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# Does *Juncus effusus* enhance methane emissions from grazed pastures on peat?

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**Abstract.** Methane ($CH_4$) emissions from drained organic soils are generally low, but internal gas transport in aerenchymatous plants may result in local emission hotspots. In a paired-sample field study at three different sites we measured fluxes of $CH_4$ with static chambers from adjacent sampling quadrats with and without *Juncus effusus* during four field campaigns. At all three sites, $CH_4$ was observed in the soil at all sampling depths (5 to 100 cm), and in most cases both above and below the groundwater table. During spring, local maxima suggested methanogenesis also took place above the water table at all three sites. We found significant $CH_4$ emissions at all three sites, but emission controls were clearly different. Across the three sites, average emission rates (±1 SE) for sampling quadrats with and without *J. effusus* were $1.47 \pm 0.28$ and $1.37 \pm 0.33\,\mathrm{mg\,CH_4\,m^{-2}\,h^{-1}}$, respectively, with no overall effect of *J. effusus* on $CH_4$ emissions. However, a significant effect of *J. effusus* was seen at one of the three sites. At this site, local $CH_4$ maxima were closer to the soil surface than at the other sites, and the upper soil layers were dryer. This could have affected both root $CH_4$ accessibility and $CH_4$ oxidation respectively, and together with limited gas diffusivity in the soil column, cause elevated $CH_4$ emissions from *J. effusus*. We conclude that *J. effusus* has the potential to act as point sources of $CH_4$ from drained peatlands, but more studies on the specific conditions under which there is an effect, are needed before the results can be used in modelling of $CH_4$ emissions.

## 1 Introduction

Undisturbed peatlands are significant sources of atmospheric methane with an estimated global emission of around $30\,\mathrm{Tg\,CH_4\,yr^{-1}}$ (Frolking et al., 2011) and local site-specific rates typically ranging up to $10\,\mathrm{mg\,CH_4\,m^{-2}\,h^{-1}}$ (Günther et al., 2013). Drainage for agriculture or forestry exposes the peat soil to oxygen and accelerates aerobic decomposition with carbon emissions of carbon dioxide ($CO_2$) rather than $CH_4$. Thus, $CH_4$ emissions are reduced partly because the activity of methanogens is attenuated in the upper oxic soil layer and partly because the oxic soil layer has a significant potential for microbial $CH_4$ oxidation (Kip et al., 2012; Segers, 1998; Ström et al., 2012). Also, methanogenesis may be attenuated as drainage increases the depth in the soil profile where the process can take place, and plant-derived carbon substrates for fermenters and methanogens at greater peat depths may be more recalcitrant than closer to the soil surface (Audet et al., 2013).

The strong influence of groundwater table on $CH_4$ emissions has been repeatedly demonstrated (e.g. Grünfeld and Brix, 1999; Moore and Roulet, 1993; Koebsch et al., 2013). A review by Couwenberg and Fritz (2012) concluded that when the water table is at 20 cm depth or below, $CH_4$ emissions are negligible. For water table depths closer to the surface, the abundance of aerenchymatous plants appeared to be a good indicator of $CH_4$ emissions (Couwenberg and Fritz, 2012) and other plant community indices may likewise have a predictive potential (Audet et al., 2013). Aerenchymatous plants provide a conduit to the atmosphere for gases dissolved in the soil water (including $CH_4$), thus bypassing the uppermost $CH_4$ oxidizing soil layers (Schimel, 1995). Henneberg et al. (2012) demonstrated that the area of permeable root surface (especially lateral roots and root tips), and not above-ground plant biomass, was rate-limiting for $CH_4$ transport in soft rush (*Juncus effusus* L.) and probably most other wetland graminoids.

While the potential of vegetation indexes as indicators of $CH_4$ emissions has been pursued in wetland ecosystems, this has not to the same extent been considered for drained organic soils where $CH_4$ emissions are generally low, negligible or even reversed to uptake of atmospheric $CH_4$ (Flessa et al., 1998; Schäfer et al., 2012). A recent study of greenhouse gas balances for eight organic soils (0.7 to 2.2 m peat depth) managed for agriculture confirmed the low or slightly negative flux of $CH_4$ from drained organic soils, with reported fluxes between –0.1 and 0.2 mg $CH_4$ $m^{-2}$ $h^{-1}$ (Petersen et al., 2012). However, there were two exceptions with high emission rates at grassland sites with a history of cattle grazing. At these sites, some sampling quadrats (55 × 55 cm) with *J. effusus* emitted significant amounts of $CH_4$ throughout the year, with emission rates of 1–5 mg $CH_4$ $m^{-2}$ $h^{-1}$, despite low water table depths. Furthermore, the flux of $CH_4$ appeared to be correlated with the biomass of *J. effusus* (Petersen et al., 2012). It was proposed that compaction of the pasture by grazing cattle had created a diffusion barrier in the soil (hindering $CH_4$ transport), and that *J. effusus* could be an important point source of $CH_4$ on organic soils used for grazing due to the aerenchymatous $CH_4$ transport capacity.

The aim of this study was to assess the possible importance of *J. effusus* tussocks as point sources for $CH_4$ emissions to the atmosphere in peat soils drained for agriculture with otherwise low emission rates. We used a paired-sample approach to compare the $CH_4$ fluxes at micro-sites with and without *J. effusus* at three grasslands with a history of cattle grazing. Sites and sampling days were selected to represent contrasting soil conditions. We hypothesized that the emission rates of $CH_4$ would be significantly higher in the presence of *J. effusus* because of $CH_4$ transport through the aerenchyma of the plants.

## 2 Materials and methods

### 2.1 Site location and experimental design

Three different Danish fen peats at Mørke (56°22′57 N, 10°24′23 E), Torsager (56°27′02 N, 9°36′46 E) and Fussingø (56°28′52 N, 9°49′37 E) with a history of grazing, and with tussocks of *J. effusus*, were selected for the study. The site at Mørke was also investigated by Petersen et al. (2012), where it was denoted E-PG. The Torsager site was located in a river valley with occasional flooding during winter, and this site had not been grazed for 3 years prior to the study. The areas selected for the gas flux measurements were fenced off to avoid disturbance from grazing cattle, and the sites were not fertilized during the 4-month monitoring period.

At each of the three sites, four plots in the pasture within a 25 m radius were selected, each with two side-by-side sampling quadrats (55 × 55 cm) for gas flux measurements. One sampling quadrat (J) included a tussock of *J. effusus*, while the other quadrat (G) had grass without *J. effusus* (Fig. 1). A slit was made in the grass turf to facilitate installation of permanent frames made of 4 mm white PVC to a depth of 10 cm. These frames served as support for static chambers during gas flux measurements (Petersen et al., 2012). To minimize disturbances of soil gas profiles during sampling, boardwalks on poles were installed in front of each plot. Each grassland site was equipped with two 50 mm diameter polyethylene piezometers with a screen at 90–100 cm depth; the piezometers were positioned between two adjacent plots as indicated in Fig. 1. Recorded groundwater levels (GWL) in each piezometer were used as a reference for both neighbouring plots. Soil molar fraction profiles of $CH_4$ (see below) were determined near one of the piezometer positions at each site.

### 2.2 Field campaigns

Four sampling campaigns were conducted during the 2010 growth season, i.e., in late May, late June, early August and mid-September. Each sampling campaign included groundwater sampling, characterization of *J. effusus* tussocks, $CH_4$ flux measurements, and determination of soil $CH_4$ molar fraction profiles.

Upon arrival at the site, GWL inside the piezometers were recorded. The piezometers were then emptied using a 12 V pump and left during gas flux measurements for fresh groundwater to enter. Around 100 mL water from the piezometers was then sampled for measurement of electrical conductivity (EC) and pH using a Cyberscan PC300 (Eutech Instruments Pte. Ltd.; Singapore). The Torsager site was flooded during the September sampling due to heavy rainfall. The standing water depth outside the piezometers was recorded, but as the floodwater had not penetrated the soil to the depth of the piezometer screen, the recorded water table did not represent the GWL in this case.

The diameter and circumference of each *J. effusus* tussock, and numbers of live and dead shoots were recorded on each of the four sampling days.

Methane flux measurements were conducted using static chambers (60 cm × 60 cm × 41 cm) constructed from white PVC as described by Petersen et al. (2012). To make a gas-tight seal during sampling, the chambers were held firmly against the permanent frames by use of elastic straps. Gas samples (20 mL) were taken via a butyl rubber septum at 15 min intervals (0, 15, 30, 45 and 60 min after deployment) using a syringe and needle, and transferred to 12 mL pre-evacuated Exetainer vials (Labco Ltd., High Wycombe, UK). Gas flux measurements were initiated between 10:00 and 12:30 a.m. In parallel with gas sampling, soil temperatures at 5, 10 and 30 cm depth were measured at each plot using

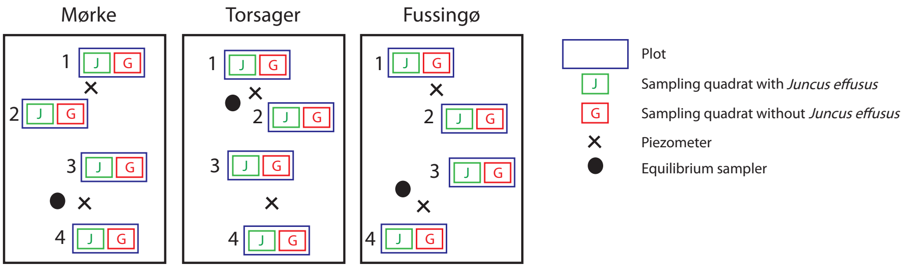

**Figure 1.** Experimental design. The three grassland sites each had four plots (1–4) consisting of two sampling quadrats for gas flux measurement with either grass alone (G) or grass with a tussock of *Juncus effusus* (J). Between each pair of plots, a piezometer was installed (x). Soil molar fraction profiles of methane ($CH_4$) were determined at five depths (from 5 to 100 cm) using equilibrium samplers (•) installed next to one of the piezometers.

a high-precision thermometer (GMH3710, Omega Newport, Deckenpfronn, Germany).

At Mørke we additionally determined $CH_4$ fluxes at the six sampling quadrats used in the long-term monitoring study reported by Petersen et al. (2012). These results were used for comparing with the original flux data from this site, but were not included in the statistical analyses presented here, which were based on the paired-sample statistical design.

Molar fractions of $CH_4$ at 5, 10, 20, 50 and 100 cm soil depth were determined using an equilibrium sampler recently described by Petersen (2014). The soil gas diffusion probe (inner diameter, 12 mm, outer diameter, 16 mm) had a 10 mL reservoir (equilibrium cell) in contact with the surroundings via a 3 mm diameter opening covered by a silicone disk (12 mm × 0.5 mm) held in place by heat-shrinkable tubing. The reservoir was connected to the soil surface via 18G stainless steel tubes with Luer-Lock fittings, one of which extended to near the bottom of the reservoir. For sampling, the reservoir was flushed with 10 mL $N_2$ spiked with 50 $\mu L\,L^{-1}$ ethylene ($C_2H_4$), while the displaced and partly diluted gas sample was collected in a 10 mL glass syringe via a 3-way valve. From the glass syringe, the sample could be transferred to a 6 mL pre-evacuated Exetainer (Labco, High Wycombe, UK). Molar fractions of $CH_4$ were corrected for dilution, which was typically in the order of 20 % as calculated on the basis of the $C_2H_4$ molar fraction. Following gas sampling, the equilibrium cell was flushed with > 100 mL $N_2$ to remove residual $C_2H_4$.

Gas samples were brought to the laboratory and analysed within 2 weeks using an Agilent 7890 gas chromatograph with a CTC CombiPal Autosampler (Agilent, Nærum, Denmark) configured as previously described (Petersen et al., 2012; Petersen, 2014). The gas stream was lead to a flame ionization detector (FID) for $CH_4$ analysis. The carrier was $N_2$ at a flow rate of 45 $mL\,min^{-1}$. The FID was supplied with 45 $mL\,min^{-1}$ $H_2$, 450 $mL\,min^{-1}$ air and 20 $mL\,min^{-1}$ $N_2$. Temperatures of column and FID were 80 and 200 °C, respectively. A separate injection with a run time of 6 min was used for analysis of $C_2H_4$.

## 2.3 Soil characteristics

By the end of the monitoring period, 30 cm sections of soil were sampled to the lower boundary of the peat layer at each plot, or a maximum depth of 132 cm (0–30, 34–64, 68–98 and 102–132 cm), using a stainless steel corer (04.15 SA/SB liner sampler, Eijkelkamp, Giesbeek, Netherlands). The soil samples were brought to the laboratory where they were homogenized. Approximately 10 g subsamples from each depth interval were then dried for 24 h at 105 °C to determine gravimetric soil moisture, and subsequently combusted at 450 °C for 3 h to determine loss-on-ignition (LOI) as a measure of soil organic matter content. Also, 10 mL subsamples of peat were mixed with 20 mL of deionized water, stirred, and then left for 22 h before measuring pH and EC.

## 2.4 Data analyses

All calculations and statistical tests were performed using R (R Core Team, 2012). Soil characteristics at the three sites were compared with Tukey's HSD tests. Methane fluxes were calculated using the HMR package (Pedersen, 2012; Pedersen et al., 2010). Observed fluxes are reported, i.e. without filtering of values below the method detection limit, in accordance with the recommendations of Parkin and Venterea (2010). Among the 120 fluxes estimated in this study, 77 were best explained by the non-linear model of HMR, whereas linear regression (LR) was used in 33 cases. Ten cases were categorized as "no flux" by the HMR software, but visual inspection of the raw data identified outliers which were removed and the data sets were then successfully reanalysed with the four remaining observations. Results are presented as mean ± standard error (SE) with indication of the number of replicates ($n$).

We used the package lme4 (Bates et al., 2012) to construct a linear mixed effect model of the relationship between $CH_4$ flux as the dependent variable and vegetation type, with plot and sampling date as fixed effects (including also interactions). As random effects we used plot (nested within site) and the interaction between plot and site. To meet the requirements of variance homogeneity prior to data analysis, the flux estimates were log-transformed after adding a constant to the initial flux value to avoid negative values (i.e. $\log(x+1)$). In preliminary runs, model effects with an $F$ value $< 1$ were sequentially removed from the model. Visual inspection of residuals plotted against the fitted values and normal QQ plots did not show any sign of violation of model assumptions of normality and variance homogeneity. $P$ values for the reduced mixed effect model were based on the Kenward-Roger approach (Kenward and Roger, 1997) using the package pbkrtest (Halekoh and Højsgaard, 2012), in which the model is tested against a model without the effect in question. Main effects were also tested against a model without interactions. In a separate analysis, site was left out as an effect, and the three sites were analysed separately.

Another linear mixed effects model was constructed to investigate relationships between $CH_4$ fluxes and the measured abiotic factors. The random effects were as above. To avoid problems with collinearity, covariates with the highest Variance Inflation Factor (VIF) were sequentially excluded from the model, using a threshold of three as suggested by Zuur et al. (2010). The following independent variables were included in the final model: soil temperature at 10 cm depth (Soil $T_{10\,\mathrm{cm}}$), groundwater level (GWL), groundwater pH ($\mathrm{pH_{GW}}$), groundwater electrical conductivity ($\mathrm{EC_{GW}}$), peat depth, soil pH at 34–64 cm depth ($\mathrm{pH_{34\,cm}}$), electrical conductivity at 0–30 cm depth ($\mathrm{EC_{soil\,0\,cm}}$), and tussock diameter ($Ø_{\mathrm{tussock}}$). Levels of significance for the model effects were again obtained using the Kenward-Roger approach for model comparison (Kenward and Roger, 1997).

## 3 Results

### 3.1 Soil characteristics

Peat depths at Torsager and Fussingø were generally at or below the maximum sampling depth of 132 cm, while at Mørke the organic layer was rather shallow with an average depth of 65 cm (Table 1). The sites also differed in average GWL which was closest to the soil surface at Mørke (i.e., at 37 cm below soil surface). The GWL in Mørke and Fussingø were relatively stable during the campaigns, ranging from 26 to 59 cm depth and 41 to 64 cm depth respectively. At Torsager the GWL increased gradually during the campaigns from a GWL at 120 cm depth during the first campaign to a water table 10 cm above the soil surface during the flood in the last campaign. The average soil temperature at 10 cm depth was slightly lower in Torsager than at Mørke and Fussingø.

Soil analyses showed differences in soil moisture, LOI, pH and $\mathrm{EC_{soil}}$ between depth intervals, and between the three sites (Table 2). Despite the higher GWL at Mørke, the soil layers generally contained less water (Table 2). This was partly due to a higher mineral content and thus dry bulk density at the two lower depths, but some loss of water due to compaction during sampling probably also occurred. Mørke had the most variable soil characteristics, and was more acidic at lower depths, with pH values as low as 3.5 in one plot (data not shown), compared to the other sites (Table 2).

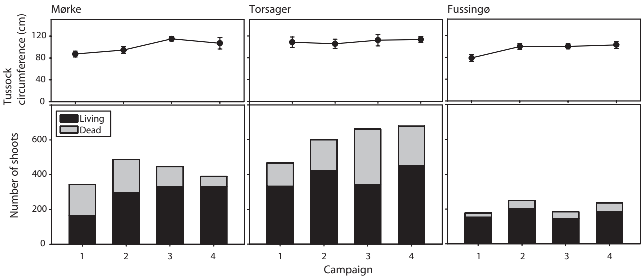

**Figure 2.** Mean circumference (± standard error, $n = 4$) and number of living and dead shoots ($n = 4$) of the tussocks in *Juncus effusus* sampling quadrats at the three sites, during the four sampling campaigns.

### 3.2 Tussocks

The characteristics of the *J. effusus* tussocks varied between sites. Generally, the tussocks at Torsager were well-defined with thick shoots and the greatest circumference (Fig. 2). The tussocks at Mørke were relatively dense, but still allowed sporadic colonization by other plant species (mostly pasture grasses). At Fussingø, tussocks were more diffuse, with slender shoots and less-defined tussocks, which allowed for colonization by other plant species (*Lotus pedunculatus*, *Rumex acetosa*, *Taraxacum* sp., *Cirsium arvense* and pasture grasses). The tussocks at Fussingø had the smallest number of shoots, and a lower proportion of dead shoots than at the other sites (Fig. 2).

### 3.3 Soil $CH_4$ profiles

Methane was present in the soil profile at all depths between 5 to 100 cm, and in most cases with significant amounts both above and below the groundwater table (Fig. 3). Air- and water-filled porosities at the sampling depths are not known, and absolute concentrations of $CH_4$ could therefore not be calculated; instead molar fractions are presented.

Methane molar fractions varied considerably between sites and sampling dates. Molar fractions were in the order of 30-fold lower at Mørke than at Torsager and Fussingø, possibly because the peat layer at Mørke was shallower and more degraded. Interestingly there was evidence for methanogenesis above the water table at all three sites at the first sampling campaign, with local maxima at 10, 50 and 20 cm depth at Mørke, Torsager and Fussingø respectively. Methane production was also evident below the GWL at all three sites, with the highest activity in spring and early summer.

The molar fraction profiles at all sites indicated that most of the $CH_4$ accumulating in the soil was oxidized before

**Table 1.** Peat depth, groundwater level depth, soil temperature at 10 cm depth and number of shoots in tussocks of *J. effusus* at the three study sites. Data are mean ± standard error ($n = 4$, $n = 8$, $n = 16$ and $n = 16$ respectively) representing spatial variability for peat depth and temporal variability within sites for groundwater level, soil temperature and tussocks of *J. effusus*.

| Site | Peat depth (cm) | Groundwater level depth (cm) | Soil temperature at 10 cm depth (°C) | *J. effusus* (shoots tussock$^{-1}$) |
|---|---|---|---|---|
| Mørke | 65 ± 7.7 | 37 ± 3.8 | 12.9 ± 0.5 | 281 ± 26 |
| Torsager | > 132[a] | 67 ± 18 | 12.5 ± 0.5 | 387 ± 28 |
| Fussingø | > 127[b] | 52 ± 3.2 | 13.1 ± 0.5 | 171 ± 8 |

[a] Peat depth in all plots in Torsager exceeded the measurement depth of 132 cm. [b] Peat depth in two out of four plots in Fussingø exceeded the measurement depth of 132 cm.

**Table 2.** Average (± standard error, $n = 4$) gravimetric soil moisture, loss-on-ignition (LOI), pH and soil electrical conductivity ($EC_{soil}$) measured at Mørke, Torsager and Fussingø.

| Depth (cm) | Mørke | Torsager | Fussingø |
|---|---|---|---|
| Soil moisture (%) | | | |
| 0–30 | 53.8 ± 6.2 a | 76.9 ± 2.0 c | 70.0 ± 3.3 b |
| 34–64 | 75.0 ± 4.8 a | 83.6 ± 1.5 b | 82.9 ± 1.4 b |
| 68–98 | 48.9 ± 14.9 a | 83.7 ± 1.6 b | 86.1 ± 0.8 b |
| 102–132 | 27.1 ± 1.8 a | 84.1 ± 1.0 b | 88.8 ± 0.6 b |
| LOI (%) | | | |
| 0–30 | 39.6 ± 11.9 a | 60.4 ± 5.8 b | 64.7 ± 7.7 b |
| 34–64 | 63.8 ± 13.6 a | 71.4 ± 2.3 ab | 80.1 ± 5.0 b |
| 68–98 | 25.4 ± 12.3 a | 65.5 ± 1.4 b | 79.9 ± 0.9 c |
| 102–132 | 3.3 ± 0.6 a | 64.3 ± 1.1 b | 77.7 ± 3.3 c |
| pH | | | |
| 0–30 | 5.68 ± 0.37 b | 5.33 ± 0.06 a | 5.70 ± 0.03 b |
| 34–64 | 5.40 ± 0.39 a | 5.60 ± 0.06 a | 5.57 ± 0.08 a |
| 68–98 | 4.80 ± 0.45 a | 5.79 ± 0.10 b | 6.14 ± 0.10 c |
| 102–132 | 5.07 ± 0.11 a | 5.80 ± 0.05 b | 6.44 ± 0.11 c |
| $EC_{soil}$ (mS cm$^{-1}$) | | | |
| 0–30 | 0.46 ± 0.07 b | 0.41 ± 0.04 ab | 0.38 ± 0.03 a |
| 34–64 | 0.70 ± 0.20 a | 0.61 ± 0.09 a | 0.96 ± 0.18 b |
| 68–98 | 0.60 ± 0.13 a | 0.62 ± 0.10 a | 0.94 ± 0.12 b |
| 102–132 | 0.63 ± 0.18 a | 0.59 ± 0.09 a | 0.93 ± 0.12 b |

Letters indicate significant ($P < 0.05$) difference within rows.

reaching the soil surface. Still, $CH_4$ molar fractions at 5 cm soil depth were above atmospheric level, especially in spring and early summer, but declined steadily during the monitoring period at all sites; at Mørke from 25 to 2.6 ppmv $CH_4$, at Torsager from 9.1 to 2.1 ppmv $CH_4$ (no data available for the last sampling campaign due to flooding), and at Fussingø from 23 to 5.1 ppmv $CH_4$.

### 3.4 Methane emissions

Methane emissions were lowest at Mørke with an average $CH_4$ flux of $0.51 \pm 0.94$ mg $CH_4$ m$^{-2}$ h$^{-1}$, while the average flux at Fussingø was $1.19 \pm 0.64$ mg $CH_4$ m$^{-2}$ h$^{-1}$. The highest fluxes were seen at Torsager with $2.55 \pm 3.20$ mg $CH_4$ m$^{-2}$ h$^{-1}$. This high mean flux was partly a result of the very high fluxes observed during the final campaign ($7.3 \pm 2.9$ mg $CH_4$ m$^{-2}$ h$^{-1}$), which coincided with flooding of the river valley where the site was located.

Across all sites and sampling campaigns, the mean emission rate for sampling quadrats with *J. effusus* was $1.47 \pm 0.28$ mg $CH_4$ m$^{-2}$ h$^{-1}$ and for sampling quadrats without *J. effusus* it was $1.37 \pm 0.33$ mg $CH_4$ m$^{-2}$ h$^{-1}$. The $CH_4$ emission patterns were analysed with a mixed-effects model (Table 3). Methane emissions varied significantly during the measurement period, but temporal dynamics differed between sites ($P < 0.001$), possibly due to the high $CH_4$ emission rates at the flooded Torsager site in September. Methane emission levels differed significantly between sites

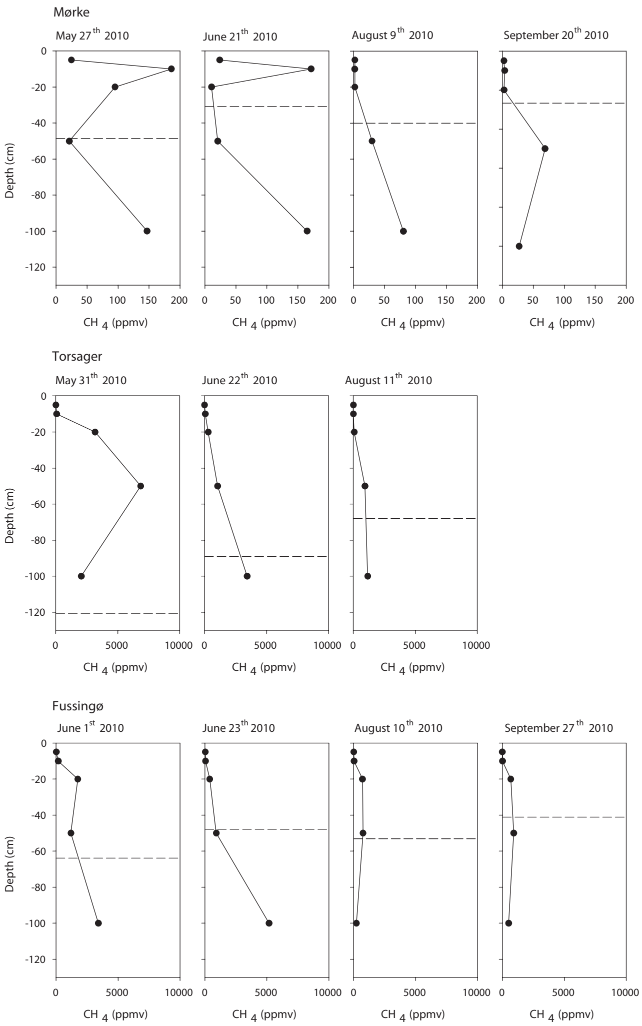

**Figure 3.** Soil methane ($CH_4$) molar fraction profiles for the three different sites at the four sampling dates. The dashed line represents the groundwater level. For Torsager measurements were not taken on the last sampling day due to excessive surface flooding. Note the different $x$ axis scale for Mørke.

($P = 0.022$), but the linear mixed model showed no effect of vegetation type across the three sites ($P = 0.531$), although some individual plots did show consistently higher $CH_4$ emissions from sampling quadrats with *J. effusus* (Fig. 4). This may account for the significant interaction between site and vegetation type ($P = 0.022$).

Analysing the three sites separately, there was a significant effect of *J. effusus* on $CH_4$ emissions at Mørke ($P < 0.001$), but not at Torsager or Fussingø (Table 4). Also, $CH_4$ emissions at Mørke were constant during the measurement period ($P = 0.283$) despite the ten-fold decline in $CH_4$ at 5 cm soil depth, whereas $CH_4$ emission rates increased significantly at Torsager ($P < 0.001$) and Fussingø ($P = 0.002$) during the sampling period.

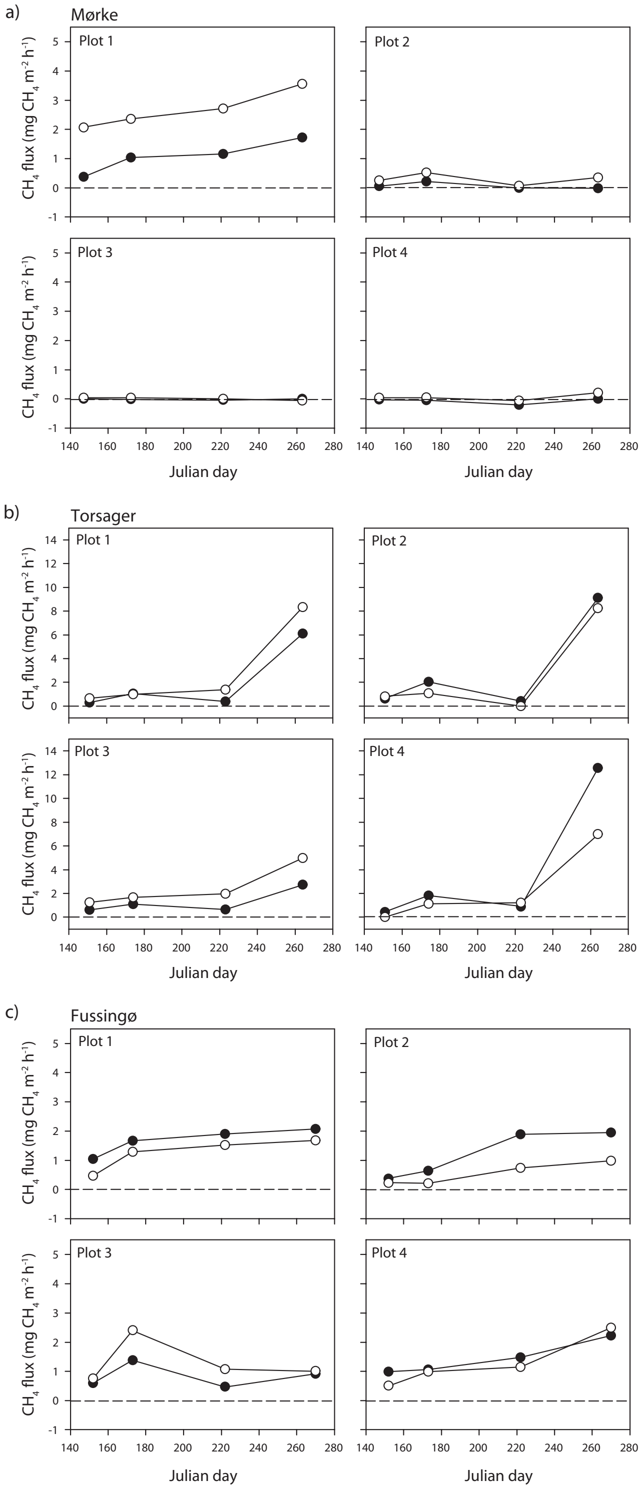

**Figure 4.** Methane ($CH_4$) fluxes at paired sampling quadrats with (-○-) and without (-●-) *Juncus effusus* at the three different sites (Mørke, Torsager and Fussingø) at the four samplings dates. Note the different $y$ axis scale in **(b)** Torsager.

**Table 3.** Effects of site, vegetation (with or without *Juncus effusus*) and sampling date on methane ($CH_4$) emission rates were evaluated using a linear mixed model. See text for a description of the model.

| Effect | df, num | df, denom | $F$ value | $P$ |
|---|---|---|---|---|
| Site | 2 | 8.4 | 6.48 | 0.022 |
| Vegetation | 1 | 3.2 | 0.51 | 0.531 |
| Sampling date | 3 | 77 | 45.8 | $<0.001$ |
| Site × Vegetation | 2 | 69 | 4.06 | 0.022 |
| Site × Sampling date | 6 | 69 | 20.3 | $<0.001$ |

The six sampling quadrats used in a previous monitoring study at Mørke between September 2008 and October 2009 (Petersen et al., 2012) were re-visited in the present study conducted during 2010. The previously observed pattern was confirmed, where a single sampling quadrat with a *J. effusus* tussock was a constant and significant source of $CH_4$ while all other sampling quadrats showed no significant flux (Fig. 5).

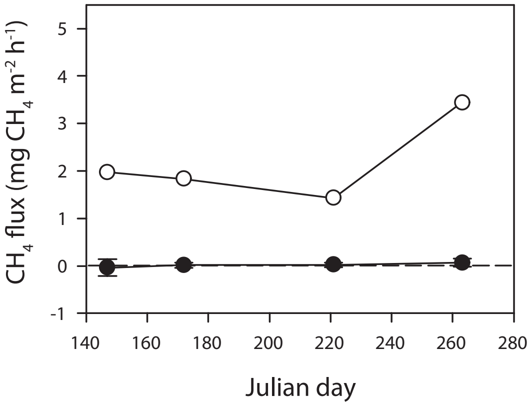

**Figure 5.** Methane ($CH_4$) emissions from the reference plots at Mørke with (-○-) *Juncus effusus* ($n = 1$) and without (-●-) *Juncus effusus* (mean ± standard error, $n = 5$) during the course of the field campaigns. The sampling positions were denoted E-PG in Petersen et al. (2012).

### 3.5 Effects of abiotic factors

The relationships between $CH_4$ emission and several abiotic factors measured during the field campaigns were examined using a linear mixed model. The explanatory variables remaining after model reduction are shown in Table 5. GWL and peat depth in particular significantly influenced $CH_4$ emission from the sites, whereas soil temperature, EC and the measured tussock characteristics did not have a significant effect on $CH_4$ emissions.

## 4 Discussion

In this study we hypothesized that local hotspots of $CH_4$ emissions from pastures drained for agriculture could develop in the presence of *J. effusus*, a wetland plant that can transport gases effectively via its aerenchyma (Henneberg et al., 2012). In wetlands, reports on the importance of aerenchymatous plants for $CH_4$ emissions differ. Most authors have found that emissions from such vegetation are enhanced (Chanton and Dacey, 1991; Greenup et al., 2000; Koelbener et al., 2010; Noyce et al., 2014; Schimel, 1995), but reduced emissions can also occur (Bhullar et al., 2013; Fritz et al., 2011; Grünfeld and Brix, 1999). However, these studies were conducted in permanently flooded wetlands or mesocosms with a high water table. We specifically addressed plant-mediated gas transport in grasslands on peat drained for agriculture which have so far received little attention. In such managed peatlands, *J. effusus* can be an important component of the vegetation. For example, during a Danish survey of soil C stocks in peat soil (Greve et al., 2014), it was found that 632 out of 4341 sites harboured > 20 *Juncus* tussucks within a 5 m radius from the soil sampling position (Mogens H. Greve, personal communication, 2015).

We used a paired-sample approach at three sites to investigate relationships between *J. effusus* and $CH_4$ emissions from grasslands on organic soil used for grazing. The hypothesis that tussocks of *J. effusus* would generally enhance $CH_4$ emissions from otherwise low-emitting areas was not confirmed. There was substantial variation in $CH_4$ emission levels between the three sites, between plots and sampling quadrats with and without *J. effusus*, and across the monitoring period. A statistically significant effect of vegetation type was only observed at the Mørke site. The elevated emissions from *J. effusus* was found from one of the four paired-sample plots (Fig. 4a) as well as in the plot previously studied by Petersen et al. (2012). In comparison to Mørke, the other two sites had significant emissions of $CH_4$ in all plots, and differences between sampling quadrats with and without *J. effusus*, though not always with higher emissions in the sampling quadrat with *J. effusus*. Thus, $CH_4$ emission potentials in grazed grasslands are spatially heterogeneous, and as shown previously (Hendriks et al., 2010), the role of aerenchymatous plants in enhancing $CH_4$ emissions to the atmosphere appears to depend on micro-site conditions.

Methane emissions, which ranged from around zero to more than 10 mg $CH_4$ m$^{-2}$ h$^{-1}$, depended significantly on groundwater level (Table 5). As would be expected, the highest emission rates were observed at Torsager after flooding, with rates equivalent to those reported from permanently flooded peatlands (Günther et al., 2013; Kim et al., 1999; Turetsky et al., 2014). Several authors have suggested that $CH_4$ emissions are insignificant when the GWL is below a certain threshold of 20 to 30 cm below the soil surface (Audet et al., 2013; Koebsch et al., 2013; Shannon and White, 1994). Such a threshold could not be confirmed in this study, where emissions of 1–3 mg $CH_4$ m$^{-2}$ h$^{-1}$ were observed with the GWL at 40–50 cm depth. Also, molar fraction profiles in-

**Table 4.** Effects of vegetation (with or without *Juncus effusus*) and sampling date on methane ($CH_4$) emission rates were evaluated using a linear mixed model for each of the three sites separately.

| | Effect | df, num | df, denom | $F$ value | $P$ |
|---|---|---|---|---|---|
| Mørke | Vegetation | 1 | 24 | 14.1 | $< 0.001$ |
| | Sampling date | 3 | 24 | 1.18 | 0.283 |
| | Vegetation × Sampling date | 3 | 21 | 0.05 | 0.985 |
| Torsager | Vegetation | 1 | 24 | 0.28 | 0.592 |
| | Sampling date | 3 | 24 | 44.8 | $< 0.001$ |
| | Vegetation × Sampling date | 3 | 21 | 0.40 | 0.753 |
| Fussingø | Vegetation | 1 | 24 | 1.47 | 0.209 |
| | Sampling date | 3 | 24 | 5.86 | 0.002 |
| | Vegetation × Sampling date | 3 | 21 | 0.09 | 0.963 |

**Table 5.** Significant effects of the relationship between methane ($CH_4$) emission rate and the measured factors that remained in the model after exclusion of model effects based on Variance Inflation Factors (VIF).

| Effects | Significance |
|---|---|
| Soil $T_{10\,\mathrm{cm}}$ | ns |
| GWL | *** |
| $\mathrm{pH}_{\mathrm{ground\,water}}$ | ns |
| $\mathrm{EC}_{\mathrm{ground\,water}}$ | ns |
| Peat depth | *** |
| $\mathrm{pH}_{34\,\mathrm{cm}}$ | ** |
| $\mathrm{EC}_{\mathrm{soil\,0\,cm}}$ | ns |
| $Ø_{\mathrm{tussock}}$ | ns |

Soil $T_{10\,\mathrm{cm}}$ – Soil temperature at 10 cm depth; GWL – groundwater level; $\mathrm{EC}_{\mathrm{ground\,water}}$ – groundwater electrical conductivity; $\mathrm{pH}_{34\,\mathrm{cm}}$ – pH at 34–64 cm depth; $\mathrm{EC}_{\mathrm{soil\,0\,cm}}$ – electrical conductivity of the soil at 0–34 cm depth; $Ø_{\mathrm{tussock}}$ – diameter of the *Juncus effusus* tussocks. *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; ns, not significant ($P > 0.05$).

dicated that $CH_4$ could be produced above the water table (Fig. 3). Schäfer et al. (2012) likewise found significant $CH_4$ production potentials both above and below the water table at the Mørke site of the present study, and at a drained bog site used for grazing. The presence of methanogens in these soil layers was later confirmed by molecular characterization of prevailing archaea (Görres et al., 2013). In our study, $CH_4$ accumulation in the soil profile above the water table was even higher at the other sites than at Mørke, and at all sites local maxima in $CH_4$ were observed above the water table. Hence, there was evidence for methanogenesis above the water table at all three sites. In addition to groundwater level, peat depth had a significant effect on $CH_4$ emissions, which is probably due to a deeper organic layer supporting a higher $CH_4$ production. Our results do not indicate an effect of soil temperature on $CH_4$ emissions, as opposed to several other studies (e.g. Moore and Dalva, 1993). First, the variation of soil temperatures presented here was low (Table 1), and second, the possible effect of temperature on $CH_4$ production may have been obliterated by the potential for $CH_4$ oxidation in the upper soil layers. Yet, temperature is generally a strong driver of $CH_4$ emissions across various ecosystems with a typical ∼ 3.5-fold rate increase per 10 °C temperature increase (Yvon-Durocher et al., 2014; Elsgaard et al., 2016).

Gas diffusivity is critical for $CH_4$ accumulation, partly by controlling the proportion of anaerobic soil volume with a potential for methanogenesis, and partly by controlling the supply of $O_2$ for $CH_4$ oxidation (Moore and Dalva, 1993; Smith et al., 2003). Capillary forces have been shown to largely saturate peat well above the water table (Grünfeld and Brix, 1999). According to Schäfer et al. (2012), the peat at Mørke was degraded to H8-H10 on the Von Post scale. In comparison, the peat at Fussingø and Torsager sites were categorized as H8 and H6, respectively. Schwärzel et al. (2002) concluded that, due to shrinkage and mineralization processes, degraded peat soils will maintain a high volumetric water content during periods of drying, and a decline in the proportion of macropores > 100 µm, which could have contributed to their ability to generate $CH_4$. The $CH_4$ accumulation we observed in the unsaturated zone during spring and early summer (Fig. 3), followed by depletion during summer and early autumn, could then be due to increasing $CH_4$ oxidation activity, or declining methanogenic activity over the season (Schäfer et al., 2012).

The positive effect of *J. effusus* on $CH_4$ emissions in Mørke cannot be fully explained from the results presented here, but contributing factors could include poor exchange of gases between soil and atmosphere, and a potential for methanogenesis above the water table. This could lead to accumulation of $CH_4$ in the *J. effusus* rhizosphere, which may extend to more than 37 cm depth (Henneberg et al., 2015). At Mørke there was a local maximum of soil $CH_4$ at 10 cm depth in May and June. This maximum was closer to the soil surface than the maxima observed at the two other sites, and well within reach of the roots of *J. effusus*. In the study of Schäfer et al. (2012), the $CH_4$ accumulation was lower in soils with *J. effusus* tussocks than in plots without *J. effusus*, which is consistent with plant-mediated transport of $CH_4$ (Chanton et al., 1989; Sorrell and Boon, 1994). We hypothesize two different scenarios causing the positive effect of *J. effusus* on $CH_4$ emissions at Mørke. First, it could be an effect of the low resistance pathway of the aerenchyma of *J. effusus* short-circuiting gas release through an otherwise compact soil with a very high resistance to gas diffusion. Second, the peat layer at Mørke was shallower, and the upper soil layers dryer, compared to the Fussingø and Torsager sites. These factors may have contributed to lower $CH_4$ production and higher potential for $CH_4$ oxidation in the upper soil layers at Mørke. If the $CH_4$ oxidation potential in the upper soil layers exceeds the amount of $CH_4$ diffusing through the soil column, all $CH_4$ can be oxidized before reaching the atmosphere, and $CH_4$ is only emitted from *J. effusus*. The fact that *J. effusus* proved to be a significant point source of $CH_4$ from the sampling point from Petersen et al. (2012) revisited in this study (Fig. 5), indicated that the positive effect of *J. effusus* on $CH_4$ emissions in Mørke is temporally consistent.

## 5 Conclusions

The importance of *J. effusus* and other similar wetland plants for enhancing $CH_4$ emissions from drained peatlands is likely to vary considerably between and within sites, depending on factors such as water table depth and the balance between $CH_4$ production and oxidation processes, along with the access of roots to rhizosphere $CH_4$. The present and previous (Petersen et al., 2012) results from Mørke represented one scenario where significant $CH_4$ production combined with root access to $CH_4$ allowed tussocks of *J. effusus* to sustain consistent elevated $CH_4$ emissions during at least two separate growing seasons, though only in some micro-sites. The absence of an effect of *J. effusus* at the other two grassland sites suggests that whether or not such plants are present is of less importance under other conditions, such as when there are high rates of $CH_4$ production and the aerenchymatous pathway does not offer a significant short-circuit compared to direct release from the soil. Since the positive effect of *J. effusus* on $CH_4$ emissions is not consistent at all sites, and the causal relationship not fully resolved, the results from this study cannot be implemented in $CH_4$ emission models at this point. The results highlight the need for more studies on the effect of aerenchymatous plants on $CH_4$ emissions from organic soils with a low water table, and on the necessary and sufficient conditions contributing to scenarios where the aerenchymatous pathway plays a significant role.

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