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Development of floating rafts after the rewetting of cut-over bogs: the importance of peat quality

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Abstract. The usual method of restoring cut-over bogs is to rewet the peat surface, but this often leads to the remaining peat layers being deeply inundated. For *Sphagnum*-dominated vegetation to develop at deeply inundated locations, it is important for floating rafts of buoyant residual peat to develop. In this study, the chemical and physical characteristics of buoyant and inundated peat collected from rewetted cut-over bog were compared. In general, buoyant peat was poorly humified; high methane (CH_4) production rates ($\geq 2\ \mu mol\ g^{-1}\ DW\ day^{-1}$) were important to ensure buoyancy. Although the peat water CH_4 concentrations increased with depth, the CH_4 production rates were higher in the uppermost peat layers. High CH_4 production rates were related positively with P concentrations and negatively with lignin concentrations. The pH to bulk density ratio (≥ 0.05) also appeared to be a good indicator of CH_4 production rates, providing an easy and cheap way to measure the variable for restoration practitioners. Our results indicated that analysing certain simple characteristics of the residual peat can greatly improve the success of the rewetting measures taken in cut-over bogs. If the analysis reveals that the residual peat is unsuitable for floating raft formation, deep inundation is inappropriate unless suitable peat from other locations can be introduced.

Introduction

Raised bogs are unique ecosystems that support distinctive plant and animal communities. World-wide, the area of raised bogs has been drastically reduced by human activities, such as peat cutting. At the beginning of the 17th century there were still 180,000 ha of raised bogs in the Netherlands (Neijenhuijs 1973), but few small relics remain. These are typically cut-over bogs that suffer the effects of water draw-down and are largely dominated by *Molinia caerulea* (Barkman 1992; Money 1995; Lamers et al. 2000). With so few natural bogs, the restoration of cut-over bogs has become important (Joosten 1995; Wheeler and Shaw 1995). The aim of restoration management is to restore the cut-over bogs to a regenerating, self-sustaining ecosystem with the appearance and composition of a ‘natural’ system (Wheeler and Shaw 1995). However, restoration is complicated, partly because little is known about the way *Sphagnum*-dominated vegetation recovers at anthropogenically disturbed sites (Joosten 1995; Money 1995; Wheeler and Shaw 1995). Successful restoration relies on the development of a dense *Sphagnum*-dominated vegetation and the formation of a new functional acrotelm (Joosten

1995; Wheeler and Shaw 1995; Money and Wheeler 1999). The spongy acrotelm has a strong self-regulating effect on the depth of the water table as a result of its high hydraulic conductivity and the ability to retain water in dry periods (Ingram 1978; Proctor 1995). To enable successful growth of *Sphagnum*, it is crucial to create stable, permanently wet, ombrotrophic conditions at the bog surface (Wheeler and Shaw 1995).

Restoration entails raising the water table by blocking drainage ditches and constructing bunds to retain precipitation (Wheeler and Shaw 1995). Often this inundates the remaining peat layers. Shallow inundation, that is, the year-round water-saturated conditions close to the ground surface (conditions that *Sphagnum* requires for optimal growth) (Wheeler and Shaw 1995; Grosvernier et al. 1997), is very difficult or impossible to achieve. Deep inundation (>0.3 m) is acceptable if the submerged *Sphagnum cuspidatum* expands rapidly, or if the residual peat floats and provides appropriate conditions for *Sphagnum* growth. But submerged *S. cuspidatum* normally grows vigorously with shallow inundation (<0.3 m) (Joosten 1995; Money 1995; Wheeler and Shaw 1995; Money and Wheeler 1999; Smolders et al. 2002a) where there is sufficient dissolved carbon dioxide (CO_2) and light (Baker and Boatman 1990; Paffen and Roelofs 1991; Wheeler and Shaw 1995; Smolders et al. 2002a).

Inundation can lead to the development of floating rafts of poorly humified peat that offer favourable conditions for *Sphagnum* growth (Joosten 1995; Money 1995; Lamers et al. 1999; Smolders et al. 2002b). Their buoyancy depends on methane (CH_4) bubbles generated by anaerobic decomposition becoming trapped in the peat (Lamers et al. 1999; Scott et al. 1999; Smolders et al. 2002b). Floating rafts are colonised initially by *S. cuspidatum* and *Sphagnum fallax* (Lamers et al. 1999) and later by other *Sphagnum* species and vascular plants (Money 1995). Deeply inundated cut-over bogs frequently lack floating peat (Meade 1992; Wheeler and Shaw 1995; Lamers et al. 1999; Smolders et al. 2002b).

Since buoyancy depends on high CH_4 production rates, it is important to know major factors limiting CH_4 production. Several studies have shown that CH_4 production is limited by peat quality (Updegraff et al. 1995; Yavitt et al. 1997; Bergman et al. 1998, 2000; Smolders et al. 2002b), temperature (Williams and Crawford 1984; Dunfield et al. 1993; Schulz et al. 1997; Bergman et al. 2000) and pH (Williams and Crawford 1984; Dunfield et al. 1993; Bergman et al. 1998; Segers 1998; Smolders et al. 2002b). Though Segers (1998) reports that the optimal pH for most methanogenic bacteria is around neutral, Williams and Crawford (1985) found that bacteria isolated from acidic *Sphagnum* peat substrates were able to produce CH_4 at pH 3.1, although they were not able to detect bacterial growth below pH 5.3. Decades of exposure to aerobic conditions, coupled with a lack of buffered groundwater frequently cause the remaining surface layers in cut-over bogs to become acidified, with pH values below 4 (Lamers et al. 1999; Smolders et al. 2002b), thereby hampering methanogenesis.

In this study we examined the mechanisms influencing the development of floating rafts by performing field observations and laboratory experiments. We also studied the chemical characteristics of buoyant and inundated peat in relation to

CH_4 production rates. We hypothesised that to be buoyant, peat must be poorly humified and have a high potential CH_4 production rate. We used our results to try to predict the buoyancy of peat substrates and to develop effective rewetting measures for cut-over bogs.

Materials and methods

Experimental sites

We used several cut-over peatlands in the Netherlands where rewetting measures had been carried out: Amsterdamse veld (52°41′50″N; 7°01′50″E), Dwingelerveld (52°49′30″N; 6°26′30″E), Haaksbergerveen (52°07′50″N; 6°46′20″E), Hatertse vennen (51°47′10″N; 5°47′30″E), Korenburgerveen (51°59′15″N; 6°39′15″E), Mariapeel (51°24′90″N; 5°54′90″E), Meerstalblok (52°41′35″N; 7°01′50″E), Pikmeeuwenwater (51°30′90″N; 6°9′90″E), Tuspeel (51°11′85″N; 5°53′55″E) and Zwart Water (51°23′50″N; 6°11′30″E). For detailed descriptions of these cut-over bogs see Schouwenaars et al. (2002).

In order to make comparisons with intact raised bogs, we included three bogs in the midlands of Ireland in this study: Clara bog (53°20′N; 7°38′E), Raheenmore bog (53°20′N; 7°20′E) and Scragh bog (53°35′N; 7°22′E).

Seasonal floating raft

Floating rafts developed spontaneously in the Haaksbergerveen nature reserve after rewetting measures had been taken. Most of these rafts are permanently buoyant, but some only float in summer. In order to reveal whether CH_4 production in summer was responsible for the observed buoyancy, methane concentrations were measured between November 1998 and June 2000 (at 0.2 and 0.5 m depth) in one of these seasonally floating rafts (for methods used, see depth profiles).

Depth profiles

At nine locations in the Netherlands (Haaksbergerveen, Korenburgerveen ($n = 2$), Zwart Water and Pikmeeuwenwater) and Ireland (Clara bog, Raheenmore bog ($n = 2$) and Scragh bog) water and peat samples were taken at three depths: 0.1, 0.5 and 1.0–3.0 m (the depth depended on the thickness of the peat profile). The peat samples were stored in airtight polyethylene bags at 4 °C until the potential decomposition rates were measured. Anaerobic peat water samples were taken using ceramic cups (Eijkelkamp Agrisearch Equipment, Giesbeek, the Netherlands), connected to 100% vacuum PVC syringes (50 ml). The first 25 ml collected was discarded to exclude internal stagnant sampler water. For CH_4 analysis, samples were taken by connecting vacuum infusion flasks (30 ml) to the ceramic cups and then the CH_4 concentrations were measured in the headspace. The pH, alkalinity, and CO_2 concentrations in the peat water were measured within 1 day (see chemical analysis), after which the samples were stored at $-20\,^{\circ}C$ until further analysis.

Chemical characteristics of the peat and methane production rate

Between April and May 2000, 30 peat samples were taken at eight locations in the Netherlands that had been subjected to inundation for at least 2 years: Haaksbergerveen ($n = 5$), Zwart Water ($n = 2$), Mariapeel ($n = 7$), Hatertse vennen ($n = 4$), Amsterdamse veld ($n = 2$), Dwingelerveld ($n = 3$), Meerstalblok ($n = 5$) and Tuspeel ($n = 2$). At 13 sites, samples were taken from floating rafts that had developed after taking rewetting measures, a further 17 samples were taken from inundated peat at sites where no floating rafts had developed. The peat samples were stored in airtight polyethylene bags at $4\,^{\circ}C$. The next day, the pH was determined in water samples squeezed from the peat. Peat water samples were taken by placing two Rhizon soil moisture samplers (10 cm; Eijkelkamp Agrisearch Equipment, Giesbeek, the Netherlands) in the peat, both connected to a 100 ml anaerobic vacuum infusion flask. The samples were analysed for nutrients and major ions (see chemical analysis). The bulk density (g DW l^{-1} FW) of the peat was determined by drying a volume of 1 l of fresh peat at $70\,^{\circ}C$ for 48 h and then measuring the dry weight. Size fractions (<1, 1–5 and >5 mm) were determined by wet-sieving homogenised peat samples (50 g) over 1 and 5 mm mesh sieves.

Potential decomposition rates (CH_4 and CO_2 production) were measured by incubating 150 g of fresh peat anaerobically in 250 ml infusion flasks sealed with airtight stoppers. For each sample incubations were carried out in triplicate. After the flasks had been filled, the gases were evacuated and then flushed with pure nitrogen gas to remove all CH_4, CO_2 and O_2 from the substrate and headspace. The evacuation and flushing were repeated several times. The flasks were kept in the dark at $20\,^{\circ}C$, and the concentrations of CH_4 and CO_2 in the headspace were measured weekly, over a period of 28 days. The CH_4 and CO_2 production rates were calculated by linear regression of the measurements and expressed on a dry weight basis.

Chemical analysis

The pH was determined with a combination pH electrode with an Ag/AgCl internal reference (Orion Research, Beverly, USA). The CH_4 was measured with ethane as an internal standard, using a Pye Unicam gas chromatograph (Unicam Cambridge, UK) equipped with a flame-photometric detector and a Porapak Q (80/100 mesh) column (Waters Chromatography, Etten-Leur, the Netherlands). The CO_2 measurements were carried out using an infrared carbon analyser (model PIR-2000, Horiba Instruments, Irvine, USA). Extinction at 450 nm was measured (Shimadzu spectrophotometer UV-120-01) for colorimetric background correction and as an estimate of humic substance concentration (Smolders et al., 2003), after citric acid had been added to a concentration of 0.6 mg l^{-1} (to prevent precipitation of metal ions). The samples were stored in iodated polyethylene bottles (50 ml) at −20 °C until further analysis.

To analyse nutrient concentrations in the peat, dried samples (48 h at 70 °C) were ground up in liquid nitrogen. Nitrogen and carbon concentrations were measured in dried samples with a CNS analyser (type NA1500; Carlo Erba Instruments, Milan, Italy). Two-hundred micrograms of the dried material was digested in sealed Teflon vessels in a Milestone microwave oven (type mls 1200 Mega, Sorisole, Italy) after addition of 4 ml HNO_3 (65%) and 1 ml H_2O_2 (30%) (Kingston and Haswell 1997). After dilution, the digestates were kept at 4 °C until analysis. Different organic matter fractions (lignin, hemicellulose, cellulose + cutine, and soluble constituents) of freeze dried peat samples were determined according to Goering and Van Soest (1970). The peat organic matter content was determined by weight loss after ignition (550 °C for 4 h).

The concentration of *o*-phosphate was measured colorimetrically with a Technicon AA II system, using ammonium molybdate (Henriksen 1965). Nitrate and ammonium were measured colorimetrically with a Traacs 800+ auto-analyser, using hydrazine sulphate (Technicon 1969) and salicylate (Grasshoff and Johannsen 1977) respectively. Potassium was measured by flame photometry (FLM3 Flame Photometer, Radiometer, Copenhagen, Denmark). Sulphur and phosphorus were determined by inductively-coupled plasma emission spectrophotometry (Spectro Analytical Instruments type FLAMEVML2-9032034, Kleve, Germany).

Data analysis

Prior to statistical analysis, data were log-transformed to make the variance less dependent on the means and to fit a normal distribution. All statistical analyses were carried out using the SPSS for Windows software package (version 10.0.7; SPSS Inc., Chicago, USA). Differences in chemical characteristics between buoyant and inundated peat were tested with independent samples *t*-test. Correlation between CH_4 concentrations and CH_4 production rate was analysed with a Pearson correlation, and described by an exponential regression analysis. Correlations between chemical characteristics of the peat and potential decomposition rate were analysed with a Pearson correlation, and significant correlations were described by a power regression analysis. For clarity of presentation, the means and standard errors (SEs) presented in the figures represent the non-transformed data.

Results

Floating raft development and methane production rate

The floating raft in the Haaksbergerveen reserve was buoyant when the CH_4 concentrations exceeded 350–400 μmol l^{-1} (Figure 1). During winter the CH_4 con-

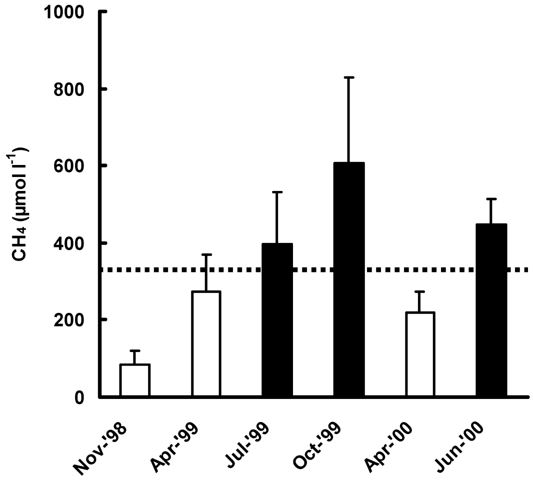

Figure 1. Peat water methane concentrations (means $\pm$ 1 SE; $n = 2$) in a floating raft showing a seasonal buoyancy pattern in the Haaksbergerveen nature reserve, the Netherlands, between November 1998 and June 2000 at 0.2–0.5 m depth. Dark bars indicate buoyancy of the raft. (t-test: $P = 0.005$).

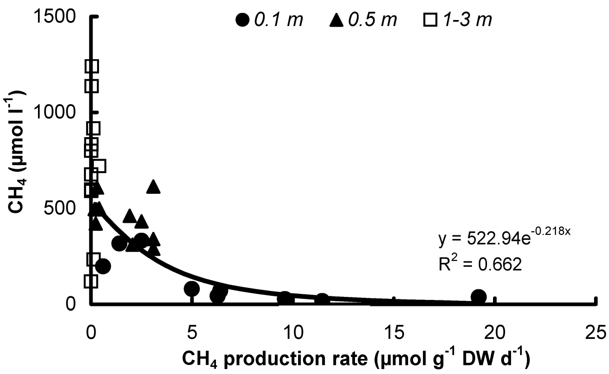

Figure 2. Methane production rates and methane concentrations measured in the peat from nine bogs in the Netherlands and Ireland at various depths (0.1, 0.5 and 1–3 m). The relation between methane production rates and methane concentrations has been described by an exponential regression analysis ($P = 0.000$).

centrations were significantly lower and the raft was inundated. Peat from the Dutch and Irish bogs revealed the highest potential CH_4 production rates in the top layer of the peat (Figure 2). The CH_4 concentrations and CH_4 production rates were inversely correlated (Pearson correlation: $R^2 = 0.608$; $P = 0.000$) in these sites.

Buoyant peat was characterised by significantly higher CO_2 and CH_4 production rates, and P and hemicellulose concentrations compared to inundated peat (Table 1). The C:P, N:P, lignin:P and lignin:N ratios were significantly lower in buoyant

Table 1. Physical and chemical characteristics (means ± 1 SE) of buoyant ($n = 13$) and inundated peat ($n = 17$) from various locations in the Netherlands. Characteristics that differ significantly are in italic (*t*-test).

	Inundated peat	Buoyant peat	
pH	4.3 ± 0.2	4.7 ± 0.2	ns
SO_4^{2-} (µmol l^{-1})	124 ± 31	87 ± 19	ns
Bulk density (g DW l^{-1} FW)	*105 ± 14*	*52 ± 5*	***
Fraction <1 mm	*0.55 ± 0.05*	*0.37 ± 0.04*	*
Fraction >5 mm	*0.36 ± 0.04*	*0.50 ± 0.03*	*
Water fraction	*0.90 ± 0.01*	*0.94 ± 0.01*	**
C (mg g^{-1} DW)	453 ± 14	458 ± 4	ns
N (µmol g^{-1} DW)	1076 ± 71	1261 ± 111	ns
K (µmol g^{-1} DW)	4.2 ± 0.8	4.6 ± 0.7	ns
P (µmol g^{-1} DW)	*6.5 ± 1.0*	*10.0 ± 1.2*	*
C:N ratio (g g^{-1})	40 ± 3	34 ± 3	ns
C:P ratio (g g^{-1})	*3276 ± 513*	*1839 ± 320*	*
C:K ratio (g g^{-1})	4306 ± 750	3469 ± 591	ns
N:P ratio (g g^{-1})	*98 ± 12*	*63 ± 6*	*
CH_4 production rate (µmol g^{-1} DW day^{-1})	*0.8 ± 0.2*	*4.4 ± 0.7*	***
CO_2 production rate (µmol g^{-1} DW day^{-1})	*1.0 ± 0.2*	*2.6 ± 0.3*	**
Total C production rate (µmol g^{-1} DW day^{-1})	*1.8 ± 0.4*	*7.0 ± 1.0*	***
Cell soluble fraction (mg g^{-1} DW)	347 ± 30	293 ± 20	ns
Hemicellulose (mg g^{-1} DW)	*226 ± 41*	*351 ± 33*	**
Cellulose + cutine (mg g^{-1} DW)	110 ± 16	109 ± 19	ns
Lignin (mg g^{-1} DW)	318 ± 29	247 ± 18	ns
Lignin:P ratio (g g^{-1})	*2590 ± 561*	*1062 ± 276*	*
Lignin:N ratio (g g^{-1})	*23 ± 3*	*15 ± 2*	*
Lignin:K ratio (g g^{-1})	3341 ± 759	2070 ± 486	ns
CH_4 production rate (µmol l^{-1} FW day^{-1})	*63 ± 16*	*203 ± 28*	***
pH:(bulk density) ratio	*0.05 ± 0.01*	*0.10 ± 0.01*	***

ns: $P > 0.05$; *$P \leq 0.05$; **$P \leq 0.01$; ***$P \leq 0.001$.

peat. Several other chemical characteristics, such as pH and N, K and lignin concentrations did not differ significantly between buoyant and inundated peat (Table 1). There also were several physical characteristics that differed between buoyant and inundated peat (Table 1). Since the CH_4, produced by decomposition processes provides buoyancy, we focussed on identifying the chemical and physical characteristics of the peat substrates determining decomposition rates.

Methane production rate and peat chemistry

In the buoyant and inundated peat substrates studied the CH_4 and CO_2 production rates were significantly correlated (Pearson's correlation: $R^2 = 0.84$; $P < 0.001$; data not shown). We focussed on the correlations between the potential decomposition rate ($CO_2 + CH_4$ production rate, henceforth called the C production rate) of the peat during anaerobic incubation and on several physical and chemical

Table 2. Some chemical and physical characteristics of the peat that significantly affect the potential decomposition rate ($CO_2 + CH_4$ production) of the peat. Relations between characteristics and potential decomposition rate are described by a power regression analysis (C production rate $= a \cdot X^b$).

X	*a*	*b*	R^2	
pH	0.002	4.738	0.452	***
SO_4^{2-} (μmol l^{-1})	68.29	−0.758	0.210	*
K (μmol g^{-1} DW)	0.516	1.212	0.427	***
N (μmol g^{-1} DW)	4.431	1.887	0.232	**
P (μmol g^{-1} DW)	0.104	1.652	0.729	***
N:P ratio (g g^{-1})	14109	−2.104	0.604	***
C:N ratio (g g^{-1})	2393	−1.930	0.321	***
C:P ratio (g g^{-1})	235466	−1.495	0.680	***
C:K ratio (g g^{-1})	18102	−1.104	0.404	***
N:P ratio (g g^{-1})	16200	−2.044	0.652	***
Hemicellulose (mg g^{-1} DW)	0.569	0.696	0.215	**
Lignin (mg g^{-1} DW)	3090824	−2.506	0.512	***
Lignin:N ratio (g g^{-1})	486.8	−1.849	0.610	***
Lignin:K ratio (g g^{-1})	3245	−0.951	0.530	***
Lignin:P ratio (g g^{-1})	10282	−1.164	0.752	***
Fraction <1 mm	0.763	−1.353	0.374	***
Fraction >5 mm	14.36	1.828	0.594	***
Water fraction	9.684	15.766	0.545	***
pH:(bulk density) ratio	209.78	1.603	0.734	***
Bulk density (g DW l^{-1} FW)	4460	−1.763	0.638	***

*$P \leq 0.05$; **$P \leq 0.01$; ***$P \leq 0.001$.

characteristics of the peat. The significant correlations were best described by a power function (Table 2).

The C production rates were significantly correlated with P concentrations and lignin:P ratios of the peat (Figure 3). High P, N and K concentrations in the peat were related positively with high C production rates (Figure 3(A) and Table 2), and as a result high C:P, C:N, C:K and N:P ratios were related negatively with the C production rates. High lignin concentrations were correlated with low C production rates, but high lignin to nutrient ratios were particularly related to low C production rates (Table 2 and Figure 3(B)). High hemicellulose concentrations correlated with high C production rates (Table 2), whereas the concentrations of cell soluble matter and cellulose + cutine did not correlate significantly with C production rates (data not shown). High concentrations of sulphate in the peat water indicated lower C production rates (Table 2).

High C production rates were related with high pore water pH values (Figure 4 and Table 2) and low peat bulk densities (Figure 5(A)). The peat's pH to bulk density ratio, showed an even stronger correlation with C production rates than pH or bulk density alone (Figure 5(B)). Substrates having a low bulk density were characterised by a substantial fraction of large peat particles (Figure 6(A)). The fraction of large peat particles (>5 mm) was related positively with high C production rates, whereas the fraction of small peat particles (<1 mm) was related negatively with the C production rates (Table 2 and Figure 6(B)).

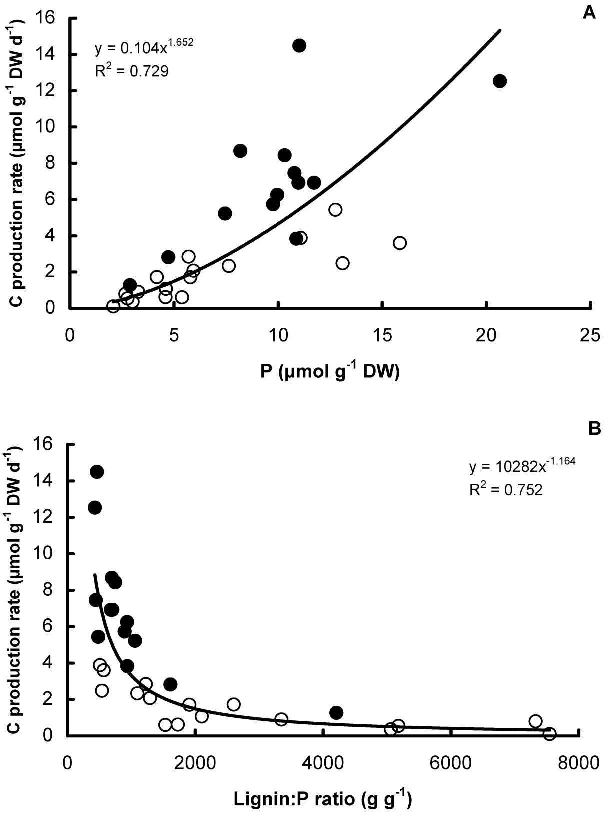

Figure 3. C production rates ($CH_4 + CO_2$), measured by anaerobic incubations, and (A) P concentrations ($P = 0.000$) and (B) lignin:P ratios ($P = 0.000$) in the peat. Each dot represents one of the peat samples that had become buoyant (•; $n = 13$) or remained inundated (○; $n = 17$) after rewetting of the peat surface. The relations between the C production rates and P concentrations and lignin:P ratios have been described by a power regression analysis.

Discussion

Floating raft formation and methane production rate

Our finding that CH_4 concentrations in peat water were much higher when the raft was floating than when it was inundated agrees with other studies (Lamers et al. 1999; Scott et al. 1999; Smolders et al. 2002b). The optimum temperature for CH_4 production in peat soils is between 25 and 30 °C (Williams and Crawford 1984; Dunfield et al. 1993; Bergman et al. 1998, 2000). However, temperature is not the only factor that accounts for summer buoyancy. The availability of easily degradable compounds (e.g., root exudates), which are important substrates for the

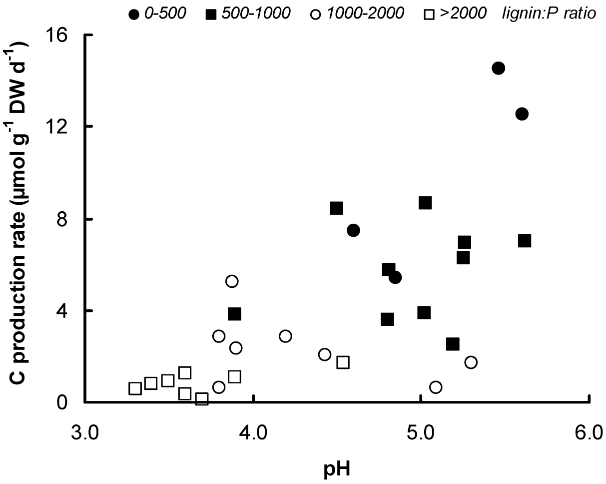

Figure 4. C production rates ($CH_4 + CO_2$) and the pH of water squeezed from the peat. Each marker represents one of the peat samples that had become buoyant ($n = 13$) or remained inundated ($n = 17$) after rewetting of the peat surface. The peat samples were divided into four categories based on their lignin:P ratios ($g\,g^{-1}$).

methanogenic bacteria also peaks in summer. Together these two factors explain most of the seasonal variation in CH_4 production rates (Bergman et al. 2000).

Most floating rafts are permanently buoyant, and their CH_4 concentrations remain high throughout the year (Smolders et al. 2002b). High CH_4 concentrations depend not only on high production rates, but also on the peat's capacity to retain the CH_4 bubbles produced. The mass of CH_4 stored in gas bubbles is estimated to be as much as three times the mass of dissolved CH_4, depending on the time of the year, and is frequently large enough to serve as a buffer between microbial production of CH_4 and the release of CH_4 to the atmosphere (Fechner-Levy and Hemond 1996). Presumably the seasonal floating raft in the Haaksbergerveen did not have the appropriate structure to retain sufficient CH_4 bubbles for buoyancy during periods with low CH_4 production rates.

Though the CH_4 concentrations in the peat profiles increased with depth (Figure 2), potential CH_4 production rates decreased with depth, indicating that superficial, relatively young, poorly humified peat supports the greatest CH_4 production rates. Other studies have also reported this decline in methanogenesis with depth (Williams and Crawford 1984; Yavitt et al. 1987, 2000). The surface layers have a high gas conductivity so that the CH_4 produced is readily vented to the atmosphere or oxidised by methanotrophic bacteria, and relatively little is retained within the peat (Segers 1998). In the deeper layers CH_4 is retained due to the low gas conductivity, and a substantial amount of CH_4 is stored (Brown et al. 1989). The CH_4 must be entrapped in the gaseous phase, since even at the pressures present in deep peat layers it is poorly soluble in water.

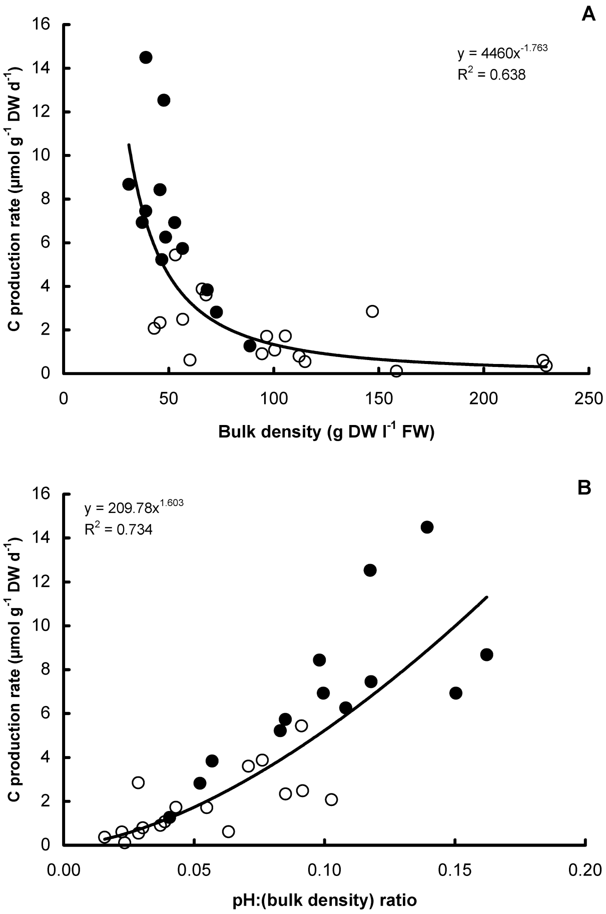

Figure 5. C production rates ($CH_4 + CO_2$) and (A) bulk density ($P = 0.000$) and (B) ratios between pH and bulk density (adapted from Smolders et al. (2002a); $P = 0.000$) of the peat. Each dot represents one of the peat samples that had become buoyant (•; $n = 13$) or remained inundated (○; $n = 17$) after rewetting of the peat surface. The relations between the C production rates and bulk density and the pH:(bulk density) ratio have been described by a power regression analysis.

Methane production rates and peat chemistry

The poor substrate quality of highly decomposed peat limits both CO_2 and CH_4 production rates, even though 95% of the peat consists of organic matter (Bridgham and Richardson 1992). Carbon mineralisation rates are usually highest in recently formed relatively coarse, light organic fractions (Hassink 1995; Van den Pol-van Dasselaar and Oenema 1999; Bozkurt et al. 2001). Since decomposition processes break down larger organic particles into smaller ones, an increase in the decomposition extent will result in the peat having a higher bulk density (Figure 6(A);

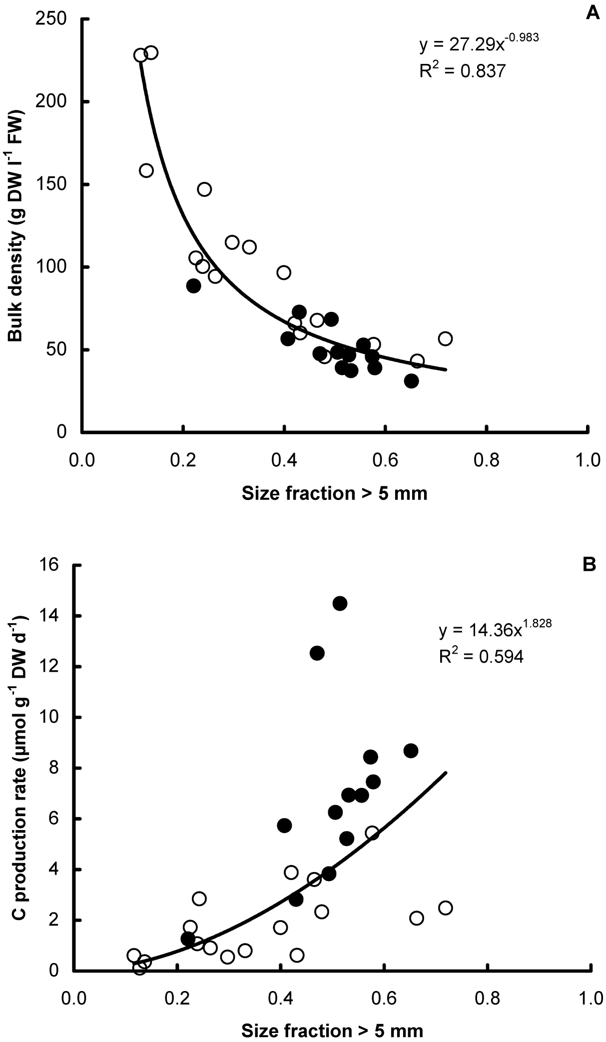

Figure 6. Bulk density (A; $P = 0.000$) and C ($CH_4 + CO_2$) production rates (B; $P = 0.000$) of the peat and the fraction of peat particles larger than 5 mm. Each dot represents one of the peat samples that had become buoyant (●; $n = 13$) or remained inundated (○; $n = 17$) after rewetting of the peat surface. The relations between the particle size and the C production rates and bulk density have been described by a power regression analysis.

Damman 1988; Wheeler and Shaw 1995; Van den Pol-van Dasselaar and Oenema 1999; Bozkurt et al. 2001). Therefore, peat with a lower bulk density is usually less decomposed and tends to have a higher potential decomposition rate than heavier peat (Bozkurt et al. 2001). This agrees with our study, where substrates having a low bulk density, a limited fraction of peat particles smaller than 1 mm and a substantial fraction larger than 5 mm, had relatively high C production rates (Table 2).

According to Grumpelt (1991), the dry bulk density of slightly decomposed peat varies between 40 and 80 $g\,l^{-1}$ and increases with continuing decomposition to 70–150 $g\,l^{-1}$ in moderately decomposed peat, and to 120–250 $g\,l^{-1}$ in highly decomposed peat. Based on this classification the average bulk density of the inundated peat was moderately decomposed (105 $g\,l^{-1}$) and that of buoyant peat was slightly decomposed (52 $g\,l^{-1}$). As heavier peat does not float as easily as lighter peat, a higher bulk density will also negatively affect peat buoyancy.

In our study, potential C production rates showed positive relationships with concentrations of P, N and K in the peat (Table 2 and Figure 3(A)). Coulson and Butterfield (1978) reported a strong correlation between the microbial decomposition of plant substrates and the N and P concentrations of the substrates. Given that nutrient availability can limit the activity of decomposing organisms, it seems likely that decomposition processes and CH_4 production rates will be hampered when C:N, C:P or C:K ratios are high, and when N, P or K concentrations are low (Swift et al. 1979; Updegraff et al. 1995; Beltman et al. 1996; Smolders et al. 2002b). Aerts et al. (2001) also have suggested that the potential decay rates of *Sphagnum* litter are controlled by N and P availability and are most strongly determined by P-related litter chemistry variables.

Our finding that peat with high lignin concentrations had low C production rates indicates that lignin increases with humification and may retard the activity of decomposing organisms (Swift et al. 1979; Bozkurt et al. 2001), resulting in a slower breakdown of organic litter (Yavitt et al. 1997; Aerts and Chapin 2000). Selective removal of the more easily metabolised carbon compounds by decomposer organisms results in larger proportions of resistant organic compounds, such as lignin, as decomposition proceeds (Bozkurt et al. 2001). Lignins from *Sphagnum* mosses are particularly rich in *p*-hydroxyphenols, which are the most stable phenolic compounds in surface peat (Yavitt et al. 2000).

Increased pH is known to enhance CH_4 production by stimulating the activity of methanogenic bacteria (Williams and Crawford 1984; Dunfield et al. 1993; Segers 1998) and by increasing the hydrolysis of organic substrates (Kok and Van de Laar 1991). The enhanced hydrolysis, in turn, results in an increased availability of substrates for methanogenic bacteria such as acetate or H_2 (Lamers et al. 1999; Smolders et al. 2002b). Yet, *Sphagnum* peat often has pH below 4 and therefore even in poorly humified peat CH_4 production rates may still be low. In our study, high C production rates occurred only at pH values above 4 (Figure 4). As Lamers et al. (1999) and Smolders et al. (2002b) have demonstrated, buffered groundwater may increase pH of the peat water, thereby enhancing microbial decomposition of the peat and CH_4 production. The influence of buffered groundwater in the peat base led to a rapid development of floating rafts in the Haaksbergerveen reserve (the Netherlands) after rewetting measures had been taken (Lamers et al. 1999).

In large parts of the Netherlands groundwater is strongly enriched with sulphate (Lamers et al. 1998). Sulphate can hamper methanogenesis because sulphate-reducing and methanogenic bacteria compete for substrates (Bhattacharya et al. 1996; Lamers et al. 1999; Smolders et al. 2002b). Although not very strong, a significant negative correlation was found between sulphate concentrations and potential C production rate (Table 2). This in accordance with the results of Lamers et al. (1999) and Smolders et al. (2002b) who showed that the presence of sulphate-enriched groundwater hampers the formation of floating rafts. Sulphate enriched (ground)water should therefore never be used to inundate bogs.

Stimulated methane production rates and the carbon balance of bogs

Bogs are important terrestrial sinks or sources of carbon and may have a potential influence on global carbon cycling (Gorham 1991; Dunfield et al. 1993). Rewetting measures can affect the carbon balance of peatlands and change these areas from carbon sinks to sources of carbon emissions to the atmosphere. Scott et al. (1999) found that the CH_4 fluxes from floating rafts were much larger than the fluxes from the pre-flood and the post-flood (submerged) peat surfaces. Since the upper peat layer of floating rafts is still anaerobic, there is less oxidation of CH_4 by methanotrophic bacteria, and the fluxes of CH_4 to the atmosphere are larger (Buttler et al. 1994). The temperature of buoyant peat can be much higher than that of inundated peat, and Crill et al. (1988) reported that tripling the soil temperature boosted the CH_4 flow by a factor of 74.

Since the cut-over bogs have been completely altered by human activities they have lost most of their function as a carbon sink. Measurements in a typical former Dutch raised bog with a shallow peat layer and vegetation dominated by *M. caerulea* revealed a net release of $97\,g\,C\,m^{-2}\,year^{-1}$ to the atmosphere (Nieveen et al. 1998). One reason that rewetting can increase carbon losses is because it stimulates anaerobic decomposition. However, if rewetting achieves its aim of increasing *Sphagnum* growth, it seems probable that ultimately these cut-over bogs will recover their function as C sink. Scott et al. (1999) noted that the extremely high fluxes associated with newly lifted peat may decrease as the floating rafts age. In time the bare floating rafts will be colonised by *Sphagnum* species that can retain large amounts of C. The increased anaerobic decomposition rates enhance the CO_2 concentrations and fluxes, and the CO_2 emitted by the peat provides a source of C for the growing *Sphagnum* (Smolders et al. 2001). Turetsky and Wieder (1999) have proved empirically that the refixation of C may be an important pathway for C cycling within peatlands, potentially capturing significant proportions of peat-produced CO_2 before it escapes to the atmosphere. In addition, the CH_4 produced can be oxidised to CO_2 by methanotrophic bacteria, thereby reducing CH_4 emission rates (Frenzel and Karofeld 2000). We therefore hypothesise that rewetting measures will increase C losses only temporarily. Ultimately, when the system has been restored to a peat accumulating system, there will be much more C fixation than there was in the unrestored cut-over bog.

Table 3. Physical and chemical prerequisites for peat able to form floating rafts after deep inundation of cut-over bogs. Data are based on the analysis of buoyant peat collected from six locations in the Netherlands ($n = 13$).

Chemical characteristics	Buoyant peat
pH	$\geq$4.0
Bulk density (g DW l^{-1} FW)	$\leq$75
Fraction <1 mm	$\leq$0.50
Fraction >5 mm	$\geq$0.40
P (μmol g^{-1} DW)	$\geq$10
C:P ratio (g g^{-1})	$\leq$3000
N:P ratio (g g^{-1})	$\leq$75
CH_4 production rate (μmol g^{-1} DW day^{-1})	$\geq$2
Total C production rate (μmol g^{-1} DW day^{-1})	$\geq$3
Hemicellulose (mg g^{-1} DW)	$\geq$220
Lignin (mg g^{-1} DW)	$\leq$300
Lignin:P ratio (g g^{-1})	$\leq$1000
Lignin:N ratio (g g^{-1})	$\leq$20
CH_4 production rate (μmol l^{-1} FW day^{-1})	$\geq$150
pH:(bulk density) ratio	$\geq$0.05

Prospects for the restoration of Sphagnum-dominated vegetation by floating raft formation

Our study has shown that if floating rafts are to develop after deep inundation of cut-over bogs, poorly humified peat must be present. Table 3 summarises some of the physical and chemical characteristics of peat that predispose peat to becoming buoyant after deep inundation. The ratio of pore water pH (squeezed from the peat) to peat bulk density appears to be a simple and reliable indicator of whether the peat is suitable for the formation of floating rafts. From our peat samples we conclude that peat that is suitable for floating raft formation has a pH above 4.0 and a bulk density below 75 g l^{-1}, resulting in a pH:(bulk density) ratio above 0.05. This pH to bulk density ratio is easy for nature managers to measure. Among the other appropriate peat characteristics for determining buoyancy are the C:P and lignin:P ratio, and the size of the peat particles (Table 3).

In most Dutch cut-over bogs, however, the residual peat is often inadequate for floating raft formation, since it is mostly the strongly humified catotelm peat which is left after peat harvesting. This strongly humified peat does not become buoyant after inundation (Smolders et al. 2002b; Tomassen et al., in press). In some areas, the surface layer of the peat including its vegetation (usually referred to by the German term *bunkerde*), has been returned after peat harvesting. After inundation, this poorly humified *bunkerde* became buoyant, providing a substrate for *Sphagnum* colonisation. In these locations, floating rafts subsequently developed, even though the residual peat was strongly humified. If no floating rafts develop and it is impossible to achieve waterlogged conditions or shallow inundation, a good option is to introduce poorly humified substrates. This measure is similar to returning the *bunkerde*. A feasibility study (Tomassen et al., 2003) has recently been carried out successfully. Poorly humified substrates derived from sod-cutting in wet heathlands and from peat cutting activities in bogs all appeared to become buoyant if pore water pH was higher than 4.5 (Tomassen et al., 2003). If the substrate was too acidic, incorporation of small amounts of lime was necessary to raise its pH and to stimulate CH_4 production and so buoyancy of the substrate (Smolders et al., 2003; Tomassen et al., 2003). Re-vegetation of the bare substrate will be important as fresh, recently produced and thus easily decomposable organic matter has to provide sufficient CH_4 to warrant buoyancy on the long term (Smolders et al., 2003).

Based on the above reported effect of several physical and chemical characteristics of the peat on C production rates, we conclude that it is possible to determine if peat has the appropriate composition for the development of floating rafts. If the remaining peat layers in a cut-over bog are very decomposed, deep inundation (>0.5 m) is not advisable unless poorly humified peat can be introduced.

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