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Interacting effects of vegetation components and water table on methane dynamics in a boreal fen

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Abstract. Vegetation and hydrology are important controlling factors in peatland methane dynamics. This study aimed at investigating the role of vegetation components — sedges, dwarf-shrubs, and *Sphagnum* mosses — in methane fluxes of a boreal fen under natural and experimental water level drawdown conditions. We measured the fluxes during four growing seasons using static chamber technique in a field experiment where the role of the ecosystem components was assessed via plant removal treatments. The first year was a calibration year after which the water level drawdown and vegetation removal treatments were applied. Under natural water level conditions, plant-mediated fluxes comprised 68-78% of the mean growing season flux (1.95 ± 0.21 g CH4 m^{-2} month-1 from June to September), of which *Sphagnum* mosses and sedges accounted for 1/4 and 3/4, respectively. The presence of dwarf shrubs, on the other hand, had a slightly attenuating effect on the fluxes. In water level drawdown conditions, the mean flux was close to zero (0.03 ± 0.03 g CH4 m-2 month-1) and the presence / absence of the plant groups had a negligible effect. In conclusion, water level acted as a switch; only in high water level conditions vegetation regulated the net fluxes. The results are relevant for assessing the response of peatland fluxes in changing climatic conditions, as water level drawdown and the consequent vegetation succession are the major projected impacts of climate change on northern peatlands.

Keywords: climate change, dwarf shrubs, methane, peatland, sedges, Sphagnum

1. Introduction

Approximately one-third of all terrestrial carbon is stored in boreal and subarctic peatlands (e.g. Yu, 2012) . While generally acting as CO_2 sinks in current climatic conditions, pristine peatlands are also the largest natural source of CH_4 into the atmosphere (Fletcher et al., 2004; Bridgham et al., 2013; Kirschke et al., 2013; Ciais et al., 2014). The carbon sink function of peatlands is mostly due to the slow decomposition rate resulting from waterlogged, anaerobic conditions sustained by a high water table level, which simultaneously favour methane production. Methane is the end product of anaerobic decomposition by strictly anaerobic methanogenic archaea. It is released from the peat into the atmosphere via diffusion through the peat column, ebullition or plant-mediated transport (Lai, 2009). A considerable part, from 20 to up to 90% (Le Mer and Roger, 2001; Pearce and Clymo, 2001; Whalen,

2005) of the methane diffusing through the upper, aerobic part of the peat layer is oxidized to CO_2 by methanotrophic bacteria (MOB) before reaching atmosphere.

Vegetation is a major factor controlling peatland methane fluxes (Koelbener et al., 2010; Ström et al., 2005, 2012). Fresh root litter and exudates are important substrates for the methanogenic microbes, and a significant proportion of the methane is formed from this easily available organic matter instead of from old, recalcitrant peat (Koelbener et al., 2010; Ström et al., 2012). Therefore, methane fluxes have a strong, positive correlation with the CO_2 uptake (Bellisario et al., 1999; Christensen et al., 2000; Rinne et al., 2018), since higher primary productivity leads to a higher input of substrate. Of the vegetation components, deep-rooting aerenchymatous species such as sedges (Cyperaceae) and aerenchymatous herbs are especially important (Leppälä et al., 2011; Ward et al., 2013). In sedge-dominated wetlands, most of the methane is released through vascular plants (Kelker and Chanton, 1997; Ding et al., 2004; Ström et al., 2005), thus bypassing the aerobic peat layer where methane oxidation takes place. On the other hand, oxygen transport through the aerenchyma to the rhizosphere may inhibit methane production (Whalen and Reeburgh, 2000; Fritz et al., 2011) and stimulate methane oxidation (King, 1994; Popp et al., 2000). The net effect of the presence of aerenchymatous species on methane fluxes is positive in most cases (Bellisario et al., 1999; Greenup et al., 2000; Rinnan et al., 2003; Couwenberg and Fritz, 2012; Ward et al., 2013), although opposite results have also been reported (Roura-Carol and Freeman, 1999; Strack et al., 2006). Although the influence of the non-aerenchymatous species on the fluxes has been studied relatively little, Gray et al. (2013) showed that plant functional groups based on more complex traits than those related to aerenchyma were good proxies of CH_4 flux. Dwarf shrubs are generally shallow rooted (Korrensalo et al., 2018a) and have a negligible methane transport capacity (Shannon et al., 1996; Garnet et al., 2005) compared to deep-rooting aerenchymatous species. In plant removal experiments, the presence of shrubs has been shown to decrease CH_4 fluxes (Ward et al., 2013; Robroek et al., 2015). *Sphagnum* mosses, in turn, have an impact on CH_4 oxidation as they host partly endophytic methanotrophs in the water-filled, hyaline cells of their leaves and stem (Raghoebarsing et al., 2005; Larmola et al., 2010; Putkinen et al., 2012).

Water level regulates the volume ratio of the aerobic and anaerobic peat and, consequently, the extent of the methane production and oxidation zones. Therefore, a positive correlation between the water level and methane fluxes has been reported in numerous studies (Moore and Roulet, 1993; Laine et al., 2007a; Pearson et al., 2015; Turetsky et al., 2014; Chimner et al., 2017). However, the relationship between the water level and methane fluxes is complex due to the vegetation – water level interaction. Because the plant communities in the wettest habitats are often associated with the sparsest vascular plant cover and lowest productivity (Waddington and Roulet, 2000; Laine et al., 2007b; Riutta et al., 2007b), less substrate for methane production is available in those communities. In the dry end of the water level gradient, fewer the roots reach the anaerobic layer of the peat (Waddington et al., 1996; Kutzbach et al., 2004). Hence, methane fluxes may also show a unimodal relationship to water level (Strack et al., 2004; Brown et al., 2014) or no relationship at all (Rask et al., 2002; Korrensalo et al., 2018b).

https://doi.org/10.5194/bg-2019-350
Preprint. Discussion started: 1 October 2019

In this study, we aim to quantify the contribution of the different components of the fen plant community, namely sedges, dwarf shrubs, *Sphagnum* mosses, and the underlying peat, to the methane fluxes in wet and dry conditions. We applied a factorial design of plant removal and water level drawdown treatments.

2. Materials and methods

2.1. Study site

The study was carried out at Lakkasuo peatland complex, an eccentric raised bog situated on the southern boreal vegetation zone (Ahti et al., 1968) in Southern Finland (61°47' N; 24°18' E). Annual precipitation in the region totals 710 mm, of which about a third falls as snow. The average temperatures for January and July are - 8.9 and 15.3 °C, respectively (Juupajoki-Hyytiälä weather station, Drebs et al. 2002).

The study site was situated on a nutrient-poor, oligotrophic, treeless fen. Surface topography in the site is uniform, mostly lawn. Sedges dominate the field layer where the most abundant species is *Carex lasiocarpa* Ehrh., other typical sedges are *Eriophorum vaginatum* L. and *Trichophorum cespitosum* (L.) Hartm. In addition to sedges, dwarf shrubs comprise a considerable proportion of the field layer. The most abundant shrub is the deciduous *Betula nana* L. and other typical shrubs are ericaceous *Andromeda polifolia* L. and *Vaccinium oxycoccos* L. The moss layer forms a continuous carpet dominated by *Sphagnum papillosum* Lindb., *S. fallax* (Klinggr.) Klinggr. and *S. flexuosum* Dozy & Molk.

2.2. Experimental design

The study was carried out during four growing seasons from 2001 to 2004. The study site was divided into two subsites, namely the wet and the drier water level drawdown (WLD) subsite, by surrounding the WLD subsite with a shallow ditch that lowered the water level by an average 17 ± 1.6 cm (22 ± 3.0 cm in 2002, 12 ± 3.4 cm in 2003 and 16 ± 1.9 cm in 2004). The first season of the study, 2001, served as a calibration year without the WLD treatment, which was implemented in April 2002.

We studied the contribution of the ecosystem components to the net CH_4 fluxes in wet and dry conditions by means of plant removal treatments. In the site, we established permanent sample plots of 56 cm × 56 cm consisting of:

- peat, *Sphagnum* mosses, sedges and dwarf shrubs (PSCD, intact vegetation, n = 8 in the wet subsite and n = 8 in WLD subsite)
- peat, *Sphagnum* mosses and sedges (PSC, dwarf shrubs removed, n = 5 + 4)
- peat and *Sphagnum* mosses (PS, sedges and shrubs removed, n = 3+3)
- peat (P, all vegetation removed, n = 4 + 4).

The plant removal treatment plots (PSC, PS and P) were established April 2002.. In the plant removal treatment plots vascular plants were cut with scissors to the level of the moss (PS plots) or peat (P plots) surface and their above-ground litter was removed. In the bare peat plots the top 1.5 cm of the *Sphagnum*

https://doi.org/10.5194/bg-2019-350
Preprint. Discussion started: 1 October 2019

moss carpet was cut off with scissors. All emerging regrowth was clipped off once a week as necessary. Over the course of the study, progressively less clipping was needed, hardly any in 2004. Prior to methane flux measurements, sedge stubble in P and PS plots was treated with paraffin wax to seal the aerenchymatous pathway of methane.

2.3. Measurements

CH_4 fluxes were measured using the closed chamber method. A stainless steel collar (56 × 56 × 30 cm) was permanently inserted into each sample plot prior to the start of the study. The collars had a water groove to allow chamber placement and air-tight sealing during the measurement. For the flux measurements, an aluminium chamber of 60 × 60 × 30 cm was placed on the water groove of the collar. After the chamber placement, a vent on the chamber roof that ensured pressure equilibration was sealed with a septum plug. A battery-operated fan circulated the air inside the chamber. A 40-ml air sample was drawn into a polypropylene syringe at 5, 15, 25 and 35 minutes after closure. The samples were stored at +4°C before analysis, which was carried out within 36 hours. Samples were analyzed with a HP-5710A gas chromatograph (GC) from 2001 to 2003 and with a HP-5890A GC in 2004. Both GCs were equipped with a 1-ml loop, 6×1/8" packed column (Hayesep Q in HP-5710A; Poropak Q in HP-5890A) and flame ionization detector. The carrier gas was helium with a flow rate of 30 mL min^{-1}. Column and detector temperatures were 40°C and 300°C, respectively. The precision of the analysis was ±0.16%, determined as the coefficient of variation of the replicate samples.

To relate the fluxes to prevailing environmental conditions, peat temperatures at 5, 10, 20 and 30 cm below the moss surface and water level in a perforated tube adjacent to each plot were measured during the flux measurements. Air and peat temperatures and precipitation were also continuously recorded in the weather station at the site. Green leaf area index (LAI) of each vascular plant species in each plot was determined with the method of Wilson et al. (2007) from April until November, as a product of the total number of leaves (counted monthly) and the average leaf size of marked individuals (measured every two weeks). Species-specific Gaussian curves were fitted to the observations to describe the continuous development of LAI throughout the season. LAI of different species were summed up to sedge, dwarf-shrub and total LAI (LAI_C, LAI_D and LAI_T, respectively). Moss cover at each plot was visually estimated annually.

In addition to CH_4 exchange, CO_2 exchange was measured in the study site. The methods and results are reported elsewhere (Riutta et al., 2007a) in more detail, but some CO_2 exchange estimates are used here to study the relationship between the CO_2 and CH_4 fluxes. In summary, net ecosystem CO_2 exchange (NEE) was measured weekly / biweekly by employing the closed chamber technique in the same plots and during the same period as the CH_4 fluxes. Measurements were carried out in both light and dark, which enabled the partitioning of the fluxes into gross photosynthesis and ecosystem respiration. We constructed nonlinear regression models for photosynthesis and respiration, with water level, temperature and LAI as explanatory factors, separately for each vegetation treatment, to reconstruct the fluxes for the whole growing season.

https://doi.org/10.5194/bg-2019-350
Preprint. Discussion started: 1 October 2019

2.4. Data analyses

CH_4 flux was calculated as the linear change in CH_4 concentration as a function of time by fitting a least-squares regression line. Of the 1300 measurements, <0.5% were rejected due to clear errors, such as leakage or problems in the GC analysis, and 2% were classified as episodic fluxes.

To reconstruct seasonal (June-September) estimates for each sample plot, the biweekly measured fluxes were linearly interpolated between measurement days and the obtained daily values were integrated. In the interpolation, rejected values and episodic fluxes were replaced with the median flux of the corresponding vegetation and water level treatment on the same measurement day. The impact of the episodic fluxes on the seasonal flux was taken into account by using the episodic values as the CH_4 flux estimates of the day they were measured. We used linear mixed effect models to test the impact of the plant removal treatments and the WLD treatment on WL, LAI and CH_4 flux. First, we tested the differences in WL, LAI_C, LAI_D, LAI_T and CH_4 flux between the wet and WLD subsites before the WLD treatment was applied (year 2001) and over the years after the WLD treatment (2002-2004), with WLD treatment, year and their interaction as potential fixed predictors. This model included only the plots with intact vegetation (PSCD). The wet subsite in 2001 was the constant against which WLD and other years were compared. Therefore, the difference between the wet and WLD treatment in the model describes the pre-treatment difference among the two subsites in calibration year 2001, and the interaction between WLD treatment and years 2002-2004 describe the impact of WLD after the treatment. Plot and date were included as crossed random effects.

Second, we tested the impact of plant removal on CH_4 flux over the years and the interaction of the plant removal treatments with the WLD treatment with data from years 2002-2004 (no plant removal treatments in 2001). For each year separately, we fitted a model with plant removal treatments, WLD treatment and the interaction between them as potential fixed predictors. A conditional F-test was used to test in each case if the full model with all fixed predictors and their interactions was significantly better ($p<0.05$) than a simpler model. Plot and date were included as crossed random effects. Resulting models are reported in Table 2. The models were fitted using the function lmer of package lme4 (Bates et al., 2015) of RStudio version 1.1.383.

3. Results

3.1. Impact of the water level drawdown

The pre-treatment water level did not differ between the wet and WLD subsites ($p=0.174$, comparison between wet and WLD treatment during the calibration year 2001) (Fig. 1a, Table 1). Following the drainage in April 2002, the water level was significantly lower in the WLD subsite ($p < 0.001$, interaction between WLD and year 2002). The WLD treatment lowered the water level by approximately 17 cm, except in July and August 2003 when a severe drought lowered the water level below the ditch, resulting in similar water levels in wet and WLD subsites. In the wet subsite, the water level during the years 2001

https://doi.org/10.5194/bg-2019-350
Preprint. Discussion started: 1 October 2019

and 2004 was similar to the long-term average of the site (Laine 2004), approximately 5 to 10 cm below the moss surface (Table 1) (Laine et al. 2004). During July and August 2002 and 2003, however, the water level was lower than the long-term average. More information on the weather conditions during the study is given in Riutta et al. (2007b).

Prior to the drainage, vegetation composition in the plots with intact vegetation (PSCD) was similar in both subsites (Table 1, Fig. 1b). In the mixed effects model, LAI_C, LAI_D and LAI_T did not differ between wet and WLD subsites in year 2001 (p-values 0.996, 0.656 and 0.878, respectively). In 2001 the peak season average LAI_T was approximately 1.0 m^2 m^{-2}, of which sedges composed 70%. The mean *Sphagnum* cover was 80%. By the third year since WLD 2004 LAI_C had decreased ($p<0.001$) and LAI_D increased ($p<0.001$) in the WLD subsite, resulting in an overall decrease in LAI_T ($p=0.007$) (Table 1, Fig. 1b).

In the PSCD plots, the pre-treatment methane fluxes did not differ between the wet and WLD subsite ($p=0.654$) (Fig. 1c). After the treatment, in 2002-2004, fluxes were significantly lower in the WLD than in the wet subsite ($p<0.001$ for all years). During the three-year WLD treatment, the mean flux was approximately 51 and 7.0 mg CH_4 m^{-2} d^{-1} in the wet and WLD subsites, respectively.

3.2. Impact of the plant removal treatments

Plant removal treatments did not lead to major changes in vegetation composition beyond the clipped target groups: the removal of the vascular plant did not affect the *Sphagnum* moss cover, and the removal of the dwarf shrubs did not change the LAI of sedges LAI_C was similar in PSC and PSCD plots (data for 2004 shown in Table 1) during all years in the wet subsite and during 2003 and 2004 in the WLD subsite (all p-values >0.05). LAI_C was higher in the PSC plots than in the PSCD plots in the WLD subsite in 2002 ($p=0.016$).

The first two years of the plant removal treatments were characterised by treatment artefacts caused by the initial disturbance of the clipping and the creation of unnatural amount of new root necromass. In the wet subsite, CH_4 fluxes were higher in the plant removal plots (P, PS and PSC) than in the intact plots (PSCD) during the first season of the removal treatments (2002), in some cases almost triple ($p<0.05$ for all treatments, Fig. 2, upper panels). The fluxes in the plant removal treatment plots also showed a stronger seasonal pattern and larger spatial variation. After the first year of removal treatments the fluxes of the P, PS and PSC plots decreased, and in 2003 P plots had a similar CH_4 flux than the intact plots ($p=0.908$), while PS and PSC plots still had a higher flux than PSCD plots ($p=0.033$ and $p=0.005$, respectively).

By the third year of the plant removal treatments (2004), the treatments had stabilised, and the contribution of the vegetation components to the fluxes could be quantified. The fluxes in all treatments showed a seasonal pattern similar to that of the intact plots. Bare peat plots had lower fluxes than the intact PSCD plots ($p<0.001$). Fluxes of the PSC plots (shrubs removed) were marginally significantly

https://doi.org/10.5194/bg-2019-350
Preprint. Discussion started: 1 October 2019

higher ($p=0.060$) than those of the PSCD plots (shrubs present). In WLD conditions, the fluxes in the plant removal plots (P, PS and PSC) were mostly lower than the fluxes in the intact PSCD plots during all three vegetation treatment years (Fig. 2, lower panel), but the differences were not significant (Table 2b). WLD and plant removal treatments had a significant interaction: in 2004 WLD lowered the fluxes more in PSC and PSCD plots than in the P plots and more in PSC plots than in the PS plots ($p<0.05$ for the interaction terms). Seasonal fluxes visualize the patterns tested with the nonlinear mixed effect models: in the WLD subsite fluxes were lower than in the wet subsite in all plant removal treatments (Fig. 3b). In wet conditions, the seasonal flux of the P and PS plots was lower than that of the PSCD and PSC plots in which vascular plants were present (Fig. 3a). Taking the fluxes from bare peat plots as a baseline, the presence of vegetation enhanced the fluxes. Compared with the situation of sedges and *Sphagna* present (PSC), the presence of shrubs (PSCD) seemed to slightly attenuate the fluxes (Fig. 3b, c). In WLD conditions, the differences between plant removal treatments were negligible. The differences between the plant removal treatments can be used as an estimate of the contribution of each plant group to the total flux, although due to the propagation of the errors, uncertainty in these estimates is large. In normal hydrological conditions, plant-mediated flux accounted for 68% ± 23% (comparison of P and PSCD plots) or 78% ± 17% (comparison of P and PSC plots) of the total growing season flux, of which *Sphagnum* mosses and sedges accounted for approximately ¼ and ¾, respectively (Fig. 3c).

The seasonal methane fluxes displayed a clear positive relationship with the seasonal net CO_2 flux (Fig. 4). The relationship was similar among the plant removal treatments in wet and dry conditions. However, the plots with intact vegetation (PSCD) were an exception; they had lower CH_4 fluxes than could have been expected based on their net CO_2 flux, pointing towards the potential suppressing effect of shrubs on CH_4 emissions.

https://doi.org/10.5194/bg-2019-350
Preprint. Discussion started: 1 October 2019

4. Discussion

4.1. The effect of the plant types and substrate on the methane fluxes in natural water level conditions

In line with the previous studies, the plant removal treatments of this study indicated that sedges were the most important plant group in regulating CH_4 fluxes. In other sedge-dominated sites, plant-mediated flux has accounted for 75 to 97% of the total flux (Schimel, 1995; Kelker and Chanton, 1997; Ström et al., 2005; Sun et al., 2012; Noyce et al., 2014) and plant removal experiments have shown that of different plant functional types, removal of graminoids cause the largest decrease on methane production and flux (Ward et al., 2013; Robroek et al., 2015). Compared to the bare peat surfaces, the presence of *Sphagnum* mosses seemed to have a slight, although not statistically significant, enhancing effect on the methane fluxes, similarly to the results of Roura-Carol and Freeman (1999). King et al. (1998) found the presence of mosses to have a slightly attenuating effect on the fluxes, while Greenup and others (2000) did not find significant differences in fluxes after *Sphagnum* removal. Based on this, the CH_4 oxidation by the loosely symbiotic methanotrophs within *Sphagnum* mosses (Raghoebarsing et al., 2005; Larmola et al., 2010; Putkinen et al., 2012) seems to play a minor role in CH_4 dynamics in our site.

Similarly to Ward et al. (2013), we found that the presence of shrubs seemed to have a slightly attenuating effect on the fluxes under natural water level conditions. Robroek et al. (2015) made a similar finding with potential methane production. In contrast, an aerenchymatous shrub, *Myrica gale*, supported similar potential methane production than a sedge, *Carex aquatilis*, and did not suppress methane flux (Strack et al., 2017). Furthermore, in line with the attenuating effect of shrubs, the methane flux: NEE ratio was lower in the plots with intact vegetation (PSCD, shrubs present) than in the other vegetation treatments. Mechanisms behind that might relate to impact of shrubs on the biomass allocation of sedges or on soil chemistry. A study on the competitive ability and biomass allocation of a wetland grass, *Molinia caerulea*, revealed that *M. caerulea* allocated more biomass to the roots when it did not face competition by shrubs (Aerts et al., 1991). Similarly, in our study, sedges in the plots where shrubs were removed may have allocated more biomass to the roots than the sedges growing in the sedge and shrub mixture. As a result, methanogenic microbes may have benefited from the higher substrate availability in the shrub removal plots (PSC). CH_4 production has a negative relationship and CH_4 oxidation has a positive relationship with the concentration of certain woody lignin compounds in peat pore water (Yavitt, 2000). In our study, this may be the reason behind the lower fluxes in the presence of the arboreals. The results concerning the attenuating effect of shrubs on methane fluxes are, however, only indicative and further, process orientated research is needed.

4.2. Delay in the plant removal treatment effect

We observed a considerable disturbance in the fluxes following the plant removal treatments. In other clipping studies in which the shoots were cut above the water level clipping either increased the CH_4 flux during the first growing season after clipping (Schimel, 1995), had no effect (Kelker and Chanton, 1997;

https://doi.org/10.5194/bg-2019-350
Preprint. Discussion started: 1 October 2019

Biogeosciences Discussions

Greenup et al., 2000) or decreased the flux (Waddington et al., 1996; Rinnan et al., 2003). The removal of the above-ground parts of vascular plants led to the gradual death of the below-ground parts and, thereby, a peak in the amount of available substrate. Methanogenesis in the study site may have been substrate limited (Bergman et al., 1998; Rinne et al., 2007), which could explain the initially high fluxes in the plant removal plots. The mass loss of *Carex* roots and rhizomes is only 10 to 45% during the first 12 months of decomposition, although the litter quality deteriorates (Scheffer and Aerts, 2000). However, after two years the mass loss can be as much as 75% of the original mass (Thormann et al., 2001), which gives more confidence in the results of the third year of the plant removal treatments. King and others (1998) likewise reported the effects of the plant removal two years after the treatment began. Shrub litter, especially below-ground litter, decomposes slower than sedge litter (Moore et al., 2007). On the other hand, the shallow roots of shrubs decompose in oxic conditions while at least the deepest sedge roots decompose in anoxic conditions, thus counteracting the differences in litter quality. Even two years after the start of the vegetation removal treatments, some shrub roots still probably remained. However, they were mostly located above the methane production zone.

4.3. Water level regulates the role of the vegetation

Experimental water level drawdown has been used to mimic climate change impact on northern peatland methane fluxes in mesocosm (Freeman et al., 1992; Blodau et al., 2004; Dinsmore et al., 2009) and in the field studies ranging from bogs to rich fens (Laine et al., 2007a; Strack and Waddington, 2007; Turetsky et al., 2008; Ballantyne et al., 2014; Munir and Strack, 2014; Pearson et al., 2015; Peltoniemi et al., 2016; Chimner et al., 2017; Olefeldt et al., 2017). In line with our results, all these studies report some level of decrease in CH_4 flux due to WLD ranging from 3 to ~20cm. Together with temperature and vegetation, water table is a major regulator of CH_4 flux (Lai, 2009; Turetsky et al., 2014). However, the mechanistic understanding of this process is still limited. While Strack et al. (2004) found only small differences in the methane production and consumption potentials between control and WLD sites, and thus attributed the the decrease in fluxes mainly to the change in the volume ratio of the anaerobic and aerobic zones, Yrjälä et al. (2011) and Peltoniemi et al. (2016) found that WLD had a stronger impact on emissions through decreasing CH_4 production, than through increasing oxidation,

In this study, the presence or absence of the plant types had no effect on the CH_4 flux in the WLD conditions. This supports the findings by Waddington et al. (1996) as well as Strack et al. (2006) that the impact of the vegetation on the fluxes is strongly dependent on the water level conditions. Our results showed that water level acts as a switch; vegetation is a major controlling factor of the peatland methane dynamics, but only in wet conditions.

5. Conclusions

Vegetation, sedges in particular, regulates the level of peatland methane fluxes in normal hydrological conditions, but this vegetation control is strongly dependent on the water level. In water level drawdown conditions methane fluxes are significantly lowered, practically to zero, and vegetation composition has

https://doi.org/10.5194/bg-2019-350
Preprint. Discussion started: 1 October 2019

no influence on the fluxes. The results are relevant for assessing the response of peatlands to changing climatic conditions, as water level drawdown and the consequent vegetation changes are the major projected impacts of climate change on northern peatlands.

Competing interests

The authors declare that they have no conflict of interest.

Data availability

The data associated with the manuscript will be published in PANGAEA repository upon publication. On request, the data can also be obtained from the corresponding author.

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https://doi.org/10.5194/bg-2019-350
Preprint. Discussion started: 1 October 2019

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Table 1. Growing season average (standard deviation) water level (WL) relative to moss surface (unit is cm), negative values indicating water level below the surface, growing season peak LAI of sedges (LAI_C) and dwarf shrubs (LAI_D), and projection cover of *Sphagnum* mosses (Spha) (units are m^2 m^{-2}) in different plant removal treatments in wet and WL drawdown subsites. Year 2001 was a calibration year without the WL drawdown and plant removal treatments, which were implemented in 2002. Vegetation treatments: PSCD - plots with intact vegetation, consisting of peat, *Sphagnum* mosses, sedges and shrubs; PSC - plots consisting of peat, *Sphagnum* mosses and sedges (shrubs removed); PS - plots consisting of peat and *Sphagnum* mosses (shrubs and sedges removed), P- plots consisting of bare peat (all vegetation removed).

		Control				WL drawdown			
Year	Vegetation	WL	LAI_C	LAI_D	Spha	WL	LAI_C	LAI_D	Spha
2001	PSCD	-7 (4)	0.7 (0.3)	0.2 (0.1)	0.8 (0.2)	-5 (3)	0.7 (0.3)	0.3 (0.2)	0.8 (0.1)
2004	PSCD	-10 (4)	0.6 (0.2)	0.3 (0.1)	0.9 (0.1)	-24 (6)	0.3 (0.1)	0.3 (0.1)	0.6 (0.2)
	PSC	-10 (5)	0.7 (0.5)		0.7 (0.2)	-29 (7)	0.8 (0.3)		0.7 (0.3)
	PS	-11 (3)			0.8 (0.2)	-26 (7)			0.7 (0.2)
	P	-7 (4)				-21 (8)			

Table 2. Parameter estimates of the linear mixed-effects model describing (a) the differences in CH_4 flux, water table (WT) and total, sedge and dwarf-shrub leaf area index (LAI_T, LAI_C and LAI_D) between control (WLD0) and water level drawdown (WLD1) subsites and years before (2001) and after (2002-2004) the WLD treatment in plots without vegetation removal and b) the differences in CH_4 flux between the vegetation removal treatments in years 2002-2004. **Vegetation treatments: PSCD – intact vegetation, PSC - plots consisting of peat, *Sphagnum* mosses and sedges (shrubs removed); PS - plots consisting of peat and *Sphagnum* (sedges and shrubs removed); P - plots consisting of bare peat (all vegetation removed).**

(a)	WT			LAI_T			LAI_C			LAI_D			CH_4 flux		
Fixed part	**Coeff.**	**SE**	**P-value**	**Coeff.**	**SE**	**P-value**	**Coeff.**	**SE**	**P-value**	**Coeff.**	**SE**	**P-value**	**Coeff.**	**SE**	**P-value**
Constant (WLD0, Year 2001)	-6.9	2.8	0.018	0.6	0.1	<0.001	0.5	0.1	<0.001	0.2	0.04	<0.001	3.1	0.5	<0.001
WLD1	1.6	1.1	0.174	0.02	0.1	0.878	0.0006	0.1	0.996	0.02	0.04	0.656	0.2	0.3	0.654
Year 2002	-8.2	3.6	0.030	0.2	0.1	0.118	0.2	0.1	0.031	-0.03	0.03	0.366	-0.3	0.6	0.571
Year 2003	-14.2	3.7	<0.001	-0.02	0.1	0.879	-0.007	0.1	0.952	-0.02	0.03	0.642	-2.0	0.6	0.002
Year 2004	-2.1	3.5	0.550	-0.1	0.1	0.364	-0.1	0.1	0.214	0.01	0.03	0.648	-1.3	0.6	0.034
WLD1*Year 2002	-16.6	0.7	<0.001	-0.06	0.05	0.173	-0.1	0.04	0.029	0.03	0.01	0.006	-2.3	0.3	<0.001
WLD1*Year 2003	-11.3	0.7	<0.001	-0.06	0.05	0.192	-0.1	0.05	0.034	0.04	0.01	0.006	-1.1	0.3	<0.001
WLD1*Year 2004	-16.3	0.7	<0.001	-0.1	0.05	0.007	-0.2	0.05	<0.001	0.05	0.01	<0.001	-2.1	0.3	<0.001
Random part															
SD (Measurement day)	7.5			0.28			0.22			0.06			1.2		
SD (Plot code)	2.0			0.25			0.21			0.09			0.5		
Residual SD	2.9			0.19			0.19			0.05			1.1		

(b)	2002			2003			2004		
Fixed part	**Coeff.**	**SE**	**P-value**	**Coeff.**	**SE**	**P-value**	**Coeff.**	**SE**	**P-value**
Constant (PSCD, WLD0)	3.8	1.1	<0.001	1.4	0.3	<0.001	1.5	0.4	<0.001
P	2.8	1.3	0.040	0.1	0.5	0.908	-0.8	0.4	0.056
PS	6.0	1.6	0.001	1.3	0.6	0.033	1.1	0.4	0.004
PSC	7.2	1.5	<0.001	1.5	0.5	0.005	0.4	0.4	0.373
WLD1	-2.2	1.0	0.036	-1.0	0.4	0.022	-1.3	0.4	0.002
P*WLD1	-4.4	1.8	0.020	-0.4	0.7	0.622	0.7	0.5	0.212
PS*WLD1	-8.2	1.9	<0.001	-1.6	0.8	0.049	-1.1	0.5	0.050
PSC*WLD1	-9.0	1.6	<0.001	-1.9	0.7	0.009	-0.6	0.5	0.256
Random part									
SD (Measurement day)	1.6			0.7			0.9		
SD (Plot code)	3.0			0.7			0.4		
Residual SD	3.8			1.3			0.9		

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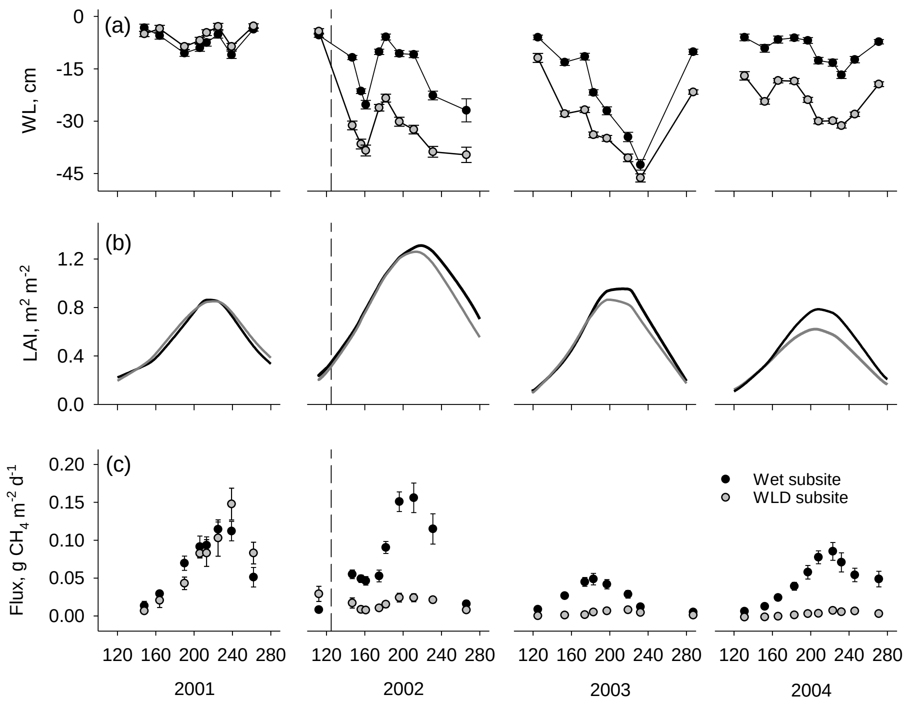

Figure 1. Mean a) water level (WL), b) leaf area index (LAI), and c) CH_4 flux in plots with intact vegetation in wet and water level drawdown (WLD) subsites. Error bars are standard errors of the mean. Units on the x-axis give the day of year. The start of the water level drawdown treatment is indicated with the vertical dashed line in 2002. Water level is negative when it is below the moss surface. Positive CH_4 fluxes indicate emission to the atmosphere.

570

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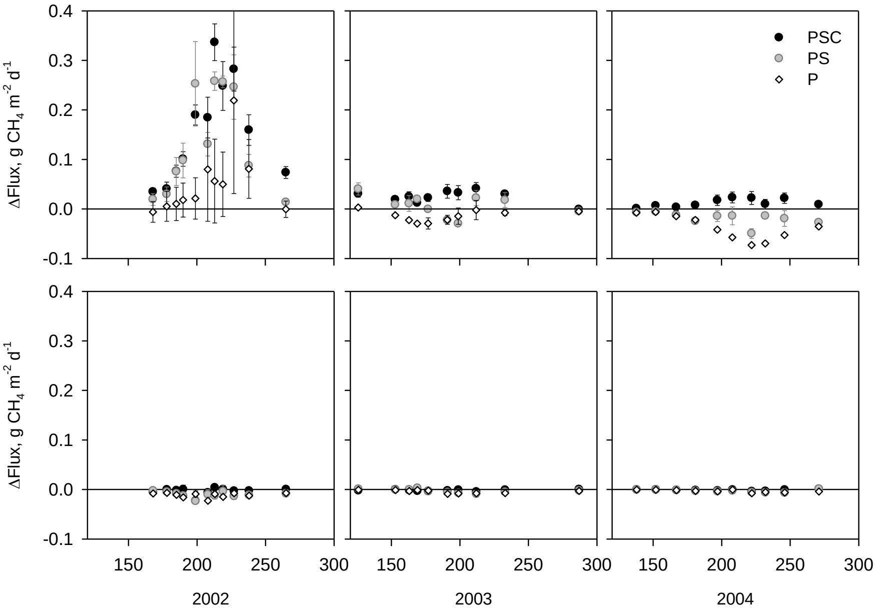

580 **Figure 2. Difference of the measured CH_4 fluxes in plots with plant removal treatments and the mean flux in the plots with intact vegetation on each measurement day in control subsite (upper panels) and water level drawdown subsite (lower panels). Positive values indicate that fluxes in the plant removal treatment plots are higher than in the intact plots. Units on the x-axis give the day of year. Error bars are standard errors of the mean. Vegetation treatments: PSC - plots consisting of peat, *Sphagnum* mosses and sedges (shrubs removed); PS - plots consisting of peat and *Sphagnum* (sedges and shrubs removed); P - plots consisting of bare peat (all vegetation removed). Intact plots consisted of peat, *Sphagnum* mosses, sedges and shrubs. Removal treatments were established in 2002.**

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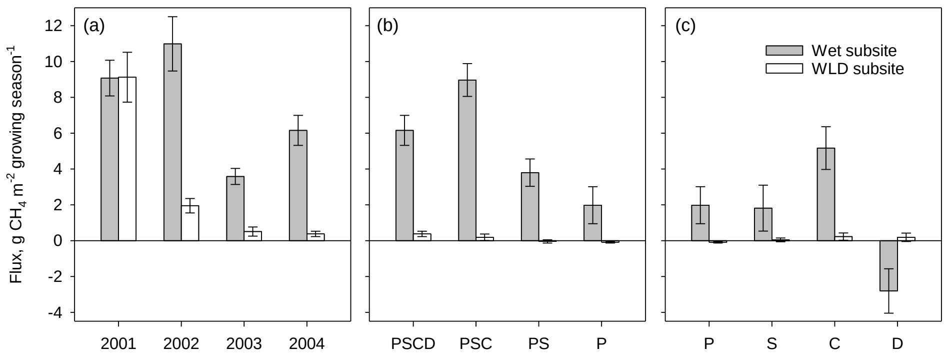

Figure 3. Seasonal (June-September) CH_4 flux (mean ± 1 standard error) in wet and water level (WLD) drawdown subsites a) in plots with intact vegetation (PSCD) during the four study years (2001 was a calibration year before the implementation of the WLD treatment), b) in different plant removal treatments plots in 2004 and c) by each plant group, the contribution of which to the total flux in 2004 was estimated from differences between the different plant removal treatments. Plant removal treatments in (b): PSCD - plots with intact vegetation, consisting of peat, *Sphagnum* mosses, sedges and shrubs; PSC - plots consisting of peat, *Sphagnum* mosses and sedges (shrubs removed); PS - plots consisting of peat and *Sphagnum* mosses (shrubs and sedges removed), P - plots consisting of bare peat (all vegetation removed). Plant groups in (c): P – bare peat, S – *Sphagnum* mosses, C – sedges, D – dwarf shrubs.

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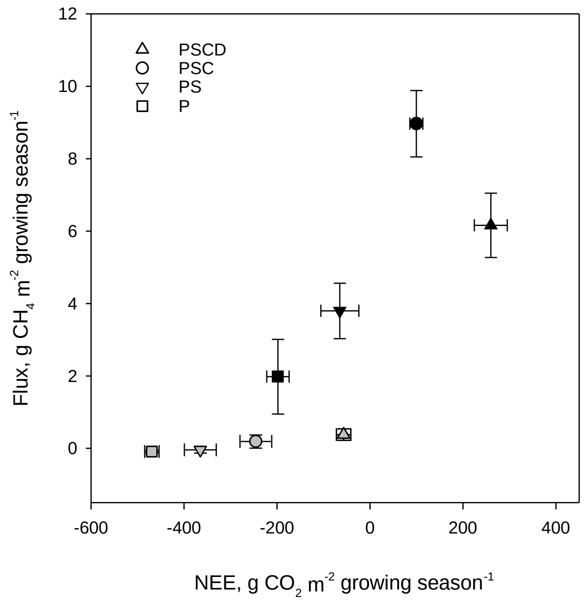

Figure 4. The relationship between the net ecosystem CO_2 uptake (NEE) and methane flux during the growing season 2004 in the different plant removal treatments in wet (black) and water level drawdown (grey) subsites. The values are means ± 1 standard error by each plant removal treatment – water level treatment combination. Vegetation treatments: PSCD - plots with intact vegetation, consisting of peat, *Sphagnum* mosses, sedges and shrubs; PSC - plots consisting of peat, *Sphagnum* mosses and sedges (shrubs removed); PS - plots consisting of peat and *Sphagnum* mosses (shrubs and sedges removed), P- plots consisting of bare peat (all vegetation removed). NEE is positive when the fen is a net sink of atmospheric CO_2. Methane flux is positive when the fen is a source of CH_4 to the atmosphere.

610