



## Determinants of spatial variability of methane emissions from wet grasslands on peat soil

AGNES VAN DEN POL-VAN DASSELAAR, MARINUS L. VAN BEUSICHEM & OENE OENEMA

*Department of Environmental Sciences, Sub-department of Soil Science and Plant Nutrition, P.O. Box 8005, 6700 EC Wageningen, the Netherlands*

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**Abstract.** Methane (CH<sub>4</sub>) emissions from soils, representing the consequence of CH<sub>4</sub> production, CH<sub>4</sub> consumption and CH<sub>4</sub> transport, are poorly characterised and show a large spatial variability. This study aimed to assess the determinants of field-scale spatial variability of CH<sub>4</sub> emissions from wet grasslands on peat soil. Mean CH<sub>4</sub> emission rates of a three-year experiment at 18 plots distributed over three sites in the nature preserve “Nieuwkoopse Plassen” on peat soil in the Netherlands were related to CH<sub>4</sub> production and CH<sub>4</sub> consumption capacities of soil layers, and to soil and vegetation characteristics. Spatial variability of CH<sub>4</sub> emissions and possible determining factors was high. Annual CH<sub>4</sub> emissions ranged from 3 to 37 g CH<sub>4</sub> m<sup>-2</sup> yr<sup>-1</sup>. Coefficients of variation (CV) of CH<sub>4</sub> emissions were on average 37% among sites and 83% within sites. Most important determinants of spatial variability were CH<sub>4</sub> production capacity (average: 211 ng CH<sub>4</sub> g<sup>-1</sup> dry soil h<sup>-1</sup>; CV: 131%) and aboveground biomass of sedges (*Carex* spp.) (average: 0.45 g dm<sup>-2</sup>; CV: 127%) ( $P < 0.01$ ). Sedges may affect CH<sub>4</sub> emissions by stimulating CH<sub>4</sub> transport from anaerobic layers to the surface via their vascular system and/or by serving as substrate for methanogens. For extrapolation of CH<sub>4</sub> emissions to larger areas, best results will be obtained by using factors that are easy to determine, like vegetation.

### Introduction

Methane (CH<sub>4</sub>) emissions from soils have been measured extensively, both from large areas using micrometeorological measurement techniques and small areas using flux chamber measurements. All these studies show high spatial variability of CH<sub>4</sub> emissions, both among and within sites (e.g. Bartlett & Harriss 1993; Bubier et al. 1993; Shurpali & Verma 1998; Van den Pol-van Dasselaar et al. 1998; Waddington & Roulet 1996). CH<sub>4</sub> emissions may vary an order of magnitude within several metres.

CH<sub>4</sub> emissions from the soil to the atmosphere are the result of the biogeochemical processes: CH<sub>4</sub> production and CH<sub>4</sub> consumption, and CH<sub>4</sub>

transport. Each of these processes is influenced by a multitude of factors (e.g. Segers 1998).  $\text{CH}_4$  production is a strict anaerobic microbial process, in which methanogenic micro-organisms reduce organic matter in the absence of other electron acceptors.  $\text{CH}_4$  production is influenced (i) by the aeration of the soil, as methanogenic micro-organisms require anoxic conditions to produce  $\text{CH}_4$ , (ii) by the presence of alternative electron acceptors, like nitrate and sulphate, (iii) by type and amount of available organic matter, and (iv) by the size of the methanogenic population.  $\text{CH}_4$  consumption is an aerobic microbial process, in which  $\text{CH}_4$  is oxidised by methanotrophs. It is influenced by the  $\text{CH}_4$  and  $\text{O}_2$  concentration in the soil, and by the size of the methanotrophic population.  $\text{CH}_4$  transport in the soil can take place via diffusion, ebullition and plants. If  $\text{CH}_4$ , produced in anaerobic layers of the soil, is transported via diffusion, a considerable part of the  $\text{CH}_4$  can be oxidised again in aerobic layers of the soil before it reaches the atmosphere. Transport via ebullition, i.e. via bubbles, and transport via plants limits the possibility of  $\text{CH}_4$  oxidation in aerobic layers. Therefore, these types of  $\text{CH}_4$  transport greatly facilitate  $\text{CH}_4$  emissions.

Even though the mechanisms of  $\text{CH}_4$  production,  $\text{CH}_4$  consumption, and  $\text{CH}_4$  transport are qualitatively reasonably well understood, quantification of determinants of spatial variability of  $\text{CH}_4$  emissions is poor. For extrapolation of results from a particular plot or field to a larger area, we need quantitative insight of the dependence of  $\text{CH}_4$  emissions on environmental factors under a wide range of conditions. Possible determinants of spatial variability are related to the scale at which these determinants dominate (Klinger et al. 1994). For example, on microscale, important determinants of  $\text{CH}_4$  emissions may be soil aeration, methanogenesis, and methanotrophy. On the scale of an individual field, important determinants may be plant growth and fluctuations in ground water table and soil temperature.

Our study aimed to assess the determinants of spatial variability of  $\text{CH}_4$  emissions on field-scale. We studied  $\text{CH}_4$  production and  $\text{CH}_4$  consumption capacities of soil layers, and soil and vegetation characteristics of 18 plots at wet grasslands in the nature preserve "Nieuwkoopse Plassen" on peat soil in the Netherlands.  $\text{CH}_4$  emissions from these 18 plots had been measured for three years (Van den Pol-van Dasselaar et al. 1998). We also included additional plots to investigate the relation between  $\text{CH}_4$  emissions and the occurrence of individual plant species, as vegetation composition is thought to be one of the main factors influencing  $\text{CH}_4$  emissions.

## Materials and methods

### *Site description and main plots*

The experimental site has been described in detail elsewhere (Van den Pol-van Dasselaar et al. 1998). In brief, in the period 1994–1996, we have measured CH<sub>4</sub> emissions from 18 main plots spread over three representative wet grasslands in the “Nieuwkoopse Plassen” area in the Netherlands with vented closed flux chambers. “Nieuwkoopse Plassen” is a nature preserve with narrow (30–80 m wide) grassland and reed fields, surrounded by ditches. Ground water level is kept near the surface via the water level in the ditches. Distances between the three sites, i.e. Drie Berken Zudde, Koole and Brampjesgat, were approximately two kilometres. Distances between plots within a site were about two metres.

### *Detailed study of main plots*

In October 1996, soil of each of the main plots was sampled. Ground water levels were then 11.5 cm below the surface at Drie Berken Zudde, 2.5 cm above the surface at Koole and 7 cm below the surface at Brampjesgat. Soil pH-H<sub>2</sub>O was measured in-situ in the field. Soil samples were stored at 4 °C and processed the next day. We studied the top layer of recently died plant material, and the layers 0–5 cm, 5–10 cm, 10–20 cm, 20–30 cm, 30–40 cm, and 40–50 cm of the soil.

We determined total aboveground biomass, and aboveground biomass per vegetation type, i.e. grasses, sedges, rushes, reed, mosses, and remainder. For soil layers up to 30 cm, we determined dry bulk density, and for Drie Berken Zudde and Brampjesgat also biomass of roots, after wet-sieving with a mesh size of 2 mm.

Each soil layer was analysed (according to Houba et al. 1995) for soil moisture content (gravimetrically after drying at 105 °C for 24 h), loss-on-ignition (550 °C for 2 h), total carbon content (850 °C for 2 h), total nitrogen and phosphorus content (both spectrophotometrically measured in digests obtained after treating a soil sample with H<sub>2</sub>SO<sub>4</sub>-salicylic acid-H<sub>2</sub>O<sub>2</sub>-Se). For Brampjesgat, we determined dissolved organic carbon by extraction with 0.1 M CaCl<sub>2</sub>.

Per soil layer, 25 g field-moist soil was incubated in a 580 ml glass bottle at 20 °C both anaerobically (N<sub>2</sub>) and aerobically (air + 100 µL L<sup>-1</sup> CH<sub>4</sub>) to determine respective CH<sub>4</sub> production and CH<sub>4</sub> consumption capacity. For Drie Berken Zudde and Koole, also both anaerobic and aerobic CO<sub>2</sub> production capacities were determined. For each bottle, a time series of CH<sub>4</sub> and CO<sub>2</sub> concentration in the headspace was obtained by sampling the headspaces

of the bottles daily for three to five days. CH<sub>4</sub> concentrations were determined either by a gas chromatograph (PU 4400), using a flame ionisation detector, or by a photo-acoustic infra-red absorption gas analyser (Brüel & Kjør 1300). There were no significant differences between results obtained with the gas chromatograph and the gas analyser, at the high concentrations found. CO<sub>2</sub> concentrations were determined by the gas analyser.

### *Additional plots*

In July 1995, 18 additional plots were selected at Koole to assess the effect of individual plant species on spatial variability of CH<sub>4</sub> emissions. We measured CH<sub>4</sub> emissions from each plot with PVC flux chambers (I.D. 20 cm, height 16 cm). Four gas samples were taken with glass syringes at regular time intervals (10 to 20 minutes) from the headspace of the chambers. They were analysed for CH<sub>4</sub> within 24 h after collection by gas chromatography using a flame ionisation detector. Also, total aboveground biomass, and aboveground biomass per individual species were assessed for each plot.

### *Data acquisition*

Annual net CH<sub>4</sub> emissions from the main plots were estimated by trapezoidal integration of CH<sub>4</sub> emissions over time (Van den Pol-van Dasselaar et al. 1998). CH<sub>4</sub> production capacity ( $\mu\text{g CH}_4 \text{ g}^{-1} \text{ dry soil h}^{-1}$ ) was calculated from linear regression of the time-course of CH<sub>4</sub> concentration in the headspace of the bottles. CH<sub>4</sub> consumption capacity ( $\mu\text{g CH}_4 \text{ g}^{-1} \text{ dry soil h}^{-1}$ ) was calculated using the first-order rate constant and an initial CH<sub>4</sub> concentration of 100  $\mu\text{L L}^{-1}$ . Net CH<sub>4</sub> emissions from the additional plots were calculated from linear regression of the time-course of CH<sub>4</sub> concentration in the headspace of the chambers.

Simple linear regression analyses were carried out with CH<sub>4</sub> emissions as dependent variable, and soil and vegetation characteristics as independent variables. Regression analyses were performed for each individual soil layer and for combinations of soil layers. Best results were obtained by using the average values of the layer 0–20 cm depth (including top layer) as independent variables. These results are presented here. For each individual site ( $n = 6$ ), the effect of a certain variable was considered significant for  $r^2 > 0.53$  ( $P < 0.05$ ) and highly significant for  $r^2 > 0.78$  ( $P < 0.01$ ). For all sites and in the experiment with additional plots ( $n = 18$ ), the effect was considered significant for  $r^2 > 0.16$  ( $P < 0.05$ ) and highly significant for  $r^2 > 0.29$  ( $P < 0.01$ ).

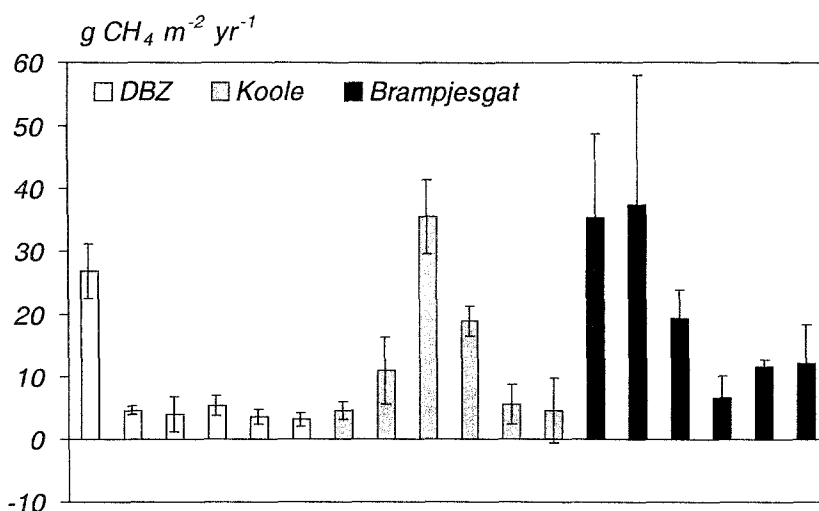


Figure 1. Mean annual net CH<sub>4</sub> emissions (g CH<sub>4</sub> m<sup>-2</sup> yr<sup>-1</sup>,  $\pm$ SD) (average of 1994, 1995 and 1996) from plots at the sites Drie Berken Zudde (DBZ), Koole and Brampjesgat.

## Results

### *Spatial variability of CH<sub>4</sub> emissions, soil and vegetation characteristics*

We found high spatial variability of CH<sub>4</sub> emissions from the main plots, both among and within sites (Figure 1). Coefficient of variation among sites was on average 37% (32% in 1994, 55% in 1995 and 25% in 1996; calculated using mean annual net CH<sub>4</sub> emissions of each individual site). Coefficient of variation within sites was on average 83% (107% for Drie Berken Zudde, 84% for Koole and 58% for Brampjesgat; calculated using annual net CH<sub>4</sub> emissions of individual plots within a site). High-emission-plots remained high-emission-plots and low-emission-plots remained low-emission-plots throughout the measurement period (not shown). The time-course of coefficients of variation within a site (not shown) indicated that spatial variability of CH<sub>4</sub> emissions was rather constant throughout the year.

Results of vegetation and soil analyses (means of the upper 20 cm of the profile) of the main plots showed a high variability (Table 1). Highest CH<sub>4</sub> production and CH<sub>4</sub> consumption capacities were found in the upper layers (Figure 2).

### *Determinants of spatial variability of CH<sub>4</sub> emissions*

In the experiment with additional plots, studying the effect of individual plant species on spatial variability of CH<sub>4</sub> emissions, CH<sub>4</sub> emissions were

Table 1. Averages and coefficients of variation of variables determined at Drie Berken Zuidde (DBZ) ( $n = 6$ ), Koole ( $n = 6$ ), Brampjesgat ( $n = 6$ ) and at all three sites ( $n = 18$ ). All soil characteristics are means of the upper 20 cm of the soil profile.

	DBZ		Koole		Brampjesgat		All	
	Avg	CV, %	Avg	CV, %	Avg	CV, %	Avg	CV, %
Annual CH <sub>4</sub> emission, g CH <sub>4</sub> m <sup>-2</sup> yr <sup>-1</sup>	8	107	13	84	20	58	14	85
CH <sub>4</sub> production capacity, ng CH <sub>4</sub> g <sup>-1</sup> dry soil h <sup>-1</sup>	5	98	162	108	466	65	211	131
CH <sub>4</sub> consumption capacity, ng CH <sub>4</sub> g <sup>-1</sup> dry soil h <sup>-1</sup>	484	27	537	44	442	28	487	36
Anaerobic CO <sub>2</sub> production capacity, $\mu$ g CO <sub>2</sub> g <sup>-1</sup> dry soil h <sup>-1</sup>	44	13	54	8	—	—	49	15
Aerobic CO <sub>2</sub> production capacity, $\mu$ g CO <sub>2</sub> g <sup>-1</sup> dry soil h <sup>-1</sup>	57	15	53	18	—	—	55	17
Loss-on-ignition, % of DM	92	4	76	14	64	5	77	17
Dissolved organic carbon, mg kg <sup>-1</sup> dry soil	—	—	—	—	1540	15	—	—
pH	3.5	3	4.9	8	5.4	3	4.6	19
N-total, g kg <sup>-1</sup>	15	7	16	17	16	4	15	12
P-total, g kg <sup>-1</sup>	0.6	8	0.9	20	1.5	5	1.0	38
Dry bulk density, mg cm <sup>-3</sup>	140	21	147	45	153	16	147	30
Aboveground biomass, g dm <sup>-2</sup>	6.0	14	3.9	19	4.8	24	4.9	26
Grass, g dm <sup>-2</sup>	0.97	45	0.93	69	1.62	42	1.17	58
Sedges ( <i>Carex</i> spp.), g dm <sup>-2</sup>	0.11	142	0.63	116	0.63	82	0.45	127
Rushes ( <i>Juncus</i> spp.), g dm <sup>-2</sup>	0.05	224	0.08	75	0.69	110	0.27	195
Reed ( <i>Phragmites australis</i> ), g dm <sup>-2</sup>	0	—	0	—	0.31	171	0.1	329
Mosses, g dm <sup>-2</sup>	4.89	11	2.15	52	1.29	74	2.77	64
Roots, mg cm <sup>-3</sup>	67	10	—	—	30	24	48	41

— = not determined

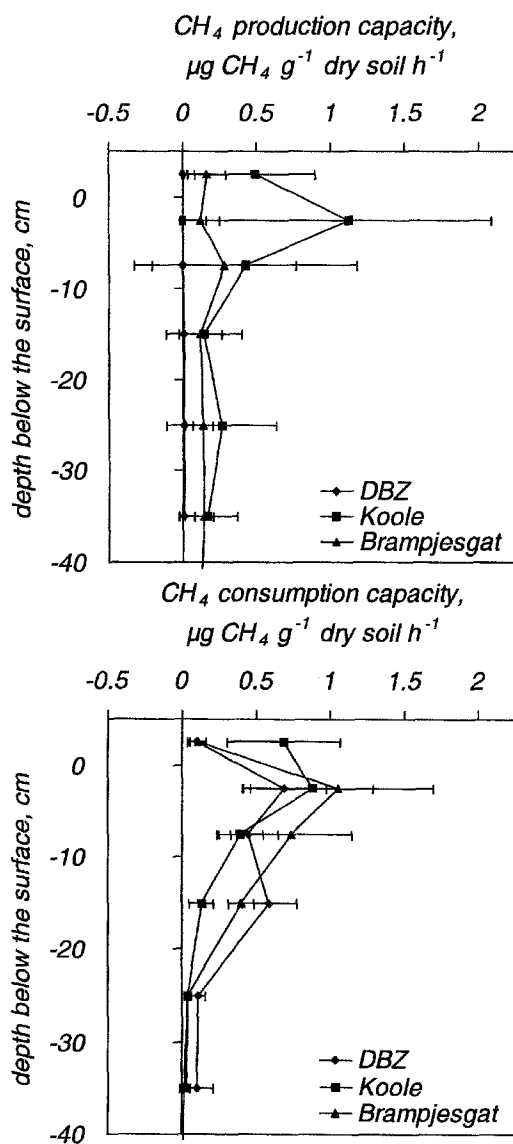


Figure 2. (a)  $\text{CH}_4$  production capacity ( $\mu\text{g CH}_4 \text{ g}^{-1} \text{ dry soil h}^{-1}$ ) and (b)  $\text{CH}_4$  consumption capacity ( $\mu\text{g CH}_4 \text{ g}^{-1} \text{ dry soil h}^{-1}$ , initial  $\text{CH}_4$  concentration of  $100 \mu\text{L L}^{-1}$ ) at incubation at  $20^\circ\text{C}$  in different soil layers of the sites Drie Berken Zudde (DBZ), Koole and Brampjesgat (layer above 0 cm is top layer of recently died plant material).

best related to *Juncus* spp. ( $P < 0.01$ ) (Figure 3). Correlations with other aerenchymatous plant species, like *Carex* spp. were not significant, but this may have been due to the limited amount of *Carex* present. Total aboveground biomass also showed a significant relation with  $\text{CH}_4$  emissions ( $P < 0.05$ ). Since relations between individual plant species and  $\text{CH}_4$  emissions were in general poor, we decided to determine biomass per vegetation type in our detailed study of the main plots, instead of per individual species.

For the main plots, mean annual  $\text{CH}_4$  emissions were positively related to  $\text{CH}_4$  production and  $\text{CH}_4$  consumption capacities ( $P < 0.05$ ), except for  $\text{CH}_4$  consumption capacity at Drie Berken Zudde.  $\text{CH}_4$  production capacity was positively related to  $\text{CH}_4$  consumption capacity ( $P < 0.05$ ) (not shown).

Main determinants of  $\text{CH}_4$  emissions differed among sites (Figure 4). At Drie Berken Zudde,  $\text{CH}_4$  emissions were best correlated with the aboveground biomass of rushes and with  $\text{CH}_4$  production capacity ( $P < 0.01$ ). At Koole,  $\text{CH}_4$  emissions were best correlated with  $\text{CH}_4$  consumption and  $\text{CH}_4$  production capacities ( $P < 0.01$ ). Also, both aerobic  $\text{CO}_2$  production capacity and aboveground biomass of sedges were positively correlated with  $\text{CH}_4$  emissions ( $P < 0.05$ ). The significant relation between  $\text{CH}_4$  emissions and aerobic  $\text{CO}_2$  production capacity suggests the importance of metabolisable organic matter in the top soil. At Brampjesgat,  $\text{CH}_4$  emissions were best correlated with  $\text{CH}_4$  consumption capacity and aboveground biomass of sedges ( $P < 0.01$ ). Other important factors were  $\text{CH}_4$  production capacity, total aboveground biomass and aboveground biomass of reed ( $P < 0.05$ ).

Combination of all sites (Figure 5) shows that  $\text{CH}_4$  emissions were positively related to  $\text{CH}_4$  production capacity, aboveground biomass of sedges ( $P < 0.01$ ),  $\text{CH}_4$  consumption capacity and pH ( $P < 0.05$ ), and negatively to aboveground biomass of mosses ( $P < 0.05$ ). The main determinant of spatial variability of  $\text{CH}_4$  emissions, other than  $\text{CH}_4$  production or  $\text{CH}_4$  consumption capacity, was aboveground biomass of sedges ( $r^2$  of 0.60,  $n = 18$ ):

$$Y = 6.7 + 3.2 * DM_{\text{sedges}} \quad (1)$$

$Y$  = mean annual  $\text{CH}_4$  emission,  $\text{g CH}_4 \text{ m}^{-2} \text{ yr}^{-1}$ ;

$DM_{\text{sedges}}$  = aboveground biomass of sedges,  $\text{g dm}^{-2}$ .

## Discussion

### *Spatial variability of $\text{CH}_4$ emissions*

Large spatial variability of  $\text{CH}_4$  emissions from wetland systems is a common phenomenon (e.g. Bartlett & Harriss 1993; Bubier et al. 1993; Waddington



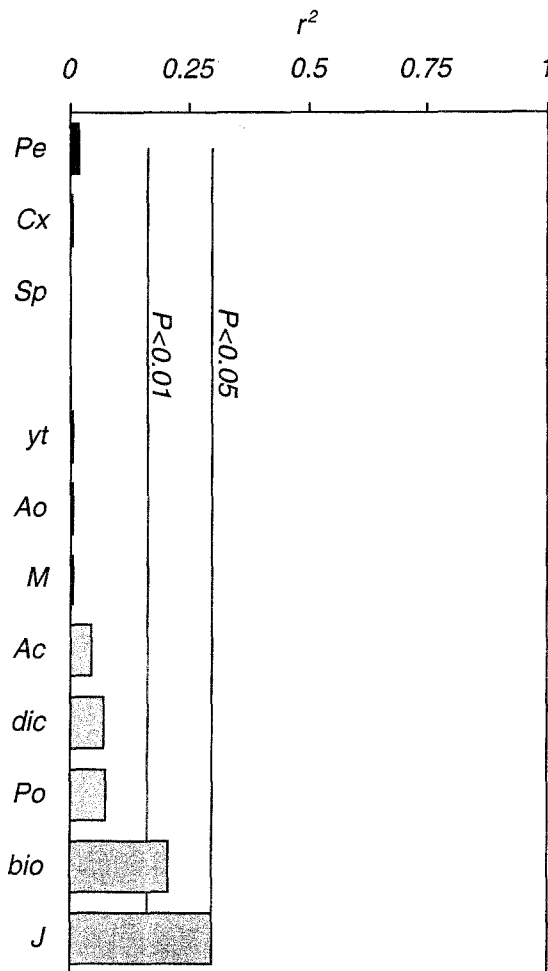


Figure 3. Coefficients of determination ( $r^2$ ) of simple linear regression analyses between  $\text{CH}_4$  emissions ( $\text{mg CH}_4 \text{ m}^{-2} \text{ d}^{-1}$ ) at the site Koole and aboveground biomass of several plant species ( $\text{g dm}^{-2}$ ). Light bars indicate a positive and dark bars a negative relationship. *Pe* = *Potentilla erecta* (L.) Räuschel; *Cx* = *Carex* spp.; *Sp* = *Sphagnum* spp.; *yt* = young tree species; *Ao* = *Anthoxanthum odoratum* L.; *M* = *Molinia caerulea* (L.) Moench; *Ac* = *Agrostis canina* L.; *dic* = Dicotyledones; *Po* = *Polytrichum* spp.; *bio* = total aboveground biomass; *J* = *Juncus* spp.

& Roulet 1996; Figure 1). However, quantification of determinants of spatial variability of  $\text{CH}_4$  emissions is poor. So far,  $\text{CH}_4$  emission measurements over several years had not been combined with a detailed study of the plots including incubation experiments, soil and vegetation analyses. Three years of measuring  $\text{CH}_4$  emissions from 18 main plots showed that the impact of variables may be rather stable throughout the year as plots with a relative high

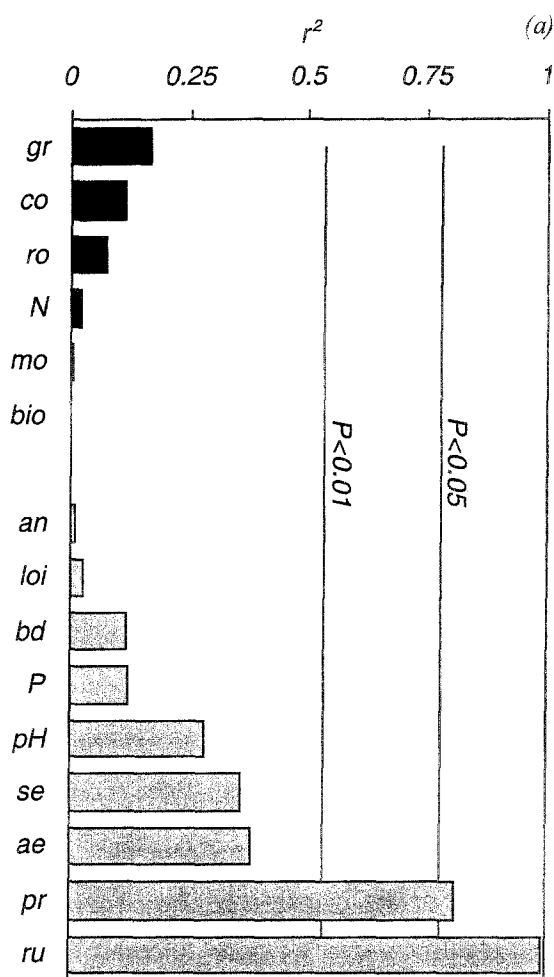


Figure 4. Coefficients of determination ( $r^2$ ) of simple linear regression analyses between mean annual net  $\text{CH}_4$  emissions ( $\text{g CH}_4 \text{ m}^{-2} \text{ yr}^{-1}$ ) and several variables at the sites (a) Drie Berken Zudde ( $n = 6$ ), (b) Koole ( $n = 6$ ), and (c) Brampjesgat ( $n = 6$ ). All soil characteristics are means of the upper 20 cm of the soil profile. Light bars indicate a positive and dark bars a negative relationship. *ae* = aerobic  $\text{CO}_2$  production capacity,  $\mu\text{g CO}_2 \text{ g}^{-1} \text{ dry soil h}^{-1}$ ; *an* = anaerobic  $\text{CO}_2$  production capacity,  $\mu\text{g CO}_2 \text{ g}^{-1} \text{ dry soil h}^{-1}$ ; *bd* = dry bulk density,  $\text{mg cm}^{-3}$ ; *bio* = total aboveground biomass,  $\text{g dm}^{-2}$ ; *co* =  $\text{CH}_4$  consumption capacity,  $\mu\text{g CH}_4 \text{ g}^{-1} \text{ dry soil h}^{-1}$ ; *doc* = dissolved organic carbon,  $\text{mg kg}^{-1} \text{ dry soil}$ ; *gr* = grasses,  $\text{g dm}^{-2}$ ; *loi* = loss-on-ignition, % of DM; *mo* = mosses,  $\text{g dm}^{-2}$ ; *N* = total nitrogen,  $\text{g kg}^{-1}$ ; *P* = total phosphorus,  $\text{g kg}^{-1}$ ; *pH* = pH; *pr* =  $\text{CH}_4$  production capacity,  $\mu\text{g CH}_4 \text{ g}^{-1} \text{ dry soil h}^{-1}$ ; *re* = reed,  $\text{g dm}^{-2}$ ; *ro* = roots,  $\text{mg cm}^{-3}$ ; *ru* = rushes,  $\text{g dm}^{-2}$ ; *se* = sedges,  $\text{g dm}^{-2}$ .

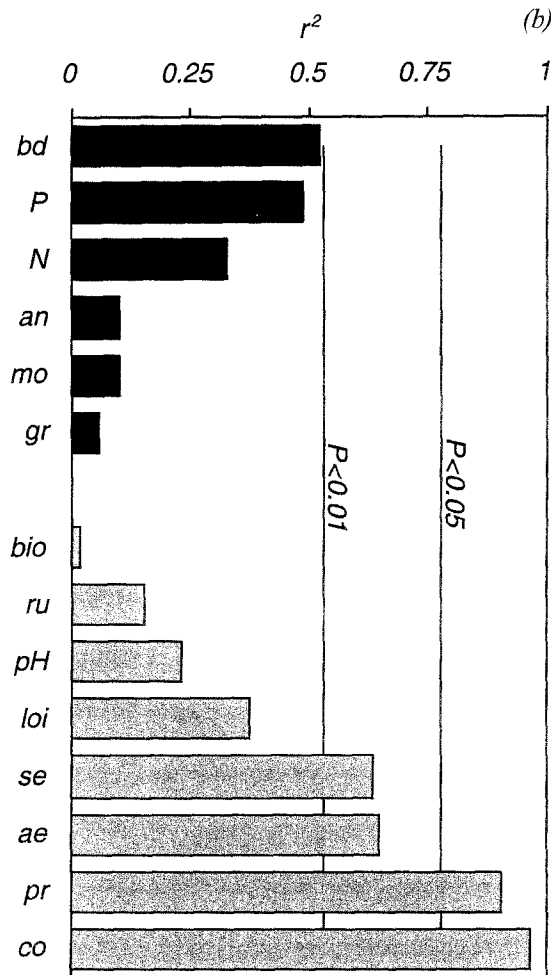


Figure 4. Continued.

emission always showed a relative high emission and plots with a relative low emission always showed a relative low emission.

#### *CH<sub>4</sub> production and CH<sub>4</sub> consumption capacity*

CH<sub>4</sub> production and CH<sub>4</sub> consumption capacity were highly variable (Table 1, Figure 2). We found that CH<sub>4</sub> emissions were significantly related to both CH<sub>4</sub> production capacity and CH<sub>4</sub> consumption capacity (Figures 4 and 5). Therefore, CH<sub>4</sub> production and consumption capacities may serve as predictors of CH<sub>4</sub> emissions. The significant relation between CH<sub>4</sub> emissions and CH<sub>4</sub> consumption capacity may be explained by the significant relation

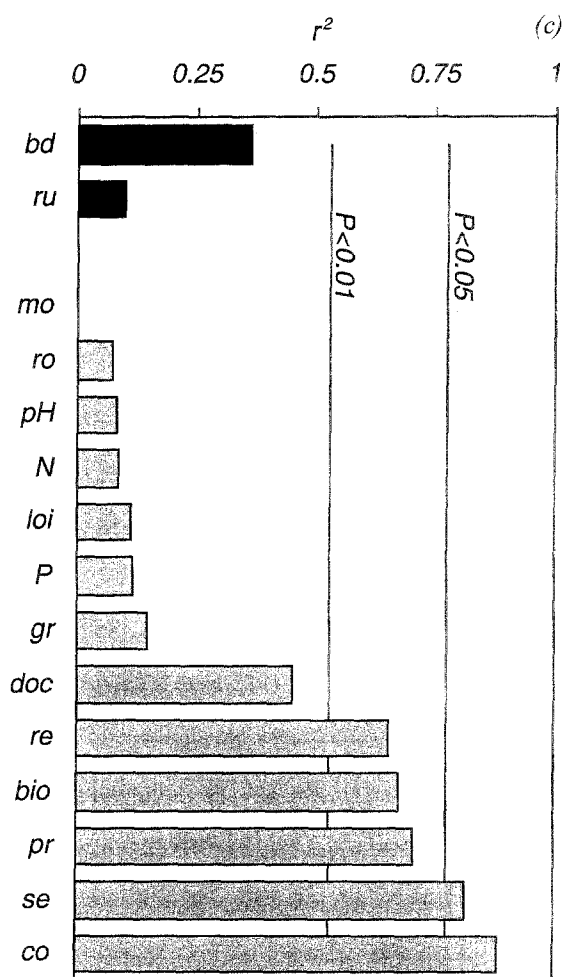


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between  $\text{CH}_4$  production capacity and  $\text{CH}_4$  consumption capacity. The latter may be explained by the dependence of  $\text{CH}_4$  consumption capacity on  $\text{CH}_4$  concentration in the soil.

Methanogenesis contributes to C mineralisation, thus  $\text{CH}_4$  production capacity may be positively related to  $\text{CO}_2$  production capacity (Moore & Dalva 1997; Schimel 1995; Yavitt & Lang 1990).  $\text{CO}_2$  production capacity is an estimate of total microbial activity, while  $\text{CH}_4$  production capacity is an estimate of the activity of methanogens. We found a significant positive relation between  $\text{CH}_4$  production capacity and  $\text{CO}_2$  production capacity at Koole. We also found that the variability of  $\text{CH}_4$  production capacity was larger than the variability of  $\text{CO}_2$  production capacity (Table 1). This indicates

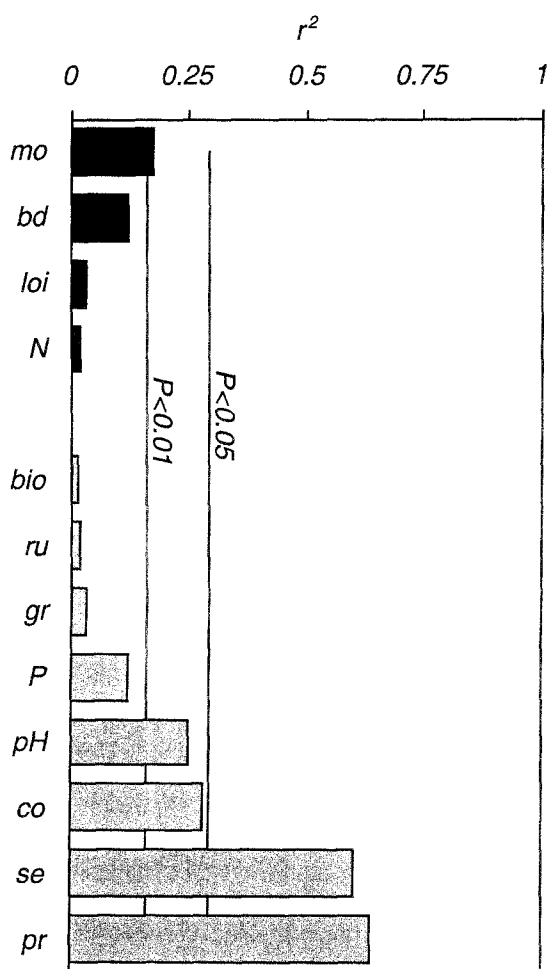


Figure 5. Coefficients of determination ( $r^2$ ) of simple linear regression analyses between mean annual net  $\text{CH}_4$  emissions ( $\text{g CH}_4 \text{ m}^{-2} \text{ yr}^{-1}$ ) of all three sites ( $n = 18$ ) and several variables. All soil characteristics are means of the upper 20 cm of the soil profile. Light bars indicate a positive and dark bars a negative relationship. Abbreviations are explained in Figure 4.

that methanogens make higher demands on quality of their substrates than the combined total microbial biomass.

If we assume that methanogenesis produces 1 mole of  $\text{CH}_4$  and 1 mole of  $\text{CO}_2$ , which is true when methanogenesis proceeds via acetate fermentation and no accumulation of fermentation products occur, then carbon mineralisation via methanogenesis was only about 1% of total anaerobic carbon mineralisation in the top layers and 5 to 10% in the deeper layers. The

increase in the contribution of methanogenesis to carbon mineralisation with depth may have been caused by increasing anaerobiosis in the field with depth, and an accompanying relative increase in the size of the methanogenic population. In a review of  $\text{CH}_4$  production, Segers (1998) found that for peat samples the ratio anaerobic C mineralisation to  $\text{CH}_4$  production may vary as much as two or three orders of magnitude.

Oxygen accelerates decomposition of dead plant material. The increase in  $\text{CO}_2$  production rates under aerobic compared with anaerobic conditions (Table 1) indicates the importance of water table and anaerobism in slowing decomposition rates. Peats which are more decomposed contain less relatively fresh plant material for methanogens and may yield lower  $\text{CH}_4$  emissions.

### *Soil characteristics*

Organic matter has been reported to be a good predictor of  $\text{CH}_4$  production capacity in peatlands, with highest  $\text{CH}_4$  emissions where organic matter is relatively labile and lowest  $\text{CH}_4$  emissions where organic matter is relatively recalcitrant (Yavitt & Lang 1990). Crozier et al. (1995) and Yavitt and Lang (1990) found a significant relation between loss-on-ignition and  $\text{CH}_4$  emissions. In our sites, loss-on-ignition was high, and therefore it may not have been a limiting factor for  $\text{CH}_4$  production. Schimel (1995) believes that soil organic matter is the main substrate for methanogens, while others believe that recently died plant material is the main substrate (e.g. Chanton et al. 1995; Whiting & Chanton 1993). Chanton et al. (1995) suggest that the main source of organic matter for methanogens is recently fixed organic compounds, most likely dissolved organic compounds produced from the decay of recently produced litter, roots and root exudation products. In correspondence with this, we found a better relationship between dissolved organic carbon and  $\text{CH}_4$  emissions than between loss-on-ignition and  $\text{CH}_4$  emissions at Brampjesgat. Unfortunately, dissolved organic carbon was not measured at the other two sites.

In incubation experiments, Wang et al. (1993) showed that  $\text{CH}_4$  emissions were highest around neutral pH. Dunfield et al. (1993) found that both  $\text{CH}_4$  production and  $\text{CH}_4$  consumption capacities were optimal at about 2 pH units higher than the native peat pH in acidic peats ( $\text{pH} < 5$ ) and 0–1 pH units higher in the more alkaline peats. They suggested that methanogens and methanotrophs are only partially adapted to acidic conditions. Jugsujinda et al. (1996) showed that soil pH was the dominant variable which influenced organic matter decomposition, low soil Eh conditions and subsequent  $\text{CH}_4$  production in flooded acid sulfate soils. In their experiments, soils with pH below 6.1 produced no significant quantities of  $\text{CH}_4$ . Even though the pH

of our plots was much lower, especially at Drie Berken Zudde (Table 1), the plots showed significant CH<sub>4</sub> production and CH<sub>4</sub> emission. We found a significant positive relation between CH<sub>4</sub> emissions and pH, but only at the combination of the three sites (Figure 5). Ranges of pH at individual sites were probably too low to detect any effects.

### *Vegetation*

Correlation between CH<sub>4</sub> emissions and plant biomass has been found in several studies (e.g. Chanton et al. 1993; Whiting & Chanton 1993). Plant biomass may affect CH<sub>4</sub> emissions, as organic material from plants may serve as substrate for methanogens. Especially roots may influence CH<sub>4</sub> production through supply of organic matter at depth via root decay and root exudation. Also, plant species with aerenchymatous tissues may directly transport CH<sub>4</sub> from the anaerobic zone of the soil to the atmosphere (e.g. Schimel 1995), thereby protecting it against oxidation. The effect of plants may however be ambiguous, as plants may also transport O<sub>2</sub> to deeper layers, leading to increased CH<sub>4</sub> oxidation. Plant communities may also control CH<sub>4</sub> fluxes in peatland ecosystems through indirect effects on the water table (e.g. Bubier et al. 1995a; Bubier et al. 1995b).

In our study, vegetation analysis yielded good results in describing spatial variability of CH<sub>4</sub> emissions. CH<sub>4</sub> emissions from the additional plots were best related to *Juncus* spp. (Figure 3). CH<sub>4</sub> emissions from the main plots were significantly related ( $P < 0.01$ ) to aboveground biomass of sedges (Equation 1; Figure 5). Strong correlations between sedge biomass and CH<sub>4</sub> emissions have been observed before (e.g. Klinger et al. 1994; Whiting & Chanton 1992). Torn and Chapin (1993) suggested that sedges are highly effective in CH<sub>4</sub> transport not only because they provide a conduit to the soil surface, but also because their large root surface and air-filled aerenchyma provide both an effective collection system and rapid diffusion path. Further on, due to the large root system of sedges, which may penetrate to more than 2 m depth (Saarinen 1996), sedges may stimulate CH<sub>4</sub> production by serving as a substrate for methanogens.

Vegetation is affected by management and environmental factors like ground water level, nutrient status and climate. These factors each have their influence on CH<sub>4</sub> emissions. Therefore, it has been suggested (e.g. Bubier et al. 1995b) that vegetation may have predictive value for CH<sub>4</sub> emissions. The use of vegetation in predicting CH<sub>4</sub> emissions has many advantages: (i) it is much easier to determine the vegetation type of a certain area than to measure all the individual factors; (ii) vegetation composition is rather stable throughout the year, while environmental factors may show considerable temporal variability; and (iii) vegetation may be remotely sensed.

### *Extrapolation*

Our results show that spatial variability of CH<sub>4</sub> emissions can be described by vegetation and soil characteristics. The effect of these variables on CH<sub>4</sub> emissions was mainly according to what we expected, although relations were often weak (Figures 4 and 5). This may be explained by the relatively small number of measurements per site ( $n = 6$ ), which may be too small to reveal possible relationships. The relative importance of influencing factors may vary independently and on different spatial scales. Probably factors, which influence CH<sub>4</sub> production, are the primary factors associated with spatial variability of CH<sub>4</sub> emissions. If conditions are favourable for CH<sub>4</sub> production, then secondary factors like temperature and CH<sub>4</sub> transport ways become important.

We found that determinants of spatial variability of CH<sub>4</sub> emissions differed among sites. Most important influencing factors were CH<sub>4</sub> production capacity and aboveground biomass of sedges (Figure 5). For extrapolation to larger areas, best results will be obtained by using factors which are easy to determine, like vegetation. When vegetation is used to predict CH<sub>4</sub> emissions, the most important factors influencing CH<sub>4</sub> emissions are considered to be also the most important ones influencing species distribution and biomass density. At the same time, vegetation also affects determinants of CH<sub>4</sub> emissions like ground water level. However, since vegetation is affected by several hydrological and physiological parameters, which also affect the processes CH<sub>4</sub> production, CH<sub>4</sub> consumption and CH<sub>4</sub> transport, vegetation can be a good predictor of CH<sub>4</sub> emissions.

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