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ORIGINAL RESEARCH

Effect of Hummock-Forming Vegetation on Methane Emissions from a Temperate Sedge-Grass Marsh

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Abstract Plants affect CH_4 emissions from wetlands by providing routes for CH_4 ventilation from the soil and its re-oxidation, the outcome depending on the vertical distribution of the plant ventilating structures as related to water level. This study investigated the effect of elevated hummocks on CH_4 emissions in a temperate wetland dominated by a hummock-forming sedge, *Carex acuta* L. Comparative measurements of CH_4 fluxes from paired plots with or without hummocks revealed a prevailing positive difference interpreted as plant-mediated fluxes. All types of CH_4 fluxes responded positively to water level with a hysteresis related to its recent dynamics. Seasonal medians of CH_4 emissions from the ecosystem, based on fluxes from both types of plots, were 15.09 and 0.11 mg m^{-2} day^{-1} in the wet year 2012 and the dry year 2014, respectively. This relatively low magnitude of CH_4 emissions, compared to values from similar habitats within the same range of water levels, is ascribed to the presence of hummocks. At water levels near the soil surface, hummocks extend above the water table and serve as aerobic microhabitats in which plant structures avoid anaerobic stress and CH_4 produced in the bulk soil and vented via deep roots can be re-oxidized.

Keywords Methane emissions · Chamber method · *Carex acuta* · Tussock · Water level · Wetland

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Introduction

Wetlands are globally important emitters of methane (CH_4), a potent greenhouse gas. Numerous recent studies have therefore attempted to quantify CH_4 emissions for different sites and conditions as well as understand their dynamics (Le Mer and Roger 2001; Lai 2009; Laanbroek 2010; Bridgham et al. 2013). Yet, much uncertainty remains in the global estimates of CH_4 emissions from wetlands and their predictions under particular situations because there are multiple determinants of CH_4 emissions which may potentially interact and can have different temporal dynamics.

The effects of vegetation cover are understood in principle. Plants promote CH_4 production by providing organic substrates for the metabolism of soil microbial populations (Whiting and Chanton 1993; Picek et al. 2007). In addition, the upward flux of CH_4 produced in the soil is partly vented to the atmosphere via the internal gas-space systems inside the plant bodies. The same plant structures improve conditions for CH_4 oxidation by facilitating oxygen transport from the atmosphere to the wetland soil (Laanbroek 2010 and references therein). As a result, plant growth forms and even plant species with different morphological and anatomical characteristics can differ in their effects on CH_4 emissions.

Plant tussocks represent an interesting growth form that determines the spatial structure of the herb layer in many types of wetlands (Perelman et al. 2003; Crain and Bertness 2005; Ervin 2007; Lawrence and Zedler 2011). Over years the tussocks can develop into elevated hummocks. The area around the hummocks can take the form of concave hollows densely covered with typical vegetation (in mires) or remain mostly flat gaps that are only sparsely vegetated if the water level stays near the surface (in some types of wet grasslands and marshes). As a result, different micro-habitats occur on the hummocks as compared with the gaps. It can be expected that they differ not only in their vegetation cover and composition, but also in the emissions of greenhouse gases. While this aspect has been studied in boreal peatlands, we have found no such information for wet grasslands or marshes.

This study examined CH_4 fluxes from hummocks and gaps in a sedge-grass marsh dominated with a tussock-forming tall sedge, *Carex acuta* L. Its aim was to assess the differences in CH_4 emissions between these two microhabitats as related to water level and the vertical structure of plant biomass within the hummocks.

Site Description

The wetland Mokré Louky (the "Wet Meadows"; 49°1′28.740″N, 14°46′13.260″E, 426 m a.s.l.) is a flat depression with an area of 450 ha located near Třeboň in the center of the Třeboň Basin Biosphere Reserve, South Bohemia, Czech Republic. The mean annual temperature and annual precipitation are 7.6 °C and 614 mm, respectively. The area is part of a large peatland complex with a peat layer of up to several meters thick superimposed on quaternary alluvial sands and clays (Jeník et al. 2002). The Wet Meadows wetland is situated in the inundation area of a large human-made lake (Rožmberk fishpond, 5 km^2). The water level is controlled by a system of ditches and thus kept stable except for periods of extreme droughts and flood events.

The study site represents the wettest northernmost part of the wetland near the fishpond, where the mean water level is near the soil surface (± 0.05 m). It used to be mown once a year but was abandoned after heavy machinery was introduced in the 1950s. The vegetation consists mainly of tall sedges (*Carex acuta* L., *C. vesicaria* L.) and wetland grasses (mostly *Calamagrostis canescens* (Weber) Roth) (Prach and Soukupová 2002; Prach 2008). After cessation of mowing 50 years ago, tussocks of *C. acuta* L. became the basis of hummocks elevated up to 0.5 m above the soil surface, leaving sparsely vegetated gaps in between. In wet years, where the water level stays above the soil surface, *C. acuta* L. predominates on hummocks and *Glyceria maxima* (Hartm.) Holmb. and *Acorus calamus* L. occur in gaps at places. In dry years, *Calamagrostis canescens* (Weber) Roth expands on the tops of the hummocks and accompanying dicot species (mainly *Barbarea stricta* Andrz., *Galium palustre* L., *Lysimachia vulgaris* L., *Persicaria hydropiper* L., and *Scutellaria galericulata* L.) spread in the gaps (Květ et al. 2002; Honissová et al. 2015).

Methods

Gas Measurement and Experimental Design

We tested the effect of plants on CH_4 emissions from the wetland in 2012 and again in 2014. CH_4 fluxes from hummocks formed by tussocks of *Carex acuta* L. were compared to plots with bare soil in gaps (further called hummocks and gaps, respectively). Six pairs of chambers were positioned on different locations of the study site (Fig. 1). Within a pair, one chamber enclosed a hummock 0.2–0.3 m high while the other was situated in an adjacent gap (about 1 m apart) (Fig. 2).

Gas emissions were estimated using two-component static chambers (Livingston and Hutchinson 1995). The chambers had an inner diameter of 0.43 m and a volume of 60 L. The base of each chamber consisted of a plastic collar permanently inserted into the soil one year before the beginning of measurements. The removable upper components were fitted to the collars at the start of each measurement and sealed airtight with a layer of water. After 40 min gas samples were taken as described below and the chambers were removed from the collars. Measurements were taken between 10:00 and 12:00 AM. Eighteen and 25 measurements were carried out from April to October 2012 and 2014, respectively, mostly at one-week intervals.

The emission chambers were constructed according to the Czech utility model no. 24236 (Equipment for the measurement of gas emissions emitted from vegetation or soil). Each chamber was equipped with a fan for internal air circulation, timer for setting the closure period and air pump for automatic air sampling. At the end of the closure period, air was sampled into a gas-tight plastic bag placed inside the chamber. The flexible gas bag eliminates problems caused by changing gas pressure during the closure period and at its end when gas is being sampled. The technical details are given in the Czech Patent and Utility Model databases (http://www.upv.cz/en/client-services/online-databases/patent-and-utility-model-databases/national-database.html).

Gas samples stored in the plastic gas bags were immediately (within 15 min) analyzed for CH_4 concentrations by a Laser gas analyzer (DT-100, Los Gatos Research inc., USA), which was available on the study site. The CH_4 concentrations were first corrected by the ideal gas law using current air temperature and air pressure. CH_4 fluxes were then calculated as a difference in CH_4 concentration in the chamber headspace over time (40 min) taking into account the chamber volume (60 L) and surface area covered (0.145 m^2). The resulting values correspond to the total CH_4 flux from the chamber including both the diffusive flux and ebullition.

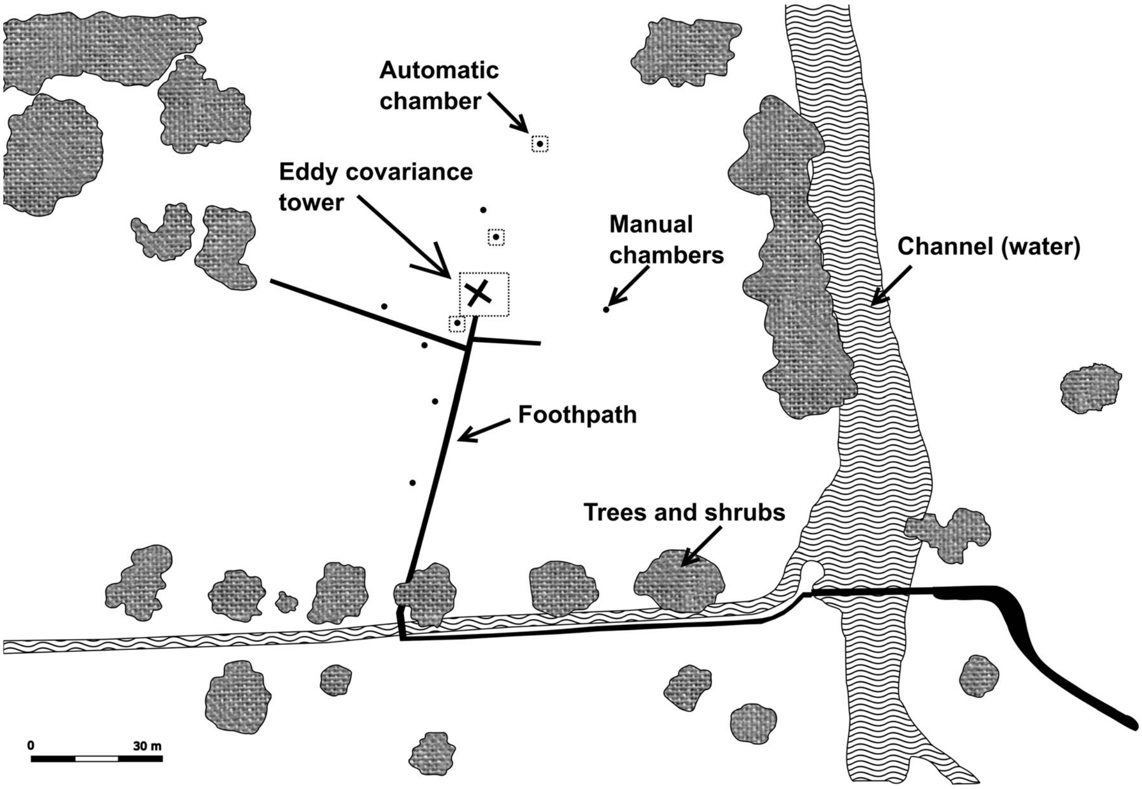

Fig. 1 Map of the study site with chamber measurement sites marked

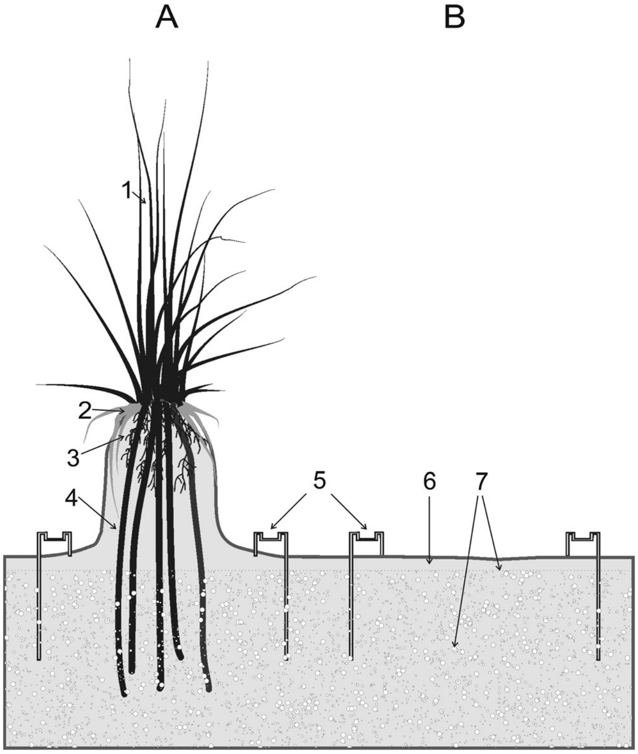

Fig. 2 Paired plots on a hummock (**a**) and in the respective gap (**b**) from which CH_4 fluxes were measured using the chamber technique. 1 – live leaf; 2 – dead leaf; 3 – richly branched root; 4 – aerenchymatous coarse root; 5 – collar; 6 – soil; 7 – water

Accompanying Measurements

The seasonal courses of precipitation, water level and soil temperatures (surface and depths of 5, 10, 20, 30 cm) were measured in a meteorological station situated in the center of the wetland (Fig. 1). The data were logged digitally on a datalogger every 30 s and averaged for 30-min intervals.

In addition, water level and soil temperature were measured manually for each sampling plot immediately after each measurement. The water level was measured inside a 1-m tall tube installed in the soil to a depth of 0.4 m next to each collar. Water level was related to the soil surface, i.e. the base of a hummock or the soil surface in a gap. The temperature was measured at a soil depth of 0.05 m. The differences in both water level and soil temperature were negligible within a pair of plots for a sampling date. Water level differed at most by 0.06 m among the six sampling locations and the meteorological station within any particular date. The values recorded on the sampling locations were used in further evaluation of the results.

The seasonal course of live aboveground plant dry weight on the plots with hummocks was followed using non-destructive measurements. Shoots of all monocot species (*Carex acuta* L., *Calamagrostis canescens* (Weber) Roth, *Glyceria maxima (Hartm.) Holmb.* and *Acorus calamus* L.) were counted in the plots four times during the 2014 vegetation season, (April, June, August and late October). The shoot numbers were then multiplied by the average dry weight of one live shoot estimated by parallel destructive measurement as described below. The biomass of dicots was negligible.

The seasonal course of live and total aboveground biomass of the plant stand was followed using successive harvests as described by Honissová et al. (2015). The samples were taken from April to November 2014 at three- to four-week intervals. On each sampling date, two 1-m^2 quadrats were randomly chosen in the study area. All the aboveground plant parts were cut at the soil surface and transported to the laboratory. The material was sorted to particular monocot species, dicots, mosses and litter. Live and dead shoots were counted for each monocot species and the plant material was then divided into live and dead parts. The fractions were dried at 85 °C to constant weight. Subsequently, the average dry weight of one live shoot was calculated for each particular monocot species by dividing the dry weight of the respective fraction by the number of shoots.

The biomass of roots and rhizomes were estimated as the amount of live material recovered from soil blocks. The samples were taken four times during the 2014 vegetation season (i.e. before the start of shoot growth in March, June, August and late October). Three types of samples (0.2 × 0.2 m in area) were taken: (1) a medium-sized, 0.2 to 0.3 m high hummock cut at the soil surface, (2) a soil block of 0.2 × 0.2 × 0.4 m (length x width x depth) beneath the hummock; (3) a 0.2 × 0.2 × 0.4 m soil block of unvegetated soil (gap) beside the hummock. The samples were taken in triplicate. The excavated soil blocks were transported to the laboratory and stored in cold until processed. No signs of change (such as shoot regrowth or root or rhizome rotting) were observed during the storage period, which lasted up to three to four weeks at maximum. The number of tillers was first counted for each tussock. The plant material was then washed free of soil and divided into live roots, live rhizomes, dead roots, and dead rhizomes of *C. acuta* L., live roots and live rhizomes of other species and dead material of other species. Live roots were distinguished from dead ones visually. In contrast to live roots, dead roots were dark brown to black or grey depending on the degree of decomposition. In addition, they were soft and filled with water which was apparent on a cross section when the root was squeezed. All fractions were dried at 85 °C to constant weight.

Data Evaluation

The effect of vegetation on CH$_4$ emissions was examined by comparing the CH$_4$ fluxes between a paired hummock and the respective gap. Positive differences were attributed to CH$_4$ fluxes mediated by plant structures and called “plant–mediated fluxes” further in the text.

In order to compare the CH$_4$ fluxes among different studies, total CH$_4$ emission rates were calculated considering the flux contributions of both hummocks and gaps weighted by their proportional area:

$$F_T = F_H . S.D_H + F_G .(1 - S.\ D_H)$$

where F_T – emission rate [mg CH$_4$-C m^{-2} day^{-1}], F_H – average CH$_4$ flux from hummocks [mg CH$_4$-C m^{-2} day^{-1}], F_G – average CH$_4$ flux from gaps [mg CH$_4$-C m^{-2} day^{-1}], S – surface area of the emission chamber [m^2], D_H – average hummock density [m^{-2}].

Direct counting of hummocks in a delineated area was difficult to perform with sufficient accuracy because of the large variation in hummock size and their irregular horizontal pattern. Therefore, we made use of the results of aboveground biomass, which was sampled considering these sources of variation (cf. previous section). The average density of the hummocks in a stand was estimated as:

$$D_H = \frac{W_H}{W_S}$$

where W_H – average seasonal maximum aboveground plant dry weight per hummock [g] and W_S – average seasonal maximum aboveground biomass of the whole stand (including both hummocks and gaps) [g m^{-2}].

The CH$_4$ flux data were analyzed using Statistica 10 (Statsoft, USA). Normality of the data was assessed with the Shapiro-Wilks test (Royston 1982a, 1982b, 1995). As the distribution of the primary data differed significantly from normality ($p < 0.01$), differences in the CH$_4$ fluxes among different locations were tested using the nonparametric Kruskal-Wallis ANOVA test with multiple comparison between groups (Kruskal and Wallis 1952). The differences in CH$_4$ fluxes between paired plots on a hummock and in the respective gap, within a particular location, were assessed using the Wilcoxon non-parametric test for paired samples (Hollander and Wolfe 1999). One-sided Wilcoxon test was used to test for positive or negative differences between the paired plots within a location.

Mutual relationships between the CH$_4$ fluxes and water level, temperature, aboveground plant dry weight, shoot numbers and their seasonal changes separately for *C. acuta* and total plant cover were explored by correlation analysis of the non-transformed data. The effects of environmental variables and plants were subsequently tested using analysis of covariance on the log-transformed CH$_4$ flux data. Water level and temperature were the continuous independent variables. The recent dynamics of the water level (either increase or decrease from the previous measurement) was a categorical effect entering in interaction with the current water level.

Results

Environmental and Plant Characteristics

The seasonal courses of water levels were without extreme events such as summer drought or flood in either year. 2012 was somewhat wetter with a maximum water level of about 0.3 m and a median of 0.03 m above the soil surface; as a result, the hummocks were partly flooded during much of the vegetation season. In contrast, 2014 was much drier with water levels below the soil surface for almost all the season with a median of 0.04 m below the soil surface (Fig. 3). Soil temperatures at the 0.05 m depth were 12.6 ± 3.9 °C and 11.8 ± 2.1 °C (mean ± standard deviation) over the 2012 and 2014 sampling periods, respectively.

The average density of hummocks was 2.5 m^{-2}. The average hummock height was 0.24 ± 0.08 m (mean ± standard deviation, $n = 56$). Total aboveground biomass increased till June and remained at its seasonal maximum till September. The seasonal maximum aboveground biomass of *C. acuta* L. was 0.18 kg m^{-2}, which accounted for about ¼ of the total aboveground biomass (Table 1).

Belowground biomass greatly varied in space, which was mainly due to differences in the size and density of the hummocks. As a result, the variation coefficient (SD/mean) was 60% for the seasonal maximum belowground biomass (Table 1). Roots of *C. acuta* L. formed more than 50% of the total belowground biomass of all species while the proportion of its rhizomes was negligible. Roots and rhizomes of other species (especially monocots) accounted for about 30% of the belowground biomass, much of them occurring within the hummocks. The biomass of live roots of *C. acuta* L. increased over the vegetation season and reached about 1 kg m^{-2} in November. About half or even more of the live root biomass occurred within the hummocks above the soil surface (Table 1).

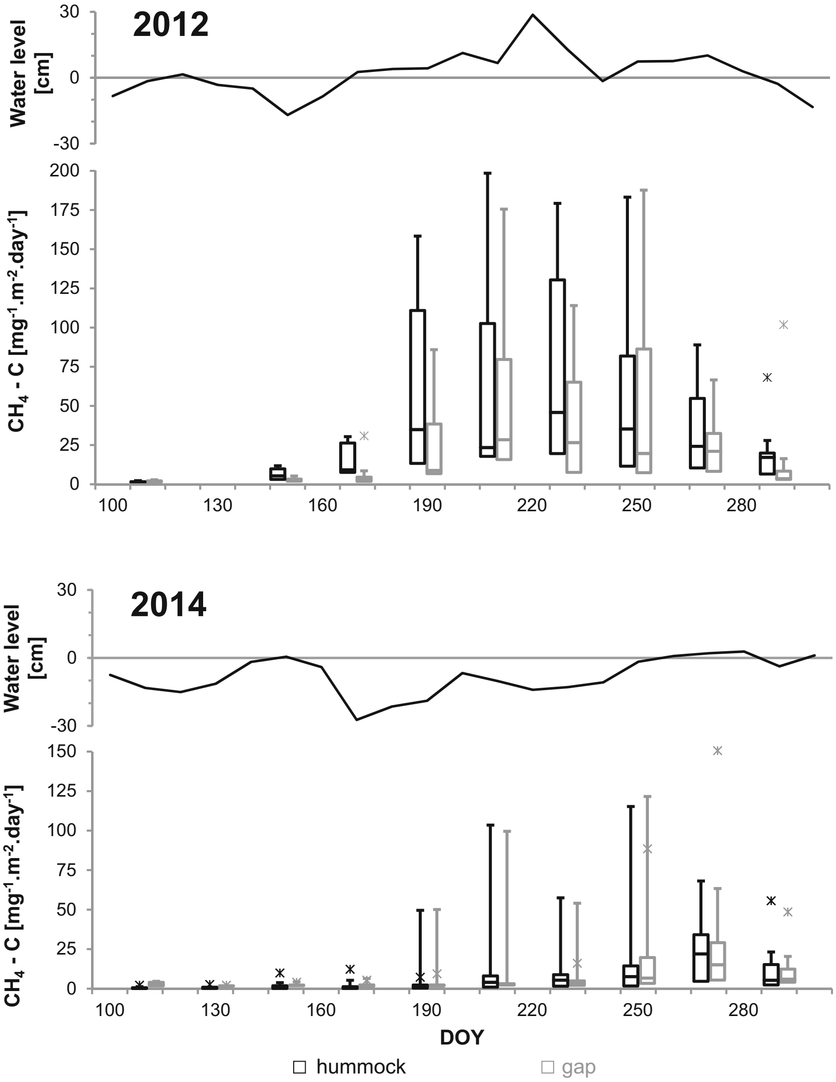

Fig. 3 Seasonal courses of water level and CH_4 fluxes from hummocks and gaps during the 2012 and 2014 vegetation seasons. The box-plots show medians, quartiles and ranges

Table 1 Plant growth characteristics of the Wet Meadows at the time of their seasonal maxima

Aboveground growth characteristics	
Total aboveground biomass [kg m^{-2}]	0.661 ± 0.103
Shoot biomass of *C. acuta* L. [kg m^{-2}]	0.180 ± 0.083
Shoot density of *C. acuta* L. [m^{-2}]	195 ± 44
Number of shoots of *C. acuta* L. per chamber (0.145 m^2)	66 ± 8
Belowground growth characteristics	
Total belowground biomass [kg m^{-2}]	2.51 ± 1.53
Belowground to aboveground ratio	0.260
Live biomass of fine roots of *C. acuta* L. [%]	2.90 ± 1.24
Live biomass of coarse roots of *C. acuta* L. [%]	52.95 ± 3.64
Dead root biomass of *C. acuta* L. [%]	9.64 ± 5.69
Live rhizome biomass of *C. acuta* L. [%]	2.06 ± 2.22
Dead rhizome biomass of *C. acuta* L. [%]	0.29 ± 0.57
Root biomass of other species [%]	11.73 ± 6.36
Rhizome biomass of other species [%]	20.43 ± 7.80
Vertical distribution of live roots of *C. acuta* L.	
Inside hummocks [%]	58.6 ± 13.2
Beneath hummocks [%]	41.4 ± 13.2

The values related to aboveground parts are means ± standard deviation of three successive harvests (of an area of 2 m^2 each) during the period of July to September. The belowground biomass reached its maximum from August to November. Values of the November sampling are given (mean ± standard deviation, $n = 3$). Total biomass denotes the sum of live and dead biomass of all plant species present. The fractions of belowground biomass are expressed as percentages of the total belowground biomass. The spatial distribution of live roots of *C. acuta* L. is based on data gathered in March, June, August and November ($n = 11$) and related to the actual live root biomass of *C. acuta* L.

Methane Fluxes

The seasonal courses of CH_4 fluxes roughly copied the seasonal water level dynamics. This was conspicuous in 2012, when the site was flooded for much of the vegetation season, but was noticeable also in the much drier year of 2014 (Fig. 3). CH_4 fluxes from hummocks were frequently greater than fluxes from gaps (Fig. 4). Positive flux differences, regarded as plant-mediated fluxes, accounted for about 60% of the cases at water levels from −0.10 to +0.05 m and as much as 80% at water levels higher than 0.05 m. Positive differences greater than 10 mg m^{-2} day^{-1} became more frequent with increasing water level and accounted for more than 50% of the cases at water levels higher than 0.05 m. Negative flux differences were less frequent than the positive ones, yet small differences (about 1 mg m^{-2} day^{-1}) occurred within the whole range of water levels recorded. Negative differences greater than 10 mg m^{-2} day^{-1} occurred predominantly at water levels above the soil surface, increasing in frequency with higher water levels. These were likely the results of ebullition from bare soil surfaces in the gaps.

Overall, significant positive differences between the hummocks and the respective gaps occurred on five out of six locations in 2012 and four locations in 2014 (Table 2). Small but significant negative differences were found on two locations in 2014. In addition to differences between the hummocks and gaps, there were also some differences among plots of the same type (Table 2). In 2012, by far the greatest CH_4 fluxes were recorded on location 4, indicating that it might be a local hotspot of CH_4 emission.

The differences in CH_4 fluxes among plots of the same type resulted also in differences in CH_4 emission rates among locations (obtained by averaging CH_4 fluxes from both hummocks and gaps weighted by the proportion of their area). In 2012, the smallest seasonal median of CH_4 emission rate (3.46 mg m^{-2} day^{-1}) was recorded on location 1 and the greatest (146.33 mg m^{-2} day^{-1}) on location 4. In 2014, the seasonal medians of CH_4 emission rate ranged from 1.06 mg m^{-2} day^{-1} on location 3 to 4.95 mg m^{-2} day^{-1} on location 4. Considering all locations together, the seasonal medians of CH_4 emission rate were 15.09 mg m^{-2} day^{-1} and 0.11 mg m^{-2} day^{-1} in 2012 and 2014, respectively.

Effects of Environmental and Plant Characteristics on Methane Fluxes

Exponential dependencies on water level were found for both types of CH_4 fluxes, i.e. fluxes from gaps and from hummocks. However, the CH_4 fluxes were generally lower at any particular water level when it was increasing than when it was decreasing (Fig. 5).

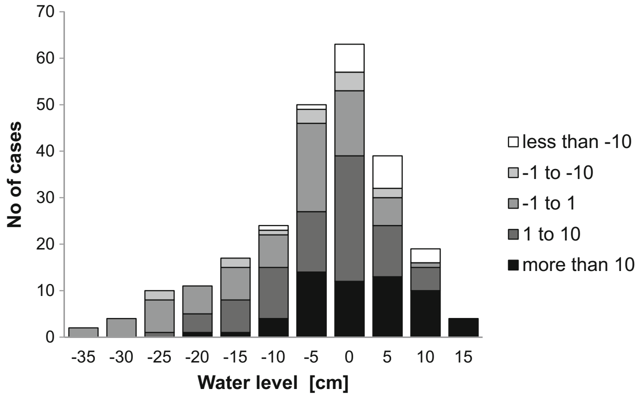

Fig. 4 Frequency of CH_4 flux differences between hummocks and gaps as related to water level. Positive values denote situations when a flux from a hummock was greater than the flux from the paired gap

The analysis of covariance confirmed the effects of water level and its recent dynamics (increase or decrease) on the CH_4 fluxes from hummocks, gaps and also the plant mediated fluxes (Table 3). In 2012, the interactions between current water level and its recent dynamics were also significant, which means that the CH_4 fluxes responded differently to water level when it was increasing or decreasing.

Apart from one exception, the effect of temperature was generally not significant. The plant-mediated CH_4 fluxes responded to the environmental variables in the same manner as fluxes from gaps and hummocks (Table 3), i.e. they were significantly affected by water level and its recent dynamics, but the effect of temperature was not proven.

Table 2 Seasonal medians of water level and CH_4-C fluxes [mg m^{-2} day^{-1}] from static chambers (0.145 m^2) positioned on hummocks and gaps, respectively

Year	Loc	n	WL	CH_4-C					
				H		G		H-G	
2012	1	17	-0.03	7.60	a	1.10	a	6.50	*†
	2	18	0.24	16.88	ac	4.57	ab	12.31	*†
	3	18	-1.65	6.95	a	6.61	abc	0.34	
	4	17	2.98	311.94	d	52.16	c	259.78	*†
	5	18	3.28	39.07	bcd	10.97	abc	28.10	*†
	6	17	-0.28	41.22	bcd	26.68	bc	14.54	†
2014	1	23	-3.78	2.23	ac	0.57	a	1.66	*†
	2	23	-4.83	0.70	a	3.50	b	-2.80	*X
	3	23	-5.66	0.83	a	1.19	ab	-0.36	*X
	4	23	-1.66	9.87	b	2.16	ab	7.71	*†
	5	23	-2.18	6.58	bc	0.73	ab	5.85	*†
	6	17	-4.83	7.17	bc	1.25	ab	5.92	†

Loc location, *n* number of measurements, *WL* water level [m]; *H* hummock, *G* gap; H-G flux difference between a paired hummock and gap. Values of CH_4-C flux followed by different letters are significantly different within a column and year at $p \leq 0.05$. Asterisks indicate significant differences in CH_4-C flux between a hummock and the respective gap at $p \leq 0.05$. Crosses indicate significantly higher (†) or lower (X) CH_4-C fluxes, respectively, from a hummock than from the paired gap at $p \leq 0.05$

The effect of plant size on the CH_4 fluxes was difficult to ascertain because the CH_4 fluxes were generally small in 2014, when the seasonal course of aboveground plant dry weight was followed. No clear-cut relationships were found between the plant-mediated fluxes and either the seasonal course of aboveground plant dry weight or aboveground production of plants on hummocks (data not shown). Only the seasonal maximum of aboveground plant dry weight of *C. acuta* L. on hummocks (taking locations as replicates, $n = 6$) was significantly correlated with the seasonal median of CH_4 flux from hummocks ($R^2 = 0.719$, df = 4, $p = 0.0329$).

Discussion

Effects of Environmental Factors on CH_4 Fluxes

Wet grasslands are characterized by mean seasonal water levels near the soil surface, though floods and droughts can cause conspicuous temporal variation (e.g., Dušek et al. 2009; Edwards et al. 2015). Our results from the wet year 2012 show that CH_4 emissions can also vary largely on the same site over time (Fig. 3) with a conspicuous part of the temporal variation being due to water level (Figs. 4, 5, Table 3). Water level was thus a crucial abiotic factor affecting CH_4 fluxes from the wetland, as found in many other studies (e.g., Bubier et al. 1993; Ding et al. 2003; Hendriks et al. 2010; Siljanen et al. 2010).

A noticeable feature was a hysteresis in the CH_4 fluxes under a particular water level depending on whether the water was increasing or decreasing (Fig. 5). A similar hysteresis was reported by Moore and Dalva (1993) and Juutinen et al. (2003) and ascribed to two main causes: (1) the time lag in the development of anaerobic conditions and (re)activation of methanogenic microorganisms that occurs under increasing water level, and (2) the duration of anaerobic microenvironments after the water level decreases, which is related to the water retention capacity of the soil.

Local hydrology can also promote the lateral and vertical movement of dissolved chemical substances such as organic substrates for methanogenesis or even CH_4 itself (Le Mer and Roger 2001). A local upward water flow might explain the high CH_4 fluxes on plot 4 in our study. The effect of temperature is considered to be an important factor affecting metabolic processes and their complexes.

The influence of temperature was also found in many studies of CH_4 emissions (e.g., Juutinen et al. 2003; Rinne et al. 2007; Moore et al. 2011; Juszczak and Augustin 2013; McEving et al. 2015). Nevertheless, we did not find any substantial changes in emissions with temperature during either vegetation season (Table 3). This can be ascribed to a fairly

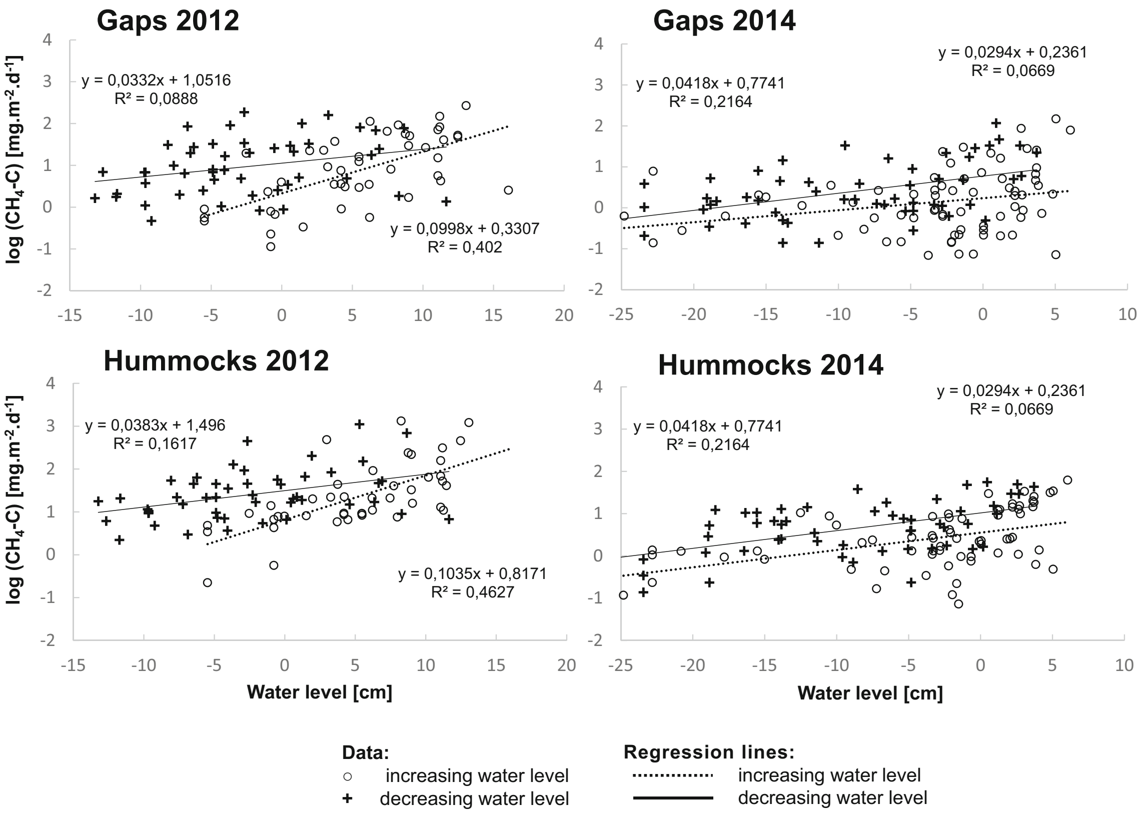

Fig. 5 Correlation analysis of log-transformed CH_4 flux data from gaps and hummocks in relation to either increasing or decreasing water levels. Regression equations and determination coefficients for decreasing and increasing water levels are given on the left and the right parts of the graphs, respectively

narrow range of temperatures during the study period compared to the variation of the flux data. Kowalska et al. (2013) also did not find any soil temperature effect on CH_4 fluxes under similar conditions.

CH_4 Flux Differences between Hummocks and Gaps

The fact that CH_4 fluxes were mostly greater from hummocks than from the paired gaps (Fig. 4) corresponds to the common knowledge that the presence of aerenchymatous vascular plants enhances CH_4 emissions (Bubier 1995; Joabsson 1999; Laanbroek 2010; Turetsky et al. 2014; McEwing et al. 2015). Nevertheless, the frequency of the opposite situation was not negligible and also requires an explanation. Small differences of the order of 1 mg m^{-2} day^{-1} in either direction are considered unimportant as they can result from heterogeneity of the soil conditions and microbial activity even within a pair of plots. The substantially greater fluxes from a gap than from a hummock that occurred at water levels above the soil surface are probably caused by CH_4 ebullition from the shallowly flooded bare soil in the gap. Surprising (though rare) was the occurrence of substantially greater fluxes from a gap than from a hummock when the water level was below the soil surface. A detailed examination of the records of CH_4-flux dynamics revealed that such situations occurred under marked and rapid changes of water levels, which could bring about episodic CH_4 fluxes (Windsor et al. 1992; Moore and Roulet 1993). Such fluxes are probably vented faster from hummocks than from gaps and this phase shift may account for the unexpected flux differences between the paired plots.

Published studies comparing CH_4 fluxes from hummocks with those from hollows are largely confined to boreal peatlands. Bubier et al. (1993), MacDonald et al. (1998), Heikkinen et al. (2002) and Kettunen (2000) detected generally lower CH_4 fluxes from hummocks (or flarks) colonized by shrubby vegetation than from hollows (or strings) with a greater occurrence of aerenchymatous vascular plants, frequently graminoids. Our study describes a different CH_4 flux pattern for a wet grassland dominated with a tussock-forming sedge, where the fluxes were generally higher from hummocks (developing from the tussocks) than from the unvegetated gaps.

The higher fluxes from hummocks were ascribed to the effects of the dominant sedge species. However, the experimental design does not allow for reaching conclusions about the relative importance of the three background mechanisms, i.e. (1) supply with organic substrates for methanogenesis, (2) upward ventilation of CH_4 and (3) downward transport of O_2 necessary for CH_4 oxidation (cf. Segers 1998; Joabsson et al. 1999). As plants supply considerable amounts of organic

Table 3 Effects of main abiotic factors on CH_4-C fluxes as indicated by the analysis of covariance applied to log-transformed flux data

Flux type	Efect	2012				2014			
		R^2	df	F	p	R^2	df	F	p
(H)	water level (WL)		1	29.751	**<0.001**		1	14.440	**<0.001**
	water level dynamics (DY)		1	17.328	**<0.001**		1	9.649	**0.002**
	WL*DY		1	7.367	**0.008**		1	0.170	0.680
	soil temperature		1	0.523	0.471		1	4.122	**0.045**
	residual		89				119		
	whole model	0.281	4	8.691	**<0.001**	0.175	4	6.298	**<0.001**
(G)	water level (WL)		1	43.224	**<0.001**		1	35.359	**<0.001**
	water level dynamics (DY)		1	21.501	**<0.001**		1	10.534	**0.002**
	WL*DY		1	9.191	**0.003**		1	0.001	0.978
	soil temperature		1	0.839	0.362		1	0.081	0.776
	residual		88				115		
	whole model	0.353	4	12.023	**<0.001**	0.262	4	10.191	**<0.001**
(H-G)	water level (WL)		1	18.954	**<0.001**		1	17.252	**<0.001**
	water level dynamics (DY)		1	7.040	**0.010**		1	8.544	**0.005**
	WL*DY		1	4.413	**0.039**		1	2.706	0.104
	soil temperature		1	0.881	0.351		1	1.402	0.240
	residual		70				77		
	whole model	0.237	4	5.428	**0.001**	0.175	4	6.298	**<0.001**

H flux from hummocks, *G* flux from gaps, (*H-G*)plant-mediated flux. R^2 determination coefficient of the whole model, *df* - degrees of freedom. Significant effects are given in bold

substrates to the soil (Kuzyakov and Domanski 2000; Picek et al. 2007; Merino et al. 2015), we can speculate that the rate of methanogenesis might be greater under the vegetation cover than on the bare soil, but this may be counteracted by a greater CH_4 oxidation rate in the rhizosphere provided it is sufficiently oxidized. The plant-related potential of CH_4 oxidation can be substantial and appears to be localized in the rhizoplane (Popp et al. 1999). The latter conclusion was supported also by Faußer et al. (2013) who found that 45% of root exodermis cells of *Phragmites australis* (Cav.) Steud. were colonized with bacteria, of which 34–47% had the potential to oxidize CH_4. Judging from the conspicuous dependence of all plant-mediated fluxes on water level and its dynamics, the upward CH_4 ventilation might predominate over the other two mechanisms when the soil is shallowly flooded.

Relation of CH_4 Fluxes to the Structure and Vertical Distribution of the Root Systems

Both the mechanism and intensity of ventilation via plants greatly depend on their anatomical and morphological structure (Laanbroek 2010). Because of their growth pattern, the tussock-forming graminoids must rely on diffusion whose rate is determined by the length of the diffusion path and the diffusivity constant. The length of the diffusion path corresponds to the length of roots and the permeable part of shoots. The diffusivity constant of a single root depends on (1) lateral permeability across the root surface tissue (or root wall), (2) the permeability of the root aerenchyma along the root (e.g. Armstrong 1971; Armstrong and Armstrong 1988; Soukup et al. 2007). In addition, the root density must be considered when relating the gas fluxes to a unit of ecosystem area.

C. acuta L. has two types of roots: (1) fine ones which are richly branched, extend to the surface water or the soil layer and presumably serve for nutrient uptake and (2) coarse, sparsely branched, positively geotropic roots whose main function is to support the plant in the substrate (Končalová 1990). In this study, the coarse roots formed the major part of live root biomass of *C. acuta* L. (Table 1) and were the sole type of roots growing in the soil beneath the hummocks, extending to depths of as much as 0.4 m. The aerenchyma of the coarse roots reaches up to 30% volume and connects to the intercellular spaces in the shoot base (Končalová 1990). As a result, the whole plant body is well permeable for gases (Končalová et al. 1988). Owing to these anatomical and morphological characteristics, *C. acuta* L. can potentially vent CH_4 produced in the soil, but also promote re-oxidation of the CH_4 by supplying oxygen to methanotrophic bacteria occurring at the root surfaces.

The vertical distribution of *C. acuta* roots may explain the magnitude of the plant mediated CH_4 fluxes as related to the water level. No plant-mediated fluxes were detected when the water level was below a soil depth of 0.2 m (Fig. 4) where roots were scarce. Fairly small amounts of CH_4 were mediated by plants at water levels between 0.2 m and the soil surface (Fig. 4), a soil layer occupied mostly with the basal parts of coarse roots. These roots have well developed aerenchyma but lateral gas exchange between the root and the soil is hindered by the low permeability of the exodermis (Končalová 1990). CH_4 fluxes were conspicuously enhanced by vegetation only at water levels above the soil surface. This indicates that root structures vented considerable amounts of CH_4 only when the basal part of the hummock was flooded. Similarly, Hendriks et al. (2010) attributed differences in CH_4 fluxes in a peat meadow to rooting depth patterns in combination with soil water level.

Methane Emissions from the Whole Ecosystem

In order to compare our results with other data on CH_4 emission for the same range of water levels, we made a review of the published values for wet grasslands, peatlands and littoral wetlands of boreal and temperate climates (Fig. 6). Among the studies included, Bubier et al. (1993), Tsuyuzaki et al. (2001) and Kettunen et al. (2000) report on the presence of hummocks or tussocks. Tsuyuzaki et al. (2001) call their subarctic sites “grassy marshlands” though they are similar to fens according to the vegetation composition.

The review found that the seasonal or summer means of CH_4 emissions ranged from 2.3 to 315 mg m^{-2} day^{-1} for mean water levels ranging from −0.06 to +0.06 m. Considering particular water depths, CH_4 emissions were among the greatest from eutrophic lake littorals while intermediate values were reached for boreal and temperate peatlands. In comparison, CH_4 emissions were relatively small in the wet grassland investigated in our study.

Arithmetic means were calculated from our data for the purpose of Fig. 6. Nevertheless, they may not be the best estimates of the average values because the CH_4-emission data were not normally distributed in this study and the arithmetic means were considerably greater than the medians. Yet, the validity of the above comparison is supported also by the fact that the median CH_4 emissions found in our study (Table 2) were generally smaller than the median values for bogs and swamps reported by Le Mer and Roger (2001), which were about 30 and 50 mg m^{-2} day^{-1}, respectively.

The relatively low CH_4 emissions found at water levels near the soil surface in our study may be due to the lack of plant ventilating structures in the bulk soil -because much of the root biomass occurs within the hummock above the soil surface. In addition, some CH_4 transported from the bulk soil via the coarse roots might be oxidized by oxygen entering the roots inside the elevated hummock where aerobic conditions occur even when the bulk soil is saturated with water.

Studies by Nishikawa (1990) and Lawrence and Zedler (2011) indicate that tussock formation in graminoids is an adaptation to prolonged flooding of the habitat. As new tillers are formed frequently from buds on the base of the mother

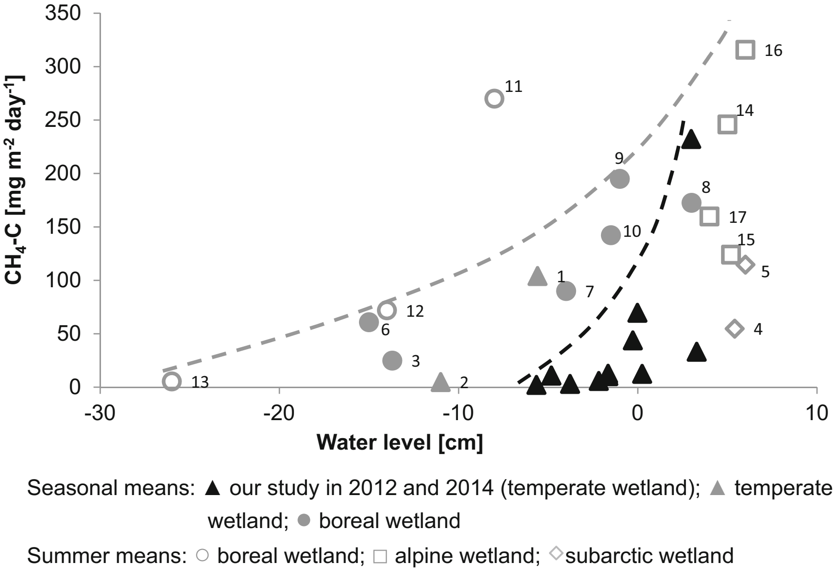

Fig. 6 Mean CH_4 fluxes from different wetland types with graminoid vegetation as related to mean water level. 1 – mesotrophic peatland (Juszczak and Augustin 2013); 2 – graminoid wetland (Askaer et al. 2011); 3 – moderately rich open low-shrub fen (Bubier et al. 1993); 4, 5 – grassy marshlands (Tsuyuzaki et al. 2001); 6, 7, 8, 9, − oligotrophic fen (Huttunen et al. 2003); 10 – oligotrophic bog – flark (Kettunen et al. 2000); 11, 12, 13 – eutrophic lake littoral (Siljanen et al. 2010); 14, 15, 16, 17 – alpine fen (Franchini et al. 2014). Dashed lines denote maximum fluxes for a given water table

tiller, further generations of tillers grow at higher elevations than the preceding ones and thus smaller parts of their roots are exposed to the deleterious effects of soil flooding. The flooding risk is reduced also for the accompanying plant species inhabiting the top of the hummocks as well as for microbial populations inside them. In the unflooded upper parts of the hummocks, aerobic conditions are promoted, CH_4 production is limited to anaerobic microzones saturated with water and CH_4 produced in deeper soil layers can be re-oxidized. These effects support the view of tussock-forming graminoids as ecosystem engineers (Crain and Bertness 2005).

Conclusions

The CH_4 fluxes from either the bare soil or the vegetated hummocks were significantly affected by water level and its recent dynamic. They were smaller when the water level was increasing than when it was decreasing. CH_4 fluxes were substantially enhanced by plants at water levels above the soil surface, when the basal parts of hummocks were flooded but the basal parts of shoots were exposed to the atmosphere.

The total CH_4 emissions from the studied wetland were smaller than reported from other studies from graminoid wetlands in temperate and boreal climates. This is attributed to the spatial structure of hummocks, in which shoots grow at elevations of 0.2 to 0.5 m above the soil surface and more than half of the belowground biomass occurs inside the hummock, i.e. also above the soil surface. At water levels near the soil surface, when much of the hummock is above water, the hummocks serve as aerobic micro-habitats in which plant structures avoid anaerobic stress and CH_4 produced in the bulk soil and vented via deep roots can be re-oxidized.

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