

Relationships between Vegetation Succession, Pore Water Chemistry and CH₄ and CO₂ Production in a Transitional Mire of Western Siberia (Tyumen Oblast)

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Abstract We present data on a transitional mire in South-Western Siberia that evolved from early thermokarst lake succession. The vegetation of the mire shows a remarkable zonation from the edges to the center. Vegetation, peat characteristics, pH and electric conductivity were recorded at 10 sites along a transect of 1.5 km. At two of the transect points with contrasting vegetation and succession stage (floating mat vs. birch forest) pore water peepers were inserted once for 3 weeks and pore waters of the upper 60 cm were analyzed for major anions and cations, and dissolved CO₂ and CH₄ concentrations. Pore waters substantially differed between the floating mat and the birch forest regarding base cation chemistry and pH whilst nutrient availability was comparable. Compared to literature, depth integrated productions (DIPs) of CH₄ and CO₂ were high for both sites but three times higher for the floating mat (CH₄ 10.89 mmol m⁻² d⁻¹, CO₂ 34.19 mmol m⁻² d⁻¹). Along with other reasons, the higher DOC input at this location seems to be responsible for the higher DIP by fueling higher microbial activity. We discuss

driving factors for biogeochemical differences between both sites and draw conclusions on CH₄ production during mire evolution.

Keywords Mire evolution · Western Siberia · Methane production · Biogeochemistry · Base cations · DOC

Introduction

The Western Siberian Lowland (WSL) is a mire region of outstanding importance and uniqueness. About 2/3 of the WSL are situated in the forest-palustrine zone, which accounts for an area of 1,800,000 km² (Kremenetski et al. 2003). The WSL includes two of the world's largest watersheds feeding the Arctic Ocean, namely the rivers Ob and Yenisey and its tributaries, and is a flat plain at elevations of about 25–95 m a.s.l which promoted excessive mire development (Turunen et al. 2001; Keddy et al. 2009).

Mire formation in the WSL began in the early Holocene during a phase of rapid warming after the Last Glacial Maximum (LGM). Permafrost melting led to round-shaped thermokarst lakes that began to paludificate due to water-level lowering under warmer climatic conditions. The lacustrine evolution of mires in the WSL is often indicated by lake sediments (e.g. Gytia) underlying the peat layers (Peregon et al. 2007).

There is no doubt about the importance of the WSL in the global carbon cycle. For example, the Great Vasyugan is the largest coherent mire in the northern hemisphere (Keddy et al. 2009; Kirpotin et al. 2009). Approximately 40 % of the world's peat deposits are stored in Siberian mires (Peregon et al. 2009); latest estimates propose that the carbon pool in the mires of the WSL is about 70.2 Pg, which accounts for

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26 % of all carbon sequestered by terrestrial ecosystems since the LGM (Sheng et al. 2004; Smith et al. 2004). However, the actual state of mire growth in the WSL is unclear and a subject of recent debate. While some authors promote a still lasting so called ‘progressive’ peatland development since the early Holocene (cf. Keddy et al. 2009), others argue that lateral extension of peatlands has stopped within the last 3000 years (e.g. Kremenetski et al. 2003). However, there is large uncertainty as the number of surveyed peat cores is low and insufficient for sound estimations (Gorham 1991; Loisel et al. 2014). With respect to underlying processes driving carbon fixation and release, even less studies are available for this area (Flessa et al. 2008; Avagyan et al. 2014).

For northern regions of Western Siberia large-scale permafrost melting and subsequent enhancement of peat decomposition is predicted in the course of climate warming (Frey and Smith 2005, Bleuten et al. 2008; Kirpotin et al. 2009). Moreover, massive CH₄ emissions from northern thermokarst lakes in permafrost landscapes add to the relevance of the region for global carbon cycling (Walter et al. 2006; Blodau et al. 2008). For southern regions of the WSL the effects of climate-change are still unclear and difficult to predict. If summer temperatures increase and precipitation decreases, like some models suggest for the forest-steppe ecotone (e.g. Tchebakova et al. 2009), lowering of water tables may also result in tremendous greenhouse-gas emissions (Peregon et al. 2007). Mire ecosystems in the southern part of the WSL can be expected as particularly vulnerable to such climate induced changes of the water table. Thus their state seems to be a suitable indicator for the effects of current and future climate change. A comparative study of CH₄ emissions from different wetland microsites (Glagolev et al. 2011) revealed that the WSL does not act as a severe CH₄ source at the global scale, but that specific microsites (i.e. ponds) tend to have substantial regional emissions. For other northern peatland areas much literature is available on the factors influencing varying CH₄ emissions between different microsites (Bubier 1995; Bubier et al. 1995; Daulat and Clymo 1998). For the WSL, in contrast, knowledge on the underlying processes is limited.

To extend current knowledge about this sparsely studied area, we investigated a transitional mire on the border between Forest-Steppe ecotone to the south and nemoral Pre-Taiga to the north, a region which is suggested to be highly affected by climate-change (Tchebakova et al. 2009; Degefe et al. 2014). The researched mire is characterized by a distinct vegetation zonation and a diversified peat stratigraphy, which was recorded at ten points along a transect of 1500 m length. For two contrasting vegetation types (floating mat vs. older birch forest) pore water depth profiles for major ions as well as for CH₄ and CO₂ were analyzed to answer the following research questions: (i) Which hydrochemical parameters determine floristic composition? (ii) Do CH₄ and CO₂ production rates differ between both sites and, if yes, what are the main

drivers? (iii) What are the implications for trace gas emissions during mire succession?

Materials and Methods

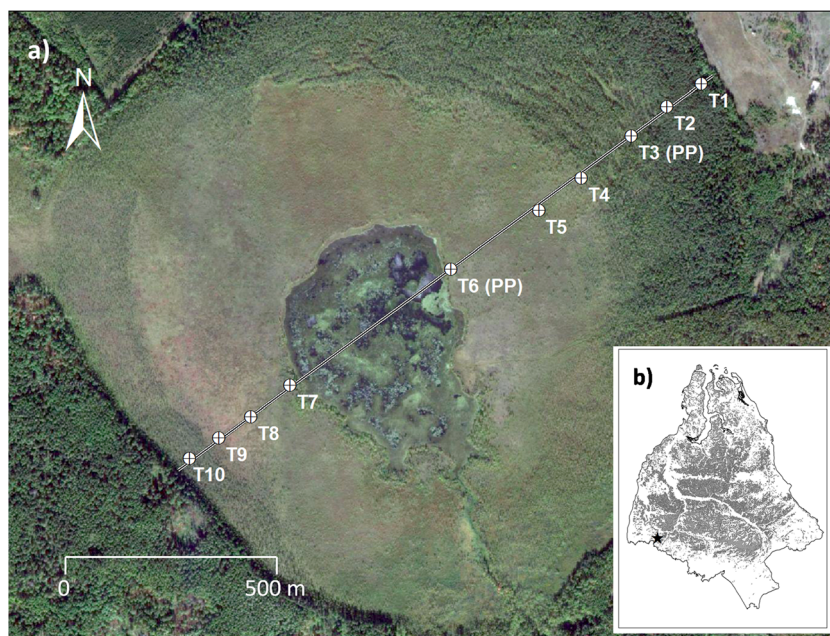
Study Site

The studied mire (‘Ishimbaevskoye’) is situated in the Tyumen Oblast directly north of its capital Tyumen (UTM 57.470620, 65.339613) and next to the village Novopokrovka (Fig. 1). It is part of the great Tarmanski mire complex which developed on the second alluvial terrace of the river Tura and has a total area of about 125,800 ha (Motorin 2012). The underlying bedrock consists of thick quaternary alluvial sand deposits. The peat deposits have mainly developed after lake succession, as indicated by *Gyttia* acting as water-logging mineral basement. Large parts of the mire complex consist of continuous percolation mires, which have been partly drained or may at least be affected by drainage of adjacent areas. Nevertheless, there are large areas of pristine sites, among them the round-shaped lake succession mires that are typical for this region of Western Siberia. The mire under study is such small, well-preserved transitional mire that shows a wide range of different trophic conditions and vegetation zones. Located within the transition between Forest-Steppe and Pre-Taiga it is part of the flat eutrophic and mesotrophic bog zone (Kremenetski et al. 2003) which has already been identified as one of Western Siberia’s main CH₄ sources (cf. Glagolev et al. 2011). To the north this zone is followed by the oligotrophic *Sphagnum*-bog zone, which crosses the WSL as a broad belt and is most relevant concerning carbon stocks (Sheng et al. 2004). The climate of the study region is strictly continental with a mean annual temperature and precipitation of about 1.8 °C and 470 mm, respectively (Degefe et al. 2014).

Vegetation and Peat Characteristics

We recorded vegetation and peat characteristics along a NE-SW transect of 1500 m that covers the major floristic and environmental gradients of the mire. Along the entire transect, we made 10 vegetation relevés in early August 2013, when vegetation development had peaked. Cover estimates of vascular plant and bryophyte species were made at a percentage scale. Plot size for vascular plants was 10 × 10 m; bryophytes were recorded inside the plot on an area of 1 × 1 m that was randomly chosen. If necessary the bryophyte vegetation of hummocks and hollows was recorded separately. The nomenclature of vascular plants is according to Rothmaler (2002) that of bryophytes according to Frahm and Frey (1992) and Laine et al. (2009). At each location of the vegetation survey, we took a peat core using a Russian peat corer. The peat profile was classified layer-wise according to major

Fig. 1 **a** Satellite image of the ‘Ishimbaevskoye’ mire (©Google Earth) with the location of the transect points and pore water peepers (PP). **b** Location of the study site (*Star symbol*) in the Western Siberian Lowland. Peatland area is indicated by grey shading. Adjusted from Smith et al. (2004)



substrate characteristics (Anon. 2005). The degree of humification was estimated for each layer following von Post (1922). If visible the occurrence and amount of macro-fossils such as seeds or leaves of specific plant taxa were recorded to document major historical changes of the vegetation. Ash layers indicating past fire events were recorded as well. Additionally, the pH and electric conductivity (EC) were measured in surface pools directly next to the borehole using a portable pH-meter (HANNA Instruments Combo Stick, HI 98129). The water-table below soil surface was measured in a small pit dug near the borehole for every transect point.

Pore Water Measurements

Pore waters were sampled after vegetation and peat sampling by the end of August 2013 using pore water peepers (PP) at two locations that markedly differed in floristic composition and thus presumably in trophic conditions (Fig. 2). One sampling site featured a light birch forest whilst the other was a floating mat dominated by *Sphagnum magellanicum* and *S. fuscum* directly next to the central lake. The PP's were type of Hesslein (1976) devices with a sampling depth down to 60 cm and a vertical resolution of 1 cm. The chambers of the PPs were filled with deionized water and covered with a permeable membrane (0.2 μm , OE 66, Schleicher & Schuell) allowing ions and gases of the adjacent pore water to diffusively equilibrate with the water inside the chambers. After preparation the PPs were carefully inserted into the peat with the uppermost chambers some centimeters above water-level and were allowed to equilibrate for 3 weeks (cf. Steinmann and Shotyk 1996).

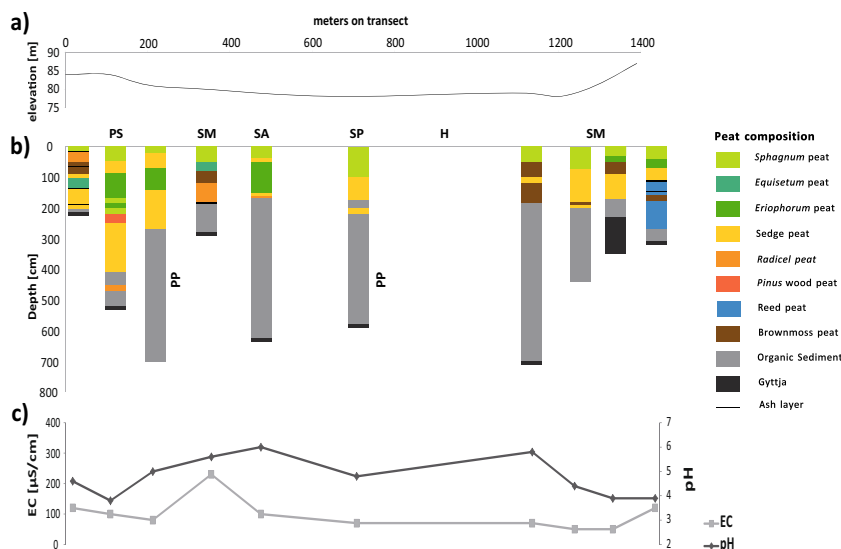
After equilibration, pore water peepers were removed and waters samples were extracted with syringes. Half of the water

samples (4 ml) of even-numbered depth stages were transferred into crimp vials together with 25 μl of 10 % HCl and sealed to preserve them for later CO_2 and CH_4 measurements. The remaining 4 ml were used for in-situ pH and redox potential measurements with a portable pH meter (WTW, pH 330, Weilheim, Germany). The water samples of odd-numbered depth stages were divided into two subsamples of 4 ml for anion and cation analysis, respectively, and kept in scintillation vials until analysis. The samples for cation analysis were also pre-treated with 25 μl of 10 % HCl to prevent oxidization of e.g. NH_4^+ . The samples for anion analysis were left untreated. All samples were immediately cooled to 5 $^\circ\text{C}$ and stored dark and cool until analysis. Gaseous CO_2 and CH_4 were measured using a gas chromatograph (SRI 8610, SRI Instruments, Torrance, USA) with methanizer and flame ionization detector (FID) in a time-frame of 1 week. The respective pore water concentration was calculated based on the volume of the head-space and the water sample applying Henry's Law [$K_{\text{H}} = 3.89 \times 10^{-2}$ (CO_2) and $K_{\text{H}} = 1.3 \times 10^{-3}$ (CH_4)] according to Stumm and Morgan (2012). The measured pH value was taken into account (cf. Beer and Blodau 2007). Anions and cations were measured by ion chromatography on a DIONEX IC-S 1100/2100 using an IonPac CS16 Analytical 5×250 mm column for cations and an IonPac AS19 Analytical 2×250 mm column for anions (both Thermo Fischer Scientific, Waltham, USA) immediately after transportation.

Data Analysis and Trace Gas Production Modelling

To explore major floristic gradients in relation to environmental variables a Detrended Correspondence Analysis (DCA)

Fig. 2 **a** Surface elevation of the mire along the transect from GPS measurements; left is northeast, right is southwest. **b** Peat composition and vegetation communities (PS = *Vaccinio uliginosi*–*Pinetalia syvestris*, SM = *Sphagnetalia magellanici*, SA = *Salicetalia auritae*, H = *Hydrocharitetalia*). The location of the pore water peepers is indicated by PP. **c** Electric conductivity and pH as measured at the transect points



was performed using PC-Ord 5.0 (McCune and Mefford 2006). For the analysis only the herb and bryophyte layers were included whilst the tree and shrub layers were excluded. The ordination was performed with squareroot-transformed data and plant species that occurred only once across the ten sampling plots were excluded. The measured environmental variables (pH, EC, peat depth and water table) were correlated with the ordination axes and complemented with weighted mean indicator values for humidity, availability of nutrients, salt tolerance, carbonate availability and variability of damping - i.e. tolerance towards fluctuating water tables. All indicator values were extracted from Didukh (2011).

The depth profiles of CH_4 and CO_2 production rates and the diffusive fluxes of CH_4 and CO_2 were calculated by inverse modeling using the model PROFILE (Berg et al. 1998). In brief, the model identifies the simplest production rate depth profile with the best fit to explain the measured concentrations at steady state, using a numerical solution of the mass conservation Eq. (1):

$$\frac{d}{dx} \left(\varphi \times D_{s,i} \times \frac{dC_i}{dx} \right) + R_i = 0 \quad (1)$$

with φ : porosity; $D_{s,i}$: sediment diffusion coefficient for dissolved species i , corrected for temperature; C_i : concentration of dissolved species i ; R_i : production rate of dissolved species i .

It has to be noted that during transient conditions, such as following water table fluctuation or non-steady state production the calculation offers only approximate estimates. Also only diffusion is considered, which leads to underestimation of CH_4 production if concentrations are high enough to allow for bubble formation, or if conduit transport of CH_4 through aerenchymatic plants occurs. Fluxes across the water table were calculated with Fick's first law. Diffusion coefficients of CO_2 ($1.93 \times 10^{-5} \text{ cm}^2 \text{ s}^{-1}$) and CH_4 ($1.73 \times 10^{-5} \text{ cm}^2 \text{ s}^{-1}$)

at 25 °C were corrected for temperature by linear interpolation and for the effect of porosity φ by $D_s = D \cdot \varphi^2$ (Lerman 1979) using bulk densities from the peat core derived at the respective location. Due to broken membranes for some depth intervals at the birch forest site, two outliers had to be excluded there. Summing up the production rates over depth, the depth integrated production (DIP) was calculated (cf. Berg et al. 1998). As consumption of sulfate by bacterial sulfate reduction may occur as a process competing with CH_4 production (Blodau 2011), we also modeled net sulfate turnover based on the concentration profiles following the same approach.

Results

Mire Topography, Vegetation and Peat Characteristics

Surface topography of the mire clearly reflected the former shoreline of the lake as indicated by the marked slopes towards the edges of the transect (Fig. 2). The general topography of the mire surface is well displayed by the topography of the underlying mineral deposits. One exception is the shallower peat found at plot T 4 which was validated by additional cores taken in adjacent areas. Peat depths ranged from 2 to 4 m but exceeded 6 m when the organic-rich sediments are included. In the central part of the mire we found *Sphagnum*-peat at the surface which was underlain by Brownmoss- or Sedge-peat. A high variability of peat types was found at the northeastern edge of the mire. The basal peat formed by sedges and *Eriophorum* remnants, followed by *Equisetum*-rich peat and then Brownmoss-peat. The upper peat layers were mainly formed by woody debris and the surface peat layer was formed by *Sphagnum*. Peat deposits rich in reeds (mainly *Typha* and *Phragmites*) were only found at the southwestern edge of the mire. At transect point T 2 we

found remarkably woody peat deposits (mainly *Pinus*) in a depth of 170 to 200 cm. Distinct ash layers were only recorded at the outer transect points (T 1, T 4 and T 10).

The DCA ordination (Fig. 3) revealed a high floristic variability with a gradient length of 3.2 for the first and 1.7 for the second axis, respectively. Axis scores of the first axis were significantly correlated with pH in surface water and water table. The second axis was correlated with the indicator values for the variability of damping and salt tolerance, tree cover and species richness. Relevés of the pine forests were located at the ombrotrophic end of the first axis. The most abundant species in pine forest were *Ledum palustre* and various Pyrolaceae such as *Orthilia secunda* and *Chimaphila umbellata*. More mesotrophic relevés with higher pH were situated on the left hand side of the ordination diagram (cf. Fig. 3). Typical plant species were e.g. *Menyanthes trifoliata*, *Equisetum fluviatile* and *Galium palustre*. The dominating bryophytes were more mesotrophic, such as *Sphagnum palustre*, *S. fallax* and *S. cuspidatum* and various brown mosses (e.g. *Hylocomium splendens* or *Aulacomnium palustre*). Plots from the central part of the mire (T 6, T 7 and T 8) were (trophically) in between forests and the *Menyanthes*-type and featured a floating mat with *Sphagnum magellanicum* and *S. fuscum* as most dominant bryophyte species. The most prominent herbs and chamaephytes were *Andromeda polifolia*, *Scheuchzeria palustris*,

Vaccinium oxycoccus, *Carex limosa*, *C. rostrata* and *Drosera rotundifolia*. The hydrophytic vegetation of the central lake was not included in the analysis, but mainly consisted of a dominant stand of *Stratiotes aloides* (cf. Fig. 4 & Online resource 1).

Chemical Composition of Pore Waters

Most prominent differences in pore water chemistry between birch forest and floating mat were found in Na^+ , Ca^{2+} , Cl^- and SO_4^{2-} concentrations (Table 1). Across the pore water profile, mean values of Na^+ ($> 4 \text{ mg L}^{-1}$) and Cl^- ($> 5.5 \text{ mg L}^{-1}$) were high for the floating mat. Ca^{2+} concentrations were slightly lower there. Sulfate, NO_3^- and PO_4^{3-} concentrations were generally low, but SO_4^{2-} and NO_3^- concentrations were slightly higher for the floating mat ($> 0.1 \text{ mg L}^{-1}$). Ammonium concentrations were intermediate with average values of about 1 mg L^{-1} . Ca:Mg ratios were higher in the birch forest than in the floating mat, but well above 3 at both sites.

In the vertical pore water profiles we found a clear maximum for most anions and cations near the water table (Figs. 5 & 6). This held true also for pH, i.e. the logarithmic H^+ ion concentrations. These maximums were more prominent at the floating mat and could not be found for K^+ and NO_3^- at the birch forest site. Compared to the birch forest, the surface

Fig. 3 DCA joint plot including vascular plants and bryophytes. The gradient length is 3.2 SD units for the first and 1.7 for the second axis. The gradient length refers to the distance between the most dissimilar relevés along the respective axis (axis 1: T5-T2, axis 2: T1-T10). Plant species and transect points (centroids) are shown in relation to the environmental gradients. A complete list of species is given in the [online resource](#)

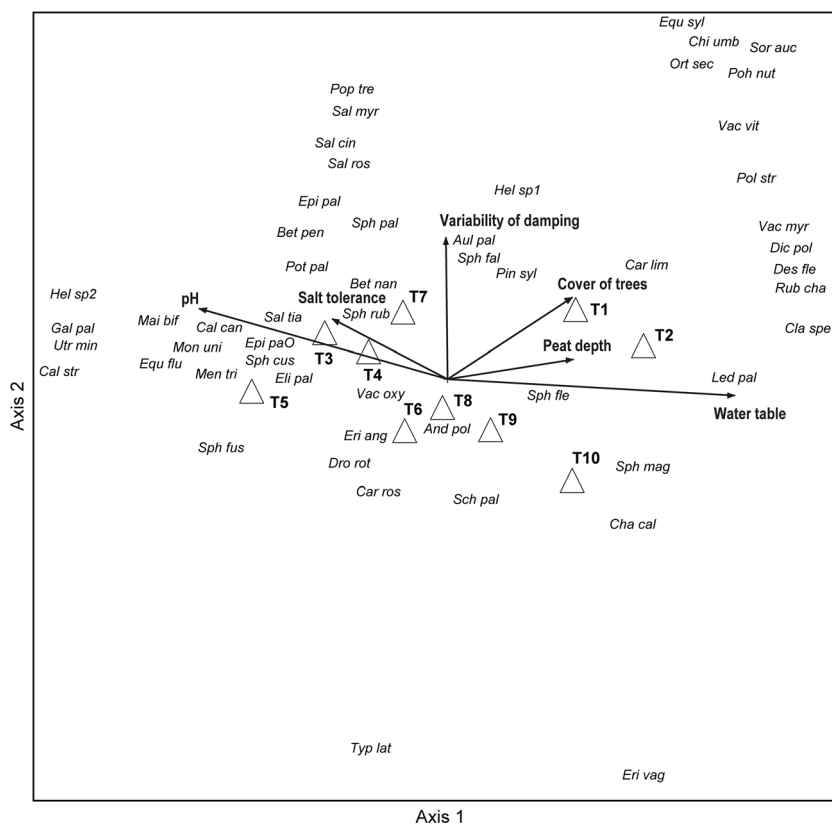




Fig. 4 Central lake with monodominant stand of *Stratiotes aloides* as viewed from sampling point ‘floating mat’

enrichment for PO_4^{3-} showed a distinct and deeper reaching peak at the floating mat. Na^+ concentrations (data not shown) revealed no clear vertical trends and showed high variability. Mg^{2+} (data not shown) showed a similar depth profile as Ca^{2+} with distinct maximum at the surface (Fig. 5).

Especially at the birch forest site major nutrients and Ca^{2+} showed more pronounced variation with depth than at the floating mat and revealed minor peaks in depths of 45 to 60 cm (Fig. 5). Sulfate concentrations were extremely low in the birch forest. In the floating mat, sulfate concentrations were still moderate with $0.01 \mu\text{mol L}^{-1}$ but distinctively higher in the upper centimeters. One consumption zone could be defined for the upper part of the floating mat with a consumption rate of about $0.5 \text{ nmol cm}^{-3} \text{ d}^{-1}$. Too low concentrations at the birch forest, however, did not allow for proper model validation at this site.

Table 1 Mean values and standard deviations (in parenthesis) for the ionic composition of both sites (–60 cm) in comparison. All values except Ca:Mg in mg L^{-1}

	Birch forest		Floating mat	
Li^+	0.0052	(0.0058)	0.0028	(0.0009)
Na^+	3.4033	(0.6390)	4.4967	(0.6437)
K^+	0.5815	(0.4658)	0.7225	(0.6086)
NH_4^+	0.9481	(0.9642)	0.9322	(0.7676)
Mg^{2+}	2.0973	(0.5244)	2.0335	(0.6308)
Ca^{2+}	7.8242	(1.8065)	6.0628	(2.0351)
Ca:Mg	3.7528	(0.3031)	3.0421	(0.5253)
F^-	0.0024	(0.0011)	0.0044	(0.0021)
Cl^-	1.6007	(1.4955)	5.7663	(4.2157)
NO_2^-	0.0025	(0.0028)	0.0018	(0.0046)
Br^-	0.0046	(0.0078)	0.0058	(0.0027)
NO_3^-	0.0306	(0.0274)	0.0535	(0.1722)
SO_3^{2-}	0.0238	(0.0210)	0.1155	(0.2800)
PO_4^{3-}	0.0019	(0.0013)	0.0020	(0.0018)

Concentrations and Production of Dissolved CH_4 and CO_2

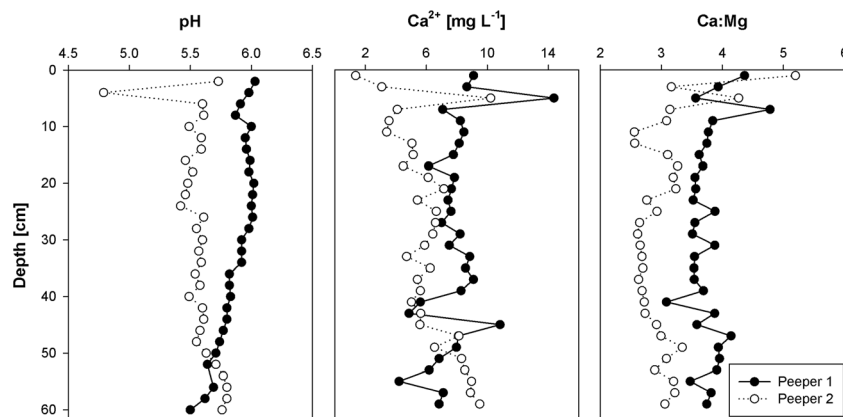
Generally, the measured CH_4 and CO_2 concentrations were quite high. The maximum concentrations were about 0.6 mmol L^{-1} for CH_4 and 4 mmol L^{-1} for CO_2 (Fig. 7). Overall, the gas concentrations were comparable between both sampling sites and revealed high $\text{CO}_2:\text{CH}_4$ ratios ranging between 5 and 14 for both sites. CH_4 showed a more continuous behavior with depth whilst CO_2 concentrations tended to be much more variable. Consequently, the modeling of production zones produced better results for CH_4 ($R^2 > 0.9$) than for CO_2 ($R^2 \leq 0.5$). At both sites the maximum production of CO_2 and CH_4 was in the upper 20 cm of the profile. While CO_2 profiles revealed no more relevant production zones at both sites, CH_4 also appeared to be produced and consumed in deeper zones of the profile especially at the floating mat. The estimated production rates were much higher for both CO_2 and CH_4 at the floating mat site. CH_4 reached a maximum production rate of $138 \text{ nmol cm}^{-3} \text{ d}^{-1}$ at floating mat compared to $37 \text{ nmol cm}^{-3} \text{ d}^{-1}$ at the birch forest. For CO_2 the maximum production rate was $158 \text{ nmol cm}^{-3} \text{ d}^{-1}$ at the floating mat and $49 \text{ nmol cm}^{-3} \text{ d}^{-1}$ at the birch forest. The DIPs for both CO_2 ($34.19 \text{ mmol m}^{-2} \text{ d}^{-1}$) and CH_4 ($10.89 \text{ mmol m}^{-2} \text{ d}^{-1}$) were threesomes higher at the floating mat compared to the birch forest (Table 2).

Discussion

Mire Evolution and Vegetation Gradients

For all surveyed peat cores the base was composed by organic and mineral lake sediments (Sapropel, Gyttia) indicating a progressive mire evolution from an early thermokarst lake after the LGM. In the early Holocene a rapid warming resulted in permafrost melting for the studied area (Velichko et al. 2002). As expected the clearest and youngest successional pattern was visible at the central part of the mire where Sedge- or Brownmoss-peat was directly overlaid by *Sphagnum*-peat, which represents the actual vegetation. At the edges of the mire, succession history was longer since the former shoreline was the likely starting point for the beginning paludification of the lake. The altering phases of vegetation succession were clearly marked by shifts in macrofossils and plant remnants indicating changes in water-table and trophic conditions. Partly, vegetation succession was fast and progressive since plant fossil assemblages changed drastically along peat core depth. At the edges of the mire ash layers of several centimeters marked severe fire events that were not limited to standing dry biomass, but also combusted the superficial peat layers, thus indicating prior phases of desiccation and lower water-tables (Lukenbach et al. 2015). Some fire

Fig. 5 Composition of pore waters with depth regarding the trophical status. Comparison between the forested site (Peeper 1) and the floating mat (Peeper 2)



events have obviously initiated abrupt shifts in vegetation (cf. Tchebakova et al. 2009). The contrasting evolution of the mire on both shores of the former lake, e.g. the occurrence of reeds only at the south-western edge of the transect, might be owed to different wind and wave exposure. For example, Riis and Hawes (2003) found that the variation in vegetation communities along lake shores is mainly explained by differences in wave exposure. In particular, the establishment of emergent macrophytes like *Typha angustifolia* or *Phragmites australis* is highly promoted by wave turbulence (Weisner 1987).

The current vegetation was characterized by a high diversity of different plant communities. Overall, the species pool was quite typical for Western Siberian mires (Walter 1977; Lapshina 2006), but it is remarkable that species of different trophic mire zones of Western Siberia coexist within one mire ecosystem. Schipper et al. (2007) found a gradual vegetation gradient in the Ob river valley mire in Western Siberia with only slightly changing species pool, which they mainly attributed to changes in hydrology. Contrastingly, we found a very distinct vegetation zonation from the former shoreline to the central lake. The main floristic gradients were related to pH

and water-table. Towards the central parts of the mire the water-table and pH increased (cf. Fig. 3) while surface elevation decreased. As the *Pinus*-forest surrounding the mire is situated topographically higher than the inner parts it is cutoff from minerotrophic water, whereas the inner parts receive some additional minerotrophic inputs. Accordingly, plant species composition changed from ombrotrophic bog species to more intermediate herb and bryophyte species in the birch forest and the willow-shrub-belt.

Geochemical Characterization

Overall, pore water chemistry indicated intermediate supply of base cations and nutrients (cf. Bendell-Young 2003). Values of pH and concentrations of major base cations (Ca²⁺, Mg²⁺) exclude a strictly ombrotrophic character for both sampled locations but suggest poor to intermediate fen conditions (Sjörs and Gunnarsson 2002, Tahvanainen 2004). Ca:Mg ratios that were well above thresholds of >1 or even >2.5 at both sites also exclude that Ca²⁺ is only supplied by rainwater (Howie and Tromp-van Meerveld 2011). This tendency is

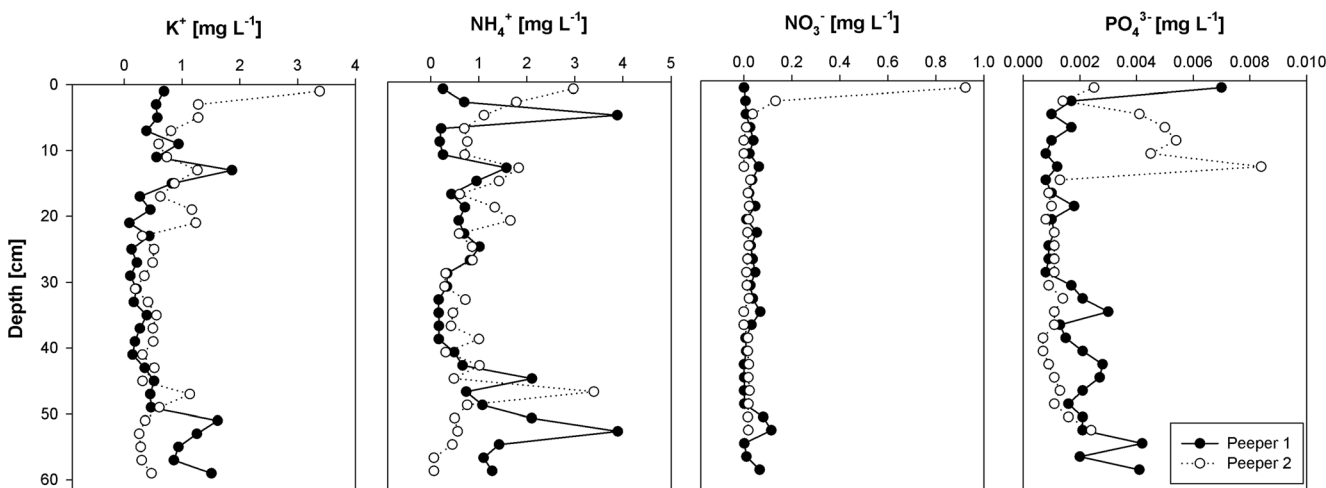


Fig. 6 Composition of pore waters with depth regarding the nutrient status. Comparison between the forested site (Peeper 1) and the floating mat (Peeper 2)

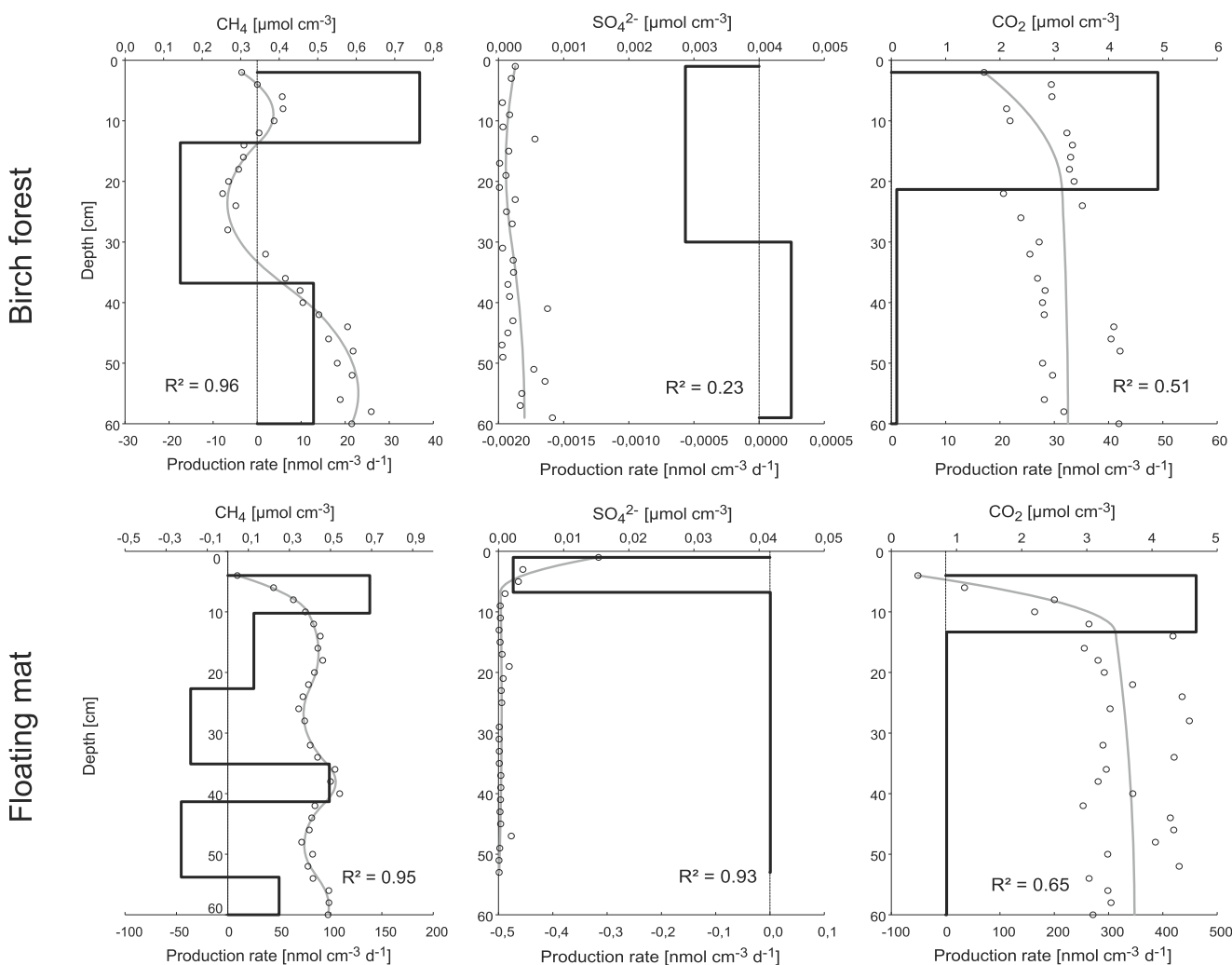


Fig. 7 Pore water profiles of CH₄, SO₄²⁻ and CO₂. Dots are measured concentrations, the lines represent modelled concentration curves by fitting of production and consumption zones (thick black lines) using PROFILE (Berg et al. 1998)

Table 2 Depth integrated pore water production of CH₄ and CO₂ below the water table (–60 cm). All values are given in mmol m⁻² d⁻¹. Some literature values are given for comparison. Note that e.g. plant respiration and plant mediated CH₄ transport add to the flux as measured by chamber methods

		CH ₄	CO ₂
Birch forest		3.21	9.87
Floating mat		10.89	34.19
Mer Bleue bog	Chamber flux	0.27	205
Ontario, Canada (Blodau et al. 2007)	DIP	0.00	1.04
Magellanic Moorland	Chamber fluxes	9.0	60.0
Patagonia, Chile (Broder et al. 2015)		1.0	40.0
WSL ponds	Chamber fluxes	195	Forest-Steppe
Russia (Glagolev et al. 2011)		135	Sub-Taiga

more striking at the forested site because the inflow of minerotrophic waters will most likely appear at the mire margins.

The pore water chemistry of the two peeper profiles differed mainly with respect to the base cation supply (cf. Ca²⁺ and Ca:Mg ratio) and pH, whereas mean concentrations of nitrogen components and PO₄³⁻ were similar. Thus, vegetation is most likely shaped by a higher supply of base cations at the birch forest (cf. Wertebach et al. 2014) which is also supported by the trophic gradient we found concerning the vegetation (Fig. 3).

We found high concentrations of Na⁺ and especially Cl⁻ at the floating mat. The drastic rise in both ions towards the open lake is obviously the result of increased evaporation in the central part of the mire which is not forested and thus subjected to higher radiation during the hot summer months. The plant indicator values for salt tolerance point in the same direction since they were also higher at the floating mat (cf. Fig. 3). Although not described for mires so far, salinization

is a well-known process for mineral soils in the study region (Kovalev 1969; Vorob'eva and Pankova 2008).

The near-surface maximum for most ions is a well described pattern and characterizes the zone of growing *Sphagna*, since peat mosses are able to create their own acidic environment by active acquisition of H^+ ions in the acrotelm (Clymo 1984; Andrus 1986). This ability is well displayed by minimum pH values in that zone. The lower pH and the stronger peak at the floating mat likely result from different *Sphagnum* species growing there (cf. Chapter 3.1). Clymo (1963) already demonstrated that the ion exchange capacity of *Sphagna* is mainly a species related trait and that ombrotrophic species have higher exchange ability than minerotrophic ones. What is true for H^+ is also true for some of the other cations (e.g. Ca^{2+} , K^+) that showed superficial enrichment; particularly the monovalent cations revealed an analogous behavior to H^+ . Monovalent cations like K^+ are highly mobile and can partly be retained at the surface of mires by living plant tissues (Damman 1978) but they are also selectively transported to the surface during dry periods (Brehm 1971) when evapotranspiration is strong. The highly variable Na^+ concentrations are quite typical as Na^+ is highly mobile and very efficiently leached from peat (Wertebach et al. 2014).

The enrichment of major nutrients in the peat surface-layer most likely results from increased (aerobic) mineralization of organic matter. Evapotranspiration and mineralization are both stronger in the non-forested central part of the mire. Higher insolation and surface temperatures are thus able to promote the increased surface enrichment there. Local maxima of ion concentrations in deeper layers of the profiles are likely caused by differences in peat composition and enhanced release of nutrients and cations from more humified peat. Some ions (e.g. Ca^{2+}) are known to be very efficiently leached from peat under anaerobic conditions (Shotyk and Steinmann 1994). For example, at the birch forest the change from nearly undecomposed *Sphagnum*- to intermediately decomposed Sedge-peat was clearly visible in the hydrochemical profile. Even under anaerobic conditions the nutrient release is suggested to be significantly higher for the sedge peat as respective contents are much higher in the plant remnants of sedges and other vascular plants compared to *Sphagna* (Schmidt et al. 2010).

Methane and CO_2 Production: Driving Factors

Compared to previous research, the measured concentrations of CH_4 and CO_2 were in a similar range as observed elsewhere, while the DIP was comparably high for both methane and CO_2 , especially at the floating mat (cf. Beer and Blodau 2007, Blodau et al. 2007; Broder et al. 2015). Taking into account further contributions to fluxes such as plant respiration and plant mediated transport of CH_4 (Joabsson and Christensen 2001), our results support the reported high CO_2

and CH_4 emissions for the region under study, as determined by chamber measurements of Glagolev et al. (2011). These observations add relevance to the role of south-western Siberian mire ecosystems in terms of carbon fluxes and cycling on regional to global scales. The observation that (thermokarst) ponds contribute the main share of CH_4 and CO_2 budgets of the WSL has been made by various authors (Walter et al. 2007; Blodau et al. 2008; Glagolev et al. 2011; Abnizova et al. 2012). Our results underline these findings and suggest high fluxes also for transitional mires. The much higher production rates we found at the floating mat compared to the successional older birch forest allow for first predictions of trace gas emissions in terms of ongoing mire development. Pore water production rates in detailed profiles allow for identification of the underlying processes.

A special yet common feature of the mire under study is the presence of a central lake in which organic material from aquatic plants accumulates and gets subjected to anaerobic mineralization processes. Manasypov et al. (2014) report high DOC concentrations from Western Siberian thermokarst lakes, which tend to increase with decreasing size of the lake and from northern to southern regions of the WSL. The supply of DOC is, along with other environmental factors, such as water table, temperature or the availability of electron acceptors for microbial respiration, a main driver of CH_4 and CO_2 production rates (Reeve et al. 1996; Blodau 2002). DOC in fens has been reported to be more reactive and labile compared to DOC in bogs (Corbett et al. 2013). Together with differences in specific plant traits affecting carbon cycling, i.e. the presence of aerenchymatic plants, significant differences in trace gas production and emissions have been reported for fens and bogs (Bellisario et al. 1999; Frenzel and Karofeld 2000).

The high CH_4 and CO_2 production rates at the floating mat are likely driven by increased DOC supply from the central lake, because only labile dissolved organic matter of small molecular size can support such high bacterial respiration (Fenchel et al. 2012). A high bacterial respiratory activity at the floating mat was further indicated by SO_4^{2-} concentration patterns that point towards bacterial sulfate reduction. Moreover, near-surface peaks of major nutrients point towards enhanced mineralization processes for that part of the mire. Besides higher DOC supply, enhanced insolation and temperatures due to the absence of tree shading at the floating mat may have also contributed to higher bacterial activity compared to the birch forest (Bubier et al. 1995; Daulat and Clymo 1998, Segers 1998). Additionally, floating mats adjust their surface to changing water tables, maintaining favorable conditions for CH_4 production even in the dry summer season (Bubier et al. 1995). Recent studies emphasized the relation between productivity, nutrient availability and CH_4 and CO_2 production (Basiliko et al. 2005, 2007). However, since we found comparable nutrient concentrations at both sites and an

even higher productivity at the birch forest we conclude that bacterial activity is rather substrate than nutrient limited. The high concentrations of Na^+ at the floating mat are able to promote methanogenesis as sodium has limiting effects on bacterial activity (cf. Basiliko et al. 2007). The redox conditions across the water column are strictly reducing for both sites as indicated by redox potentials <70 mV from a depth of 4 cm downwards (Thompson et al. 2009). Methane production is thus promoted as strictly anaerobic conditions are necessary (Fetzer et al. 1993). The high CH_4 production rates at the floating mat are even more striking when considering the higher sulfate concentrations close to the water-table. Sulfate favored as the electron acceptor over CO_2 for mineralization of small organic acids and, thus, typically methanogenesis is suppressed under high concentrations of sulfate (Blodau 2011; Estop-Aragones et al. 2013). Therefore, high rates of methanogenesis in the presence of well detectable sulfate concentrations indicate a high supply of labile substrates in the floating mat, e.g. by lake-derived DOC or by root exudates (cf. Knorr et al. 2015).

According to Glagolev et al. (2011) in the WSL ponds have the highest methane emission followed by fens and poor fens with intermediate emissions and finally forested ombrotrophic bogs (Ryams) with negligible emissions. As this displays the course of mire development from an early thermokarst lake to a Ryam we would propose that the main factor influencing these regional emissions is the lake DOC input and its cutoff during succession to an ombrotrophic Ryam.

The depth profiles of CO_2 production rates showed quite analogous patterns at both sites. The main production in the upper part of the profile is mainly attributed to heterotrophic bacterial respiration. As mentioned above bacterial activity and supply of substrates are supposed to be higher at the floating mat which should lead to higher CO_2 production rates as well. Zones of CH_4 consumption, especially at the floating mat, might be due to the presence of aerenchymatic plants (e.g. *Scheuchzeria palustris*, *Carex spec.*) which transport O_2 to deeper peat layers and promote outgassing of CH_4 (Bellisario et al. 1999; Frenzel and Karofeld 2000). This is supported by the high CO_2 : CH_4 ratios that we found for both sites, as ratios >5 are indicative for prevalent methane outgassing (Broder et al. 2015). In the applied simple mass conservation approach, outgassing of CH_4 cannot be included and thus is only identified as a consumption zone.

Conclusion

Round shaped transitional mires that evolved from thermokarst lake succession represent special ecosystems concerning vegetation, hydrochemistry and evolution. They feature wetland ecosystems with a wide range of trophic conditions and thus harbor a high diversity of plant communities.

The floristic gradient is mostly related to base cation supply and pH. Evolution of these mires is characterized by ongoing successional processes that are markedly affected by fluctuating water-tables and fire events. According to Glagolev et al. (2011) wet micro-landscapes like the floating mat under study contribute 70 % of the WSL regional CH_4 emissions while ombrotrophic ridges and ryams only contribute little, even if they have the greatest aerial share.

The findings of our study underline the importance of ponds and wet micro-landscapes and allow for first predictions of trace gas emissions in the course of mire succession. We showed that CH_4 emissions are strongest in early phases of mire development, in which a central lake is still present. In the course of ongoing succession towards a forested bog ecosystem we observed a decrease in CH_4 production rates due to decreasing DOC input. Drawing an evolutionary line from an early thermokarst pond to a forested bog (Ryam) we expect an ongoing decrease of CH_4 production and emission, since the DOC input decreases and the trophic conditions change to ombrotrophic. Nevertheless, we are well aware that this hypothesis needs further confirmation by more detailed studies on methanogenetic pathways in Western Siberian mires of different succession stage. Our findings demonstrate that ponds and thermokarst lakes in the WSL act as relevant methane sources and thus may be able to positively feedback global warming. Moreover, transitional mires of the Forest-Steppe and Sub-Taiga zone may serve as reference ecosystems for effects of climate change-induced permafrost melting in northern ecosystems. For this kind of space-for-time substitution further research in the southern part of Western Siberia would be promising, particularly as current research is mostly restricted to northern regions or the oligotrophic (peat) bog zone.

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