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Species-specific effects of vascular plants on carbon turnover and methane emissions from wetlands

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Abstract. Species composition affects the carbon turnover and the formation and emission of the greenhouse gas methane (CH_4) in wetlands. Here we investigate the individual effects of vascular plant species on the carbon cycling in a wetland ecosystem. We used a novel combination of laboratory methods and controlled environment facilities and studied three different vascular plant species (*Eriophorum vaginatum*, *Carex rostrata* and *Juncus effusus*) collected from the same wetland in southern Sweden. We found distinct differences in the functioning of these wetland sedges in terms of their effects on carbon dioxide (CO_2) and CH_4 fluxes, bubble emission of CH_4, decomposition of ^{14}C-labelled acetate into $^{14}CH_4$ and $^{14}CO_2$, rhizospheric oxidation of CH_4 to CO_2 and stimulation of methanogenesis through root exudation of substrate (e.g., acetate). The results show that the emission of CH_4 from peat–plant monoliths was highest when the vegetation was dominated by *Carex* (6.76 mg CH_4 m^{-2} h^{-1}) than when it was dominated by *Eriophorum* (2.38 mg CH_4 m^{-2} h^{-1}) or *Juncus* (2.68 mg CH_4 m^{-2} h^{-1}). Furthermore, the CH_4 emission seemed controlled primarily by the degree of rhizospheric CH_4 oxidation which was between 20 and 40% for *Carex* but >90% for both the other species. Our results point toward a direct and very important linkage between the plant species composition and the functioning of wetland ecosystems and indicate that changes in the species composition may alter important processes relating to controls of and interactions between greenhouse gas fluxes with significant implications for feedback mechanisms in a changing climate as a result.

Introduction

Species composition has important implications for ecosystem functioning and affect carbon and energy exchange as well as greenhouse gas fluxes. 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 and Gorbenko 1992; Christensen et al. 1999; Oechel et al. 2000). In general, these ecosystems are 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 favour anaerobic decomposition and make wetlands significant sources of atmospheric CH_4.

Vascular plants in combination with their effects on CO_2 dynamics through photosynthesis and respiration also affect important processes relating to CH_4 dynamics, e.g., production, consumption and transport. Details of the mechanisms behind these relationships are, however, still poorly known. Various studies have attributed the relationship to different mechanisms, such as (1) *stimulation of methanogenesis by increasing C-substrate availability*. A fairly large amount of the carbon assimilated by vascular plants through photosynthesis can be allocated belowground. For example, in Alaskan tussock tundra, between 47 and 92% of the biomass was found to end up in this pool depending on plant species (Shaver and Kummerow 1992). It has been shown in a ^{14}C-labelling experiment on the dry ombrotrophic parts of the Stordalen mire in northern Sweden that between 37 and 69% of recent assimilates had been released as $^{14}CO_2$ or was found in more rapidly decomposable pools, e.g., dissolved organic carbon in the pore water or in hair roots, after 32 days (Olsrud and Christensen 2004). Once released to the soil, these rapidly decomposable carbon pools can serve as substrate for fermenting bacteria and, ultimately, have a substantial effect on CH_4 production in the soil (Joabsson et al. 1999; Ström et al. 2003). Vascular plants continuously release a wide range of labile carbon compounds from their root system, including mucilage, ectoenzymes, organic acids, sugars, phenolics and amino acids (Marschner 1995). An organic acid of particular interest in this respect is acetate, which is frequently mentioned as a substrate of major importance for the methanogens (Oremland 1988; Boone 1991; Ferry 1997; Bellisario et al. 1999; Avery et al. 2003; Ström et al. 2003). It has been reported, however, that methanogens in northern wetlands do not use acetate or C1 compounds as substrate. Instead these compounds accumulate throughout the season with acetate as the primary organic end product of fermentation (Hines et al. 2001). 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). Furthermore, stable isotope techniques have shown that a significant fraction of emitted CH_4 is derived from recently fixed carbon and suggested the importance of the acetate fermentation pathway, which is thought to dominate over CO_2 reduction when fresh organic material is utilized (Chanton et al. 1995; Bellisario et al. 1999; Chasar et al. 2000). (2) *CH_4 consumption* through oxidation. Plant species adapted to wetland conditions often develop oxygen-transporting gas spaces (aerenchyma), which provide an internal pathway for the exchange of gases between above water and submerged parts of the plant (Končalová 1990; Armstrong et al. 1991). The diffusion of O_2 from the shoots to the roots via the aerenchyma can result in considerable amounts of O_2 in the rhizosphere (Weißner et al. 2002). Consequently, CH_4 oxidizing bacteria (methanotrophs) can live within the rhizosphere and oxidize CH_4 that otherwise would travel unimpeded through the plant. The plants are in this way shielding the

atmosphere from the release of additional CH_4 (Chanton and Dacey 1991; King 1992). (3) *Enhanced CH_4 transport*. 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 and Rudolph 1998; Bellisario et al. 1999).

It is of vital importance to understand how individual vascular plant species affect these different components of the carbon cycling in wetland ecosystems. This will in future 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. Thus, the main objective of this study was to investigate the individual effects of vascular plant species on the carbon cycling in a wetland ecosystem. Focusing mainly on (1) How individual plant species affect the fluxes of CO_2 and CH_4. (2) To what extent stimulation of methanogenesis by increasing C-substrate availability and CH_4 consumption are affected by individual plant species. To address these questions we used a combination of laboratory methods and controlled environment facilities and studied the effects of three different vascular plants collected from the same wetland in southern Sweden on CO_2 and CH_4 fluxes, decomposition of ^{14}C-labelled acetate and C-substrate availability through root exudation.

Materials and methods

To study the species-specific effects of vascular plants on the fluxes of CO_2 and CH_4 we collected peat–plant monoliths dominated by three different vascular plants, i.e., *Carex rostrata* Stokes (will onwards be referred to as *Carex*), *Eriophorum vaginatum* L. (*Eriophorum*) and *Juncus effusus* L. (*Juncus*), from a peat forming wetland surrounded by deciduous forest by the lake 'Fjällfotasjön' in south Sweden (55°32′ N, 13°17′ E). Similar techniques of bringing in peat cores for laboratory CO_2 and CH_4 flux experiments have been used previously (Billings et al. 1982; Thomas et al. 1996; Daulat and Clymo 1998; Christensen et al. 2003; Ström et al. 2003). The technique used in this study allowed a detailed comparison of gas fluxes and emission patterns between the monoliths. However, the laboratory set-up and instrumentation only allowed simultaneous measurements on three monoliths and thus prevented an otherwise desired replication.

Monolith sampling and laboratory set-up

The monoliths were sampled before the start of the growing season on the 26th February 2002 (average temperature −1.2 °C) in aluminium frames (25L * 25W * 40D cm, length * width * depth) that were inserted into the ground and lifted containing the peat–plant monoliths. Within 3 h after removal from the field site the monoliths were transported to the laboratory

and placed in a temperature controlled growth room with day/night rhythm of 13/15 °C and a 12 h photoperiod with light intensity of 300 μmol m^{-2} s^{-1}. The somewhat low light intensity was considered realistic since the monoliths were collected from a field site surrounded by deciduous forest. Through small additions of distilled water the depth of the water-table below the moss surface was constantly kept at the level measured in the field: 10 cm for *Eriophorum* and *Carex* and 2 cm for *Juncus*. 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 aluminium frames with silicone sealing the monoliths were hermetically sealed, whereupon they were continuously flushed with ambient air at an average flow rate of 0.80 l min^{-1}. The Plexiglas chambers each had a volume of 13 l and the headspace gas was turned over at a rate of 3.7 times per hour. The air humidity was maintained at a constant level. Flowstat, rotameters and solenoid valves controlled the airflow. A photoacoustic (IR) multigas analyser (INNOVA 1312) operated continuously and recorded the concentration of CO_2 and CH_4 in the input and output air. A PC was used for data logging and for controlling the solenoid valves (Christensen et al. 2003). Flux measurements of CO_2 where started one week after sampling of the monoliths on the 5th March 2002 and of CH_4 an additional 10 days later on the 15th of March.

At the end of the experiment the above ground biomass in the monoliths was harvested, divided into plant species and dried in 40 °C for 2 weeks before weighing. The below ground biomass was not harvested due to high levels of radioactivity following the ^{14}C-acetate labelling. Throughout the duration of the experiment the soil (5 cm below the water table) and air temperature (5 cm above the peat surface) in the monoliths was continuously logged.

Monolith pore water sampling

To determine the amount of labile substrate, i.e. acetate, in the monoliths pore water was sampled continuously over the experimental period. Pore water samples (2 ml) were drawn; from the centre of the monolith through permanently installed stainless steel tubes positioned with 4 cm intervals between 2 and 22 cm below the water level. The samples were immediately filtered through a sterile pre-rinsed Acrodisc PF 0.8 μm/0.2 μm filter into N_2-flushed vials, shaken for 1 min and analysed for acetate using an anion exchange HPLC system equipped with a column system from Dionex, including the analytical column AS11 (4 mm, P/N 044076).

^{14}C-acetate labelling of the monoliths

To determine whether acetate was a substrate for CH_4 and CO_2 formation in the monoliths and to what extent the formation was affected by plant species

we injected the monoliths with ^{14}C-labelled acetate and monitored the subsequent emissions of $^{14}CH_4$ and $^{14}CO_2$, this technique has been previously used by Ström et al. (2003).

The labelling was started 48 and 55 days after the monoliths where brought in from the field: the 15th of April for *Eriophorum* and *Juncus* and 22nd of April for *Carex*. To the 10 cm depth (below the water table) of each monolith we added 96 ml of an ^{14}C-acetate solution composed of 1.21 kBq ml^{-1} [2-^{14}C] acetic acid Na-salt and an unlabelled mixture of 100 μM acetic acid and 100 μM Na-acetate; a mixture which resulted in a pH (4.75) very close to the natural pH of the monoliths (4.53 $\pm$ 0.13). Before addition the ^{14}C-acetate solution was flushed with N_2, to remove oxygen from the solution. The ^{14}C-acetate solution was distributed in a grid over the 10 cm depth through four channels closed by septa, by inserting an injection tube (1.5 mm in diameter) 18 cm into the monolith and injecting 1.5 ml ^{14}C-acetate solution for every 1 cm that the tube was pulled out of the monolith over a length of 16 cm (Ström et al. 2003).

To continuously trap 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 $Na_2{}^{14}CO_3$ or $NaH^{14}CO_3$) and a tube-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) (Christensen et al. 2003; Ström et al. 2003). The traps were changed periodically starting 4 h and ending 672 h (28 days) following ^{14}C-acetate addition and counted for radioactivity by liquid scintillation (Packard Tri-Carb 2100TR liquid scintillation analyser) using alkali compatible scintillation cocktail (OptiPhase, 'HiSafe'3, Wallac). 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 $^{14}CH_4$.

During the labelling period the average contribution of bubbles to the total emission was calculated using a statistical method based on frequency analysis of the instant flux values (see Appendix A).

Plant root exudation

To investigate the contribution of easily degradable substrate for CH_4 formation, e.g., acetate, from plant roots to their rhizosphere we collected *Eriophorum*, *Carex* and *Juncus* at the field site. This was done simultaneously with the monolith sampling on 26th of February 2002. We chose plants of similar size to the individual plants in the monoliths and placed 15 replicates of each species and an additional set of 15 blanks without plants in the same growth room and under identical conditions to the monoliths. The plants were grown hydroponically under unsterile conditions in rhizosphere microcosms composed of 60 ml polypropylene tubes filled with a weak nutrient solution composed to simulate the pore water at the field site. The solution level in the microcosms was adjusted daily and changed in total once every week.

When growth of fresh undisturbed roots was observed in all plant containing microcosms (first on 19th March), the nutrient solution was completely exchanged for fresh solution. Following 24-h of incubation the solution in the microcosms was sampled immediately filtered through a sterile Acrodisc PF 0.8 μm/0.2 μm filter (pre-rinsed with 40 ml of distilled H_2O to remove any organic acid contaminants) and analysed for acetate according to the HPLC-method described above. The sampling procedure was repeated on three consecutive days, where after, the plants were harvested and dried in 40 °C dried in 40 °C for 2 weeks before weighing.

Results

Monolith characteristics

The above ground biomass of the *Eriophorum* monolith was completely dominated by this species. Of the total 21.4 g total dry weight 94% was *Eriophorum* and the remaining 6% consisted solely of *Carex*. In the *Carex* monolith the total aboveground biomass (10.3 g) consisted of 77% *Carex* and 23% graminoids. While, in the *Juncus* monolith the total aboveground biomass (12.5 g) consisted of 91% *Juncus* and 9% *Carex*.

The temperature setting of the growth room resulted in a soil temperature (5 cm below the water table) of at daytime 13.0 ± 0.3 (°C ± Standard deviation) and during night 12.9 ± 0.3. The corresponding air temperatures were: daytime 14.8 ± 0.8, during night 13.7 ± 1.0 and the daily average were 14.2 ± 1.1. The daily average air temperature corresponded well with the 1961–1990 daily average measured at the Sturup weather station (5 km from the field site) for late spring and summer in south Sweden: May 10.6 °C, June 14.4 °C and July 16.0 °C (Alexandersson et al. 1991).

Monolith flux measurements

The 2.5 month long incubation of the peat–plant monoliths show how the exchange rates (the difference between maximum and minimum CO_2 flux in a given day) of CO_2 increases for all three species as the vegetation develops from spring to summer (Figure 1). It further shows that all three monoliths were sources of CH_4 throughout the incubation period (Figure 2). In May when the vegetation in all three monoliths was fully developed and the exchange rates of CO_2 had stabilized it was obvious that the magnitude of the CO_2 exchange as well as the CH_4 emission was species-specific (Table 1). During this period the *Carex* and *Eriophorum* monoliths were in total sources of CO_2 to the atmosphere in spite of a negative daytime NEE, whereas, the *Juncus* monolith was a sink for CO_2 (Figure 1 and Table 1). The May mean values of daytime NEE, respiration and CH_4 emission for the three species were not correlated with the

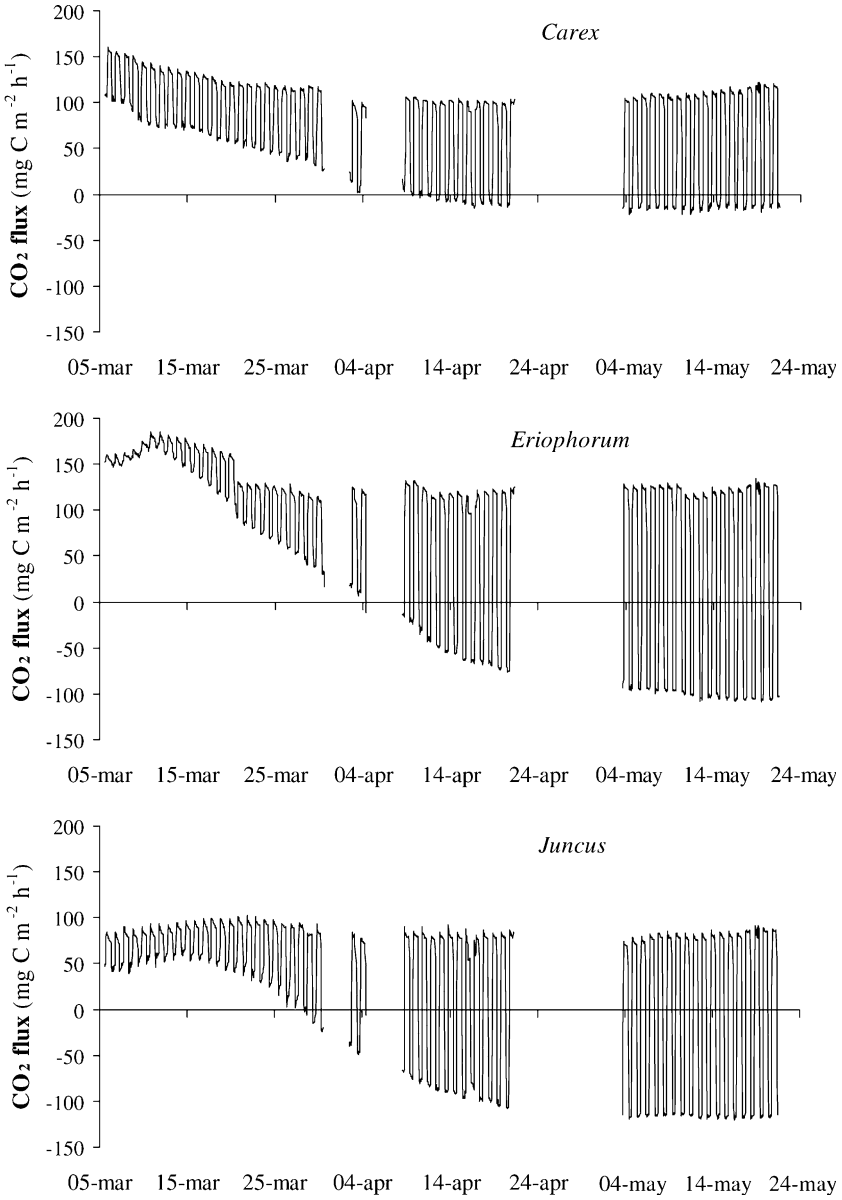

Figure 1. The CO_2 fluxes of three peat–plant monoliths, dominated by *Carex rostrata*, *Eriophorum vaginatum* and *Juncus effusus*, grown under constant light and temperature conditions over a >2.5 month period. Positive values on the CO_2 flux means respiration and loss of C to the atmosphere and negative values represent photosynthesis.

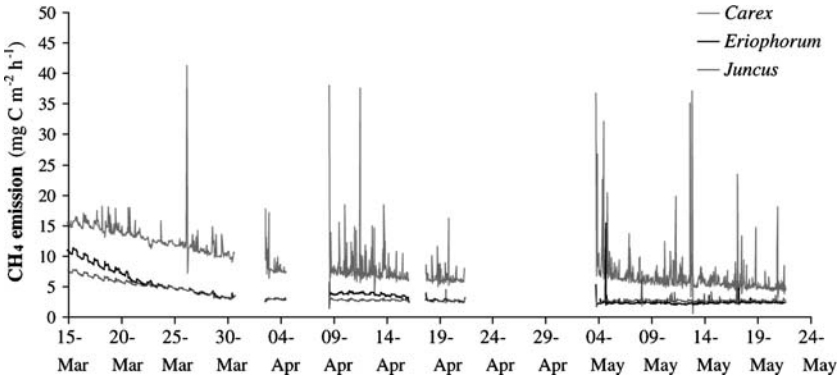

Figure 2. The CH_4 fluxes of three peat–plant monoliths dominated by *Carex rostrata*, *Eriophorum vaginatum* and *Juncus effusus*, grown under constant light and temperature conditions over a >2 month period.

Table 1. The May means of CO_2 and CH_4 fluxes from three peat–plant monoliths dominated by *Carex rostrata*, *Eriophorum vaginatum* and *Juncus effusus* grown under constant light and temperature conditions.

	NEE (mg C m^{-2} h^{-1})	Respiration (mg C m^{-2} h^{-1})	Photosynthesis (mg C m^{-2} h^{-1})	CH_4 emission (mg C m^{-2} h^{-1})
Carex	− 13.4 ± 0.6	107.9 ± 1.1	− 121.3 ± 1.1	6.76 ± 0.47
Eriophorum	− 103.7 ± 1.6	119.0 ± 1.5	− 222.7 ± 1.8	2.38 ± 0.03
Juncus	− 118.5 ± 0.7	76.6 ± 1.2	− 195.1 ± 1.4	2.68 ± 0.02

Positive values mean loss of C to the atmosphere. NEE = net ecosystem exchange during daytime.

above ground plant biomass in the monoliths at the end of the experiment. A correlation between calculated photosynthetic rate and biomass was, however, indicated although not significant due to the lack of replication ($n = 3$).

In accordance with the findings for CO_2 the CH_4 emission seemed to be species-specific and differ between the monoliths (Figure 2). Throughout the experimental period the CH_4 emission was highest from the *Carex* monolith (Figure 2 and Table 1) as well as the average contribution of bubbles to the total emissions, which was 23.4% of total emission for the monolith dominated by *Carex*, 3.5% for *Eriophorum* and undetectable for *Juncus*.

Plant root exudation

The contribution of easily degradable substrate for CH_4 formation, i.e., acetate, from plant roots to their rhizosphere was found to vary between species. The formation rate of acetate in the rhizosphere microcosms with *Eriophorum* contained more than 7 times more acetate ($p \leq 0.0002$, ANOVA followed by Tukey's test for multiple comparison) than the *Carex* and *Juncus* microcosms that did not differ significantly (Figure 3).

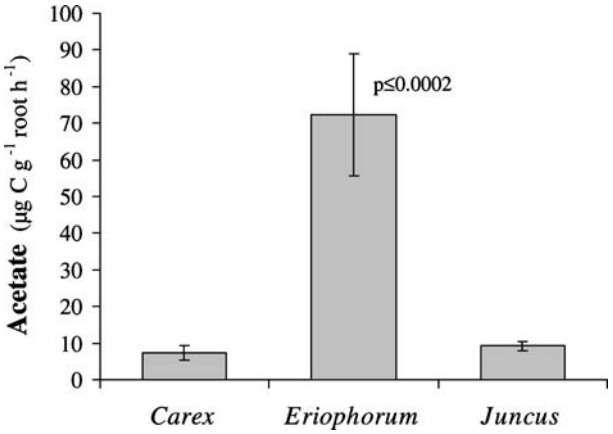

Figure 3. The formation rate of acetate (μg C g^{-1} dry root h^{-1} ± SE, n = 15) in root microcosms containing *Carex rostrata*, *Eriophorum vaginatum* and *Juncus effusus* grown under constant light and temperature conditions and sampled for three consecutive days. The p-value over the *Eriophorum* bar indicates that this species differed significantly from the other two.

Monolith pore water sampling

The total amount of labile substrate, i.e. acetate, in the monoliths was also found to be species-specific and consequently differed between the three monoliths: *Eriophorum* (60.1 ± 2.7, mg C l^{-1} pore water ± SE) > *Juncus* (22.3 ± 2.6) > *Carex* (3.7 ± 0.4). Furthermore, the depth distribution of acetate in the monoliths varied between the three species (Figure 4).

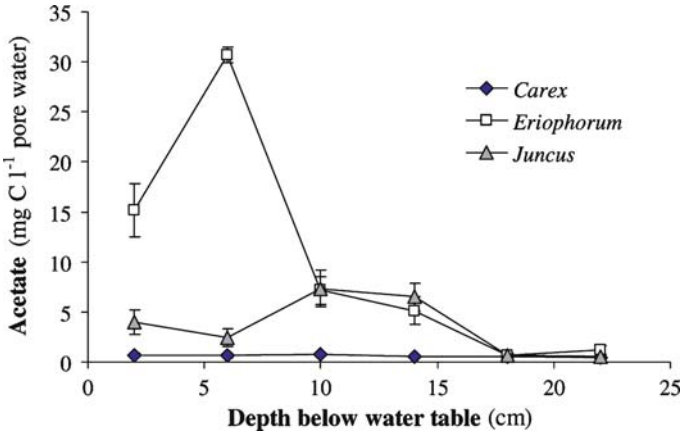

Figure 4. The concentration profile of acetate (mg C l^{-1} pore water ± SE, n = 6) in the pore water of three peat–plant monoliths, dominated by *Carex rostrata*, *Eriophorum vaginatum* and *Juncus effusus*, grown under constant light and temperature conditions.

^{14}C-acetate labelling of the monoliths

The addition of ^{14}C-labelled acetate to the monoliths resulted in emission of different $^{14}CH_4/^{14}CO_2$ ratios depending on plant species. In both the *Eriophorum* and the *Juncus* monoliths the added ^{14}C-acetate was emitted almost entirely as $^{14}CO_2$, whereas, it in the *Carex* monolith was emitted mostly as $^{14}CH_4$ (Figure 5). We added [2-^{14}C] acetate ($^{14}CH_3$-COO^-), which should result exclusively in $^{14}CH_4$ emission if no oxidation to $^{14}CO_2$ takes place provided that acetate is degraded by the aceticlastic reaction that reduces the methyl group to CH_4 while the carboxylic group is oxidized to CO_2 (Boone 1991). Consequently, it was possible to estimate the rhizospheric oxidation of $^{14}CH_4$ to $^{14}CO_2$ in the monoliths: *Eriophorum* and *Juncus* >90% and *Carex* 20–40%.

The relationship between CH_4 emission and substrate availability

If the emission of CH_4 from the monoliths depended only on substrate quality we would expect to find the highest emission rates from the monolith with the highest acetate concentration, i.e., *Eriophorum*. In contrast, when the acetate concentration in the monoliths was correlated with the mean CH_4 emission on the respective sampling dates (27 March, 3 and 17 April) the result indicated a negative correlation between CH_4 emission and substrate availability (Figure 6a). However, if we assume that 90% of the produced CH_4 is oxidized in both the *Eriophorum* and *Juncus* monoliths (Figure 5) but only 30% in the *Carex* monolith the Gross CH_4 Production (GCP), i.e., the potential CH_4 emissions if no CH_4 is oxidized, may be estimated. When the acetate concentration in the monoliths was correlated with GCP the result was a positive relationship that fitted to a Michaelis–Menten equation (Figure 6b).

Discussion

The measurement technique we used in this study allowed a detailed comparison of gas fluxes and emission patterns between the monoliths and the three plant species. The laboratory set-up and instrumentation only allowed simultaneous measurements on three monoliths and thus prevented an otherwise desired replication. To achieve a full comparison and understanding of how vegetation types and individual species affect fluxes of CO_2 and CH_4 from ecosystems replication of the monoliths would be required. However, through the results presented in this study we can show indications that species composition may have dramatic effects on ecosystem functioning.

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

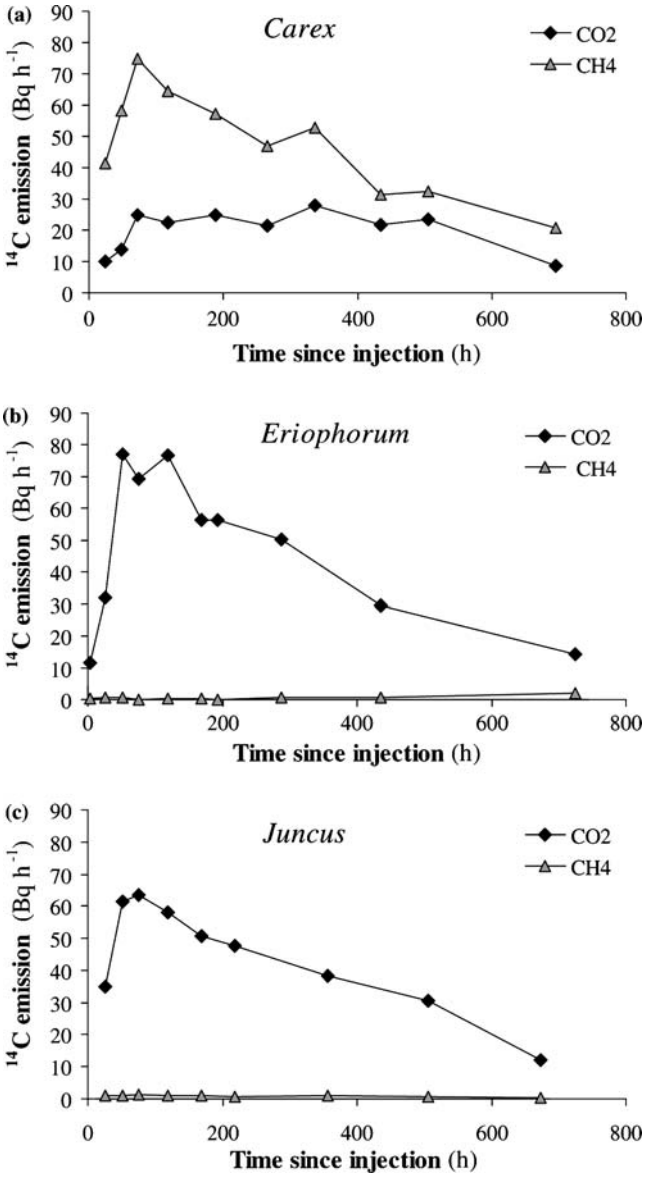

Figure 5. The emission of $^{14}CH_4$ and $^{14}CO_2$ (Bq h^{-1}) from three peat–plant monoliths, dominated by *Carex rostrata*, *Eriophorum vaginatum* and *Juncus effusus* and grown under constant light and temperature conditions, following addition of ^{14}C-acetate 10 cm below the water-table at time zero.

associated with recent production and to a stimulation of methanogesis (Whiting and Chanton 1993; Chanton et al. 1995; Waddington et al. 1996; Christensen et al. 2000). Joabsson and Christensen (2001) demonstrated a

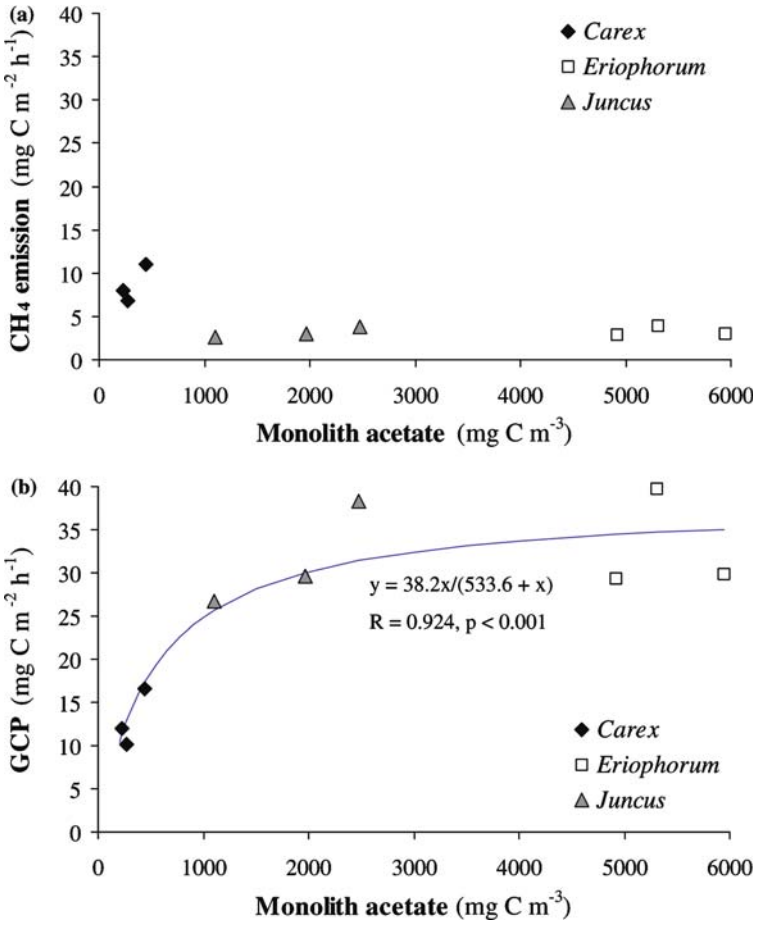

Figure 6. The pore water concentration of acetate (mg C m^{-3}) in three peat–plant monoliths, dominated by *Carex rostrata*, *Eriophorum vaginatum* and *Juncus effusus*, in relation to (a) the emission of CH_4 from the monoliths and (b) the calculated gross CH_4 production (GCP), i.e., the potential CH_4 production if no oxidation would occur in the peat profile. The values represent three individual sampling dates (March 27, April 18 and May 9). A Michaelis–Menten equation is fitted to the values in panel B.

higher CH_4 flux from control than from shaded plots in a wetland in NE Greenland and also showed a positive correlation between NEE and CH_4 flux. In contrast we find here that in May when fluxes from the monoliths had stabilized the *Carex* monolith that was the smallest sink for CO_2 and that had the lowest photosynthetic rate, was the largest source for CH_4 (Table 1 and Figure 2). Methane transport through vascular plants is frequently mentioned as one of the major pathways for CH_4 emissions from wetlands (Schimel 1995; Frenzel and Rudolph 1998; King et al. 1998; Bellisario et al. 1999; Greenup

et al. 2000). We have previously shown that CH_4 emissions from a wetland in NE Greenland correlated positively with the biomass of *Eriophorum scheuchzeri*, whereas no correlation with the biomass of another dominating sedge, *Dupontia psilosantha*, could be demonstrated (Joabsson and Christensen 2001). Therefore, a positive relationship between CH_4 emissions and increasing photosynthetic rates as the green biomass builds up could be expected in our experiment. In disagreement with these findings, we find a decrease in CH_4 emissions from the middle of March when all three monoliths increased in greenness and biomass (Figures 1 and 2). We discuss potential mechanisms for this negative relationship between net CH_4 flux and aboveground plant biomass in more detail below. The lack of consistency in these findings, where presence of some species leads to an increase in CH_4 emission whereas presence of others leads to a decrease supports the proposed importance of species-composition in controlling CH_4 emissions from wetland ecosystems.

Acetate is frequently mentioned as a substrate of major importance to methanogens (Oremland 1988; Ferry 1997; Bellisario et al. 1999; Avery et al. 2003; Ström et al. 2003). 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 et al. 2001). In a previous study in NE Greenland we found that ^{14}C-acetate added to a peat–plant monolith collected at the study site was decomposed to $^{14}CH_4$ (Ström et al. 2003). The result from the present study further shows that acetate is a substrate for CH_4 formation (Figure 5a) but stresses the importance of species composition in this respect. All three monoliths emitted CH_4 but only from the *Carex* dominated monolith was the ^{14}C from ^{14}C-labelled acetate recaptured as $^{14}CH_4$. In the two monoliths dominated by *Eriophorum* and *Juncus* $>90\%$ of the added ^{14}C-acetate was recaptured as $^{14}CO_2$, presumably due to rhizospheric oxidation of $^{14}CH_4$ to $^{14}CO_2$.

It could, however, be argued that the emissions of $^{14}CO_2$, following addition of ^{14}C-labelled acetate, was due not to rhizospheric oxidation of $^{14}CH_4$ to $^{14}CO_2$ but instead to aerobic decomposition of the ^{14}C-labelled acetate directly to $^{14}CO_2$. Although, an additional explanation could be that the unlabelled CH_4 that was emitted from the *Eriophorum* and *Juncus* monoliths originates mainly from CO_2 reduction and that aceticlastic methanogenesis were of less importance in these two monoliths. However, independent of CH_4 production pathway our results clearly show that presence of *Eriophorum* and *Juncus* results in lower emissions of CH_4 than the presence of *Carex* and, thus, stresses the importance of species composition for the CH_4 emissions from wetlands.

Weißner et al. (2002) determined the release of oxygen from *Juncus effusus* plants allowing us to attempt to estimate whether the release of the *Juncus* plants in our monolith could be high enough to account for an $>90\%$ rhizospheric oxidation. Assuming their release rate (0.8 mg O_2 g^{-1} h^{-1}) we can estimate the potential release of the *Juncus* plants in our monolith to 145 mg O_2 m^{-2} h^{-1}. If we compare the GCP (gross CH_4 production) during

May (Figure 6b) to the actual release from the *Juncus* monolith during this month (Table 1) an oxidation rate of 2.2 mmol CH_4 m^{-2} h^{-1} is suggested. At this rate of oxidation the O_2 requirement would be 4.4 mmol m^{-2} h^{-1} (141 mg O_2 m^{-2} h^{-1}), which is within the range of the estimated potential oxygen release from *Juncus* in our monolith.

Considerable amounts of the methane that is produced in anoxic soil can be oxidized while passing through oxic zones: estimates generally ranging between 20 and 99% (Lombardi et al. 1997; Frenzel and Karofeld 2000; Popp et al. 2000; Le Mer and Roger 2001). Oxidation may be as important as production in controlling net CH_4 emissions (Frenzel and Karofeld 2000). Plant-associated microbial activities dominate the CH_4 oxidation in most wetlands since the methanotrophs are enriched in the rhizosphere and live in close association with the plants (Frenzel 2000). Our results indicate that the oxidizing capacity of the monoliths was dependent on plant species (Figure 5). This could be due to differences between the plant species in the size of their root system or in their oxygen transporting efficiency. (Weißner et al. 2002) showed that the oxygen release from *Juncus effusus* grown in hydroponic systems was governed by the size of the aboveground biomass and not significantly affected by the total size of the root system. In accordance with these findings we found a slight decrease in CH_4 emissions during March, when the monoliths increased in biomass and greenness. However, our experiment shows that species composition was clearly more important in determining the oxidizing capacity than simply plant-biomass. We found that $>90\%$ of added [2-^{14}C] acetate was oxidized in the *Eriophorum* monolith, which had the highest aboveground biomass. However, the oxidizing rate was equally high in the *Juncus* monolith and much lower (20–40%) in the *Carex* monolith, which both had similar aboveground biomasses. This indicates that species-specific characteristics of the root system or the oxygen transporting capacity of the plant species were the main determining factor.

As previously stated acetate is frequently mentioned as a substrate of major importance for the methanogens (Oremland 1988; Boone 1991; Bellisario et al. 1999). We have previously demonstrated that the positive correlation between CH_4 emissions from a wetland in NE Greenland and the biomass of *Eriophorum scheuchzeri* was at least in part related to higher substrate (acetate) availability for the methanogens in the root vicinity of this species (Ström et al. 2003). These results offered further support for the proposed importance of certain vascular plant species as suppliers of easily available substrates for the methanogenic bacteria (van Veen et al. 1989; Jackson and Caldwell 1992; Whiting and Chanton 1992; Chanton et al. 1995; Joabsson et al. 1999; Greenup et al. 2000). In the individual plant incubations of this study we also found a much higher acetate formation rate in the root vicinity of *Eriophorum vaginatum* than in the root vicinity of the other two species (Figure 3). Subsequently, we also found much higher acetate concentrations in the *Eriophorum* dominated monolith than in the monoliths dominated by *Carex* and *Juncus* (Figure 4). In this study, however, we found a negative relationship between

substrate in the form of acetate and CH_4 emissions from the monoliths (Figure 6a). Thus, our results might at the first sight seem to indicate that there is no stimulation of methanogenesis by increasing C-substrate availability and that, in opposition to previous findings, the photosynthetic rate and production of vascular plant does not effect CH_4 emissions from wetlands. However, if we take the rhizospheric oxidation into consideration and calculate the gross CH_4 production if there was no oxidation we find that this correlates with the amount of acetate that is found in the pore water of the monoliths (Figure 6b). This indicates that although CH_4 emissions seem be primarily controlled by rhizospheric oxidation CH_4 production may be largely dependent on substrate availability.

Chapin and Shaver (1985) studied the growth response of tundra plant species to environmental manipulations in the field. They found that each species showed a different pattern of growth response to alteration in light, air temperature and nutrients. Therefore, it is hard to predict how the functioning of individual species or the species composition of ecosystems will respond to environmental changes. The current climate change scenario predicts an increased CO_2 concentration in the atmosphere, increased temperature and increased atmospheric deposition rates. Although little is known about the interacting effects of climate change, nitrogen deposition and increasing atmospheric concentration of CO_2 on the demography of sedges (Saarinen 1998) wetland plant community composition and quite possible also the biodiversity is likely to change in response to future climate change with implications for carbon cycling as a result. Although, seasonal flux patterns needs further attention our results show that a change in species composition from for example *Eriophorum* to *Carex* can lead to a much higher CH_4 emission from the ecosystem during the summer. This, in brief, clearly indicates that changes in species composition can have far reaching consequences for carbon cycling and CH_4 emissions in wetland ecosystems.

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Appendix A

Estimation of the bubble component in CH_4 emission

To separate the observed CH_4 emission into gas ebullition (GE) and steady emission (SE) we used a statistical method based on frequency analysis of

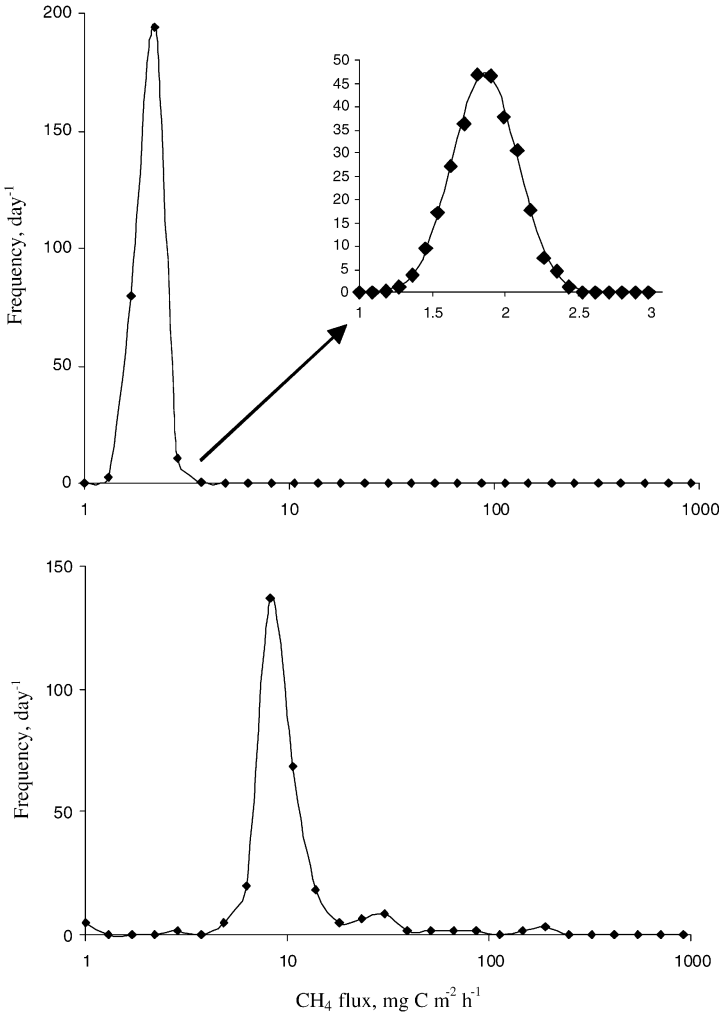

Figure 7. The basis for the statistical frequency analysis of instant CH_4 flux values. Panel A shows a scenario where the bubble component is considered negligible and panel B shows a scenario where the bubble component is considered to be sufficient.

instant flux values (Figure 1). In model experiments we found that these values have a normal distribution around average when SE is stable and GE negligible (Figure 7). In moments of gas bubble release the GE instant fluxes values are shifted out of the normal distribution curve and may form subsequent frequency peaks. But even in this case the first peak may be used for estimation of SE. In practice we used medians of the first frequency peaks as SE, averages upon all the data as total emission (TE) and their difference as GE (GE = TE − SE).

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