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

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Abstract
This paper investigates how vascular plants affect carbon flow and the formation and emission of the greenhouse gas methane (CH4) 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 CH4 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 CH4 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 CH4, 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 14C-labelled acetate injected at the depth of methanogenic activity. After 4 h, 14CH4 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 CH4 formation.

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

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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 (CO2) and methane (CH4) with the atmosphere (Panikov & Gorbenko, 1992; Christensen et al., 1999; Oechel et al., 2000). Tundra wetlands are generally net sinks for atmospheric CO2 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 CH4 production and the atmospheric input of CH4 from these regions account for about 10% of the total CH4 sources globally (Reeburgh & Whalen, 1992).

It is well recognized that the presence of vascular plants affects CH4 exchange between wetland ecosystems and the atmosphere, because plants affect important aspects of CH4 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
rhizosphere can lead to the inhibition of methanogenesis and oxidation of CH₄ to CO₂ (Chanton & Dacey, 1991; Watson et al., 1997; Frenzel, 2000). However, at the same time CH₄ transported in the aerenchyma escapes oxidation to CO₂, 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 muckleage, 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 CH₄ 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 CO₂ to CH₄ (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 precursor to CH₄ 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 CH₄ 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 CH₄ 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 H2O to remove any organic acid contaminants) into 10 mL glass vials, transported to the lab, flushed with N2 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 CH4 production**

The potential CH4 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 N2 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 CH4 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).

**14C-acetate labelling of a peat-plant monolith**

To determine whether acetate was a substrate for CH4 formation in the fen, we collected a peat-plant monolith from the field site, injected it with 14C-labelled acetate and monitored the subsequent emissions of 14CH4 and 14CO2 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 × 24W × 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...
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 dm$^3$ min$^{-1}$. The Plexiglas chamber volume was 13 dm$^3$ and the headspace 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 kBq 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}$COONa (Amersham Biosciences, Piscataway, New Jersey, USA). A mixture was chosen since we wanted to trace all CH$_4$ formed 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 ± 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$_2$ m$^{-2}$ h$^{-1} ± SE$))
compared to control ($-854\pm40$) 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 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).

14C-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 14C-acetate injection at 9 cm, a diffusion of radioactivity to 6 and 12 cm could be observed (Fig. 4a) and 14CH$_4$ started to be emitted from the monolith (Fig. 4b). After 24 h, the concentration of 14C-acetate in the pore water of the monolith peaked at 12 cm and emission of both 14CO$_2$ and 14CH$_4$ could be observed from the monolith. After 48 h, the 14C-acetate in the pore water at 6 cm peaked, whereupon, at both 6 and 12 cm it decreased slowly throughout the

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**Fig. 2** Formation rate of acetate ($\mu$mol g$^{-1}$ dry root h$^{-1}$ ± SE, $n=6$) in root microcosms containing *Eriophorum scheuchzeri* (Erioph) grown in the control and shaded experimental plots and *Dupontia psilosantha* (Dupon) grown only in the control plots. The number over the bars shows the mean (mg CO$_2$ m$^{-2}$h$^{-1}$ ± SE) photosynthetic rate (calculated as NEE - respiration) in August for each treatment.

**Fig. 3** Potential CH$_4$ production (mg CH$_4$ g$^{-1}$ day$^{-1}$ ± 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$^{-1}$ ± 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).
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, \(R^2 = 0.943, P < 0.001\)), 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\(_2\)-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 \(^{14}\)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*.  

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**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\(_4\) (\(\circ\)) and CO\(_2\) (\(\square\)) from the monolith following addition of \(^{14}\)C-acetate to the 9 cm depth at time zero.

**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 some studies, it has been observed that the CH₄ 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 methanogenesis (Whiting & Chanton, 1993; Chanton et al., 1995; Waddington et al., 1996; Christensen et al., 2000). Joabsson & Christensen (2001) demonstrated a higher CH₄ flux from control than from shaded plots in the Zackenberg wetland and also showed a positive correlation between net ecosystem exchange (NEE) and CH₄ 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 CH₄ 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 CO₂ 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 CH₄ emission from the ecosystem. In further support of this reasoning, we found a very strong correlation between the potential CH₄ production at anoxic peat depths and the acetate concentration in the pore water of that depth (Fig. 3a). When the same potential CH₄ 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 ¹⁴C-acetate added to a peat-live plant monolith collected at the study site in NE Greenland was decomposed to ¹⁴CH₄ (Fig. 4b).

Acetate is usually degraded by the aceticlastic reaction, in which the methyl group is reduced to CH₄ while the carboxylic group is oxidized to CO₂ (Boone, 1991). From the results of our study it is obvious that acetate is a predecessor to CH₄ (Fig. 4b) and the very close correlation between CH₄ and CO₂ 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 CH₄ oxidation to 10%. However, it cannot be excluded that some acetate is decomposed to CO₂ in the oxic vicinity of plant roots, whereupon the methanogens use CO₂ as a substrate for CH₄ formation. Instead, we propose separate additions of ¹³CH₄-COO⁻ and CH₄-¹²COO⁻-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 ¹⁴C-acetate labelling study. However, regardless of the pathway to CH₄ formation and lack of replication, our results clearly show that acetate can be a predecessor to CH₄ 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, CH₄ emission rates, and the potential CH₄ production of the peat, are dependent on substrate quality and we document the linkage between root exudation of labile carbon, e.g. acetate and CH₄ 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 CH₄ emissions in northern wetland ecosystems.

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