




# Environmental Controls on CO<sub>2</sub> Exchange along a Salinity Gradient in a Saline Boreal Fen in the Athabasca Oil Sands Region

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## Abstract

Understanding the controls on carbon dioxide (CO<sub>2</sub>) exchange within saline boreal fens, appropriate natural analogs for landscape reclamation in areas affected by salinization in the Athabasca Oil Sands Region, can provide insights into the biogeochemical and carbon sink functioning of constructed wetlands under saline conditions. Hence, this study aims to assess net ecosystem exchange (NEE), ecosystem respiration (R), and gross ecosystem productivity (GEP) of peatland and open-water areas within a saline boreal fen near Fort McMurray (Alberta, Canada) to determine environmental controls on CO<sub>2</sub> fluxes using community-scale CO<sub>2</sub> measurements along a salinity gradient. Strong positive correlations between NEE, GEP, leaf area index within peatland, and between GEP and vegetation density within open-water areas (ponds) were observed, demonstrating the importance of vegetation properties for carbon uptake. Strong negative correlations were found between NEE, GEP, R and water table depth and electrical conductivity within peatland. In contrast, GEP and R were positively correlated with phosphate concentrations in ponds, and electrical conductivity had no effect on CO<sub>2</sub> fluxes within ponds. In peatlands, links between CO<sub>2</sub> exchange and environmental factors were influenced by microtopography, and complex relationships between NEE, GEP, R and environmental variables were observed within depressions.

**Keywords** Saline fen · Gross ecosystem productivity · Carbon dioxide exchange · Ecosystem respiration · Salinity · Athabasca Oil Sands region

## Introduction

Peatlands play an important role in global carbon (Roulet 2000; Blodau 2002; Limpens et al. 2008) water (Price and Waddington 2000; Price et al. 2005), and nutrient cycles (Bridgman et al. 1996) and have been exploited by humans over many centuries for fuel, agriculture and forestry (Turetsky 2002). However, anthropogenic disturbance has

increased dramatically in the twentieth century as demand for mineral resources in the world economy has risen (Dubinski 2013). Large areas of the boreal zone have been affected by the growing mining industry. In particular, one of the world's largest mining-induced boreal peatland losses is occurring in the Athabasca Oil Sands Region (AOSR) (Alberta, Canada) where vegetation and surficial deposits have been completely removed for the development of open-pit mines from more than 700 km<sup>2</sup> of boreal land (Rooney et al. 2012), of which peatlands comprise 50% (Vitt et al. 1996).

After mine closure, oil companies are obligated by the Government of Alberta to reclaim disturbed areas to lands with “equivalent land capability”, which means that “the land is to have the same ability to support various land uses after conservation and reclamation, but the individual land uses do not have to be identical” (Province of Alberta 2003). About one third of post-mined lands must be reclaimed back to wetlands to restore pre-disturbance landscape diversity (Alberta Environment 2008). As reclamation requires total reconstruction of a whole ecosystem at the landscape scale (Johnson and

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Miyanishi 2008), a firm grasp on environmental processes in boreal ecosystems is essential for the reclamation success (Environment and Parks 2015). Consequently, there is a growing interest in better understanding natural ecosystems that can provide suitable targets for reclamation. In particular, saline boreal fens, groundwater fed peatlands with increased salt content, have been suggested as appropriate models for reclamation of areas with elevated salinity (e.g., Purdy et al. 2005; Wells and Price 2015a, b), which is commonly caused by salts derived from saline tailings and reclamation materials in the AOSR (Ketcheson et al. 2016).

Saline fens are rare ecosystems that have been reported from Western Boreal Plains (Grasby and Betcher 2002; Purdy et al. 2005; Trites and Bayley 2009a, b). These fens are slightly acid to neutral chloride dominated peatlands (Stewart and Lemay 2011; Volik et al. 2017a) with notable salinity gradients associated with the discharge of groundwater from pre-Quaternary saline aquifers (Wells and Price 2015a, b). Salinity has a strong effect on fen vegetation and controls the distribution of plant communities (Trites and Bayley 2009a) as dissolved salts decrease water availability for plants by decreasing the osmotic potential of the soil solution, and some ions (e.g., chloride, sodium) become toxic at certain concentrations (Cooper 1984; Neill 1993; Curco et al. 2002; Willis and Hester 2004; Neubauer 2013); moreover, salinity can interfere with nutrient uptake and redistribution (Silberbush and Ben-Asher 2001). Ridge-depression patterns, coupled with an abundance of depressed open-water areas (ponds), are common features of saline fens (Wells and Price 2015a), and water cycling within fens is influenced by such microtopography (Wells and Price 2015a; Phillips et al. 2016). Microtopographical heterogeneity and increased salinity may have an effect on carbon cycling in saline fens because microtopography can modify carbon dioxide (CO<sub>2</sub>) fluxes (e.g., Waddington and Roulet 1996; Petrone et al. 2011), and notable differences in magnitude and direction of CO<sub>2</sub> exchange between ponded and vegetated areas within peatlands have been reported (Pelletier et al. 2015). In addition, elevated salt content can affect plant productivity and litter decomposition (Trites and Bayley 2009b). Despite some improvement in our understanding of the ecohydrological and biochemical functioning of saline fens, there is a paucity of information about CO<sub>2</sub> exchange within the fens. Carbon uptake, coupled with its long-term storage is one of the primary ecological services provided by peatlands including fens, so a better understanding of the carbon dynamics of saline fens is necessary to ensure that these ecosystems targeted by reclamation plans provide equivalent ecosystem services to those destroyed by mining.

Currently, it has been suggested that evaluation of functional characteristics (e.g., hydrologic regulation, biogeochemical transformation, primary production and decomposition) of constructed fens (functional-based approach) can better reflect

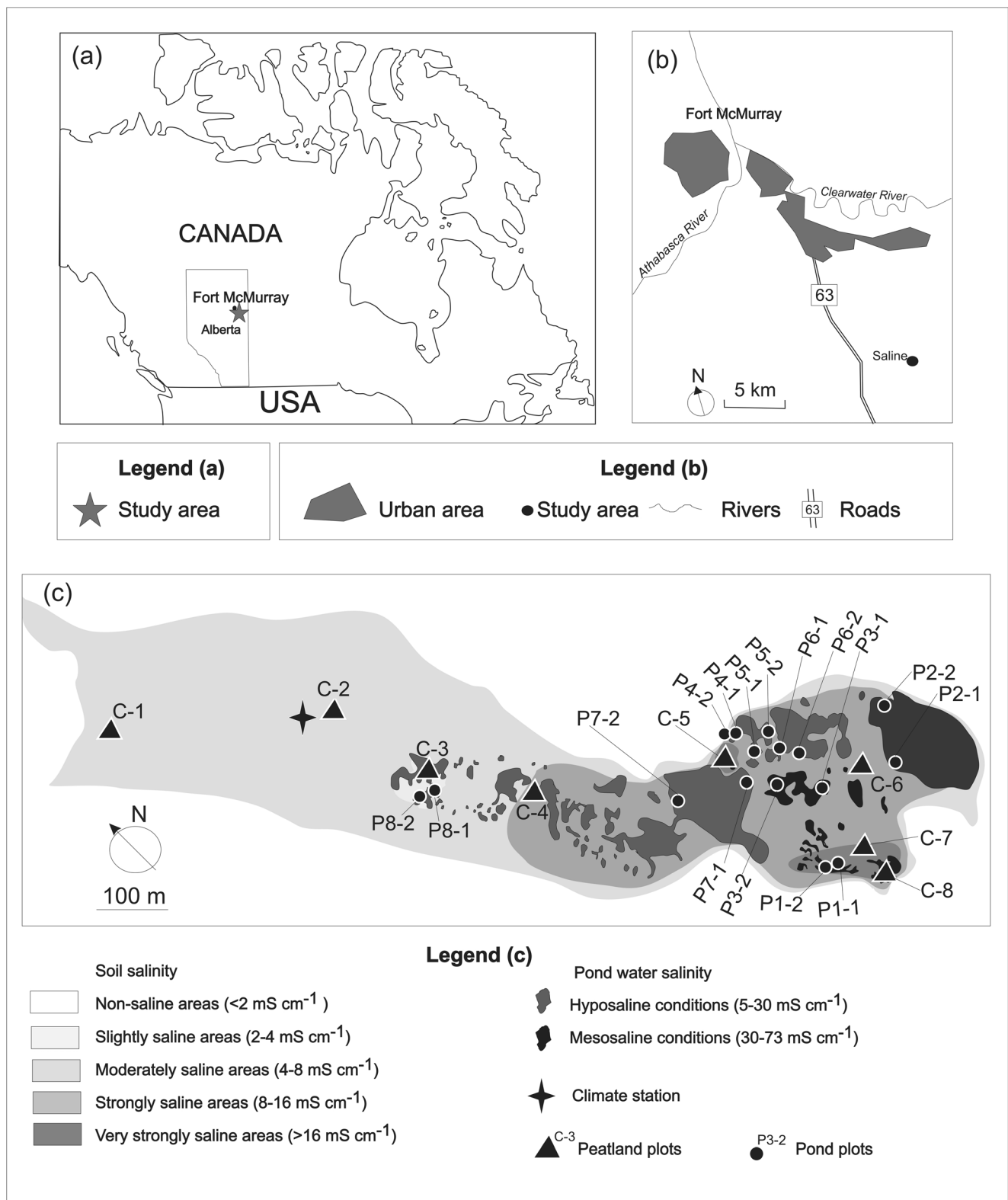
the state of the fens comparatively to assessment of their vegetation community structure (indicator species approach), and rates of gross photosynthesis and ecosystem respiration have been recognized as variables that are useful for assessment of functioning of the fens (Nwaishi et al. 2015). Consequently, better understanding of the relationship between salinity, vegetation and CO<sub>2</sub> fluxes in saline fens is necessary to set carbon storage benchmarks against which reclaimed fens can be evaluated (Environment and Parks 2015). In addition, the main drivers of saline fen productivity would allow reclamation plans to target environmental conditions that maximize the rate of carbon uptake despite the negative effect of salinity stress on plant growth. Further, evaluation of variability in productivity and CO<sub>2</sub> exchange in saline boreal fens under different environmental conditions will help to predict how constructed saline fens will respond to natural and anthropogenic changes.

Thus, this study aims to characterize the environmental controls on CO<sub>2</sub> fluxes in a saline boreal fen in the AOSR using community-scale measurements along a salinity gradient. The main objectives are: 1) to determine how electrical conductivity (EC), water table depth (WTD), soil moisture (SM) and temperature (ST), peat hydrophysical properties, nutrient availability, and vegetation influence net ecosystem exchange (NEE), ecosystem respiration (R), and gross ecosystem productivity (GEP) within different microtopographic forms within peatland; 2) to assess effect of changes in vegetation, water depth (WD), EC, pH, water temperature (WT), dissolved oxygen (DO) and nutrient concentrations on NEE, GEP and R within open-water areas (ponds); and 3) to identify key features of CO<sub>2</sub> exchange under saline conditions that can be useful for improvement of saline fen construction in the post-mined setting in the AOSR.

## Materials and Methods

### Study Site

This study was conducted at a saline peatland (hereafter, Saline Fen) 10 km south of the city of Fort McMurray (56°34'28.84" N, 111°16'38.39" W), Alberta, Canada (Fig. 1 a, b). The site is situated within the Boreal Plain Ecozone, which is characterized by a subhumid continental climate. At Fort McMurray, mean annual temperature and mean annual precipitation based on 1981–2010 normals, are 0.2 °C and 460 mm respectively (Environment Canada 2015). Saline Fen is a 27 ha elongated fen with a prominent ridge-depression pattern in the northern portion, and abundant shallow ponds in the central and southern portions of the peatland. The fen, with an average pH of 6.5–7.5 demonstrates a notable range of salinity; electrical conductivity of sodium chloride-dominated groundwater varies from more than 60 mS cm<sup>-1</sup> in



**Fig. 1** **a** Regional map showing the location of the study site within Alberta, Canada; **b** map showing location of Saline Fen near Fort McMurray, Alberta; **c** map of the study site, including locations of peatland and pond sites

the southern part to  $19 \text{ mS cm}^{-1}$  in the northern part (Wells and Price 2015b) (Fig. 1c). According to soil salinity

classification (Abrol et al. 1988), the northern part of the fen is characterized by slightly ( $2-4 \text{ mS cm}^{-1}$ ) and moderately

saline (4–8 mS cm<sup>-1</sup>) conditions while the southern part has strongly (8–16 mS cm<sup>-1</sup>) to very strongly saline (>16 mS cm<sup>-1</sup>) conditions (Fig. 1). The distribution of plant communities closely follows this salinity gradient. Slightly saline areas are dominated by mosses and shrubs (*Alnus* spp., *Salix* spp., *Betula* spp.) regardless of topographic position. Ridges with moderately saline conditions are dominated by Baltic rush (*Juncus balticus* Willd.), sweetgrass (*Hierochloa hirta* ssp. *arctica* (J. Presl) G. Weim.) and narrow reed grass (*Calamagrostis stricta* (Timm.) Koeler) while moderately saline depressions are dominated by seaside arrow grass (*Triglochin maritima* L.) and hastate-leaved orache (*Atriplex prostrata* Boucher ex de Candolle). Strongly saline areas are dominated by foxtail barley (*Hordeum jubatum* L.), *Puccinellia nuttalliana* (Schult.) Hitchc. and sea plantain (*Plantago maritima* L.) on the ridges, or by *T. maritima* in the depressions (Volik et al. 2017b). Very strongly saline areas are dominated by *P. maritima* and horned seablite (*Suaeda calceoliformis* (Hook.) Moq.) on ridges, or *T. maritima* and samphire (*Salicornia rubra* Nelson) on depressions.

Numerous open-water areas (ponds) with salinity from 2 to 50 ppt were situated predominantly in the southern and central parts of the fen. The ponds were shallow (average depths of 0.4–0.5 m) and small (surface area up to 1.2 ha). Most of the large ponds had irregular shapes, while small ponds were typically circular and located in deep depressions with steep margins. Some ponds had a semi-permanent regime and dried out during the late summer. According to limnological salinity classification scheme (Last and Ginn 2005; Herbert et al. 2015), ponds situated in the northern part of the fen can be characterized as hyposaline (5–30 mS cm<sup>-1</sup>) whereas ponds in the southern part were mesosaline (30–73 mS cm<sup>-1</sup>) (Fig. 1). Eight ponds with mean EC ranging from 5 to 44 mS cm<sup>-1</sup> were selected for this study (Fig. 1). Hyposaline ponds were dominated by *Staurosirella pinnata* (Ehrenberg) D.M. Williams & Round and *Staurosira venter* (Ehrenberg) Cleve & J.D. Möller while *Navicymbula pusilla* (Grunow) Krammer, *Halamphora coffeaeformis* (Agardh) Levkov, *Platessa salinarum* (Grunow) Lange-Bertalot, *Anomoeoneis costata* (Kützinger) Hustedt, *Navicula peregrina* (Ehrenberg) Kützinger, *Craticula halophila* (Grunow) D.G. Mann, *Diploneis stroemii* Hustedt, *Parlibellus cruciculus* (W. Smith) Witkowski, Lange-Bertalot & Metzeltin) were dominant in mesosaline ponds (Volik et al. 2017a). *T. maritima* occurred around hypo- and mesosaline ponds while *S. rubra* grew around mesosaline ponds only. Emergent vegetation was more abundant in hyposaline ponds and included *Typha angustifolia* L., *Bolboschoenus maritimus* (L.) Palla and *Schoenoplectus tabernaemontani* (C.C. Gmel.) Palla while mesosaline ponds were lacking emergent vegetation. Submergent vegetation in hypo- and mesosaline ponds was presented predominantly by *Stuckenia pectinata* (L.) Böerner and *Ruppia maritima* L. (Volik et al. 2018).

## Community-Scale CO<sub>2</sub> Fluxes

In May 2015, fourteen community-scale peatland plots (eight within ridges and six within depressions) were selected along a salinity gradient for CO<sub>2</sub> flux measurements (see Fig. 1 and Online Resource (Table S1) for details). Each plot ( $n = 14$ ) was equipped with a semi-permanent polyvinyl chloride collar (height of 15 cm and inside diameter of 19 cm) that was inserted 10 cm into the peat. In addition, sixteen pond plots were selected for measurements of CO<sub>2</sub> flux along a salinity gradient using a floating chamber; no collars were installed, but each of the pond plots ( $n = 16$ ) was marked with a stake (see Online Resource (Table S2) for details).

Community-scale CO<sub>2</sub> fluxes were measured using enclosed dynamic Plexiglass chamber (volume 0.01 m<sup>3</sup>) equipped with a fan for cooling and mixing of air inside (Brown et al. 2010). Peatland and pond plots were used for measuring CO<sub>2</sub> fluxes associated with net ecosystem exchange (NEE) (full sun) and dark respiration of the above-ground vegetation, coupled with soil respiration (with non-transparent cover). During flux measurements at the peatland sites, a chamber was placed in a 3 mm channel on the top side of the collar and sealed with water to prevent air exchange (Brown et al. 2010). In the pond sites, the chamber was equipped with a Styrofoam float and placed directly on the water surface reaching approximately 3 cm into the water column. The measurements at each peatland plot were twice per month from May to August 2015, and for each pond plot measurements were taken twice per month from June to August. Sampling period for pond plots was shorter due to limited access to ponds in May. All measurements were collected between 9 am and 4 pm under PAR ranging between 1300 and 1700  $\mu\text{mol m}^{-2} \text{s}^{-1}$ .

CO<sub>2</sub> concentration, air temperature, photosynthetically active radiation (PAR) and relative humidity within the chamber were measured using an EGM-4 Infrared Gas Analyzer (IRGA) (PP-Systems, Amesbury, MA, USA) (PP-Systems 2009) (Fig. S1). CO<sub>2</sub> flux was measured for two minutes, with a 1 s sampling period and 30 s recording interval. Average values of PAR and air temperature over measuring time were used for statistical analysis. Each sampling event at each plot included three replicates (i.e., three 2-min measuring runs at the collar, and the chamber was ventilated between measurement runs). Obtained CO<sub>2</sub> concentration data were visually checked (using scatterplots) for normality and used for development of non-linear regression models that were assessed using coefficient of determination ( $r^2 \geq 0.75$ ) and ANOVA ( $p$  value  $\leq 0.05$ ) (Kutzbach et al. 2007).

CO<sub>2</sub> flux was calculated by multiplying the gas volume within the chamber by the change in CO<sub>2</sub> concentration per unit time and dividing by ground surface measurement area (Lund et al. 1999; Solondz et al. 2008; Strack et al. 2014). As EGM-4 measures the concentration in ppm sec<sup>-1</sup>, the change



in CO<sub>2</sub> concentration was converted to mass per unit volume by multiplying it by the molar mass and dividing by the molar volume.

$$F = \Delta C \frac{M V}{N A} CF \quad (1)$$

where  $F$  is CO<sub>2</sub> flux (mg m<sup>-2</sup> s<sup>-1</sup>),  $\Delta C$  is change in the chamber headspace CO<sub>2</sub> concentration (ppm sec<sup>-1</sup>),  $A$  is the area of the chamber (m<sup>2</sup>),  $M$  is the molar mass of CO<sub>2</sub> at standard temperature and pressure (STP) (4401 × 10<sup>6</sup> mg mol<sup>-1</sup>),  $N$  is the molar volume of a gas at STP (0.0224 m<sup>3</sup> mol<sup>-1</sup>),  $CF$  is the conversion factor from parts per million to mole (1 ppm = 10<sup>-6</sup> mol),  $V$  is the corrected gas volume within the chamber (m<sup>3</sup>) calculated as,

$$V = \frac{273.15 P (V_{ch} + V_c)}{1013.25 (273.15 + T)} \quad (2)$$

where  $P$  is atmospheric pressure (mbar),  $T$  is air temperature (°C),  $V_{ch}$  is volume of the chamber (m<sup>3</sup>),  $V_c$  is volume of the collar (m<sup>3</sup>) calculated based on the average height of the collar aboveground.

Gross ecosystem production (GEP) was calculated as,

$$GEP = NEE + R \quad (3)$$

where  $NEE$  is net CO<sub>2</sub> flux and  $R$  is flux associated with respiration of the aboveground vegetation and soil respiration (Kutzbach et al. 2007). Our sign convention is that positive  $NEE$  indicates carbon uptake by ecosystem, and both  $GEP$  and  $R$  are given positive signs.

## Environmental Variables

Environmental conditions (wind speed and direction, air temperature, atmospheric pressure, precipitation, net radiation) at Saline Fen were obtained from the climate station equipped with Gill Windmaster Pro sonic anemometer, LI-7200 Enclosed Path CO<sub>2</sub>/H<sub>2</sub>O Analyzer, Kipp and Zonen NR-lite, Onset HOBO Pro V2 Temp/Rh, Onset Hobo RG3 tipping bucket. To assess the control of environmental variables on CO<sub>2</sub> fluxes, measurements of water table depth (WTD), soil moisture (SM), and soil temperature (ST) (at 0, 5, 10 cm), and electrical conductivity (EC) were taken adjacent to collars simultaneously with flux measurements. Water table depth measurements were made with a 1.5 m long blow stick (0.001 m increments) in wells that were constructed out of 2.5" PVC tubing cut to 30 cm and installed within 1 m from each collar ( $n = 14$ ). SM and ST were measured using handheld probes HH2 Meter (Delta-T Devices) and Type K thermocouple probe and meter (HH200, Omega Scientific, USA), respectively. EC was measured in the field by EC<sub>1:5</sub> tests for which 1 part peat was mixed with 5 parts distilled water, and the EC of the solution was tested using handheld probe (YSI ProPlus, YSI Incorporated, USA); peat EC was calculated by

applying the EC<sub>1:5</sub> conversion factor with respect to peat moisture content and texture (Rayment and Higginson 1992). Plant root simulator (PRS) probes (Western Ag Innovations Inc., Saskatoon, Canada) were used to quantify the availability of major anions and cations. PRS probe consists of a plastic applicator handle with an ion exchange resin membrane that can be buried into soil to measure ion supply in situ with minimal disturbance (Western Ag 2014). PRS probes were inserted 10 cm below the peat surface for three weeks in July and August 2015. Within 24 to 72 h after the field incubation, each probe was cleaned with distilled water, placed in a polyethylene bag and stored in a cool, dry location until shipped to Western Ag Innovations for analysis.

Pond water EC, water temperature, pH, dissolved oxygen (DO) and chlorophyll *a* concentrations were measured simultaneously with flux measurements using a handheld probe (YSI Professional Plus; YSI Incorporated, USA). Surface water (from ~ 20 cm) samples from each site were collected simultaneously with flux measurements. The water samples were filtered (0.45 µm cellulose acetate filters) within 24 h of collection and frozen (for major ion analysis and soluble reactive phosphorus (SRP), NO<sub>3</sub><sup>-</sup> and NH<sub>4</sub><sup>+</sup>) or acidified (for total N and P). Samples were analyzed in the Biogeochemistry Lab at the University of Waterloo (major ions on DIONEX ICS3000; nutrients on Bran Luebbe AA3, Seal Analytical, Seattle, U.S.A., Methods G-102-93 (NH<sub>4</sub><sup>+</sup>), G-109-94 (NO<sub>3</sub><sup>-</sup> and NO<sub>2</sub><sup>-</sup>), G-103-93 (SRP)).

## Vegetation Sampling

All species at each peatland collar were identified and percent cover was estimated (point-intercept method (Rich et al. 2005)), but only species with an abundance >1% are considered in this study. The leaf area index (leaf surface area per unit soil surface area, LAI) of each vegetated collar was measured after flux measurements using AccuPAR LP-80 Ceptometer (Decagon Devices, Inc). In September 2015, vegetated collars were harvested to a depth of 20 cm to quantify above and belowground biomass. Aboveground vegetation was clipped and oven dried at 60 °C for 2 days and then weighed to estimate aboveground biomass (AB). Coarse roots were removed manually while fine roots were separated by washing through a 1 mm mesh sieve. The roots were oven dried at 60 °C for 2 days and weighed to estimate belowground biomass (BB). Seasonal increase in belowground biomass (BBI) was accessed using the soil core in-growth method (Neill 1992). In May 2015, 5 peat cores (height of 10 cm and diameter of 5 cm) were taken near each vegetated collar; all live plant roots were removed and the peat was put back in the original hole. After recollecting the cores in September 2015, all live roots were removed, oven dried at 60 °C for 2 days and weighed to estimate BBI. 5 short (20 cm) peat cores were taken near vegetated collars and analysed for soil

organic matter (SOM), bulk density (BD), porosity (Po) and specific yield (Sy). For pond sites, plant identification and vegetation density (VD, as percent cover) estimation under the floating chamber was conducted along with flux measurements.

## Statistical Analyses

Principal components analysis (PCA) was used to identify the main environmental gradients and to reduce the dimensionality of environmental measurements. Due to a skewed distribution, all data except water table depth and pond depth were log-transformed while water table depth and pond depth were square-root transformed prior to ordination analysis. In this study, non-parametric tests were used because 1) visual inspection (frequency distribution (histogram)) and normality tests (Shapiro-Wilk test and Anderson-Darling test) of the data distribution suggested non-normal data distribution; 2) median scores better represent the central tendency for the data; 3) several outliers that cannot be removed from dataset were detected. As such, the Mann–Whitney U-tests was used to detect differences in environmental variables, NEE, GEP and R between ridges and depression, as well as differences in NEE, GEP and R between hyposaline and strongly saline pond sites. Differences in NEE, GEP and R between slightly to moderately saline, strongly saline, and very strongly saline sites within peatland were determined by the Kruskal–Wallis test. Probability values obtained from nonparametric tests were alpha corrected using a Bonferroni correction. Due to relatively small sample size, alpha level was set to 0.05 to detect any significant relationship between variables. Spearman's rank correlation coefficient ( $r_s$ ), a nonparametric measure of rank correlation between two variables was used to determine relations between NEE, GEP, R and environmental variables. To assess the extent to which the variables that strongly correlated (as revealed by Spearman's correlation) with NEE, R, and GEP were direct drivers of CO<sub>2</sub> fluxes, a non-parametric Spearman's semi-partial correlation analysis was performed to control for the main environmental covariates. All statistical analyses were performed using PAST 3.06 (Hammer et al. 2001) except semi-partial correlation that was performed using RStudio (RStudio Team 2015).

## Results

### Spatial Variability in CO<sub>2</sub> Fluxes

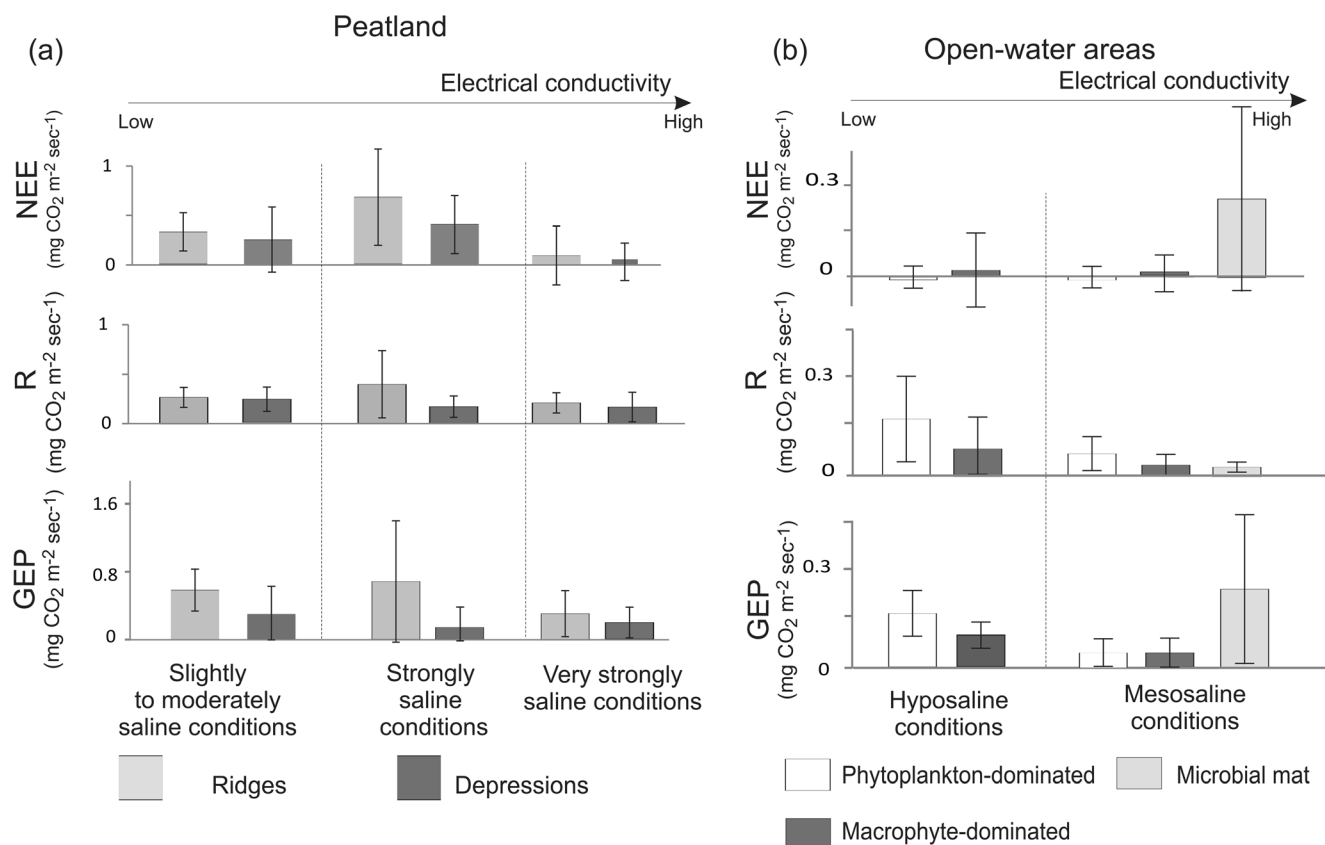
Significant differences ( $p < 0.05$ ) in NEE, GEP, and R between slightly to moderately saline, strongly saline, and very strongly saline sites were observed. The mean NEE of peatland sites varied from 0.06 mg CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup> (SD 0.19) within depressions with very strongly saline conditions to

0.94 mg CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup> (SD 0.30) within strongly saline ridges (Fig. 2a). The highest mean R (0.39 mg CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup> (SD 0.34)) was observed within strongly saline ridges (Fig. 2a) while very strongly saline depressions had the lowest R of 0.15 mg CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup> (SD 0.14) (Fig. 2a). GEP of peatland sites ranged from 0.21 mg CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup> (SD 0.17) within depressions with very strongly saline conditions to 0.71 mg CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup> (SD 0.83) within strongly saline ridges (Fig. 2a). Overall, ridge sites had significantly higher ( $p < 0.05$ ) NEE, GEP, and R than depressions (Fig. 2).

Hyposaline and mesosaline ponds were characterized by significant differences ( $p < 0.05$ ) in NEE, GEP, and R. Sites with microbial mats had significantly higher ( $p < 0.05$ ) mean GEP (0.21 mg CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup> (SD 0.05)) and NEE (0.24 mg CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup> (SD 0.05)) compared to phytoplankton- and macrophyte-dominated sites while R (0.18 mg CO<sub>2</sub> m<sup>-2</sup> s<sup>-1</sup> (SD 0.05)) was significantly higher ( $p < 0.05$ ) within phytoplankton-dominated sites compared to macrophyte-dominated sites and sites with microbial mat (Fig. 2b).

### Controls on CO<sub>2</sub> Fluxes within Peatland

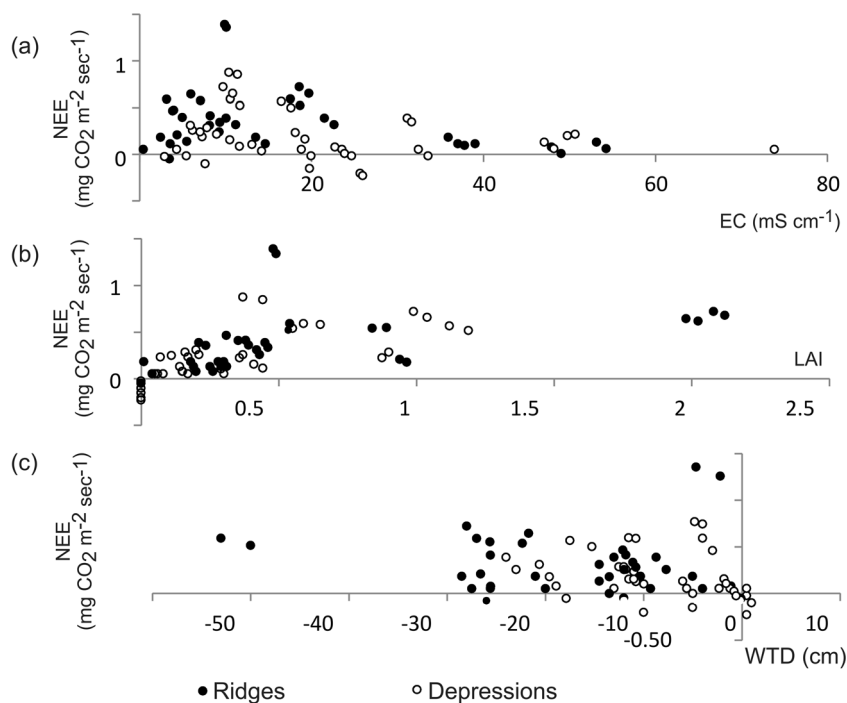
Variability in NEE, GEP, and R with respect to EC, WTD, SM, ST, LAI, and PAR within the peatland is shown in Online Resource (Figure3, Online Resource (Figs. S2–S4)). PCA revealed that the main environmental gradients within ridges were associated with LAI and WTD (PC 1), and EC (PC 2) that together contribute 60.8% of variance while within depressions the gradients were related to SM, WTD and LAI (PC 1), and EC (PC 2) that accounts for 62.8% of the variation (Online Resource (Table S3)). Ridges were characterized by significantly lower ( $p < 0.05$ ) EC comparatively to depressions. Significant differences ( $p < 0.05$ ) in WTD, SM, and LAI between ridges and depressions were found while ST was similar ( $p > 0.05$ ) between microtopographic forms; GEP and NEE were strongly positively correlated ( $r_s > 0.6$ ,  $p < 0.05$ ) with LAI within both ridges and depressions whereas NEE, R, and GEP were all negatively correlated ( $r_s < -0.5$ ,  $p < 0.05$ ) with EC in both depressions and ridges (Fig. 3; Online Resource (Table S4)). Both WTD and SM showed strong negative correlations ( $r_s < -0.5$ ,  $p < 0.05$ ) with NEE and GEP within depressions; however, within ridges only WTD demonstrated a strong negative correlation ( $r_s < -0.5$ ,  $p < 0.05$ ) with NEE, GEP and R (Fig. 3; Online Resource, (Table S3)). LAI within ridges and depressions remained strongly significantly correlated with NEE ( $r_s > 0.6$ ,  $p < 0.05$ ) and GEP ( $r_s > 0.6$ ,  $p < 0.05$ ) after controlling for EC, SM and WTD (Online Resource (Table S5)). Within ridges and depressions, correlation between NEE, GEP, R and EC remained significant ( $r_s > -0.5$ ,  $p < 0.05$ ) after controlling for LAI, WTD, and SM, and similarly, correlation between NEE, GEP and WTD was significant ( $r_s > -0.5$ ,  $p < 0.05$ ) after controlling for EC, LAI, and SM. Relations between NEE, GEP



**Fig. 2** Net ecosystem exchange (NEE), gross ecosystem productivity (GEP) and ecosystem respiration (R) within peatland (a) and open-water areas (b). Positive NEE values indicate CO<sub>2</sub> uptake. Vertical bars represent the standard deviation. Observed NEE, GEP, and R were

significantly different ( $p < 0.05$ ) between ridges and depressions as well as between slightly to moderately saline, strongly saline, and very strongly saline sites

**Fig. 3** Variations in net ecosystem exchange (NEE) with (a) electrical conductivity (EC), (b) leaf area index (LAI), (c) water table depth (WTD). Positive NEE values indicate CO<sub>2</sub> uptake



and SM were significant ( $r_s > -0.5$ ,  $p < 0.05$ ) after controlling for EC, WTD, and LAI within depressions only (Online Resource (Table S5)).

Soil properties (BD, Po, Sy) were generally similar ( $p > 0.05$ ) along a salinity gradient and between microtopographical forms, and only SOM of very strongly saline sites was significantly lower ( $p < 0.05$ ) than at less saline sites; moreover, mean SOM was also significantly higher ( $p < 0.05$ ) within ridges than depressions (Online Resource (Table S4)).

No significant differences in mean aboveground biomass (AB), belowground biomass (BB) between ridges and depressions were found; however, differences in BB were significant ( $p < 0.05$ ) along a salinity gradient. Increases in belowground biomass (BBI) were significantly higher ( $p < 0.05$ ) within ridges (Online Resource (Table S4)), and BBI was significantly different ( $p < 0.05$ ) along a salinity gradient.

Ridges were characterized by significantly higher ( $p < 0.05$ ) availability of total nitrogen (TN),  $\text{NH}_4^+$ ,  $\text{NO}_3^-$ ,  $\text{K}^+$ , P, Fe, Mn, S, Zn,  $\text{Ca}^{2+}$ , and  $\text{Mg}^{2+}$  (Online Resource (Fig. S5)). Along a salinity gradient, significant differences ( $p < 0.05$ ) in the availability of TN,  $\text{NH}_4^+$ ,  $\text{K}^+$ , Fe, Al, S,  $\text{Ca}^{2+}$  were observed. PCA of the soil chemistry data showed that within ridges the first PC axis represented gradients related to nitrogen and sulphur availability while the second PC axis was associated with phosphorous and iron availability; these two axes accounted for 48.5% of variance. Within depressions, the gradients found along the first two axes were associated with manganese (PC1), calcium and magnesium (PC2) availability and together accounted for 55.5% of the variation (Online Resource (Table S3)). Depressions were characterized by strong positive correlations ( $r_s > 0.6$ ,  $p < 0.05$ ) between all R, NEE, GEP and Mn,  $\text{Ca}^{2+}$ ,  $\text{Mg}^{2+}$  availability though these elements were also negatively correlated ( $r_s < -0.5$ ,  $p < 0.05$ ) with EC (Online Resource (Table S6)). No significant correlations between nutrient availability and the response variables NEE, GEP or R was evident within ridges, however.

### Controls on $\text{CO}_2$ Fluxes within Open-Water Areas

Variability in NEE, GEP, and R with respect to pond water EC, WD, WT, pH, DO and chlorophyll *a* concentrations, and VD within open-water areas is shown in Online Resource (Figs. S6–S8). PCA showed that the main environmental gradients within ponds were associated with vegetation density and EC (PC1) and nitrates, ammonium and phosphates concentrations (PC2), and the first two PC axes accounted for 61.9% of variance (Online Resource (Table S3)). Significant differences ( $p < 0.05$ ) in EC and chlorophyll *a* concentration between hyposaline and mesosaline ponds were found. However, WD, WT, DO, pH, and VD were not significantly different in hyposaline and mesosaline ponds. WD, EC WT, DO, and pH were similar ( $p > 0.05$ ) within unvegetated,

macrophyte-dominated sites and sites with a microbial mat, but significant differences ( $p < 0.05$ ) in vegetation density and chlorophyll *a* concentrations between these ponds were observed.

Nutrient concentrations in hyposaline and mesosaline ponds are shown in Online Resource (Fig. S9). Mesosaline ponds had significantly higher ( $p < 0.05$ ) concentration of  $\text{SO}_4^{2-}$ ,  $\text{K}^+$ ,  $\text{Mg}^{2+}$ ,  $\text{Ca}^{2+}$ ,  $\text{Na}^+$ ,  $\text{Cl}^-$ ,  $\text{NH}_4^+$ ,  $\text{NO}_3^-$ ,  $\text{PO}_4^{3-}$ . No significant differences in  $\text{SO}_4^{2-}$ ,  $\text{K}^+$ ,  $\text{Mg}^{2+}$ ,  $\text{Ca}^{2+}$ ,  $\text{Na}^+$ ,  $\text{Cl}^-$  between non-vegetated, macrophyte-dominated sites and sites with a microbial mat were found, but sites with a microbial mat had significantly higher ( $p < 0.05$ )  $\text{NO}_3^-$  and  $\text{PO}_4^{3-}$  concentrations and significantly lower  $\text{NH}_4^+$  concentration compared to non-vegetated, macrophyte-dominated sites. In ponds, over the study season, both GEP and R correlated strongly positively ( $r_s > 0.5$ ,  $p < 0.05$ ) with vegetation density and phosphate concentration (Online Resource (Table S7)), and these relations remained strong and significant ( $r_s > 0.5$ ,  $p < 0.05$ ) after controlling for other environmental variables (EC, nitrates and ammonium concentrations) (Online Resource (Table S8)).

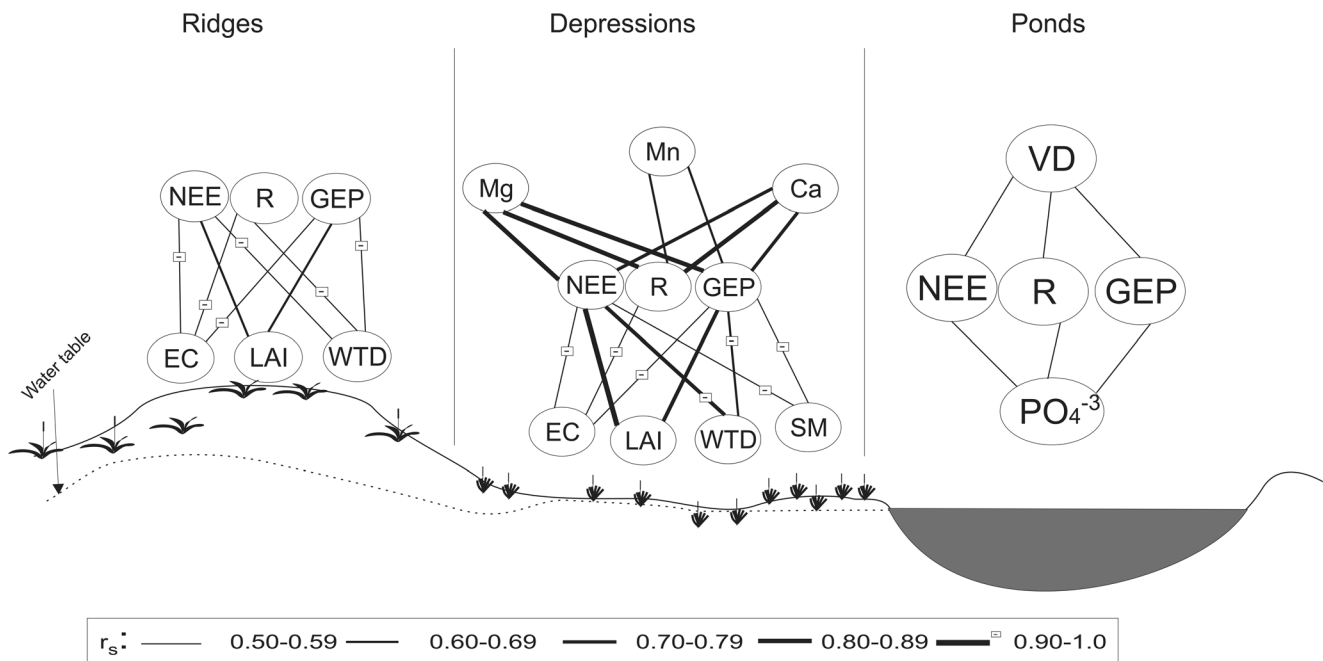
## Discussion

Construction of sustainable peatlands in post-mined oil sands landscapes is a multifaceted task that requires the re-establishment of key ecosystem functions including carbon capture and storage through biological processes, primarily photosynthesis. The results presented in this study show that  $\text{CO}_2$  uptake in a natural saline fen depends on the complex interactions between plant communities and environmental variables (primarily, WTD, EC, and nutrient availability) (Fig. 4). Moreover, the data illustrate that peatland microtopographic heterogeneity has a strong influence on the relationship between  $\text{CO}_2$  exchange and environmental conditions.

### $\text{CO}_2$ Fluxes within Peatland

Vegetation has been repeatedly shown to influence carbon fluxes (e.g., Picek et al. 2007; Koelbener et al. 2010; Strilesky and Humphreys 2012; Andrews et al. 2013). Although an effect of vegetation on methane emission in the studied fen was not prominent (Murray et al. 2017), in our study, strong positive correlations between  $\text{CO}_2$  fluxes and LAI (Table S4) suggest that vegetation properties are important for  $\text{CO}_2$  exchange. LAI, an index that represents an area of carbon and water surface exchange and is useful for assessment of vegetation community structure (Vose et al. 1994) was considered as one of the most important drivers of  $\text{CO}_2$  fluxes. LAI was positively correlated with NEE and GEP (Figs. 4, 7; Online Resource, Table S4) and it was found to





**Fig. 4** Correlations between net ecosystem exchange (NEE), gross ecosystem productivity (GEP), ecosystem respiration (R) and environmental variables (electrical conductivity (EC), water table depth (WTD), soil moisture (SM), leaf area index (LAI), availability of calcium ( $\text{Ca}^{2+}$ ), manganese (Mn) and magnesium ( $\text{Mg}^{2+}$ ) (measured by PRS Probes), concentration of phosphates ( $\text{PO}_4^{3-}$ ), vegetation density (VD))

within depressions, ridges and ponds in the studied saline fen. Only strong significant correlations are shown. Strength of the relationship ( $r_s$ ) has been shown as the width of a line. Negative correlation is indicated by “-” sign. Negative correlation between NEE, GEP, R, and WTD indicates higher NEE, GEP, and R associated with shallower water table

explain a substantial portion of the variation in GEP and NEE within both ridges and depressions as revealed by semi-partial correlation (Online Resource; Table S5). This is consistent with the findings of Lund et al. (2010) and Humphreys et al. (2006) and Goud et al. (2017) suggesting that increased  $\text{CO}_2$  uptake is often associated with increased LAI. Notably, in the studied saline fen, LAI was negatively correlated with EC within ridges and depressions, and BB and BBI were significantly lower under very strongly saline conditions, and this is consistent with a negative effect of elevated salt content on plant growth. For example, it has been shown that salinity suppresses an increase in plant biomass, coupled with photosynthetic rates (Sperling et al. 2014; Sutter et al. 2014) and affects LAI even within the same species growing under higher salinity levels (Phillips et al. 2016). Within ridges, LAI seems to be affected by WTD and soil moisture as revealed by a strong negative correlation. This can be explained by the dominance of species that are not tolerant to prolonged inundation (e.g., *J. balticus*, *H. jubatum*, *P. maritima*) that have been reported to have reduced biomass under waterlogged conditions (Cooper 1982; Montemayor et al. 2015).

Negative correlations between NEE, GEP, R and EC (Fig. 4), coupled with higher GEP in the less saline part of the fen is consistent with previous findings that salinity is one of the most important factors that can affect plant productivity and  $\text{CO}_2$  exchange in coastal and prairie wetlands (Neill 1993; Curco et al. 2002; Willis and Hester 2004; Neubauer 2013).

Notably, in the studied saline fen, LAI was negatively correlated with EC within ridges and depressions, and this is consistent with a negative effect of elevated salt content on plant growth in non-wetland ecosystems (Sperling et al. 2014) and marshes ((Sutter et al. 2014); moreover, the strong negative correlation between EC and LAI is consistent with previous work at Saline Fen (Phillips et al. 2016) that reported a negative relationship between salinity and LAI, even within the same species (*T. maritima*). A negative correlation between R and EC within ridges and depressions (Fig. 4) could result from reduced plant respiration due to reduced vegetative biomass resulting from higher EC (Online Resource; Table S1) as well as from the negative impact of elevated salt content on microbial activity that has been previously documented in coastal wetlands (e.g., Rejmankova and Houdkova 2006; Tripathi et al. 2006). However, previous study in Saline Fen suggested that salinity encourage decomposition as revealed by positive correlation between dissolved organic carbon (DOC) concentration and EC (Khadka et al. 2015, 2016). This discrepancy may be related to relatively narrow EC range (from ~0.5 to ~3.5  $\text{mS cm}^{-1}$ ) used for study of DOC dynamics by Khadka et al. (2015, 2016). Also, it has been shown that high salinity ( $\text{EC} > 3.5 \text{ mS cm}^{-1}$ ) hinders microbial activity, reducing the consumption of DOC and resulting in higher concentrations (Mavi et al. 2012).

Wetland productivity is known to be tied tightly to the moisture regime, as driven by the WTD (Wallen et al. 1988;

Hilbert et al. 2000). Several field studies have shown a positive correlation between primary productivity and WTD (Szumigalski and Bayley 1996). Notably, the relationship between productivity and WTD can be influenced by microtopography: within hummocks and ridges elevated above the water table, higher primary productivity is associated with a lower water table, whereas in depressions (lawns and hollows) primary productivity is higher during wet conditions (Alm et al. 1997; Strack et al. 2006). In contrast, in this study, a strong negative correlation between GEP and WTD was observed in both ridges and depressions (Fig. 4; Online Resource (Table S4)) and such correlation remained significant after controlling for EC (Online Resource (Table S5)) suggesting that WTD can be considered one of the controls on GEP. Such negative correlation between WTD and GEP within ridges can be explained by the dominance of flood-sensitive species (e.g., *J. balticus*, *H. jubatum*) (Cooper 1982; Montemayor et al. 2015), so the higher water table can reduce GEP. A negative correlation between GEP and WTD within depressions can be associated with prolonged flooding that hinders oxygen diffusion into roots from soil, causing a shift from aerobic respiration to energy-inefficient anaerobic respiration in flood-tolerant species (Reddy and DeLaune 2008). Such increased energy demand often results in an energy deficit affecting photosynthetic activity, water and nutrient adsorption and distribution (Pezeshki and DeLaune 2012) and thus, root growth as revealed by significantly lower BB and BBI within very strongly saline depressions. Consequently, although inundation-tolerant species such as *T. maritima* can survive within depressions, their productivity can be reduced due to energy depletion.

Carbon exchange is known to be linked to nutrient dynamics, and increased nutrient availability is often associated with increased productivity (Bonan and Van Cleve 1992; Mack et al. 2004). In this study, we observed strong positive correlation between magnesium, manganese, and calcium availability and GEP, NEE and R within depressions (Fig. 4; Online Resource (Table S6)). Such correlation can be expected as magnesium, manganese, and calcium play important role in photosynthesis, nitrogen and phosphorous assimilation, and cell formation (Rydin and Jeglum 2013), and thus are tightly connected to plant productivity and respiration. Moreover, Mg, Ca, and Mn availability can be limiting for plant productivity within depressions, as their availability is decreased under anaerobic conditions, and salinity coupled with higher pH can also yield reductions in Mg, Ca, and Mn supply (Cooper 1984; Stueben et al. 2004; Rydin and Jeglum 2013).

### CO<sub>2</sub> Flux within Open-Water Areas (Ponds)

Our results suggest that CO<sub>2</sub> flux in ponds is more strongly influenced by vegetation properties (such as vegetation

density) and community composition than by environmental variables. While CO<sub>2</sub> uptake rates were notably higher in ponds with macrophyte cover, low CO<sub>2</sub> uptake was observed in ponds lacking submergent vegetation, and this can be expected due to the absence of photosynthetic macrophytes that coincides with what was reported from salt marshes (Miller et al. 2001; Moseman-Valtierra et al. 2016). Although phytoplankton productivity and respiration are important components of carbon cycling in aquatic ecosystems (Kobayashi et al. 2013), microalgae are not likely the main contributors to CO<sub>2</sub> uptake within ponds as suggested by the low productivity of plankton-dominated ponds and the weak correlation between GEP and chlorophyll concentrations. The highest CO<sub>2</sub> uptake was observed in a mesosaline pond (South Pond) that had excessive benthic microbial mats (Fig. 2b). Such photosynthetic microbial mats are known from saline environments (Ley et al. 2006; Kunin et al. 2008; Burow et al. 2013), and have high primary production rates that are comparable to rates of tropical rain forests (Guerrero and Mas 1989). Our findings suggest that microbial mats are likely important contributors to CO<sub>2</sub> fluxes, but further detailed studies of community composition and the main pathway of carbon through the microbial community are required for better understanding of role of microbial mats in carbon cycling within open-water areas in saline boreal fens.

Strong significant positive correlations between GEP, R, and phosphates observed in this study (Fig. 4) and such relations remained strong and significant after controlling for other variables (Online Resource (Table S8)) suggesting that phosphate concentration had strong effect on CO<sub>2</sub> fluxes. This was expected as P is a key nutrient in aquatic ecosystems, and increased ecosystem production is often associated with P load (Wetzel et al. 2001; Elser et al. 2007). However, this is in contrast to saline prairie lakes and wetlands that are often N-limited (Sahm et al. 2009). Although our study has shown that EC had a strong effect on primary productivity within peatlands, EC was not a controlling parameter for CO<sub>2</sub> fluxes; moreover mesosaline ponds had higher GEP than hyposaline ponds.

### Implications for Fen Construction in AOSR

Microtopography plays an important role in the regulation of water drainage, water table position and salinity within constructed wetlands (BGC Engineering Inc. 2010); in addition, our study revealed that microtopography plays an important role in regulation of CO<sub>2</sub> fluxes within peatland areas. Because topographic heterogeneity is one of the desired features of constructed wetlands (Wylynko and Hrynshyn 2014), development of appropriate planting scheme (a construction document that shows the position, variety and quantity of plants to be planted within constructed wetlands) that will support the highest possible CO<sub>2</sub> uptake within different

microtopographic forms is of paramount importance. Our results suggest that *J. balticus*, *C. stricta* and *H. jubatum* support high CO<sub>2</sub> uptake within ridges while *T. maritima* and *A. prostrata* are the most productive in depressions. However, a more detailed study with a wide range of plant species is required to determine the most appropriate species composition with respect to the height, slope, aspect and general shape of microtopographical forms.

The EC gradient across the studied fen had a strong impact on biologically dependent carbon uptake (Fig. 2), with decreasing biomass production from more saline to less saline parts of the fen. Within peatland plant productivity varied greatly due to differences in WTD, and a strong negative effect of elevated EC (>15 mS cm<sup>-1</sup>) coupled with prolonged flooding on primary productivity and respiration was found. Consequently, although the accumulation of organic matter under saline conditions depends mainly on the presence of a high water table (Trites and Bayley 2009a), continuous waterlogging especially in areas with EC > 15 mS cm<sup>-1</sup> should be avoided in constructed fens, as it can reduce CO<sub>2</sub> uptake.

This study suggests that vegetation cover is of paramount importance for CO<sub>2</sub> exchange within ponds, and ponds with dense macrophyte cover had higher GEP comparatively to phytoplankton-dominated ponds. Given this, fen design should ensure pond construction is favourable for vegetation establishment. Salt-tolerant *S. pectinata* seems to be useful for increasing carbon uptake within open-water areas in constructed fens, but further studies are required to determine the most suitable species composition under different salinity levels. Because aquatic areas within western boreal forests have increased evaporative losses (Devito et al. 2012), and dense macrophyte cover can result in more intense evapotranspiration and a consequent decline in water level (Xu et al. 2014), macrophyte control through planting and harvest seems to be necessary for achieving the highest possible GEP that would not affect water balance in constructed ponds. Although productivity of planktonic algae seem to be low in the studied ponds, benthic microbial mats were associated with the highest GEP suggesting possible usefulness of the microbial mats for increasing productivity in constructed open-water areas. Microbial mats may be suitable for mesosaline ponds where growth of macrophytes is limited due to salt content; however, detailed study of role of the mats in carbon transformation in ponds is necessary to determine their usefulness for wetland construction in AOSR.

### Limitation of the Study

CO<sub>2</sub> fluxes in this study represent point samples of midday fluxes and cannot be extrapolated to diurnal or seasonal

carbon balances (Heijmans et al. 2001), but to provide representation of average mid-day fluxes to compare relative fluxes across the salinity gradient (Petrone et al. 2011). Although CO<sub>2</sub> exchange is an important part of carbon balance of fens, this study did not aim to characterize carbon sequestration and carbon balance of the fen, but sought to reveal the main environmental factors that influence NEE and R. This study was focused on environmental controls on CO<sub>2</sub> fluxes along a salinity gradient, so sampling across a wide range of EC, rather than multiyear repetitions, was considered to be more essential for the study. Further continuous measurements of CO<sub>2</sub> fluxes are required to reveal diurnal and annual changes in carbon uptake and release that are crucial for proper characterization of carbon sequestration within the site. Despite some improvement in our understanding of the methane emission and DOC biogeochemistry in Saline Fen (Khadka et al. 2015, 2016; Murray et al. 2017), further studies of CH<sub>4</sub> fluxes and DOC production that will include full range of EC at the fen are necessary for accurate estimation of carbon balance of the site.

### Conclusion

Notable differences in CO<sub>2</sub> fluxes between ridges, depressions, and ponds reveal obvious spatial heterogeneity in saline fen carbon dynamics. Vegetation properties, WTD, and EC were identified as the main controlling factors on CO<sub>2</sub> fluxes within peatland. Microtopography was important for CO<sub>2</sub> fluxes, largely through its alteration of relations between CO<sub>2</sub> exchange and environmental factors, and more complex relationships between NEE, GEP, R and environmental variables were observed within depressions. Within open water areas (ponds), changes in CO<sub>2</sub> fluxes were mostly associated with vegetation density and phosphate concentration. This study illustrated importance of appropriate choice of vegetation communities for open-water areas within constructed fens; moreover, the results suggested that development of planting schemes with respect to microtopographical differences will help to support carbon capture within constructed fens.

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