and spread as a thin layer into the bottom of a 600 ml infusion bottles with a glass stick to avoid diffusion limitation and anoxic nodules in samples.

### 2.2. Methane production and oxidation potentials

The bottles for methane production and oxidation potentials were kept unshaken at 20°C temperature in laboratory conditions. The methane oxidation bottles were first allowed to dry in open air for 4 h, after which the bottles were sealed with rubber stoppers and the initial methane concentration in the bottles was adjusted to 100 µl l<sup>-1</sup>. The oxygen concentration in the bottles was not regulated. The methane concentrations in the gas phase of all bottles were measured 4–7 times during the first 10 d of incubation using a Shimadzu GC-14-A gas chromatograph equipped with a flame ionization detector. The methane production and oxidation rates were calculated from the linear and log-linear least-square fits, respectively, of measurements from three parallel peat samples and normalized to dry weight of peat. The oxidation rate was expressed as a first order reaction constant that is the regression coefficient to the log transformed concentration correlated against time.

A *t*-test for the regression slopes was used to determine whether a specific reaction rate was significantly

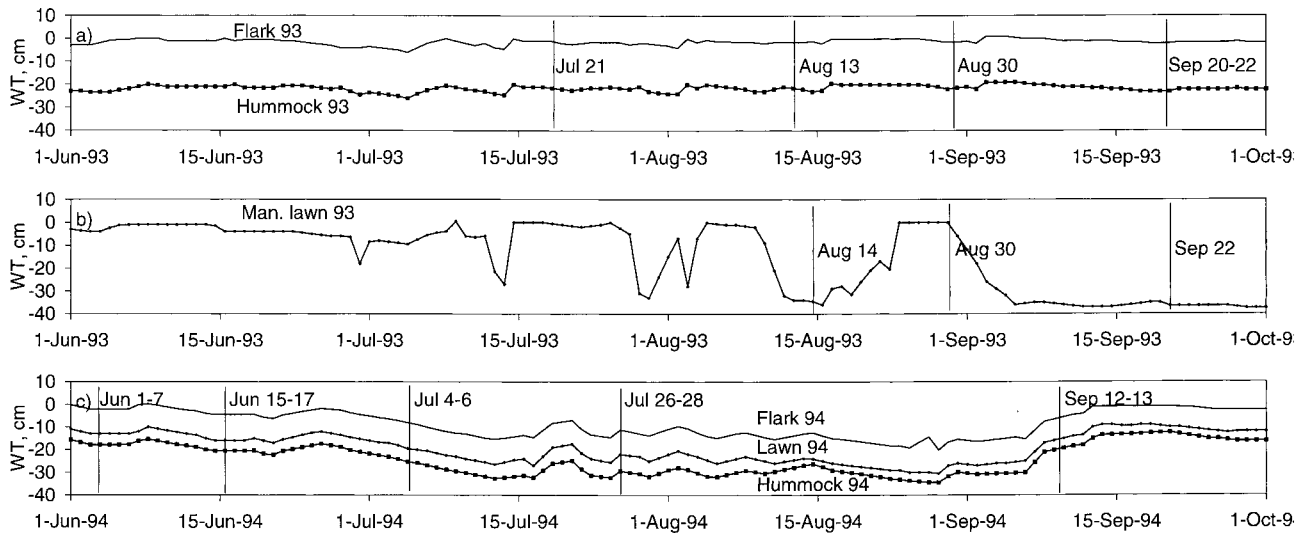


Fig. 1. Seasonal water table patterns in (a) the virgin hummock and flark in the fen during summer 1993, (b) the lawn where the water table was manipulated in the fen during summer 1993 and c) the virgin hollow, lawn and hummock in the bog during summer 1994.

different from zero and whether two reaction rates differed from each other. N varied between 12 and 18 and the probability value of 0.01 was used throughout the paper.

### 2.3. Water table patterns

We assumed that in profiles where water table (=WT) had varied less than 5 cm during the 30-d

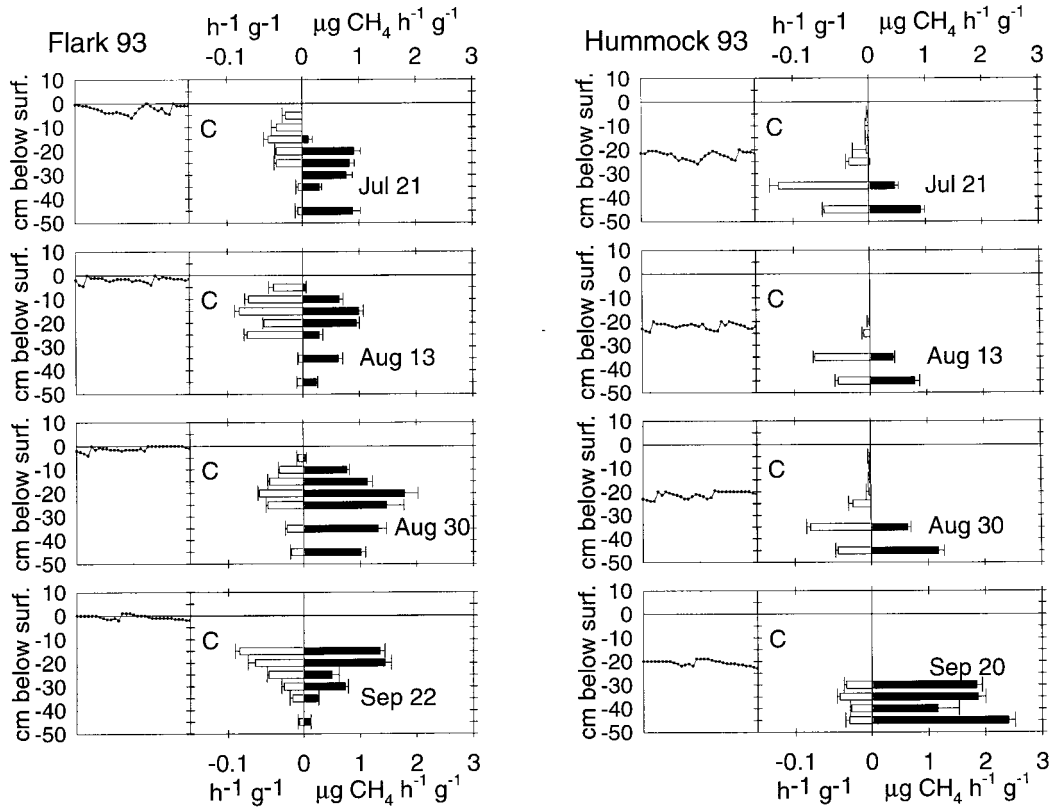


Fig. 2. The WT pattern during the 30-d period before peat collection and the oxidation and production potentials with standard errors from three parallel samples in the flark and the hummock during summer 1993 in the fen. The zero level is the peat surface. As WT remains constant, the profiles are marked with 'C' and the layers above WT are permanently unsaturated and the layers below WT permanently saturated.

period preceding the peat collection (later referred to as 'profiles with constant WT' and marked with 'C' in Figs. 2,4,5) the methane production and oxidation reaction rates in the peat profiles had reached an equilibrium in relation to current WT. If the variations exceeded 5 cm ('profiles with varying WT' marked with 'V' in Figs. 3–5), we assumed that equilibrium had not been reached. In profiles with constant WT, the layers above the water level are referred to as permanently unsaturated layers and the layers below the water level as permanently saturated layers. In profiles with varying WT, temporarily unsaturated layers refer to layers that have become unsaturated after a water level draw-down and temporarily saturated layers to layers that have become saturated after a rise in water level.

In the fen, WT at the virgin sites varied only little during the season 1993 (Fig. 1a). In the lawn microsite of the fen, WT was artificially lowered to 30–40 cm below the peat surface during August and September, but the low water level was not continuously maintained (Fig. 1b).

In the bog, the water tables showed a strong seasonal pattern during summer 1994 (Fig. 1c). Till the beginning of July, WT varied within a few centimeters, but between 6 and 11 July, a drop by about 10 cm occurred. After 11 July, WT remained low till the end of July, the only exception being the temporary rise of 5 cm on 23 July. In August, WT remained low, rising by 15 cm towards mid-September.

### 3. Results

#### 3.1. Methane production and oxidation potentials in profiles with constant WT

In all profiles with constant WT (marked with 'C' in Figs. 2,4,5), the production and oxidation potentials in the permanently saturated layers below water level were at least an order of magnitude greater than potentials in the permanently unsaturated layers above the water level. In the permanently unsaturated layers, the production potentials remained below  $10 \text{ ng CH}_4 \text{ h}^{-1} (\text{g d.w.})^{-1}$  and the oxidation potentials below  $-0.01 \text{ h}^{-1} (\text{g d.w.})^{-1}$  throughout the season, except the slightly higher values in the hummock profile on 17 June 1994. In the layer at water table, production potentials up to  $60 \text{ ng CH}_4 \text{ h}^{-1} (\text{g d.w.})^{-1}$  and oxidation potentials up to  $-0.05 \text{ h}^{-1} (\text{g d.w.})^{-1}$  were measured. In the permanently saturated layer 0–30 cm below the WT, the production potentials ranged from  $0.1$  to  $2.4 \text{ } \mu\text{g CH}_4 \text{ h}^{-1} (\text{g d.w.})^{-1}$  and oxidation potentials from  $-0.010$  to  $-0.120 \text{ h}^{-1} (\text{g d.w.})^{-1}$ . In a few exceptional cases, i.e. in uppermost layers of lawn and hollow on 1 and 2 June and in the hummock profile

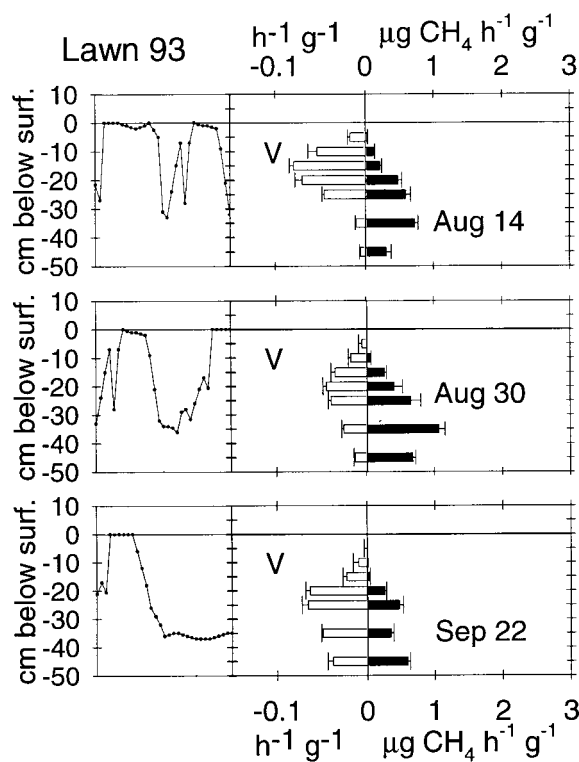


Fig. 3. The WT pattern during the 30-d period before peat collection and the oxidation and production potentials with standard errors from three parallel samples in the lawn where water table was manipulated during summer 1993 in the fen. The zero level is the peat surface. As WT varies, the profiles are marked with 'V'.

on 6 July 1994 from the bog slightly lower production potentials were detected. In the few profiles where saturated layers deeper than 30 cm below WT were measured, the production potentials varied from  $0.01$  to  $1.3 \text{ } \mu\text{g CH}_4 \text{ h}^{-1} (\text{g d.w.})^{-1}$  and oxidation potentials from nonsignificant rate to  $-0.03 \text{ h}^{-1} (\text{g d.w.})^{-1}$  (data not shown in Fig. 2).

In the saturated layers of fen profiles, the production potentials increased towards the autumn. The production potentials ranged from  $0.1$  to  $1.0 \text{ } \mu\text{g CH}_4 \text{ h}^{-1} (\text{g d.w.})^{-1}$  from June to early August, while in late August and September the range was from  $1.0$  to  $2.4 \text{ } \mu\text{g CH}_4 \text{ h}^{-1} (\text{g d.w.})^{-1}$ .

#### 3.2. The production and oxidation potentials in relation to WT fluctuations

##### 3.2.1. Responses to a downwards shift in water level

In the fen, only a few days after the artificial water level draw-down (Fig. 3, 14 August), the oxidation potentials in the temporarily unsaturated lawn layers did not differ from potentials in the permanently saturated flark layers. The production potentials in the temporarily unsaturated lawn layer 0–20 cm below peat surface accounted for 16–41% of the permanently

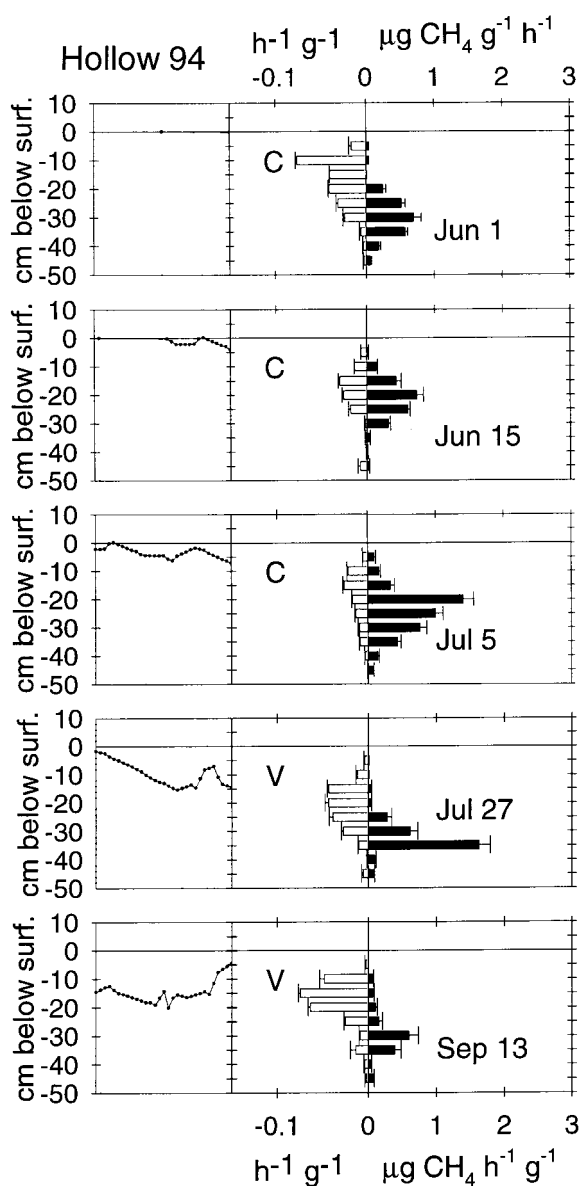


Fig. 4. The WT pattern during the 30-d period before peat collection and the oxidation and production potentials with standard errors from three parallel samples in the hollow during summer 1994 in the bog. The zero level is the peat surface. When WT remains constant, the profiles are marked with 'C' and the layers above WT are permanently unsaturated and the layers below WT permanently saturated. When WT varies, the profiles are marked with 'V'.

saturated flank potentials, but were significantly greater than production potentials in the permanently unsaturated layers.

In the bog, after the 2-week period of low water level starting in mid-July, the production potentials in the temporarily unsaturated hollow layer 0–10 cm and oxidation potentials in the temporarily unsaturated hollow layer 0–5 cm had decreased to the values of permanently unsaturated layers (Fig. 4, 27 July). The oxidation potential in the temporarily unsaturated

layer 5–10 cm accounted for 32% of potentials in the same layer before the water level draw-down.

In dry (lawn and hummock) microsites of the bog, the potentials in temporarily unsaturated layers survived the 2 weeks of low water level better than in the wet (hollow) microsite (Fig. 5, 26–28 July). In the temporarily unsaturated lawn layers, production potentials did not differ from potentials in the permanently saturated lawn layers before water level draw-down. The production potentials in temporarily unsaturated hummock layers 20–30 cm had decreased to 20–50% of production potentials in the same hummock layers before the water level draw-down. Oxidation potentials in the temporarily unsaturated lawn layers 20–35 cm and hummock layers 25–30 cm had fallen to 50–70% of the potentials before the water level draw-down.

In the fen, more than 6 weeks after the start of artificial water table lowering, production and oxidation potentials in the temporarily unsaturated lawn layers 15–45 cm below peat surface had survived and were significantly greater than in the permanently unsaturated layers (Fig. 3, 22 September). In temporarily unsaturated layers 0–15 cm, production and oxidation potentials had disappeared being similar to potentials in permanently unsaturated layers. The maximal oxidation potential occurred in the layer 20–25 cm below peat surface, i.e. one layer deeper than in profile on 30 August, indicating a transition towards an equilibrium in relation to the new water level.

### 3.2.2. Reactivation of potentials after a rise in water level

In the fen, no recovery was observed in the lawn profile where peat profile had become water saturated a few days before peat collection after 2 weeks of unsaturation (Fig. 3, 30 August). Throughout the temporarily saturated profile (Fig. 3, 30 August), the production and oxidation potentials were similar or lower than in the temporarily unsaturated profile (Fig. 3, 14 August) despite the fact that on 14 August most of the layers were above and on 30 August below the water level. In the temporarily saturated layer 0–5 cm, the production and oxidation potentials were similar to permanently unsaturated layers. In the layers 5–20 cm, the production potentials accounted for 10–35% of the potentials in the permanently saturated layers. The maximal oxidation potential was observed in layer 15–20 cm below peat surface, i.e. one layer deeper than in the profile on 14 August, reflecting adaptation to water level draw-down but not to the rise in water level.

After a temporary rise in water level on 23 July in the bog, the oxidation potentials in the hummock layers 10–20 cm and lawn layers 5–15 cm below peat surface (Fig. 5, 26–28 July) were greater than the potentials in the same layers before the temporary rise.

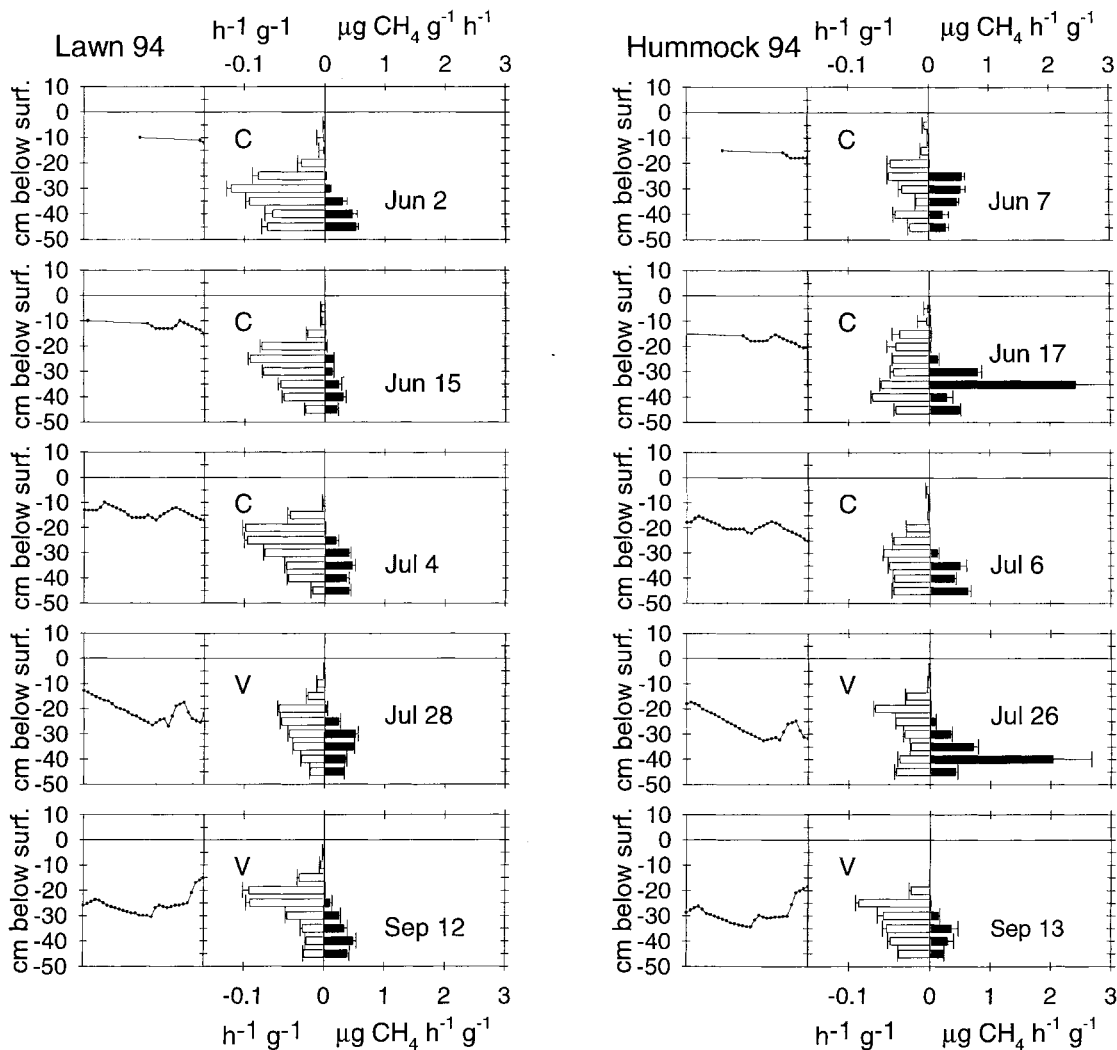


Fig. 5. The WT pattern during the 30-d period before peat collection and the oxidation and production potentials with standard errors from three parallel samples in the lawn and the hummock during summer 1994 in the bog. The symbols and organization of the graphs are the same as in Fig. 4.

When the low water level period in the bog was followed by a rather slow 15 cm rise starting at the end of August, the production and oxidation potentials in the temporarily saturated layers 5–20 cm of the wet (hollow) microsite (Fig. 4, 13 September) were greater than the potentials in the same layers before the rise in water level.

The hummock and lawn profiles did not show evidence of reactivation after the rise in water level (Fig. 5, 12–13 September), as both production and oxidation potentials were in all cases either similar or smaller than potentials during the low water level. The temporarily saturated hummock layers 0–20 cm and the lawn layers 0–15 cm showed potentials similar to permanently unsaturated layers. The production potentials in temporarily saturated hummock layer 20–30 cm accounted for 14–42% of the potentials in these layers during the low water level and 3–32% of the po-

tentials in these layers when the layers were permanently saturated. In the newly saturated lawn layers 15–25 cm the potentials accounted for 48–51% of the potentials in the layers when the layers were permanently saturated.

### 3.3. Maximal potentials

In profiles with constant WT, the depth of maximal production and oxidation potentials showed a strong relation to 30-d average water level. Maximal production occurred on average about 20 cm below water level (regression  $P = 0.86WT - 20.6$ ,  $r^2 = 0.93$ ,  $P < 0.001$ ,  $n = 17$ , see Fig. 6a) and oxidation potential 10 cm below water level (regression  $O = 1.03WT - 10.5$ ,  $r^2 = 0.89$ ,  $P < 0.001$ ,  $n = 17$ , see Fig. 6b). In profiles with varying WT, neither maximal production depth nor maximal oxidation depth was

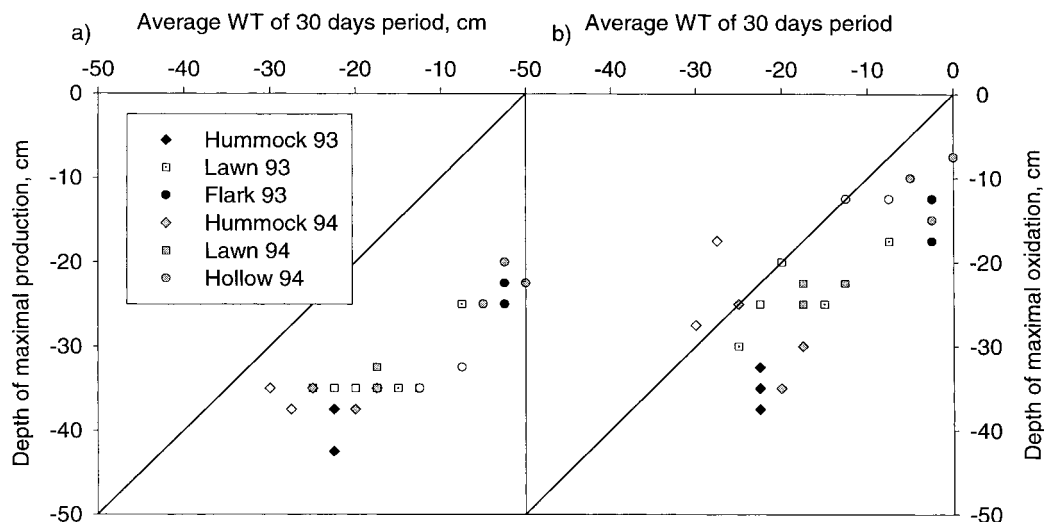


Fig. 6. The maximal (a) production and (b) oxidation zone versus the average water level during the 30-d period before the peat collection. The lines represent situations where maximal potentials coincidence to water level. Closed symbols indicate profiles with constant WT (marked with 'C' in Figs. 2–5) and open symbols profiles with varying WT (marked with 'V' in Figs. 2–5).

statistically related to water level ( $n = 9$ ,  $P > 0.05$ ). Generally, the dryer microsites showed their maximal production closer to the water level than the wetter.

#### 4. Discussion

Our study shows that methane production and oxidation potentials in the peat profile decrease very slowly during periods of low water level and consequent unsaturation. On the other hand, also the reactivation of the potentials after a rise in water level is slow if the potentials had already considerably decreased and conditions in peat profile had become more suitable for reduction of alternative electron acceptors (Segers and Kengen, 1998). Overall, our results show that both methane producers and oxidizers are well adapted to their natural environment where water level typically shows both short-term fluctuations and a seasonal pattern. The lag in reactivation of methane production in layers that become saturated after a 1-week period of unsaturation resulted in low methane fluxes during rising water table as observed in the laboratory study by Moore and Dalva (1993). The extremely slow dynamics both in the decrease of potentials after the water level draw-down and in the reactivation after a rise in water level indicate that methanogenic and methanotrophic bacteria are attached to peat particles and remain in the same layer of peat matrix even though water table shows fluctuations.

In profiles where water table had not varied, the vertical pattern and the range in production potentials were similar to earlier studies (Yavitt et al., 1988, 1990; Moore and Knowles, 1990; Bubier et al., 1993;

Dunfield et al., 1993; Roulet et al., 1993; Valentine et al., 1994; Sundh et al., 1994, 1995; Moore et al., 1994; Nedwell and Watson, 1995; Segers, 1998) when the different normalizations are taken into account. Maximal production potential occurred 20 cm below the water table consistently with the results of Roulet et al. (1993) and Sundh et al. (1994). Maximal oxidation potentials were detected higher in the profile, on average 10 cm below the water level where apparently both methane and oxygen concentrations are high, in accordance with Bubier et al. (1993) and Sundh et al., (1994).

When the water table did not vary considerably, the production potentials tended to increase towards the autumn (see also Sundh et al., 1994). This pattern supports the hypothesis of accumulation of suitable carbon in peat towards the autumn due to reduced activity of methanogenic bacteria in low in situ temperatures (Valentine et al., 1994; Saarnio et al., 1997). The reactivation of methane-producing bacteria in laboratory temperature then results in higher production potential (Yavitt et al., 1988; Valentine et al., 1994). In addition to the substrate accumulation, an increase in the size of methanogenic community could contribute to the higher production potentials towards late summer (Svensson and Rosswall, 1984; Whiting and Chanton, 1993).

The water level directly determines the moisture conditions in peat (Weiss et al., 1998) and the volumetric water contents in the unsaturated layers varies from 60% near the peat surface to 90% near the water level. A change in water level is reflected to the moisture in peat profile and a new equilibrium is rapidly reached. When the water table decreases, a smaller portion of the peat pores is water filled and oxygen

can more efficiently diffuse into peat profile. According to our study, the methanogenic and methanotrophic bacteria still seem to survive. As extreme anaerobic bacteria, the methanogens probably cannot grow in oxic peat layers, but they seem to retain their viability during periods of unsaturation as our data and earlier results from paddy soils indicate (Mayer and Conrad, 1990). The deeper peat layers, however, even when exposed to air by decreasing water table, remain very close to saturation providing anoxic microenvironments for methanogens which at least partly explains the survival of production potentials in unsaturated layers. The faster decrease in the potentials near the peat surface compared to potentials in deeper layers is directly related to the shorter distance to peat surface and the consequently more rapid oxygen diffusion to the newly unsaturated layers. Methanotrophic bacteria need oxygen, but can survive in anoxic conditions (Roslev and King, 1994), so it is not surprising that we found oxidation potentials to be less affected by WT fluctuations than production potentials.

In addition to the direct effect on moisture and oxygen concentrations in peat profile, the changes in water level might affect the amounts of substrate. After the water level draw-down, increased aerobic degradation in the unsaturated layers consumes the carbon compounds that in anoxic conditions would promote methane production. The reduction in substrates then decreases the methane production potential. Methane oxidation potential may also be reduced by a decrease in methane concentration in unsaturated peat layers. On the other hand, a temporary rise followed by a downward shift in water level may liberate methane from deep layers (Moore and Dalva, 1993) so that methane oxidation may be reactivated by the substrate peak as the lawn and hummock data from the bog indicate.

We are not aware of any studies reporting the immediate effects of water level changes to potentials. The study by Roulet et al. (1993) compares the potentials in an undrained and drained bog and hence analyzes the effects of a long-term water level draw-down. In the undrained site, the saturated layer 0–50 cm below peat surface showed production potential while in the drained site, the unsaturated layer 0–50 cm below peat surface did not. Oxidation potentials were less affected by the water level draw-down and maximal oxidation occurred deeper in the drained site than in the undrained site. All these findings support our results.

The duration of the anticipated more frequent summer droughts is decisive for methane release rates in peatlands. If the drought prevails for a period shorter than 1 month, methane production potential can survive and the production is rapidly reactivated after the water level rises. Consequently, methane fluxes soon

would recover. However, if the duration of a drought period approaches 2 months, methane production potentials are eliminated from the peat profile. As the reactivation of already reduced potentials is slow, the methane fluxes remain low for weeks after a rise in water level, reducing the potential climatic feedback of boreal peatlands.

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