The effect of vascular plants on carbon turnover and methane emissions from a tundra wetland

LENA STRÖM, ANNA EKBERG*, MIKHAIL MASTEPANOV and TORBEN RØJLE CHRISTENSEN

*GeoBiosphere Science Centre, Department of Physical Geography and Ecosystem Analysis, Lund University, Sölvegatan 12, SE-223 62 Lund, Sweden (*Formerly Joabsson)*

Abstract

This paper investigates how vascular plants affect carbon flow and the formation and emission of the greenhouse gas methane (CH_4) in an arctic wet tundra ecosystem in NE Greenland. We present a field experiment where we studied, in particular, how species-specific root exudation patterns affect the availability of acetate, a hypothesized precursor of CH_4 formation. We found significantly higher acetate formation rates in the root vicinity of *Eriophorum scheuchzeri* compared with another dominating sedge in the wetland, i.e. *Dupontia psilosantha*. Furthermore a shading treatment, which reduced net photosynthesis, resulted in significantly decreased formation rates of acetate. We also found that the potential CH_4 production of the peat profile was highly positively correlated to the concentration of acetate at the respective depths, whereas it was negatively correlated to the concentration of total dissolved organic carbon. This suggests that acetate is a substrate of importance to the methanogens in the studied ecosystem and that acetate concentration in this case can serve as a predictor of substrate quality. To further investigate the importance of acetate as a predecessor to CH_4, we brought an intact peat-plant monolith system collected at the field site in NE Greenland to the laboratory, sealed it hermetically and studied the decomposition of ^{14}C-labelled acetate injected at the depth of methanogenic activity. After 4 h, $^{14}CH_4$ emission from the monolith could be observed. In conclusion, allocation of recently fixed carbon to the roots of certain species of vascular plants affects substrate quality and influence CH_4 formation.

Keywords: acetate, arctic wetlands, methane emission, methanogens, substrate quality, vascular plant effects

Introduction

The arctic tundra covers only about 5% of the global land area, but approximately 12–14% of the world's total pool of soil organic carbon is tied up in these soils (Post *et al.*, 1982; Oechel & Vourlitis, 1997). Therefore, northern wetland ecosystems play an important role in the global carbon budget and have a great potential for exchange of the greenhouse gases carbon dioxide (CO_2) and methane (CH_4) with the atmosphere (Panikov & Gorbenko, 1992; Christensen *et al.*, 1999; Oechel *et al.*, 2000). Tundra wetlands are generally net sinks for atmospheric CO_2 due to the prevailing waterlogged, anoxic and cool conditions that effectively reduce decomposition rates and favour the formation of peat. These conditions, however, at the same time make tundra wetlands ideal sites for CH_4 production and the atmospheric input of CH_4 from these regions account for about 10% of the total CH_4 sources globally (Reeburgh & Whalen, 1992).

It is well recognized that the presence of vascular plants affects CH_4 exchange between wetland ecosystems and the atmosphere, because plants affect important aspects of CH_4 dynamics, e.g., production, consumption and transport (Joabsson *et al.*, 1999). Cortical oxygen-transporting gas spaces (aerenchyma) can often be observed in plant species adapted to wetland conditions (Končalová, 1990; Armstrong *et al.*, 1991). The release of oxygen from roots to the

Correspondence: Lena Ström, fax + 46 462224011, e-mail: lena.strom@nateko.lu.se

rhizosphere can lead to the inhibition of methanogenesis and oxidation of CH_4 to CO_2 (Chanton & Dacey, 1991; Watson *et al.*, 1997; Frenzel, 2000). However, at the same time CH_4 transported in the aerenchyma escapes oxidation to CO_2, since it is transported directly from the anoxic zone to the atmosphere without having to pass through the oxic zone of the peat (Frenzel & Rudolph, 1998; Bellisario *et al.*, 1999).

A considerable amount of the carbon assimilated by vascular plants through photosynthesis can be allocated below ground. For example, in Alaskan tussock tundra, between 47% and 92% of the biomass was allocated below ground depending on plant species (Shaver & Kummerow, 1992). Furthermore, a wide range of labile carbon compounds are continuously released from the plant root system, including mucilage, ectoenzymes, organic acids, sugars, phenolics and amino acids (Marschner, 1995). Once released to the soil, these compounds can serve as an easily available substrate for the methanogenic bacteria and have a substantial effect on CH_4 production in the soil (Joabsson *et al.*, 1999). It might seem paradoxical that the addition of carbon compounds by vascular plants could be of any importance in a peat-accumulating system that already consists of more than 90% organic carbon. However, a large fraction of the organic material at the peat depths where methanogenesis takes place is often old and recalcitrant (Hogg, 1993; Christensen *et al.*, 1999). Methanogenic bacteria use only a few small molecules supplied as the end products of the metabolic activities of other microbes as substrate. While some methanogens reduce CO_2 to CH_4 (Boone, 1991), others use the methyl groups of organic molecules, e.g. acetate, as a substrate for methanogenesis (Oremland, 1988; Boone, 1991; Bellisario *et al.*, 1999). However, it has lately been reported that methanogens in northern peatlands do not use acetate or C1 compounds as a substrate. Instead, these compounds accumulate throughout the season with acetate as the primary organic end product of fermentation (Hines & Duddleston, 2001).

It is of vital importance to understand how individual vascular plant species affect the carbon cycling of ecosystems and, furthermore, how they respond to changes in their environment. In future, this will promote an increased understanding of the possible feedback mechanisms that vegetation responses or changes in species composition might impose on the global climate and future climatic change. The main objectives of this study were to (1) investigate how the photosynthetic rate of vascular plants affected the exudation of recently fixed carbon from their roots and (2) to determine whether the exuded carbon was a predecessor to CH_4 in an arctic wet tundra ecosystem in

NE Greenland. Several studies have previously proposed the importance of certain vascular plant species as suppliers of easily available substrates for the methanogenic bacteria (van Veen *et al.*, 1989; Jackson & Caldwell, 1992; Whiting & Chanton, 1992; Chanton *et al.*, 1995; Greenup *et al.*, 2000, Joabsson & Christensen, 2001). In accordance with these previous suggestions, we hypothesized that vascular plants release labile carbon, e.g. acetate, to their root vicinity, and that acetate is a precursor of CH_4 formation in the studied ecosystem.

Materials and methods

Field experiments

Study site
The site was positioned in the Zackenberg valley, NE Greenland (74°30′N, 21°00′W), which according to the floristic division and vegetation zonation of Bay (1997) belongs to the middle arctic zone. The site was established in a continuous fen in 1998 and maintained throughout the summers of 1999 and 2000. The experiments and samplings reported in this article were performed in July–August 2000 and represent the concluding part of the experiments conducted in this site. The vascular plant vegetation in the site was completely dominated by three sedge species, *Eriophorum scheuchzeri* Hoppe., *Carex subspathacea* Wormskj. and *Dupontia psilosantha* (Rupr.) Hult. A more detailed description of the site can be found in Joabsson & Christensen (2001) and a more detailed description of the valley can be found in Christensen *et al.* (2000). Briefly, the seasonally thawed organic layer was 20–30 cm thick underlain by permafrost. The position of the water table normally varied between 3 and 5 cm below the peat surface. In the area, daily air temperature generally had a positive mean during June to August and during the experimental period the mean air temperature varied between 4.5 °C and 7.0 °C.

Treatment and sampling
The site consisted of twelve 1×1 m plots, where six were shaded with hessian (sack-cloth) and six acted as unshaded controls. The shading treatment aimed to reduce photosynthetically active radiation (PAR) and lower the photosynthetic rate (calculated as NEE – respiration) of the vascular plants. Air and soil temperature did not differ significantly between treatments, but relative humidity was approximately 5% higher in the control plots (Joabsson & Christensen, 2001).

To investigate the contribution of easily degradable substrate for CH_4 formation (e.g. acetate) from plant

roots to the surrounding pore water, we designed an experimental set-up where the exudation from individual plant species could be determined under field conditions. Peat water-filled rhizosphere microcosms were constructed, which allowed the growth of roots from a single plant isolated from other plants. The microcosms were constructed from 12 mL polypropylene vessels, which could be lifted from the peat and opened in the bottom to allow water change. The peat water (pH = 6) that we used to fill the microcosms consisted of pore water, which was collected from the fen and allowed to settle so that it contained no large peat particles. To ensure that the bacterial community and nutrient conditions was as near natural as possible, no other measures was taken to purify the peat water. In each of the six control and six shaded plots, we placed a rhizosphere microcosm containing two shoots of *Eriophorum scheuchzeri* and a blank microcosm without plants. In each of the six control plots, we also placed a microcosm containing two shoots of *Dupontia psilosantha*. All plants had been carefully transplanted from the peat next to the plots into the microcosms. The water level in the microcosms was adjusted daily.

When growth of fresh undisturbed roots was observed in all plant containing microcosms (two weeks after transplantation), the plants were allowed to adapt for one additional week before the start of sampling. The peat water sampling procedures were as follows: (1) on the 15th of August, the peat water in plant-microcosms and blanks was completely exchanged for fresh peat water. (2) Twenty-four hours later on the 16th of August, the peat water in the microcosms was fully sampled and exchanged for fresh peat water. (3) The procedure (steps 1 and 2) was repeated on the 17th and 18th of August. Immediately after sampling, the peat water from the microcosm was filtered through a sterile Acrodisc PF 0.8/0.2 μm filter (prerinsed with 40 mL of distilled H_2O to remove any organic acid contaminants) into 10 mL glass vials, transported to the lab, flushed with N_2 for 1 min (to ensure oxygen-free conditions in the vial headspace) and frozen.

On the 10th and 17th of August 2000, we also collected pore water from the soil profiles in each of the 12 experimental plots. Water was collected from stainless-steel tubes permanently inserted into the peat at 5, 10, 15, 20 and 25 cm depth. The tubes were emptied of standing water and, thereafter, we sampled 2 mL of water and filtered and treated the samples as described above.

Lab experiments

Potential CH_4 production
The potential CH_4 production (Sundh et al., 1994) was measured on peat cores (4 cm diameter) collected on the 5th of August 2000. The cores were brought back to the field station lab and divided into 5 cm sections extending down to 25 cm depth. From each section, samples of 5–10 g wet weight were transferred to 130 mL glass bottles amended with 20 mL of demineralized water. The flasks were flushed with pure N_2 in order to create anoxia and incubated at approximately 15 °C. Headspace gas samples (5 mL) were withdrawn through butyl rubber stoppers and analysed for CH_4 by gas chromatography within 3 h after the collection of the peat cores and then repeatedly for 5 consecutive days. The results have been previously reported in Joabsson & Christensen (2001) and are used here as a comparison to acetate concentrations in the soil profile.

Analysis of organic acids and DOC
Samples were transported, still frozen, to Lund where organic acids were analysed using an anion exchange HPLC system equipped with a column system from Dionex, including the analytical column AS11 (4 mm, P/N 044076). A more detailed description of the HPLC system and method can be found in Ström et al. (1994). Dissolved organic carbon (DOC) in the samples was also determined (Shimadzu, TOC-500, Kyoto, Japan).

^{14}C-acetate labelling of a peat-plant monolith
To determine whether acetate was a substrate for CH_4 formation in the fen, we collected a peat-plant monolith from the field site, injected it with ^{14}C-labelled acetate and monitored the subsequent emissions of $^{14}CH_4$ and $^{14}CO_2$ from the monolith. The schematic laboratory set-up of the monolith and the basic experimental design can be seen in Fig. 1. The great difficulties in obtaining monoliths from this remote site in NE Greenland prevented an otherwise desired replication of the experiment.

Monolith collection and set-up
The monolith was collected on the 24th of August 2000 and transported to the laboratory in Lund, Sweden, within 48 h after removal of the monolith from the field site. The monolith was sampled in an aluminium frame ($24L \times 24W \times 15D$ cm, length × width × depth) that was inserted into the ground and lifted containing the peat-plant monolith. At the laboratory in Lund, the water level was re-adjusted to resemble field conditions (3 cm below the peat surface). To ensure a dormant period for the vegetation, the monolith was kept in a dark (no ambient light) temperature-controlled growth room at 5 °C. After 5 months, the temperature was increased to 10 °C and the monolith was exposed to 300 μmol m^{-2} s^{-1} of photosynthetically active radiation. A water-bath was placed between the light source and the monolith to absorb thermal radiation and
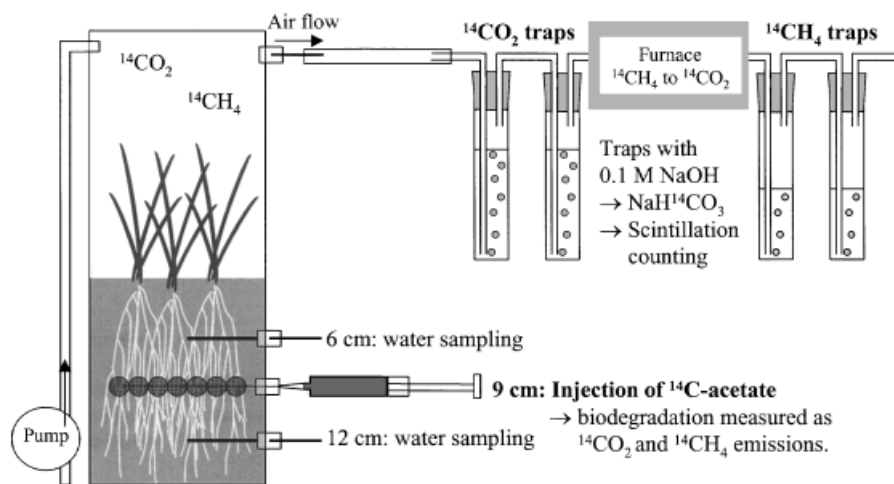
Fig. 1 A schematic drawing of the experimental monolith set-up used for determination of ^{14}C-acetate biodegradation.

minimize diurnal temperature variations. By attaching transparent Plexiglas covers to the monolith with silicone sealing the monolith was hermetically sealed, whereupon, it was continuously flushed with ambient air at an average flow rate of $0.80 \, \text{dm}^3 \, \text{min}^{-1}$. The Plexiglas chamber volume was $13 \, \text{dm}^3$ and the head-space gas was turned over at a rate of 3.7 times per hour.

Monolith treatment and pore water sampling

Pore water samples were drawn from the centre of the monolith through permanently installed stainless-steel tubes positioned 6, 9 and 12 cm below the peat surface, sterile filtered into N_2-flushed vials, shaken for 1 min and frozen to await analysis of acetate according to the previously described HPLC method.

On 29 of March 2001, 80 mL of $1.21 \, \text{kBq} \, \text{mL}^{-1}$ ^{14}C-acetate was added to the 9 cm depth as a mixture of 50% $^{14}CH_3$-COONa and 50% CH_3-^{14}COONa (Amersham Biosclences, Piscataway, New Jersey, USA). A mixture was chosen since we wanted to trace all CH_4 formed from acetate independent of whether its immediate precursor was acetate or $^{14}CO_2$ formed from acetate fermentation. The ^{14}C-acetate solution was distributed in a grid over the 9 cm depth through four channels closed by septa, by inserting an injection tube (1.5 mm in diameter) 22 cm into the monolith and over a length of 20 cm injecting 1 mL ^{14}C-acetate solution for every 1 cm that the tube was pulled out of the monolith (Fig. 1). To ensure an addition that caused as little changes in the chemical composition of the monolith as possible, the ^{14}C-acetate was flushed with N_2, to remove oxygen from the solution, and added in the ambient acetate concentration and pH of the 9 cm depth (60.0 μM, pH = 6). The ambient acetate concentrations of the 9 cm depth was determined on 5 consecutive days immediately prior to labelling and equal to 59.65 ± 3.09 (μM $\pm$ SE).

During the experiment, we continuously monitored the ^{14}C concentration in DOC in the pore water at 6 and 12 cm (Fig. 1). Pore water samples were drawn as described previously, whereupon, 1 mL was counted for radioactivity by liquid scintillation (PerkinElmer Tri-Carb 2100TR liquid scintillation analyser, PerkinElmer, Boston, MA, USA) using alkali compatible scintillation cocktail (OptiPhase 'HiSafe'3; Wallac, PerkinElmer, Boston, MA, USA).

To trap continuously any emitted $^{14}CO_2$ and $^{14}CH_4$, 10% of the outflow air was successively passed through two containers of NaOH (80 mL of 0.1 M; traps $^{14}CO_2$ as $NaH^{14}CO_3$) and a furnace (850 °C) to oxidize $^{14}CH_4$ to $^{14}CO_2$, which was subsequently trapped in two more containers of NaOH (40 mL of 0.1 M) (Fig. 1). The traps were changed periodically and counted for radioactivity as follows: 4 h following ^{14}C-acetate addition and, thereafter, with 24 h intervals until 240 h had passed, 48 h intervals until 384 h had passed, 72 h intervals until 528 h had passed and finally one last sampling 672 h (28 days) following ^{14}C-acetate addition. We did not find radioactivity in the second of the two $^{14}CO_2$ traps and can be certain that no $^{14}CO_2$ spilled over to the furnace and $^{14}CH_4$ traps and was mistaken for $^{14}CH_4$.

Results

Treatment effects

The shading treatment reduced photosynthetically active radiation (PAR) by about 60% during the duration of the season (July to August). PAR was for example reduced by 65% on the 19th of August and the difference was highly significant ($P < 0.001$). Subsequently, the photosynthetic rate was significantly lower ($P < 0.001$) in shaded (-505 ± 27 (mg $CO_2 \, \text{m}^{-2} \, \text{h}^{-1} \pm$ SE))

compared to control (-854 ± 40) plots in August (Fig. 2). Photosynthetic rates were calculated as NEE (net ecosystem exchange) minus respiration, which were continuously measured as previously reported in Joabsson & Christensen (2001).

The root adjacent zone

Of the two sedges tested in this experiment, *E. scheuchzeri* had the greatest effect on the acetate concentration in its root vicinity. The formation rate ($\mu mol\,g^{-1}$ dry root h^{-1}) of acetate was significantly higher (*t*-test, $P = 0.029$) in the root vicinity of *E. scheuchzeri* than in the root vicinity of *D. psilosantha* (Fig. 2). Furthermore, the formation rate of acetate was related to the photosynthetic rate and significantly (*t*-test, $P = 0.006$) lower in *E. scheuchzeri* containing microcosms in the shaded than in the control treatment (Fig. 2).

Soil profiles

At anoxic depths in the peat profile, the concentration of acetate seemed to be a good predictor of substrate quality for CH_4 formation. The potential CH_4 production of the peat profile was highly positively correlated to the acetate concentration at the respective depths (Fig. 3a, $R = 0.968$, $P < 0.001$), whereas it was negatively correlated to the concentration of DOC (Fig. 3b, $R = -0.887$, $P = 0.003$). The 5 cm depth was excluded from the correlation since very little (< 0.5 mL of the desired 2 mL) or no sample was retrieved from this depth. Furthermore, since the 5 cm depth obviously
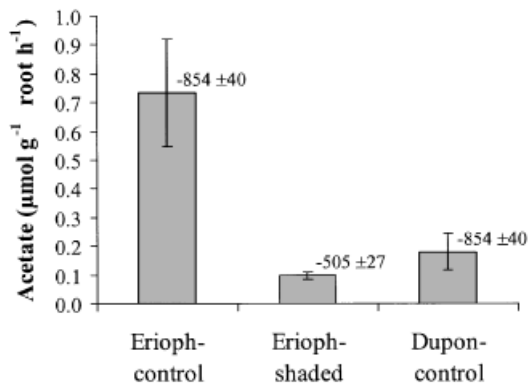
Fig. 3 Potential CH_4 production (mg $CH_4\,g^{-1}\,day^{-1} \pm SE$, $n = 6$) in the soil profile of control (open symbols) and shaded (filled symbols) treatments plotted against the acetate (a) and DOC (b) concentration ($\mu mol\,L^{-1} \pm SE$, $n = 6$, mean of two sampling dates, i.e. 10th and 17th of August 2000) at the respective depths (5, 10, 15, 20 and 25 cm).

was positioned above or just at the water table we concluded that this depth was within the oxic zone (Beckmann & Lloyd, 2001) of the peat and, thus, had no influence on CH_4 formation. For detailed results on CH_4 emissions and potential CH_4 production, see Joabsson & Christensen (2001).

^{14}C-acetate labelling of a peat-live plant monolith

When the monolith was brought out of the dark and cold all green vegetation had withered. At the start of the labelling experiment, the monolith had a green and fully developed vegetation.

Four hours after ^{14}C-acetate injection at 9 cm, a diffusion of radioactivity to 6 and 12 cm could be observed (Fig. 4a) and $^{14}CH_4$ started to be emitted from the monolith (Fig. 4b). After 24 h, the concentration of ^{14}C-acetate in the pore water of the monolith peaked at 12 cm and emission of both $^{14}CO_2$ and $^{14}CH_4$ could be observed from the monolith. After 48 h, the ^{14}C-acetate in the pore water at 6 cm peaked, whereupon, at both 6 and 12 cm it decreased slowly throughout the

Fig. 2 Formation rate of acetate ($\mu mol\,g^{-1}$ dry root $h^{-1} \pm SE$, $n = 6$) in root microcosms containing *Eriophorum scheuchzeri* (Erioph) grown in the control and shaded experimental plots and *Dupontia psilosantha* (Dupon) grow only in the control plots. The number over the bars shows the mean (mg $CO_2\,m^{-2}\,h^{-1} \pm SE$) photosynthetic rate (calculated as NEE – respiration) in August for each treatment.
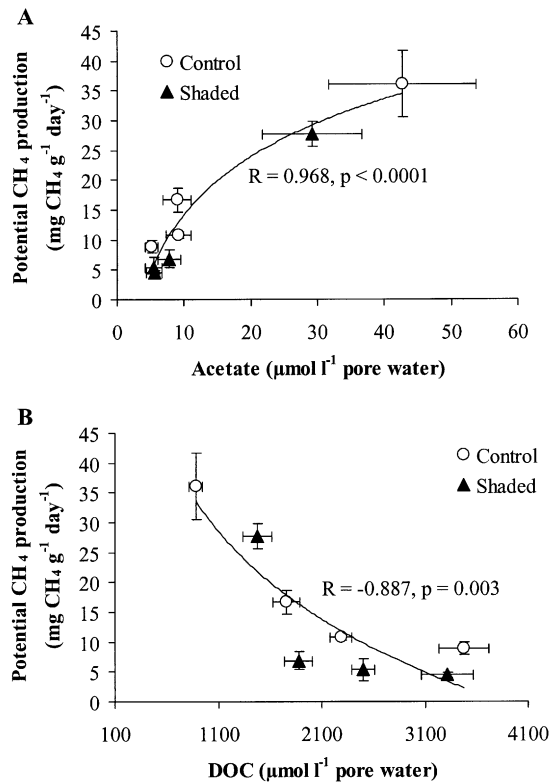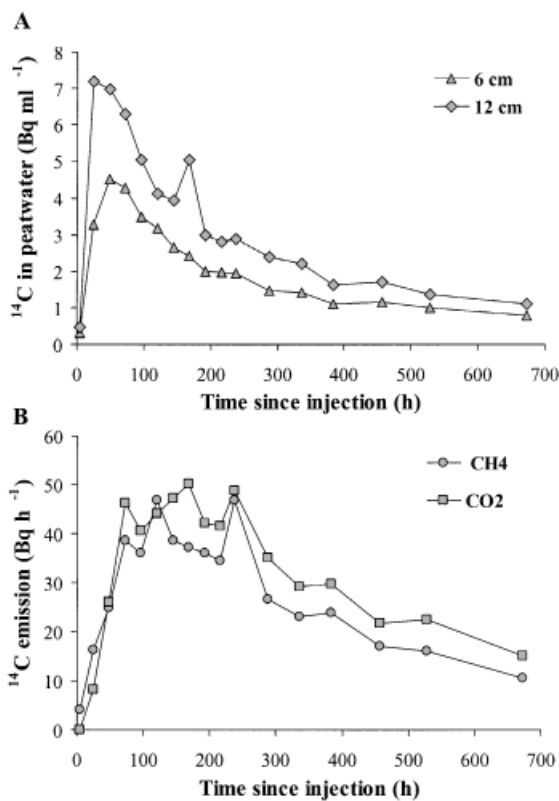
A

B

Fig. 4 Panel (a) Concentration of ^{14}C-acetate ($Bq\,mL^{-1}$) in pore water at the 6 cm ($\triangle$) and 12 cm ($\diamond$) depth of the monolith following addition of ^{14}C-acetate to the 9 cm depth at time zero. Panel (b) Emission of ^{14}C as CH_4 ($\bigcirc$) and CO_2 ($\square$) from the monolith following addition of ^{14}C-acetate to the 9 cm depth at time zero.

remainder of the experiment (Fig. 4a). Gas emission of both $^{14}CH_4$ and $^{14}CO_2$ was highest between 72 and 240 h following ^{14}C-acetate addition and, thereafter, slowly decreased throughout the remainder of the experiment (Fig. 4b). The emission of $^{14}CO_2$ and $^{14}CH_4$ was strongly correlated (Fig. 5, $R = 0.943$, $P < 0.001$), diverging 20% from a 1:1 relationship due to somewhat higher $^{14}CO_2$ emission. When the experiment was brought to an end an estimated 37% of the added radioactivity had been emitted from the monolith as $^{14}CO_2$ and $^{14}CH_4$.

Acetate is usually degraded by the aceticlastic reaction, in which the methyl group is reduced to CH_4 while the carboxylic group is oxidized to CO_2 (Boone, 1991). We added a 1:1 mixture of $^{14}CH_4$-COO$^-$- and CH_4-$^{14}COO^-$- labelled acetate, and, therefore, the aceticlastic pathway would result in a 1:1 relationship between the emission of $^{14}CO_2$ and $^{14}CH_4$ from the monolith. However, if oxidation of $^{14}CH_4$ to $^{14}CO_2$ occurs in the oxic zone of the peat, it will cause a decrease in emitted $^{14}CH_4$ and an equally large increase

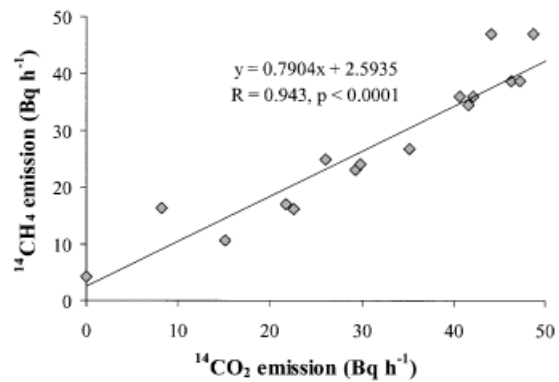**Fig. 5** Correlation between $^{14}CH_4$ and $^{14}CO_2$ emission ($Bq\,h^{-1}$) from the monolith following addition of ^{14}C-acetate to the 9 cm depth.

in emitted $^{14}CO_2$. According to the equation for the linear relationship between $^{14}CO_2$ and $^{14}CH_4$ emission shown in Fig. 5, $^{14}CH_4 = 0.7904 \times {}^{14}CO_2$. Thus, allowing these assumptions to be made the oxidation can be calculated as $(1 - 0.7904)/2 = 0.10$, i.e. 10%.

Discussion

Methane transport through vascular plants is frequently mentioned as one of the major pathways for soil–atmosphere CH_4 fluxes in wetlands (Schimel, 1995; Frenzel & Rudolph, 1998; King *et al.*, 1998; Bellisario *et al.*, 1999; Greenup *et al.*, 2000). Increased emissions from vegetated areas are primarily attributed to plant-mediated transport of CH_4 produced at anoxic peat depths through the aerenchymatous tissue of sedges directly to the atmosphere (King *et al.*, 1998). *Eriophorum* species are often mentioned as being particularly effective transporters of CH_4 (Schimel, 1995; Frenzel & Rudolph, 1998; Greenup *et al.*, 2000). We have shown earlier that CH_4 emission correlates positively to the biomass of *E. scheuchzeri*, whereas no correlation with the biomass of *D. psilosantha* can be demonstrated (Joabsson & Christensen, 2001). In this study, we show that the positive correlation between CH_4 and *E. scheuchzeri* found in Joabsson & Christensen (2001) seems to be, at least in part, related to higher substrate availability for the methanogens in the root vicinity of this species (Fig. 2). Thus, our results give further support to the proposed importance of certain vascular plant species as suppliers of easily available substrates for the methanogenic bacteria (van Veen *et al.*,1989; Jackson & Caldwell, 1992; Whiting & Chanton, 1992; Chanton *et al.*, 1995; Joabsson *et al.*, 1999; Greenup *et al.*, 2000), although it cannot be excluded that the plant-mediated transport of CH_4 is also higher in *E. scheuchzeri* than in *D. psilosantha*.

In some studies, it has been observed that the CH_4 emission from wetland ecosystems is positively correlated with net ecosystem productivity (NEP), presumably because a higher NEP leads to a higher input of substrates associated with recent production and to a stimulation of methanogesis (Whiting & Chanton, 1993; Chanton et al., 1995; Waddington et al., 1996; Christensen et al., 2000). Joabsson & Christensen (2001) demonstrated a higher CH_4 flux from control than from shaded plots in the Zackenberg wetland and also showed a positive correlation between net ecosystem exchange (NEE) and CH_4 flux. Our results show that the acetate formation rate was much higher in E. scheuchzeri microcosms in control than in shaded plots (Fig. 2), indicating that higher photosynthetic rates in control plots lead to higher allocation of carbon to the root zone and, subsequently, to higher acetate formation rates in the root vicinity of E. scheuchzeri in this treatment (Fig. 2). We sampled on three consecutive days, each day for 24 h. On each sampling day, we found higher acetate formation rates in E. scheuchzeri microcosms than in blanks in the control treatment, indicating that the acetate originated from recently fixed carbon. Stable isotope techniques have shown that a significant fraction of emitted CH_4 is derived from recently fixed carbon (Chanton et al., 1995) and suggested the importance of the acetate fermentation pathway, which is thought to dominate over CO_2 reduction when fresh organic material is utilized (Bellisario et al., 1999; Chasar et al., 2000). It is reasonable to assume that the ultimate fate of the acetate we found in the root vicinity of E. scheuchzeri will be CH_4 emission from the ecosystem. In further support of this reasoning, we found a very strong correlation between the potential CH_4 production at anoxic peat depths and the acetate concentration in the pore water of that depth (Fig. 3a). When the same potential CH_4 production was correlated to DOC, we instead found a strong negative correlation, indicating that the quality of DOC decreased with the degree of decomposition (Fig. 3b).

Acetate is frequently mentioned as a substrate of major importance to methanogens (Oremland, 1988; Bellisario et al., 1999). There have recently been findings that methanogens in northern wetlands in general do not consume acetate, but that it instead accumulates in the peat water throughout the season (Hines & Duddleston, 2001). Our result, however, further supports the importance of acetate as a substrate even in high northern wetlands and shows that ^{14}C-acetate added to a peat-live plant monolith collected at the study site in NE Greenland was decomposed to $^{14}CH_4$ (Fig. 4b).

Acetate is usually degraded by the aceticlastic reaction, in which the methyl group is reduced to CH_4 while the carboxylic group is oxidized to CO_2 (Boone, 1991). From the results of our study it is obvious that acetate is a predecessor to CH_4 (Fig. 4b) and the very close correlation between CH_4 and CO_2 emissions (Fig. 5) from our monolith suggests a dominance of the aceticlastic reaction. In the result section, we suggested a dominance of the aceticlastic pathway and calculated the CH_4 oxidation to 10%. However, it cannot be excluded that some acetate is decomposed to CO_2 in the oxic vicinity of plant roots, whereupon the methanogens use CO_2 as a substrate for CH_4 formation. Instead, we propose separate additions of $^{14}CH_4$-COO^-- and CH_4-$^{14}COO^-$-labelled acetate to determine these relationships more accurately and in more detail. The great difficulties in obtaining monolith replicates from NE Greenland prevented an otherwise desired replication of the experiments presented and certainly calls for further work testing the findings of our ^{14}C-acetate labelling study. However, regardless of the pathway to CH_4 formation and lack of replication, our results clearly show that acetate can be a predecessor to CH_4 in the studied ecosystem.

In conclusion, our results demonstrate that the amount of labile carbon, e.g., acetate, found in the root vicinity of vascular plants is dependent on plant species and photosynthetic rates. We also show that in the studied arctic ecosystem, CH_4 emission rates, and the potential CH_4 production of the peat, are dependent on substrate quality and we document the linkage between root exudation of labile carbon, e.g. acetate and CH_4 formation. Thus, potential human-induced climatic changes affecting vascular plant species composition, biomass or carbon allocation can have far-reaching consequences for substrate quality, carbon cycling and CH_4 emissions in northern wetland ecosystems.

References

Armstrong W, Justin SHFW, Beckett PM, Lythe S (1991) Root adaptation to soil waterlogging. *Aquatic Botany*, **39**, 57–73.

Bay C (1997) Floristic division and vegetation zonation of Greenland of relevance to a circumpolar arctic vegetation map. In: *Proceedings of The Second Circumpolar Arctic Vegetation Mapping Workshop, Arendal, Norway, 19–25 May 1996* (Occasional Paper No. 52, pp. 27–31. Institute of Arctic and Alpine Research, University of Colorado.

Beckmann M, Lloyd D (2001) Mass spectrometric monitoring of gases (CO_2, CH_4, O_2) in a mesotrophic peat core from Kopparås Mire, Sweden. *Global Change Biology*, **7**, 171–180.

Bellisario LM, Bubier JL, Moore TR (1999) Controls on CH_4 emissions from a northern peatland. *Global Biogeochemical Cycles*, **13**, 81–91.

Boone DR (1991) Ecology of methanogesis. In: *Microbial Production and Consumption of Greenhouse Gases: Methane, Nitrogen Oxides, and Halomethanes* (eds Rogers JE, Whitman WB), pp. 57–70. American Society for Microbiology, Washington, DC.

Chanton JP, Dacey JWH (1991) Effects of vegetation on methane flux, reservoirs, and carbon isotopic composition. In: *Trace Gas Emissions by Plants* (eds Sharkey TD, Holland EA, Mooney HA), pp. 65–92. Academic Press, San Diego.

Chanton JP, Bauer JE, Glaser PA *et al.* (1995) Radiocarbon evidence for the substrates supporting methane formation within northern Minnesota peatlands. *Geochimica et Cosmochimica Acta*, **59**, 3663–3668.

Chasar LS, Chanton JP, Glaser PH, Siegels DI (2000) Methane concentration and stable isotope distribution as evidence of rhizospheric processes: comparison of a fen and bog in the glacial lake agassiz peatland complex. *Annals of Botany*, **86**, 655–663.

Christensen TR, Friborg T, Sommerkorn M (2000) Trace gas exchange in a high arctic valley 1: variations in CO_2 and CH_4 flux between tundra vegetation types. *Global Biogeochemical Cycles*, **14**, 701–714.

Christensen TR, Jonasson S, Callaghan TV, Havström M (1999) On the potential CO_2 releases from tundra soils in a changing climate. *Applied Soil Ecology*, **11**, 127–134.

Frenzel P, Rudolph J (1998) Methane emission from a wetland plant: the role of CH_4 oxidation in Eriophorum. *Plant and Soil*, **202**, 27–32.

Frenzel P (2000) Plant-associated methane oxidation in rice fields and wetlands. In: **Vol. 16** (ed. Schink B), pp. 85–114. Kluwer, New York.

Greenup AL, Bradford MA, McNamara PN, Ineson P, Lee JA (2000) The role of Eriophorum vaginatum in CH_4 flux from an ombrotrophic peatland. *Plant and Soil*, **227**, 265–272.

Hines ME, Duddleston KN (2001) Carbon flow to acetate and C_1 compounds in northern wetlands. *Geophysical Research Letters*, **28**, 4251–4254.

Hogg EH (1993) Decay potential of hummock and hollow Sphagnum peats at different depths in a Swedish raised bog. *Oikos*, **66**, 269–278.

Jackson RB, Caldwell MM (1992) Shading and the capture of localized soil nutrients: nutrient contents, carbohydrates and root uptake kinetics of a perennial tussock grass. *Oecologia*, **91**, 457–462.

Joabsson A, Christensen TR, Wallén B (1999) Vascular plant controls on methane emissions from northern peatforming wetlands. *Trends in Ecology and Evolution*, **14**, 385–388.

Joabsson A, Christensen TR (2001) Methane emissions from wetlands and their relationship with vascular plants: an Arctic example. *Global Change Biology*, **7**, 919–932.

King JY, Reeburgh WS, Regli SK (1998) Methane emission and transport by arctic sedges in Alaska: Results of a vegetation removal experiment. *Journal of Geophysical Research*, **103**, 29083–29092.

Konĕalová H (1990) Anatomical adaptations to waterlogging in roots of wetland graminoids: limitations and drawbacks. *Aquatic Botany*, **38**, 127–134.

Marschner H (1995) *Mineral Nutrition of Higher Plants* 2nd edn. Academic Press, London.

Oechel WC, Vourlitis GL (1997) Climate change in northern latitudes: alterations in ecosystem structure and function and effects on carbon sequestration. In: *Global Change and Arctic Terrestrial Ecosystems* (eds Oechel WC, Callaghan T, Gilmanov T, Holten JI, Maxwell B, Molau U, Sveinbjörnsson B), pp. 381–401. Springer, New York.

Oechel WC, Vourlitis GL, Hastings SJ, Zulueta RC, Hinzman L, Kane D (2000) Acclimation of ecosystem CO_2 exchange in the Alaskan Arctic in response to decadal climate warming. *Nature*, **406**, 978–980.

Oremland RS (1988) Biogeochemistry of methanogenic bacteria. In: *Biology of anaerobic microorganisms* (ed. Zehnder AJB), pp. 641–703. John Wiley, New York.

Panikov NS, Gorbenko AJu (1992) The dynamics of gas exchange between soil and atmosphere in relation to plant-microbe interactions: fluxes measuring and modeling. *Ecological Bulletins (Copenhagen)*, **42**, 280–287.

Post WM, Emanuel WR, Zinke PJ, Stangenberger AG (1982) Soil carbon pools and world life zones. *Nature*, **298**, 156–159.

Reeburgh WS, Whalen SC (1992) High latitude ecosystems as CH_4 sources. *Ecological Bulletins*, **42**, 62–70.

Shaver GR, Kummerow J (1992) Phenology, resource allocation, and growth of arctic vascular plants. In: *Arctic ecosystems in a changing climate. An ecophysiological perspective* (eds Chapin III FS, Jefferies RL, Reynolds JF, Shaver GR, Svoboda J), pp. 193–211. Academic Press, Inc., San Diego.

Schimel JP (1995) Plant transport and methane production as controls on methane flux from arctic wet meadow tundra. *Biogeochemistry*, **28**, 183–200.

Ström L, Olsson T, Tyler G (1994) Differences between calcifuge and acidifuge plants in root exudation of low-molecular organic acids. *Plant and Soil*, **167**, 239–245.

Sundh I, Nilsson M, Granberg G, Svensson BH (1994) Depth distribution of microbial production and oxidation of methane in northern boreal peatlands. *Microbial Ecology*, **27**, 253–265.

van Veen JA, Merckx R, van de Geijn SC (1989) Plant and soil related controls of the flow of carbon from roots through the soil microbial biomass. *Plant and Soil*, **115**, 179–188.

Waddington JM, Roulet NT, Swanson RV (1996) Water table control of CH_4 emission enhancement by vascular plants in boreal peatlands. *Journal of Geophysical Research*, **101**, 22775–22785.

Watson A, Stephen KD, Nedwell DB, Arah JRM (1997) Oxidation of methane in peat: kinetics of CH_4 and O_2 removal and the role of plant roots. *Soil Biology and Biochemistry*, **29**, 1257–1267.

Whiting GJ, Chanton JP (1992) Plant-dependent CH_4 emission in a subarctic Canadian fen. *Global Biogeochemical Cycles*, **6**, 225–231.

Whiting GJ, Chanton JP (1993) Primary production control of methane emission from wetlands. *Nature*, **364**, 794–795.