Plant species from mesotrophic wetlands cause relatively high methane emissions from peat soil

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Abstract Plants can influence methane emissions from wetland ecosystems by altering its production, consumption and transport in the soil. The aim of this study was to investigate how eight vascular plant species from mesotrophic to eutrophic wetlands vary in their influence on CH_4 emissions from peat cores, under low and high N supply. Additionally, we measured the production of low-molecular-weight organic acids (LOA) by the same species (also at low and high N supply), because LOA form a substrate for methanogenesis. There were considerable differences among species in their effects upon rates of CH_4 emission. Six of the species (*Eriophorum latifolium* Hoppe, *Potentilla palustris* (L.) Scop., *Anthoxanthum odoratum* (L.) s. str., *Carex rostrata* Stokes, *Carex elata* All., *Carex acutiformis* Ehrh.) increased CH_4 emissions up to five times compared to control peat cores without plants, whereas two species (*Phalaris arundinacea* L., *Phragmites australis* (Cav.) Trin. ex Steud.) had no effect. There was a weak negative correlation between plant biomass and CH_4 emission. N addition had no significant general effect upon CH_4 emission. LOA production varied considerably among species, and tended to be highest for species from mesotrophic habitats. LOA production was stimulated by N addition. We conclude that some species from mesotrophic wetlands tend to cause higher CH_4 emissions than species from eutrophic wetlands. This pattern, which contradicts what is often mentioned in literature, may be explained by the higher LOA production rates of species adapted to less productive habitats.

Keywords Adaptation · Biomass · Ecological traits · Greenhouse gas · Nitrogen · Organic acids · Peat · Root exudation · Vascular plants

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Introduction

Methane (CH_4) is an important greenhouse gas, estimated to be responsible for almost 20% of the radiative forcing from long-lived and globally mixed greenhouse gases (IPCC 2007). Natural wetlands are among the most important sources of CH_4, estimated to account for 90% of natural emissions and one third of total emissions (IPCC 2007).

Plants can have a strong effect upon the emission of CH_4 from wetland ecosystems, apparently because they influence the production, consumption and transport of CH_4 in the soil (Christensen et al. 2003;

Joabsson et al. 1999; Saarnio et al. 2004; Ström et al. 2003; Whiting and Chanton 1992). In some cases, as much as 90–98% of the CH_4 efflux from inundated sites has been associated with vascular plants (Joabsson et al. 1999; Verville et al. 1998). Three main mechanisms are known through which vascular plants influence CH_4 emissions from wetland soils: (1) plant roots continuously release organic compounds into the rhizosphere, which are easily available C-sources for methanogenesis (Ström et al. 2003); (2) CH_4 moves through the aerenchyma tissue of the roots, rhizomes and dead or living stems to the atmosphere, thereby escaping oxidation in aerobic soil layers—the conduit or chimney effect (Verville et al. 1998); (3) plants bring oxygen into the rhizosphere, which inhibits methanogenic archaea, and fuels CH_4 oxidation (Van der Nat and Middelburg 1998). Only a few plant species have been studied for their influence on CH_4 emission; however, these have shown large variation (Ding et al. 2005; Joabsson and Christensen 2001; Laine et al. 2007; Ström et al. 2005), suggesting that changes in the species composition of wetlands—either as a consequence of climate change or through some other process—could have a considerable effect on CH_4 emissions (Christensen et al. 2004; Johansson et al. 2006). But to be able to predict such effects, more species need to be investigated and the relative importance of the various mechanisms by which plants influence CH_4 emissions need to be better understood.

Many wetlands throughout the world are subjected to nutrient enrichment, which may increase the productivity of the vegetation and lead to changes in species composition (Bedford et al 1999, Olde Venterink et al 2002, Galloway et al 2004, Bragazza et al 2006). Some authors have concluded that CH_4 emissions tend to increase with increasing wetland productivity because rates of root exudation, as well as and gas exchange via the conduit effect, are likely to be larger for big plants than for small ones and hence to be positively related to plant biomass (cf. Ding et al. 2003; Joabsson and Christensen 2001; Waddington et al. 1996; Whiting and Chanton 1993). However, it could also be argued that, because plant roots tend to produce more exudates under nutrient-poor conditions as a mechanism to increase phosphorus availability (Hinsinger 2001; Lu et al. 1999; Marschner 1998; Neumann and Römheld 1999; Ström 1997), CH_4 emissions are likely to be higher in nutrient poor wetlands. In view of the different mechanisms by which plants may influence

CH_4 emissions, it is unclear whether there is a general tendency for species of eutrophic sites to enhance CH_4 emission more than species from mesotrophic sites, or vice versa.

The main aim of this study was to investigate how eight vascular plant species from meso- to eutrophic wetlands vary in their influence upon CH_4 emissions. Additionally, we investigated whether N fertilisation influences the effects of plants on CH_4 emission. In a separate experiment we investigated how the selected plant species differ in root production of low-molecular-weight organic acids (LOA). It was our objective to evaluate the effects of differences in plant biomass production, fertility of the natural habitat, as well as root LOA production of the species. Our hypotheses were:

(I)   Vascular plants increase CH_4 emissions from peat.
(II) N fertilisation results in higher CH_4 emission rates because it stimulates plant productivity and it may also increase root exudation because of induced P-limitation.
(III) Plant species from eutrophic wetlands have a larger effect upon CH_4 emission rates than species from less productive wetlands. This hypothesis is based on the assumption that plant size has a larger effect upon emissions than inherent species differences in production of root exudates.

Materials and methods

Experiment I: Influence of plant species on CH_4 emission from peat cores

This first experiment was designed to compare the influence of eight plant species on CH_4 emission from peat soil. We compared the following species with each other and with a control (bare soil): *Eriophorum latifolium* Hoppe, *Potentilla palustris* (L.) Scop., *Carex rostrata* Stokes, *Anthoxanthum odoratum* (L.) s. str., *Carex elata* All., *Carex acutiformis* Ehrh., *Phragmites australis* (Cav.) Trin. ex Steud., and *Phalaris arundinacea* L. The species differ with respect to fertility of the habitats in which they normally occur, varying from mesotrophic to eutrophic wetlands. We ordered the species according to the fertility indication values of Ellenberg et al. (1991) and Bakkenes et al. (2002) (see Appendix A). *Anthoxanthum odoratum*, *Phalaris*

arundinacea and *Phragmites australis* were grown from seeds collected in the field (NE Switzerland), *Carex rostrata*, *Carex elata* and *Carex acutiformis* were propagated from tillers collected in the field. Wild types of *Potentilla palustris* and *Eriophorum latifolium* were bought commercially (Die Wildstaudengärtnerei, Eschenbach, Switzerland).

Plants were grown in undisturbed peat cores (one plant per core, or in the case of *Eriophorum latifolium* two small plants). Peat for the experiment was taken from a wet, mesotrophic fen in Nussbaumen near Frauenfeld, Switzerland, where atmospheric N-deposition is 15–20 kg ha^{-1} y^{-1} (BUWAL 2005). Although it would have been convenient to use a homogenised peat-substrate, the processes of sieving and mixing of peat would have severely altered the microbial community and increased carbon mineralization. We therefore decided to grow the plants in intact peat cores, accepting that inhomogeneities in the substrate would probably lead to variation among replicates. To minimize this variation, all material was collected from a small (10 m^2) area where the top 40 cm of the soil had been removed the week before. Peat cores (2.2 l) were collected by driving PVC cylinders (19 cm depth, 12.2 cm diameter) into the peat, taking care not to compact the material, and closing the bottoms with gas-tight lids.

Half of the cores in the experiment were fertilized with N (100 mg N (NH_4NO_3) per pot during the experiment), while the other half remained unfertilized (equally distributed among plant species and bare soil). We fertilized with N because it was growth-limiting: in a preliminary experiment using the same peat material, *Anthoxanthum odoratum* plants were supplied with N, P, N+P, and growth was compared with an unfertilized control. Only the addition of N caused a significant increase in biomass (ANOVA: $F_{(1,17)}=23.48$; $P=0.0015$). At the end of the experiment NH_4, NO_3, PO_4 and K concentrations were measured in the soil solution of five fertilised and five unfertilised cores. Nitrate was below the detection limit, whereas NH_4, PO_4 and K concentrations were on average 0.13, 0.03 and 0.54 mg/l in unfertilised, and 0.20, 0.02 and 0.50 mg/l in the fertilised treatments respectively.

The experiment was carried out in a greenhouse in Zurich, Switzerland, between June and October 2006. The water level in the cylinder was maintained at 2 cm below the peat surface, throughout the experiment with deionised water. This could be monitored from outside by means of a tube connected to the base of the peat core. There was no visible growth of algae. All treatments were replicated ten times, yielding a total of 180 pots (eight species+bare control soil * two (with/without N) * ten replicates).

Methane emissions were measured using a closed chamber technique. Pots were placed in water-filled vessels (32 cm in diameter; 4 cm high) twelve hours before sampling. In order to take air samples, Plexiglas chambers were placed on top of the vessels immediately before the sampling. Chambers of two different volumes were used (15.2 or 27.1 litre), depending on the size of the plants. Head-space samples were taken with syringes through a rubber stopper with an inbuilt three-way stopcock. Samples were instantly transferred into evacuated vials with rubber septa. Four samples were taken from each pot at six-minute intervals. Methane concentrations were determined using a gas chromatograph (6890 N, Agilent Technologies, California, USA) equipped with a Porapak Q column (80/120 mesh) and a flame ionization detector. Samples were injected using an auto sampler (222xc Sample Changer, Gilson, Wisconsin, USA) and calibrated with several calibration gases injected every nine to 12 samples. The CH_4 emission rate of each pot was determined by linear regression of the four repeated headspace CH_4 concentrations in the chamber. In case of significant methane emission rates R^2-values were high (generally>0.7). If emission rates were very low or negligible, R^2-values could also be low (<0.5) due to bias around zero. The sampling of one full replicate (eight species+one control times two N treatments=18 pots) took half a day; thus all 180 pots were sampled over five consecutive days. We varied the sample time of different species throughout the day. The CH_4 emission rates of all cores were measured for all cores between 25 and 30 September 2006.

After the CH_4 measurements, the roots and shoots of all plants were harvested, dried at 70ºC for 48 h, and weighed.

Experiment II: Organic acid production of plant species

In a second experiment, we grew the same eight plant species in nutrient solutions to determined interspecific differences in the production of low molecular

weight organic acids (LOA) such as acetate, formate and oxalate. These LOAs may either be exuded directly by roots or, more likely, result in the fermentation of larger acids and carbohydrates from plant root exudates (Dessureault-Rompré et al. 2007). The plants used for this experiment had been grown on peat cores collected from the same 10 m^2 as in Experiment I. They had been growing in the same greenhouse and for the same period (five months) as the plants in Experiment I. At the time for harvesting of Experiment I, we transferred the plants into nutrient solutions. Plants were grown in a low-N or a high-N nutrient solution to simulate differences in N availability, just as in Experiment I. The Low-N solution was a 1/10 dilution of a full strength solution containing 57 g/l Ca (NO$_3$)$_2$·4H$_2$O, 12.7 g/l NH$_4$NO$_3$, 13.2 g/l HK$_2$PO4, 26.6 g/l MgSO$_4$·7H$_2$O, 0.1 g/l ZnSO$_4$·7H$_2$O, 0.02 g/l CuSO$_4$·5H$_2$O, 0.5 g/l H$_3$BO$_3$, 0.02 g/l NA$_2$MoO$_4$·H$_2$O and 4.4 g/l Cl$_3$Fe (Modified Hoagland solution after Steiner 1961). The high-N solution contained twice as much NH$_4$NO$_3$ (and therefore had a N:P ratio of 10 instead of 5). All other nutrients were the same in both N-treatments. Both N treatments were replicated four times in a full factorial design, yielding 64 plants (eight species * two N treatments * four replicates). The plants grew in the nutrient solutions for three weeks; the solutions were exchanged weekly. After three weeks, all plants had produced new roots and the nutrient solutions were exchanged for the last time. Subsequently after three days of incubation, samples were taken and analysed for acetate, formate, oxalate, citrate, malate, lactate and propionate by ion chromatography (Dionex autosampler system, AS 11 column, eluent generator: potassium hydroxide (1 to 60 mM), flow: 1.5 ml min^{-1}). Unfortunately, all plants of *Potentilla palustris* died in the nutrient solution, so that no data were obtained for this species.

Statistics

Differences in CH$_4$ emission and LOA production rates were tested by means of one-way ANOVAs. All data were log-transformed. ANOVAs were carried out with species and nitrogen as factors and root biomass and/or shoot biomass as co-variables. For analyses that included the pots without plants (control), or target variables calculated per gram biomass (root or shoot), only the factors species and nitrogen were fitted. All models were determined by the AICc criterion

(Burnham and Anderson 2002). Multiple comparisons between pairs of means were carried out with the Tukey test (Zar 1999). All analyses were performed using the statistical software R, version 2.6.2 (R Development Core Team 2006).

Results

Variation in biomass among plant species and effect of N addition (Experiment I)

Biomass varied widely among the eight plant species (Fig. 1), with *Carex elata, Carex acutiformis, Phragmites australis* and *Phalaris arundinacea* having significantly higher shoot and root biomasses than *Eriophorum latifolium, Potentilla palustris* and
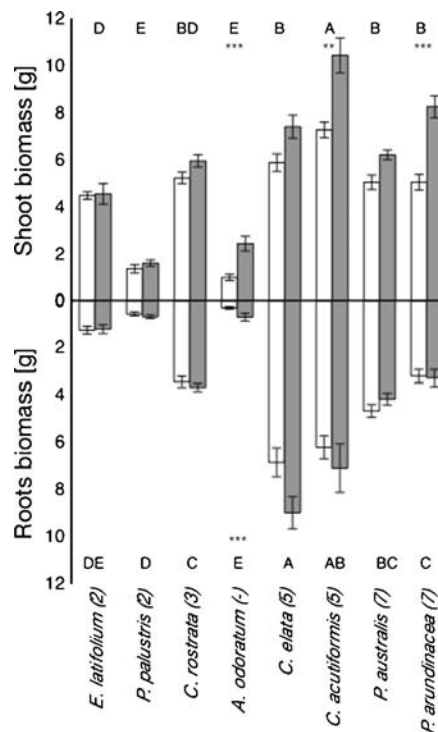

Fig. 1 Mean root and shoot biomass (dry) of the eight wetland plant species of the experiment with plants in peat cores. Species are ordered according to the fertility index (N-values) of Ellenberg et al. (1991) increasing from left to right (see Appendix A). White bars are unfertilised plants, shaded bars are N-fertilised. Error bars show SE of 10 replicates. Stars indicate significant differences in biomass of a species due to N fertilisation (*$P \leq 0.05$; **$P \leq 0.01$; ***$P \leq 0.001$), letters show significant differences between species ($P \leq 0.05$)

Anthoxanthum odoratum. However, it was not always the species from mesotrophic habitats (*Eriophorum latifolium*, *Potentilla palustris* and *Carex rostrata*) that produced the lowest biomass (Fig. 1). N addition significantly increased the shoot biomass of *Anthoxanthum odoratum*, *Carex acutiformis* and *Phalaris arundinacea* ($F_{(1,144)}=53.42$, $P<0.001$), and also the root biomass of *Anthoxanthum odoratum* ($F_{(1,140)}=5.81$, $P<0.05$).

Effects of vascular plants on CH_4 emission (Experiment I)

CH_4 emissions were up to five times higher from peat cores with *Eriophorum latifolium*, *Potentilla palustris*, *Carex rostrata*, *Anthoxanthum odoratum*, *Carex elata* and *Carex acutiformis* than from control cores with no plant (Fig. 2a, Table 1). However, the emission rates of two species—*Phragmites australis* and *Phalaris arundinacea*—were not significantly higher than the control. CH_4 emission rates tended to be higher with species from mesotrophic wetlands (species with Ellenberg N values 2-5) than with species from eutrophic wetlands (species with Ellenberg $N=7$) (Fig. 2a). Also, plant species from mesotrophic wetlands, such as *Eriophorum latifolium* and *Potentilla*

palustris, had significantly higher CH_4 emission rates per gram total biomass than *Phragmites australis* and *Phalaris arundinacea* (Fig. 2b, Table 1).

Phalaris arundinacea was the only species for which there was a significant positive relationship ($R^2=0.302$) between CH_4 emissions and shoot biomass (Fig. 3, interaction effects Table 1). The combined data for all species showed a weakly negative relationship (Fig. 3). Correlation between root biomass and CH_4 emission showed a similar pattern as for shoot biomass (data not shown).

The N treatment had no significant consistent effect on CH_4 emission rates (Table 1), either on a per plant or per unit biomass basis, although N application increased the biomass of some species.

Variation in rhizospheric LOA production among species and upon N addition (Experiment II)

Rhizospheric production of low molecular weight organic acids (LOA) differed considerably among plant species (Fig. 4a; Table 2). *Carex elata* had by far the highest LOA production, but *Eriophorum latifolium* and *Carex rostrata* with high-N supply also had a higher production of LOA than *Carex acutiformis*, *Phalaris arundinacea* and *Phragmites australis*
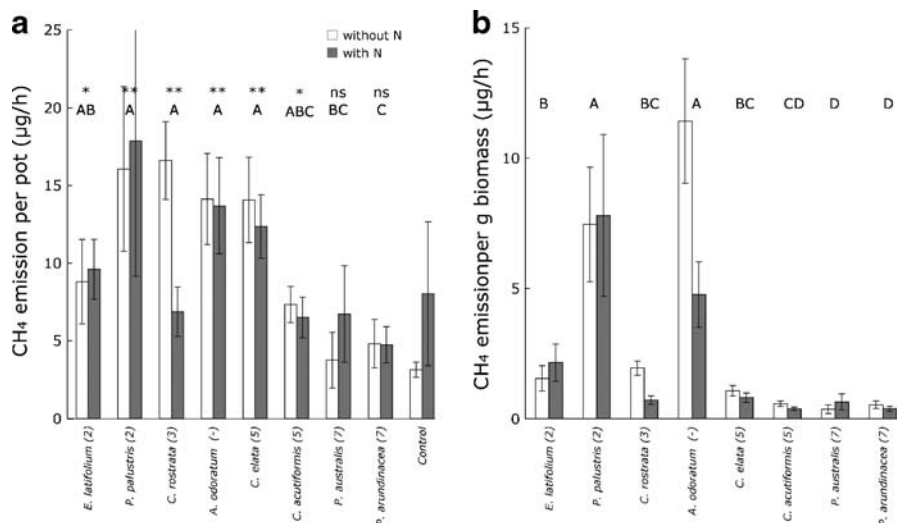

Fig. 2 Mean CH_4 emission rates from peat cores with different plant species of European wetlands, as calculated per pot (**a**), or per g total dry plant biomass (**b**). Species are ranked according to the fertility index (N-values) of Ellenberg et al. (1991); values shown in brackets after species name (see Appendix A). Error bars show SE of 10 replicates. In A: *Stars* indicate

whether CH_4 emission rates of a species were significantly higher compared to the control pots (peat cores without plants) (*$P \leq 0.05$; **$P \leq 0.01$; ***$P \leq 0.001$). *Letters* indicate significant ($P \leq 0.05$) differences in CH_4 emission rates between species (the N treatment had no significant effect on CH_4 emission rates)

Table 1 Effects of species, nitrogen and biomass on CH_4 log transformed emission rates (ten replicates per treatment). The results from three ANOVAs either include or exclude control (soil without plant) treatments. Model evaluations were based on the AICc criterion (Burnham and Anderson 2002)

Source	CH_4 per pot without control			CH_4 per pot with control			CH_4 per g biomass without control		
	df	MS	F	df	MS	F	df	MS	F
Species	7	11.10	**5.26*****	8	13.17	**3.51*****	7	33.38	**12.77*****
Nitrogen	1	1.64	0.78	1	4.13	1.10	1	7.96	3.05
Shoot biomass	1	19.20	**9.06****	nf			nf		
Root biomass	1	0.82	0.39	nf			nf		
Species x Nitrogen	7	5.83	**2.75***	nf			nf		
Species x Shoot b.	7	9.11	**4.30*****	nf			nf		
Residuals	135	2.12		170	3.76		151		

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

(Fig. 4a). In the low N treatment, *Carex rostrata*, *Anthoxanthum odoratum* and *Carex elata* had higher production rates of LOA than *Phalaris arundinacea*, *Phragmites australis*. Generally, species from mesotrophic wetlands tended to produce more LOA than species from eutrophic wetlands, both in absolute terms and per gram plant or root biomass (Fig. 4). Independently of species, total LOA production was not correlated with biomass (Table 2).

Overall, a high N addition caused a significantly higher LOA production than the low N treatment (Table 2). Acetate and formate were the most important organic acids. Whereas production of both acids was similar in the low N treatment, acetate production was significantly higher than formate production in the high N treatment (Appendix B). Whereas species-specific effects on acetate were very similar to those on total LOA production, there were no species effects on formate production.

Discussion

Vascular plants can influence CH_4 emissions from wetlands by altering the production, consumption and transport of CH_4 in the soil (Christensen et al. 2003; Joabsson et al. 1999; Saarnio et al. 2004; Ström et al. 2003; Whiting and Chanton 1992), but different species have been found to vary in the extent and how they influence CH_4 emissions (Ström et al. 2005; Verville et al. 1998). Our experiment supports our first hypothesis—that plants strongly influence the rate of CH_4 emission from wetland soils, and they

also confirm that there are large differences among species in this respect: whereas six of the eight species significantly increased CH_4 emissions compared to bare peat, two species had no detectable effect (Fig. 2a). We found indications that the difference among species is related to variation in root exudate production, and hence to the influence of the plants on production of CH_4, as we will discuss below.
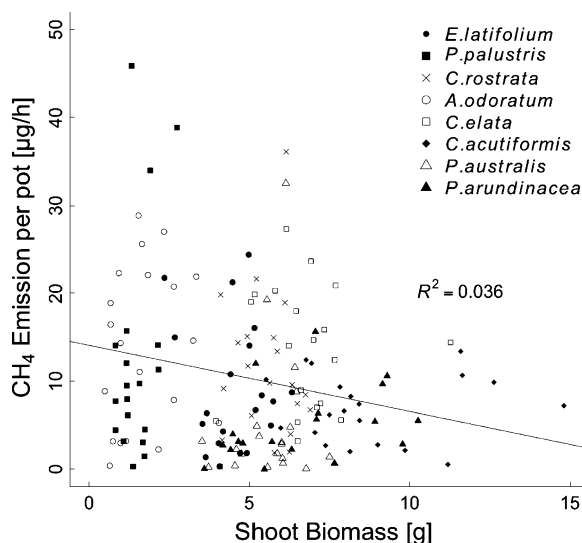

Fig. 3 Methane emission rates plotted against shoot biomass, for eight plant species together. There was a weakly negative correlation between CH_4 emission and shoot biomass. Since the N treatment had no significant effect on CH_4 emission rates, data from both fertilized and unfertilized treatment were included
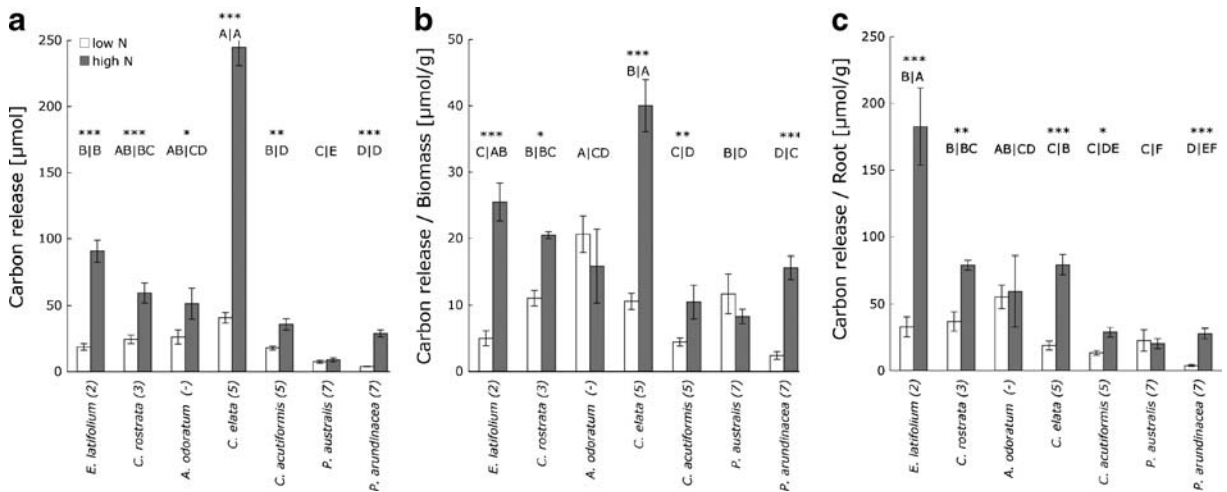
Fig. 4 Mean total of rhizospheric production (+/− SE) of low molecular weight organic acids (LOA) of eight wetland species in nutrient solution during three days, as calculated per plant (a), per gram total dry biomass (b), or per gram dry root biomass (c). Species are ordered according to the fertility index (N-values) of Ellenberg et al. (1991) increasing from left to right (see Appendix A). LOA is expressed here as the cumulative carbon release by the plants. Error bars show SE of 4 replicates. Significant effects of N addition are indicated with stars (* $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$). Letters show differences among the plant species. The letters on the right side compare plant species exposed to the high N treatment, the letters of the left side compare the species from the low N treatment

Whiting and Chanton (1993) found evidence that CH_4 emission rates increase as the net production of wetland vegetation increases. Similarly, Chanton et al. (1997) found a strong positive correlation between CH_4 emission and living aboveground biomass of rice plants. These positive relationships have been interpreted as indicating that CH_4 emissions increase with the increasing primary productivity (Bouchard et al. 2007; Dacey et al. 1994; Greenup et al. 2000). We only found a positive correlation between shoot-biomass and CH_4 emission rates for one species (Phalaris arundinacea), and no significant relationships for the other seven (Fig. 3), just as Joabsson and Christensen (2001) and Ström et al. (2005) did for some other wetland species. The combined data for all our species actually showed a weak negative correlation between aboveground biomass and CH_4 emission (Fig. 3). Similarly, Bouchard et al. (2007) found decreasing CH_4 emission rates with increasing biomass production of emergent plants in a mesocosm experiment, and such a negative relationship is also evident in the data of Van der Nat and Middleburg (1998), albeit with

Table 2 ANOVA tables for the effects of species and the nitrogen treatment on rhizospheric production of low molecular weight organic acids (log transformed) of seven wetland plant species. The target variable was either LOA production per plant, LOA production calculated per gram dry total biomass or LOA production per gram dry root biomass

Source	LOA production per plant			LOA production per g total biomass			LOA production per g root biomass		
	df	MS	F	df	MS	F	df	MS	F
Species	6	5.9	**73.9***	6	1.8	**11.7***	6	4.1	**20.6***
Nitrogen	1	17	**215.9***	1	9.3	**60.5***	1	12.8	**65.2***
Shoot biomass	1	0.0001	0.002	nf			nf		
Root biomass	1	0.12	1.5	nf			nf		
Species x Nitrogen	6	0.93	**11.7***	6	1.7	**11.1***	6	1.4	**7.0***
Residuals	41	0.08		42	0.15		42	0.20	

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

only two species. If biomass were strictly correlated with CH$_4$ emission, we would expect a constant CH$_4$ emission per gram biomass for all plant species (Fig. 2b), but our experiment revealed that the two species with the lowest biomass—*Potentilla palustris* and *Anthoxanthum odoratum*—had much higher CH$_4$ emissions per unit of biomass than other species (Fig. 1). Overall, therefore, our results are more consistent with those of Bouchard et al. (2007), who found a negative relationship between CH$_4$ emission and biomass, than with those of Whiting and Chanton (1993). We conclude that in wetland ecosystems biomass alone is not a reliable predictor of CH$_4$ emissions because some species enhance CH$_4$ emissions more strongly than others with similar or higher biomass (Joabsson et al. 1999; Ström et al. 2003). Possible reasons for this are that some species supply more substrate for methanogenic archaea than others, or provide a more effective conduit for CH$_4$ transport (Greenup et al. 2000); and some species may even reduce CH$_4$ emissions by causing strong rhizospheric oxidation because of high belowground biomass (Hirota et al. 2004).
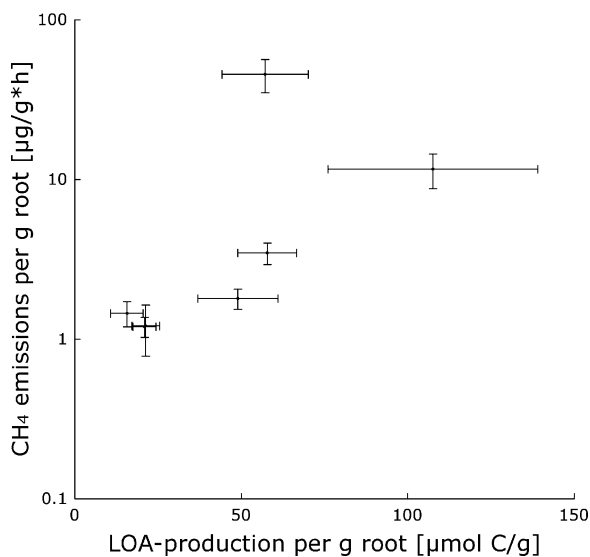

Fig. 5 Mean CH$_4$ emission rates per gram plant root (Experiment I) versus mean rhizospheric production of low molecular weight organic acids per gram plant root (Experiment II) after three days. Data points are average values of the two nitrogen treatments (with/without N, and low/high N). Error bars represent SE of 8 and 20 replicates for LOA-production and CH$_4$ emission, respectively

Contrary to our hypothesis, species from mesotrophic wetlands tended to show higher CH$_4$ emission rates than species from eutrophic wetlands (Fig. 2). Moreover, in Experiment II there was a tendency for species causing high CH$_4$ emission rates to have high rates of LOA production as well (Fig. 5). Although we have to be cautious in linking the two experiments—for example, because nutrient availabilities and LOA production in soil may not be the same as in a nutrient solution (Jones 1998)—our results suggest that CH$_4$ emissions are strongly influenced by the differing rates of root exudation from wetland plants (Chanton et al. 1995; Ström et al. 2003). Root exudation in plants is likely to be influenced not only by plant size—with bigger plants producing more exudates in absolute terms (Jones et al. 2004)—but also by the ecological characteristics of a species. Plants adapted to low nutrient availability, particularly of phosphorus, may produce more exudates (Bais et al. 2006; Hinsinger 2001; Lu et al. 1999; Marschner 1998; Neumann and Römheld 1999). In absolute terms, total production of organic acids per plant was not correlated with shoot biomass in our experiment (Table 2). Species adapted to mesotrophic habitats had higher LOA production than species of eutrophic habitats, particularly in the N-fertilized treatment (i.e. likely P-limited conditions) both per gram of root as well as in absolute terms (Fig. 4). Thus, the assumption implicit in our third hypothesis—that plant size is more important than habitat adaptation—was incorrect. We note, however, that besides this general pattern, some species like *Carex elata* in our study may have exceptionally high exudation rates under specific environmental (e.g. P-limited) conditions. We do not have an explanation why this specific species showed such a high exudation rate.

The reason that plants tend to produce more exudates in nutrient-poor conditions is thought to be in order to increase phosphorus availability (Bais et al. 2006; Hinsinger 2001; Lu et al. 1999; Marschner 1998; Neumann and Römheld 1999; Ström 1997). This idea is consistent with the finding that N fertilisation stimulates root exudation (Henry et al. 2005) since this causes a shift in the relative availabilities of N and P in the direction of P limitation. This might have stimulated some species in Experiment II to enhanced production of root exudates. Consequently, we also found that N addition increased the production of organic acids in some species in this experiment.

However, we did not observe any significant effect of N addition upon CH_4 emission rates in Experiment I although the underlying mechanisms of a higher biomass and higher LOA production were observed. Hence, our hypothesis predicting a higher CH_4 emission upon N-addition has to be rejected. Similar to our results, Silvola et al. (2003) found no significant effect of NH_4NO_3 on CH_4-emissions from oligotrophic peatlands. Effects of chemical N-fertilisers on CH_4 formation, consumption and emission are complex and often contradictory. In other studies, negative and positive effects of NO_3 and/or NH_4 additions on CH_4 emissions were observed (cf. Le Mer and Roger 2001).

The finding that there was no difference in CH_4 emissions between *Phalaris arundinacea* and *Phragmites australis* and bare soil is surprising, since these species revealed high CH_4 emission rates under field conditions (Kankaala et al. 2004; Wilson et al. 2008). This inconsistency may be due to differences between the experimental conditions and those in the field, for example in plant size, rooting depths and age. To make a direct comparison between different plants species, and to show mechanistic differences among these species, we chose relatively young plants and kept conditions such as water table and peat volume the same for all species. Perennial plants might act differently when they grow older, and the water table (2 cm below surface) might not have been optimal for all species. Also, LOA production may differ seasonally and this may vary among species. Furthermore, we noted that the CH_4 emission rates in our peat cores (0.4–1.5 mg m^{-2}h^{-1}) were rather low compared to reported rates from other peat soils, and were in the order of magnitude observed (on average below 1.7 mg m^{-2}h^{-1}) for ombrotrophic peatlands (Greenup et al. 2000). Therefore the effect of plants on CH_4 emission through the chimney effect or soil oxidation may have been smaller than in wetlands with higher CH_4 production rates in the soil. In contrast, the effect of plants through rhizospheric exudation of C compounds may have been relatively larger than in other peat soils with higher concentrations of available carbon for methanogenesis. Hence, our peat cores were particularly suited for testing differences among plants with respect to the latter mechanism, but care should be taken in transferring our results to plants growing under field conditions.

Despite intensive research, global estimates of CH_4 emissions from wetlands vary widely, from 100 to 231 Tg CH_4 / year (IPCC 2007). Our results show that the species composition of wetland vegetations are important in differentiating CH_4 emissions, just as shown in other studies (Ström et al. 2005, Bouchard et al. 2007). Ecological traits of plants may be more important than absolute biomass in determining the influence of wetland plants upon CH_4 emissions. Taking into account the functional properties of plants offers scope to improve global estimates of CH_4 emissions from wetlands. Our results suggest that emission rates tend to be relatively high under environmental conditions promoting a high production of root exudates, such as P-limitation or alkaline soil conditions (Dakora and Phillips 2002; Jones et al. 2004).
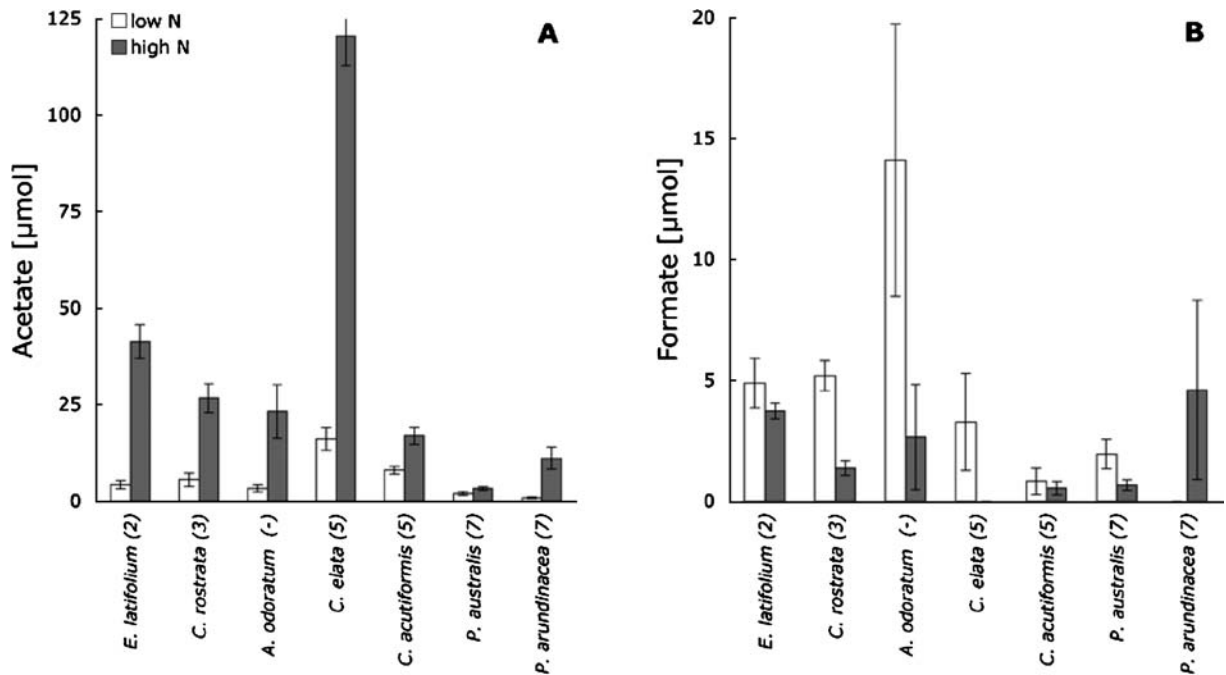
Appendix A

The eight plant species used in the experiments with their Ellenberg- and MOVE N indicator values (Bakkenes et al. 2002; Ellenberg et al. 1991). MOVE values are based on Ellenberg values. A dataset of 100'000 vegetation relevees from the Netherlands served as a base for the calculation of these values.

Species	Ellenberg N-value	MOVE N-value
Eriophorum latifolium	2	–
Potentilla palustris	2	4.07 (±0.96)
Carex rostrata	3	4.02 (±1.17)
Anthoxanthum odoratum	–	4.47 (±1.06)
Carex elata	5	4.93 (±1.00)
Carex acutiformis	5	5.14 (±0.97)
Phragmites australis	7	5.52 (±1.22)
Phalaris arundinacea	7	6.14 (±0.72)

Appendix B

Mean total acetate (**A**) and formate (**B**) production (+/− SE) per plant of eight wetland species in nutrient

solution during three days. Species are ordered according to the fertility index (N-values) of Ellenberg et al. (1991) increasing from left to right (see Appendix A). Notice the different scales in **A** and **B**.

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