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Plant functional group effects on peat carbon cycling in a boreal rich fen

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Abstract Dominant plant functional groups (PFGs) found in boreal rich fens include sedges, grasses, horsetails, and cinquefoils (obligate wetland shrubs). Precipitation regime shift and permafrost thaw due to climate change will likely trigger changes in fen plant community structure through shifts in these PFGs, and it is thus crucial to understand how these PFGs will impact carbon cycling and greenhouse gas dynamics to predict and model peatland-climate feedbacks. In this study, we detail the above and belowground effects of these PFGs on aspects of carbon cycling using a mesocosm approach. We hypothesized that PFGs capable of aerating the rhizosphere (sedges, horsetails, and grasses) would oxidize the belowground environment supporting higher redox potentials, a favorable environment for decomposition, and higher CO_2:CH_4 in pore water and gas efflux measurements than PFGs lacking aerenchyma (cinquefoil, unplanted control). Overall, sedges, horsetail and grasses had an oxidizing effect on rhizosphere pore water chemistry, producing an environment more favorable for methanotrophy during the growing season, as supported by an approximate isotopic enrichment of pore water methane ($\delta^{13}CH_4$) by 5‰, and isotopic depletion in pore water carbon dioxide ($\delta^{13}CO_2$) by 10‰, relative to cinquefoil treatments. Cinquefoil and unplanted control treatments fostered a reducing environment more favorable for methanogenesis. In addition, cinquefoil appeared to slow decomposition in comparison with the other PFGs. These findings, paired with PFG effects on oxidation–reduction potential and CO_2 and CH_4 production, point to the ability of rich fen plant communities to moderate biogeochemistry, specifically carbon cycling, in response to changing climatic conditions.

Keywords Peatlands · Carbon cycling · Trace gas · Vegetation · Boreal ecosystems · Climate change

Abbreviations

APEX	Alaska peatland experiment
BIX	Biological index
CH_4	Methane
CO_2	Carbon dioxide

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DOC	Dissolved organic carbon
DOM	Dissolved organic matter
ESC	Electron shuttling capacity
HIX	Humification index
NDVI	Normalized difference vegetation index
PFG	Plant functional group
Sr	Spectral ratio
SUVA	Specific ultraviolet absorbance
TI	Tryptophan index
TN	Total nitrogen

Introduction

Peatlands are common landscape features in boreal North America. Cool, hypoxic and acidic conditions as well as the input of plant litter that is difficult to decompose have resulted in the accumulation of soil organic matter in these ecosystems, with peatlands storing an estimated one-third of the terrestrial soil carbon (Gorham 1991; Yu 2012). As climatic change disproportionately affects northern landscapes (Steward et al. 2013), changes in temperature and hydrology (Hinzman et al. 2005) will likely cause plant community shifts in northern peatlands, as has been demonstrated by numerous studies (Minkkinen et al. 1999; Weltzin et al. 2001; Laiho et al. 2003; Brancaleoni and Gerdol 2014; Churchill et al. 2014; Pedrotti et al. 2014; Potvin et al. 2014; Dieleman et al. 2015; McPartland et al. 2019). These vegetation community shifts may have consequences for belowground carbon cycling linkages (Jassey et al. 2013; Radu and Duval 2018). In fact, recent studies have demonstrated that plant community structure alone can have a stronger effect on belowground carbon cycling than established environmental drivers like temperature (Ward et al. 2015; Dieleman et al. 2017).

A growing number of studies have found plant functional groups (PFGs) to be an effective predictor of carbon cycling dynamics in northern peatlands (Chapin III et al. 1996; De Deyn et al. 2008; Ward et al. 2009). Mosses, particularly *Sphagnum* spp., are a widely studied PFG in peatland science (Crum and Planisek 1992; Asada et al. 2003; Basiliko et al. 2004; Turetsky et al. 2008, 2012; Dieleman et al. 2015). Two main vascular PFGs have been widely studied in peatland literature, namely ericaceous shrubs (e.g., *Vaccinium* spp., *Chamadaphne* spp., etc.) and sedges (e.g., *Carex* spp.). Shrubs in the Ericaceae family are characterized by recalcitrant leaves and shallow roots with mycorrhizal associates. Belowground linkages to carbon cycling in ericoid shrubs include the capability to suppress decomposition in the rhizosphere due to antagonistic relationships between soil saprotrophs and ericoid fungal mycorrhizal associates (Gadgil and Gadgil 1975; Read et al. 2004; Romanowicz et al. 2015; Wiedermann et al. 2017). Sedges are monocots with a graminoid form and are known to contain aerenchymous tissue that can passively aerate the soil rhizosphere. The oxidized rhizosphere can increase the availability of energetically favorable electron acceptors needed to support relatively rapid, aerobic decomposition and methanotrophy in an otherwise anoxic environment (Holzapfel-Pschorn et al. 1986; Whiting and Chanton 1992; King et al. 1998; Strack et al. 2017). Conversely, sedges also release labile root exudates into deep peat horizons, which stimulate trace gas production as a form of rhizosphere or microbial priming (Mary et al. 1993; Chanton et al. 1995; Glaser and Chanton 2009). The net effect of both the addition of electron acceptors (O_2) and electron donors (labile carbon) by sedges appears to have different consequences for carbon cycling depending on site, experiment, and other environmental variables.

Understanding the differential impacts of ericoid shrub and sedge PFGs has helped us better understand the complex controls of carbon cycling in many northern peatlands (Schaepman-Strub et al. 2009; Kuiper et al. 2014; Noyce et al. 2014; Potvin et al. 2014; Wiedermann et al. 2017). However, past studies of these PFGs have largely taken place in bogs and poor fens at the ombrotrophic end of the peatland gradient. In contrast, few studies have explored the importance of PFGs in more minerotrophic rich fens. Rich fens are one of the most common boreal peatland types in western North America (Vitt et al. 2000), and are an increasingly dominant component of the Alaskan landscape (Lara et al. 2016). Moreover, carbon cycling in these systems has been shown to be more sensitive to vegetation than in other types of peatlands (Turetsky et al. 2014).

Rich fens are commonly dominated by sedges, but understudied PFGs like horsetail (e.g., *Equisetum fluviatile*), marsh cinquefoil (e.g., *Comarum palustre*), and grasses (e.g., *Calamagrostis* spp.) (Rydin and Jeglum 2013) can also make up significant

percentages of the plant community. Horsetail is part of an ancient phenology of plants belonging to the family Equisetaceae that reproduces by spores. The silica-containing stems of the plant are divided into a series of hollow segments that rise perpendicularly from a horizontal subterranean rhizome which maintains the hollow, segmented structure (Hauke 1979). Marsh cinquefoil is an obligate non-ericoid wetland shrub in the family Rosaceae (USDA 2018). It is characterized by sprawling stems that run above and below the water table, often parallel to the earth, rooting shallowly along the length of the stem and rising up to produce small clumps of stems and leaves. In contrast, grasses such as *Calamagrostis* spp. form dense root clumps and have been purported to contain aerenchymous tissue (Landhäusser and Lieffers 1994). The effects of these widely prevalent yet understudied PFGs on carbon cycling dynamics may be key for understanding indirect effects of climate change on rich fens through changes in plant community composition.

By understanding the effects of PFGs we can better understand the large degree of variation in anaerobic carbon cycling observed in many peatland soils, perhaps via impacts on organic terminal electron acceptors. The ratio of CO_2:CH_4 production should be 1:1 under anaerobic conditions that support methanogenesis (Conrad 1999); however, multiple studies report CO_2:CH_4 values in excess of 1:1 under these conditions (Valentine et al. 1994; Vile et al. 2003; Keller and Bridgham 2007; Estop-Aragonés et al. 2013; Fan et al. 2013; Kane et al. 2013; Olefeldt et al. 2017). A growing body of literature indicates that dissolved and solid-phase organics may be responsible in part for these trends by functioning as regenerable electron acceptors in peats with fluctuating oxidation–reduction (redox) conditions (Keller and Takagi 2013; Klupfel et al. 2014). In fact, a recent study by Agethen et al. (2018) demonstrated that in situ regeneration of dissolved organic electron acceptors in peatlands, caused in part by cyclic rewetting and root activity of various aerenchymous plants, suppressed methane production. However, exactly how different PFGs mediate these redox conditions controlling trace gas production is poorly resolved in rich fen ecosystems.

Here, we investigate PFG effects on trace gas production, decomposition, dissolved and solid phase organic matter, pore water and litter leachate chemistry, and peat redox dynamics in a mesocosm experiment. Specifically, we hypothesized that PFGs capable of aerating the rhizosphere via aerenchyma or hollow rhizomes (sedges, horsetails, and grasses) would oxidize the belowground environment supporting higher redox potentials, a favorable environment for decomposition, and higher CO_2:CH_4 in pore water and gas efflux measurements than in PFGs lacking aerenchyma (cinquefoil, unplanted control). Conversely, we hypothesized that PFGs without these traits would be associated with lower redox potentials, an unfavorable environment for decomposition, and lower CO_2:CH_4 ratios.

Materials and methods

Mesocosms

To test our hypotheses, 30 mesocosms were created using four dominant PFGs typical of rich fens in central Alaska. The PFGs included sedge (*Carex atherodes* Spreng.), grass (*Calamagrostis* spp. Michx), horsetail (*Equisetum fluviatile* L.), and cinquefoil (*Comarum palustre* L.). Unplanted mesocosms were also used as controls ($n = 6$ for all treatments). A mesocosm approach allowed us to control for peat microform (hummocks, hollows, and lawns), which strongly influences carbon cycling in a natural peatland setting (Strack et al. 2006a; Hribljan et al. 2017). In this study, all mesocosms consisted of peat collected from lawns. Peat and plants for the mesocosm experiment were collected in June 2017 from Pixie Fen (WGS 84: 64°42′04″N 148°16′50″W), a rich fen with pH 5.7–6.1 just outside of the Bonanza Creek Experimental Forest southwest of Fairbanks, Alaska. Pixie Fen is situated in a narrow alluvial plain within the floodplain of the Tanana River, and is characterized by *Sphagnum* and brown moss species in addition to the dominant plant species listed above. There are no trees within the fen except for a central island of birch and aspen. Interior Alaska experiences large temperature fluctuations, with a mean annual temperature of − 2.9 °C and 269 mm of rain per year (Hinzman et al. 2006). The growing season is short, ranging from around mid-May to mid-August. In June, daylight reaches > 21 h/day.

Peat was collected from within one area of the fen with an expanse of lawn microtopography (25 m × 10 m) to a depth of approximately 30 cm,

transported to Fairbanks, and homogenized by hand to remove large roots. Individual plants from the same area were carefully removed from the fen with a shovel in order to maintain the health of the fine roots. These were transported in water back to Fairbanks and randomly assigned to the relevant mesocosm treatment. Two to five individual plants of the same species were planted in homogenized peat in 3.8 L (roughly 17 × 26.5 cm) glass jars (approximately 1.2 kg peat dry mass equivalent per jar) with a spigot 3 cm from the base of the jar. The number of plantings in each mesocosm was based on the visually assessed consistency of biomass going into each jar. For example, horsetails and sedges occupy much less space than cinquefoils or grasses, so more individuals were planted in those mesocosms to attain a similar plant density per jar as the other treatments. Measured differences in biomass were accounted for in statistical analyses (described below). Peat was gently but firmly packed around the plants to a constant height within the jar, and leveled to control for microtopographical effects (i.e., creating a "lawn" environment in each mesocosm as opposed to hummocks and hollows). Approximately 40 cm of vinyl tubing was secured around the spigot using plumber's tape covered with electrical tape. The tubing was wrapped around the jar and secured 3 cm below the location of the peat surface within the jar to maintain the water level within the jars at a constant, as conducted by Dieleman et al. (2017). This design also allowed for water flow through every time more water was added, mimicking fen system hydrology (constant inflow and outflow from surface/groundwater). Each jar was wrapped with a white canvas shroud to exclude light. The water levels within the mesocosms were checked throughout the week, depending on the weather (more often on hot, dry days). Water for the mesocosms was collected approximately bi-weekly from a rich fen with standing water about 1 km from the source site and stored in opaque plastic jugs. Mesocosms were randomly assorted in a fenced-in open area on the University of Alaska (Fairbanks) campus, exposed to all the natural elements that would be present at Pixie Fen. The mesocosms were established in early June 2017 and the experiment was ended in September 2017 to coincide with senescence in the field.

Two weeks after the initiation of the mesocosm experiment, decomposition bags consisting of a pre-weighed Whatman 0.2 μm cellulose filter inside a 1 × 1 mm screen 8.5 × 9.5 cm mesh bag were installed into each mesocosm to a depth of 10 cm. Bags were removed at the close of the mesocosm experiment (after 13 weeks of decomposition), gently rinsed to remove peat, and dried at 65 °C before weighing the remains of the filter to determine mass loss by decomposition. An overview of measurements collected throughout the course of the study is summarized in Table 1.

Pore water collection and analysis

Pore water samples were collected on three dates during the growing season after allowing 1 month for plant acclimation (July 14, 20, and 27, 2017) and once during fall senescence (September 2017). A stainless steel "sipper" (0.52 cm diameter tubing with 2 cm slotted region at the end), was carefully inserted into the peat to the bottom of the mesocosm (a depth of 20 cm below the peat surface), about 5 cm from the main plant stems. Pore water was drawn up through the sipper into a syringe that was rinsed first with deionized (DI) water, then with sample prior to aliquot collection. The first aliquot was used to measure the oxidation–reduction potential of the water using an oxidation–reduction (Eh) probe (Hach Co., Loveland, Co., USA, Intellical MTC301) connected to a sealed and sample-purged flow-through cell, following Romanowicz et al. (2015). All Eh values were normalized to a pH of 7 (Eh7), based on pH–Eh relationships for Quinhydrone (Bier 2009). The second aliquot was injected into a 125 mL dinitrogen gas flushed and evacuated Wheaton® glass vial capped with a butyl rubber septa via a 0.45 μm Whatman syringe filter and needle. The needle hole was immediately covered with vacuum grease and wrapped in parafilm upon removal of the needle. A third aliquot was filtered into 60 mL high density polyethylene (HDPE) Nalgene bottles for analysis of ions and organic acids (Dionex® ICS-2000 ion chromatograph with an IonPac AS11 separator column; Thermo Fisher, Sunnyvale, CA). The final pore water aliquot was run immediately on a field spectrophotometer using SpectraWiz® spectroscopy software (StellarNet Inc., Tampa, FL). Ultraviolet absorbance at λ = 195–1000 nm were determined using a 1 cm quartz cuvette averaged over five reads.

Headspace gases were collected from the glass pore water vials within 2 h of field collection. Bottles were

Table 1 Summary of measurements collected throughout the duration of the study

Activity/measurement	Data obtained	# campaigns
Chamber measurements	CH_4, CO_2 efflux	4
Pore water collection	$^{13}CO_2$, $^{13}CH_4$, DOC, TN, spectral DOC characterization, ions, organic acids	4
Oxidation–reduction potential	Eh7, monitoring treatment separation	7
Peat cores	Electron shuttling capacity of peat	2
Decomposition assays	Mass decomposed over study period	1
Biomass measurements	Aboveground and belowground biomass	1
Leaf extract characterization	Spectral character of leaf tea extracts	1
Peat mass	Bulk density	1
FTIR	Inherent peat characterization	1

shaken vigorously for 1 min, after which two aliquots of 12 mL of gas were removed and injected into dinitrogen gas flushed and pre-evacuated 12 mL Exetainer™ vials. Isotopic composition ($\delta^{13}C$) and concentrations of CO_2 and CH_4 in gas samples were measured at the UC Davis Stable Isotope Facility, CA, USA.

The remaining gas-stripped pore water samples were stored upside down on ice packs and shipped to the Northern Research Station in Houghton, MI, USA for further processing. Pore water was extracted from each of the Wheaton vials and run on a fluorometer (Horiba–Jobin–Yvon Aqualog C; Horiba Co., Edison, NJ) to simultaneously collect UV–Vis absorbance and florescence spectra. Run parameters were excitation: 240 to 600 nm in 3-nm increments; emission: 212 to 608 nm by 3 nm bandpass; integration time = 0.25 s. Samples with absorbance greater than 0.6 at λ 254 ($A_{254} > 0.6$) were diluted with DI water, such that they were $0.20 < A_{254}$ (sample) < 0.6 to satisfy the assumption of detector linearity required by modeling (Stedmon and Bro 2008; Lawaetz and Stedmon 2009). Data post-processing and correction for inner filter effects were as described in detail by Veverica et al. (2016), following Stedmon and Bro (2008) and Lawaetz and Stedmon (2009). Absorbance and fluorometric indices were calculated to characterize dissolved organic matter in all pore water samples. The remaining pore water was acidified to pH 2 with concentrated HCl acid and analyzed for dissolved organic carbon and total dissolved nitrogen (TDN) on a Shimadzu® Total Organic Carbon Analyzer with a TDN module (Shimadzu Scientific Instruments, Columbia, MD).

Trace gas flux measurements

Chambers for dark CO_2 and CH_4 efflux measurement were constructed from 10.2 cm inner diameter × 61.5 cm opaque polyvinyl chloride (PVC) pipe to create an exact fit between the top of the mesocosm and the chamber. Due to the small size of the chambers, no internal fans were installed. Chambers were lined with closed cell foam weather stripping to ensure a complete seal. Dark static chamber CO_2 efflux measurements (Carroll and Crill 1997) were collected using an Infrared Gas Analyzer (IRGA; EGM-4; PP-Systems International, Amesbury, MA). Changes in CO_2 concentrations were measured in the headspace of each chamber for ~ 3 min. Methane efflux was measured by taking a syringe of gas from a collection tube with a stopcock attached to the chamber every 5 min for 30 min. Gas was mixed within the collection tube and chamber prior to final sample using a syringe. Methane was analyzed within 24 h on a gas chromatograph (Varian 3800 FID detector; Varian Analytical Inc., Palo Alto, CA) calibrated with three concentration standards daily (0, 10.22, and 100 ppm). Standards were run every 14 samples to ensure read accuracy. Each flux was examined visually for linearity and none were discarded ($R^2 \geq 0.50$).

Peat core collection for electron shuttling assay

Small sharpened PVC corers 1.9 cm in diameter and 20 cm long were used to core the mesocosms twice within the time period of the experiment, once on July 24 and again on September 25. Sharpened PVC corers

were rotated as inserted, to cut the peat. Inserted corers were capped, allowing suction to remove intact core, and upon extraction the bottom end was flushed with pore water extracted from the bottom of the hole from whence the core came and capped (PVC end caps). Closed PVC tubes were placed within the holes created by core collection to minimize further impact to the mesocosms. Cores were shipped on ice to Chapman University (Orange, CA, USA) where electron shuttling assays were performed on the peat, as described in detail by Keller and Takagi (2013). Briefly, capped PVC cores were brought into an anaerobic chamber (Coy Laboratory Products, Grass Lake, MI) for processing. The cores were opened, pore water was decanted into 50 mL centrifuge tubes and peat was transferred to plastic weigh boats where it was gently mixed with forceps. Approximately 3 g of field-moist peat was added to the 50-mL centrifuge tubes containing pore water. Tubes were removed from the anaerobic chamber and centrifuged at 4100 rpm for 5 min. The centrifuge tubes were returned to the anaerobic chamber, pore water was decanted and filtered (Whatman GF/F) and 0.25 mL of filtered pore water was added to 1 mL of 5 mM ferric iron complexed with nitriloacetic acid (Fe(III)-NTA). The resulting formation of Fe(II) was measured using buffered ferrozine (0.1% ferrozine in HEPES buffer, pH 7.0) to quantify dissolved electron shuttling capacity (ESC). Fifteen mL of 5 mM Fe(III)-NTA was added to the centrifuge tubes still containing peat, tubes were shaken, removed from the anaerobic chamber and centrifuged at 4100 rpm for 5 min. A 0.10 mL aliquot of the supernatant was used to measure Fe(II) using ferrozine to quantify ESC. The centrifuge tubes were dried to constant mass and solid-phase ESC was corrected for dissolved ESC by the pore water in the peat sample.

Plant biomass and ancillary measurements

Stem counts, plant heights, and depth to peat from the top of mesocosm jars were measured twice during the experiment, once on July 9 and again on July 27. Dimensions were used to calculate air volume for gas efflux measurements. Upon take-down of the mesocosm experiment, aboveground biomass and belowground biomass were separated from the peat and dried to constant mass at 65 °C. The remaining peat was bagged and shipped to the Northern Research Station in Houghton, MI (USA) where it was frozen. This peat was used to calculate peat bulk density and moisture content. A subset of peat samples was analyzed using Fourier-transform infrared spectroscopy (Nicolet iS5 Series FTIR; Thermo Fisher Scientific) to test if inherent properties of the peat changed throughout the experiment, using the wavelength ratio 1060 cm^{-1}:1620 cm^{-1} (polysaccharides/lignin) to calculate a substrate quality index (Basiliko et al. 2007; Hribljan et al. 2017). Leaf extracts were made from the aboveground biomass of each treatment by soaking 5 g dry mass equivalent of aboveground material (leaves and stems) in 50 mL of DI water for 72 h at 7 °C. Extracts were filtered through 0.45 µm Whatman filters. Leaf extracts were characterized for dissolved organic carbon quality, as described below.

Pore water and leaf extract characterization

A suite of absorbance and fluorometric indices were calculated to describe dissolved organic matter in pore water samples and leaf extracts. Specific ultraviolet absorbance (SUVA) was calculated by dividing absorbance at $\lambda = 254$ by DOC concentration (SUVA 254) to evaluate changes in pore water aromaticity (Weishaar et al. 2003). Absorbance index E2:E3 (absorbance at λ250/absorbance at λ365) was calculated, along with SUVA 254, using both the fluorometer and the field spectrophotometer to evaluate the character of dissolved organic matter (DOM). E2:E3 expresses an inverse relationship to molecular size of DOM (De Haan and De Boer 1987; Avagyan et al. 2014). Fluorometric indices of statistical importance to this study include the humification index (HIX) (Ohno 2002), biological index (BIX) (Huguet et al. 2009), and tryptophan index (TI) (Fellman et al. 2009), and were calculated as described in detail by Veverica et al. (2016).

Statistical analysis

We monitored Eh7 conditions for three campaigns in June to track experiment equilibration, which was reached in July (Appendix Fig. 6). All statistical analysis and graphing was completed in R version 3.4.1 open source software, using packages nlme (Pinheiro et al. 2014), lsmeans (Lenth 2016), and ggplot2 (Wickham 2016). Spearman's correlations

were run among all variables to identify potential relationships. Type II mixed effects models (nlme function lme) were run on all measurements to test differences among plant functional type treatments for a given response variable (CH_4 and CO_2 efflux; concentration and isotopic fractions of CH_4 and CO_2 in pore water; oxidation–reduction potential (Eh7); fluorometric indices BIX, HIX, TI, and E2:E3; DOC and TDN; and ions). All mixed effects models used belowground biomass and plant treatment as fixed effects, and individual mesocosm I.D. as a random effect to account for repeated measurements. Changes in belowground biomass co-occurring with PFG treatment were accounted for by running belowground biomass as the first effect in the fixed effects models. Residuals were visually inspected for normal distribution and data were log transformed when necessary to meet model assumptions. Models were run separately by season; July data (3 campaigns) were pooled for the growing season model, and September data (1 campaign) were run separately for the end-of-experiment (late season) model. Multiple comparisons of means and Tukey Honest Significant Difference Test (HSD) post hoc analysis was used to compare treatments using the R package lsmeans (adjust = "tukey"), the results of which are found in Appendix Table 4. Statistical significance was accepted at $p < 0.05$, and trending relationships $0.05 < p < 0.07$.

Results

Belowground biomass, which varied by PFG, strongly affected CO_2 efflux, CH_4 concentration in pore water, $\delta^{13}CO_2$ in pore water, SUVA 254, BIX, E2:E3, TDN, C:N ratio, phosphate, and chloride concentrations throughout the entire season (Table 2). Eh7 was significantly lower (more reduced) in the unplanted and cinquefoil treatments (-100 ± 100 mV and -50 ± 60 mV, respectively) than in the sedge treatment in September (202 mV $\pm$ 7; Table 2; Fig. 1; Appendix Fig. 6).

Across all treatments, there was a negative relationship between Eh7 and pore water CH_4 (Fig. 2). There were significant PFG effects on Eh7 and pore water CH_4 (Table 2). When adjusted for PFG treatment, there was still a significant effect of Eh7 on CH_4 (ppmv) in analysis of covariance ($F = 12.99$, $p < 0.001$). The slopes between Eh7 and CH_4 (ppmv) for PFGs that transport gases via aerenchyma or hollow stems ranged from -4.5 to 6.7 ppmv CH_4/mV, while the cinquefoil treatment had a slope of -1.2 ppmv CH_4/mV (Fig. 2), although there was no significant interaction between PFG and Eh7 in determining CH_4 concentrations ($F = 0.47$, $p = 0.76$). Most varied were the sedge treatment, which produced lower concentrations of pore water CH_4, and the unplanted treatment, which produced higher concentrations of CH_4 over a similar Eh7 range—suggestive that CH_4 concentrations were not caused strictly by environmental conditions but likely by the presence/absence of PFGs (Fig. 2). Sedges had a significantly lower concentration of pore water CH_4 than the unplanted treatment ($p = 0.0048$) and trended lower than the cinquefoil treatment ($p = 0.0576$) after accounting for changes in Eh7 (mixed effects model, $F = 4.28$, $p = 0.009$). The cinquefoil and unplanted treatments trended toward higher and more erratic CH_4 concentrations and lower Eh7 (Fig. 2).

After the effects of belowground biomass were accounted for, the plant treatments had a significant ($p < 0.0005$) effect on pore water $\delta^{13}CO_2$ (sedges and horsetail significantly more depleted than the cinquefoil and unplanted treatments, grasses falling in between); pore water $\delta^{13}CH_4$ (sedges, horsetail, and grasses less depleted than cinquefoil and unplanted treatments; Fig. 3); TDN (plant treatments had lower TDN than the unplanted treatment); and pore water C:N ratios (all plant treatments had higher ratios than the unplanted treatment) throughout the entire season (Table 2; Appendix Table 4).

Although surface chamber-based measurements yielded no significant differences in gaseous CO_2:CH_4 ratios, sedges did produce significantly higher rates of CO_2 efflux during the growing season than cinquefoil and unplanted treatments (Appendix Table 4). Additionally, sedges produced a pore water CO_2:CH_4 ratio larger (July mean 30 ± 20 and September mean 200 ± 200) than expected (1:1). This ratio was significantly larger than cinquefoil and unplanted treatments in both peak growing season (means 7 ± 4, 8 ± 6 respectively) and at the end of the experiment (means 7 ± 3, 10 ± 5 respectively).

Methane efflux was not significantly related to biomass or treatment. However, belowground biomass and treatment (during the mid-season measurements) influenced pore water CH_4 concentrations (Table 2).

Table 2 Results of mixed effects modeling investigating plant functional group controls on gas and chemistry measurements from July (3 campaigns) and September (1 campaign) mesocosms

Predicted variable	Mid-season		Late-season	
	F-value	*p*-value	*F*-value	*p*-value
CH_4 Efflux	0.165	0.6941	0.452	0.5184
	1.876	0.1989	1.105	0.4113
CO_2 Efflux	46.63	< **0.0001**	126.58	< **0.0001**
	1.401	0.2842	8.67	< **0.0001**
CH_4:CO_2 Efflux	2.346	0.1599	1.067	0.3287
	0.61	0.6659	1.112	0.4085
ppmv CH_4 in pore water	8.482	**0.0076**	7.495	**0.0115**
	5.439	**0.0029**	2.08	0.115
ppmv CO_2 in pore water	9.819	**0.0045**	0.308	0.5842
	2.63	0.0594	0.711	0.5927
δ^{13}CH4	15.96	**0.0005**	2.079	0.1623
	17.69	< **0.0001**	20.361	< **0.0001**
δ^{13}CO2	48.071	< **0.0001**	152.994	< **0.0001**
	14.801	< **0.0001**	34.177	< **0.0001**
Eh_7	0.287	0.597	25.86	< **0.0001**
	7.616	**0.0004**	7.223	**0.0006**
SUVA (254)	6.748	**0.0158**	61.815	< **0.0001**
	1.111	0.3742	16.751	< **0.0001**
BIX	5.91	**0.0229**	12.908	**0.0015**
	2.32	0.0856	12.223	< **0.0001**
HIX	1.74	0.1996	12.307	**0.0018**
	0.271	0.894	26.048	< **0.0001**
TI	3.143	0.0889	3.907	0.0597
	6.692	**0.0009**	2.826	**0.0472**
E2:E3	6.994	**0.0142**	14.473	**0.0009**
	1.013	0.4202	2.654	0.0578
DOC	0.782	0.3854	25.679	< **0.0001**
	1.095	0.3816	20.84	< **0.0001**
TDN	12.463	**0.0017**	34.037	< **0.0001**
	7.502	**0.0005**	19.763	< **0.0001**
Pore water C:N ratio	27.032	< **0.0001**	60.17	< **0.0001**
	16.388	< **0.0001**	28.97	< **0.0001**
Phosphate	3.509	**0.0733**	No data	
	4.516	**0.0073**	No data	
Chloride	6.682	**0.0162**	No data	
	6.641	**0.001**	No data	

Shown first for each variable is the response (F-value and *p* value) to below-ground biomass; second is the response of the variable to the PFG treatment after accounting for below-ground biomass. Significant values are highlighted in bold text

The highest pore water CH_4 concentrations were seen consistently in the unplanted and cinquefoil treatments, whereas sedges generally exhibited the lowest pore water gas concentrations throughout the experiment but for CO_2 concentration in September.

Dissolved organic carbon concentration (DOC) paired with SUVA 254 results suggest that sedges and horsetail presence resulted in lower concentrations of DOC with less aromatic carbon, whereas cinquefoil and unplanted treatments resulted in high concentrations of DOC composed of more aromatic

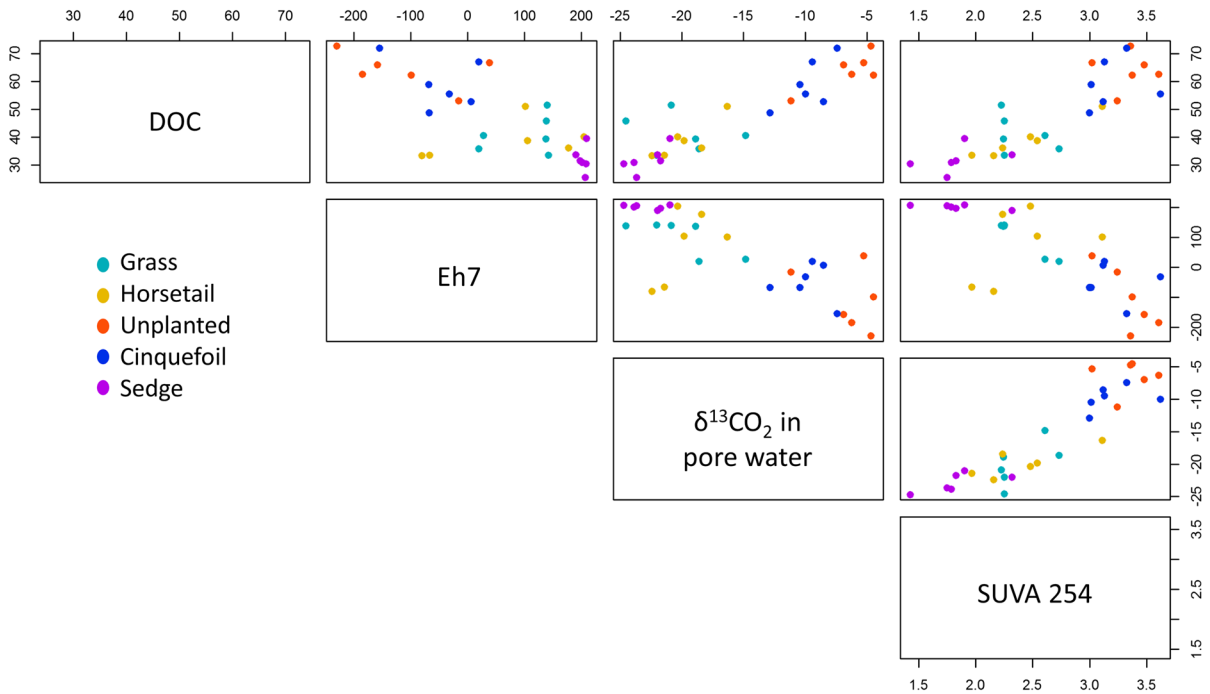

Fig. 1 Correlations between carbon quantity (DOC) and quality (SUVA 254), which influence environmental conditions (Eh7) and carbon reaction pathways ($\delta^{13}CO_2$). DOC is correlated with Eh7 ($R^2 = -0.53$, $p < 0.01$), $^{13}CO_2$ ($R^2 = 0.83$, $p < 0.01$), and SUVA 254 ($R^2 = 0.73$, $p < 0.01$). Eh7 is correlated with $^{13}CO_2$ ($R^2 = -0.62$, $p < 0.01$) and SUVA 254 ($R^2 = -0.59$, $p < 0.01$), and SUVA 254 is correlated with $^{13}CO_2$ ($R^2 = 0.83$, $p < 0.01$)

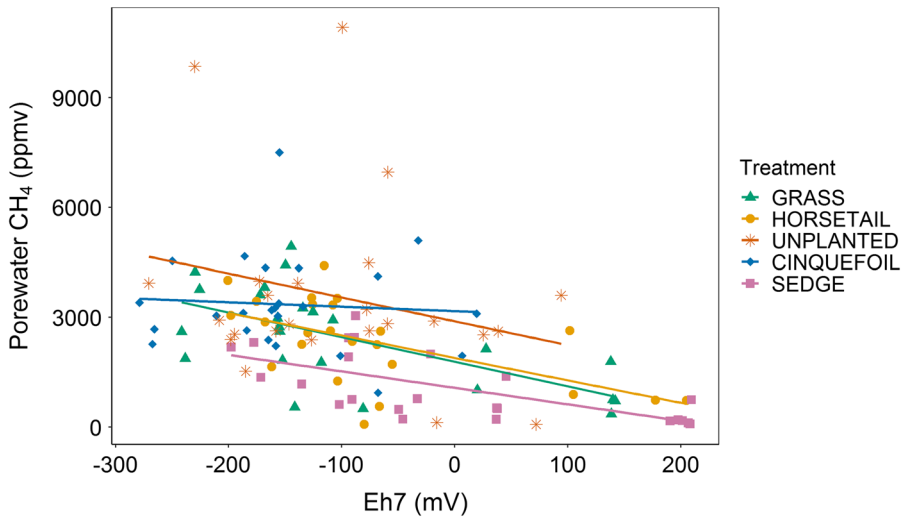

Fig. 2 Negative relationships between pore water Eh7 and [CH_4] by plant functional group. (overall $R^2 = 0.23$, $p < 0.001$). Sedges: $y = -4.504x$ (SE = 1.068) + 1073.447 (SE = 142.690), $p < 0.05$. Grass: $y = -6.724x$ (SE = 1.771) + 1788.319 (SE = 275.627), $p < 0.05$. Horsetail: $y = -6.139x$ (SE = 1.850) + 1892.782 (SE = 243.595), $p < 0.05$. Cinquefoil: $y = -1.207x$ (SE = 3.544) + 3171.111 (SE = 601.967), $p = 0.74$. Unplanted: $y = -6.513x$ (SE = 5.260) + 2893.146 (SE = 736.769), $p = 0.23$. Shown are data from all four campaigns

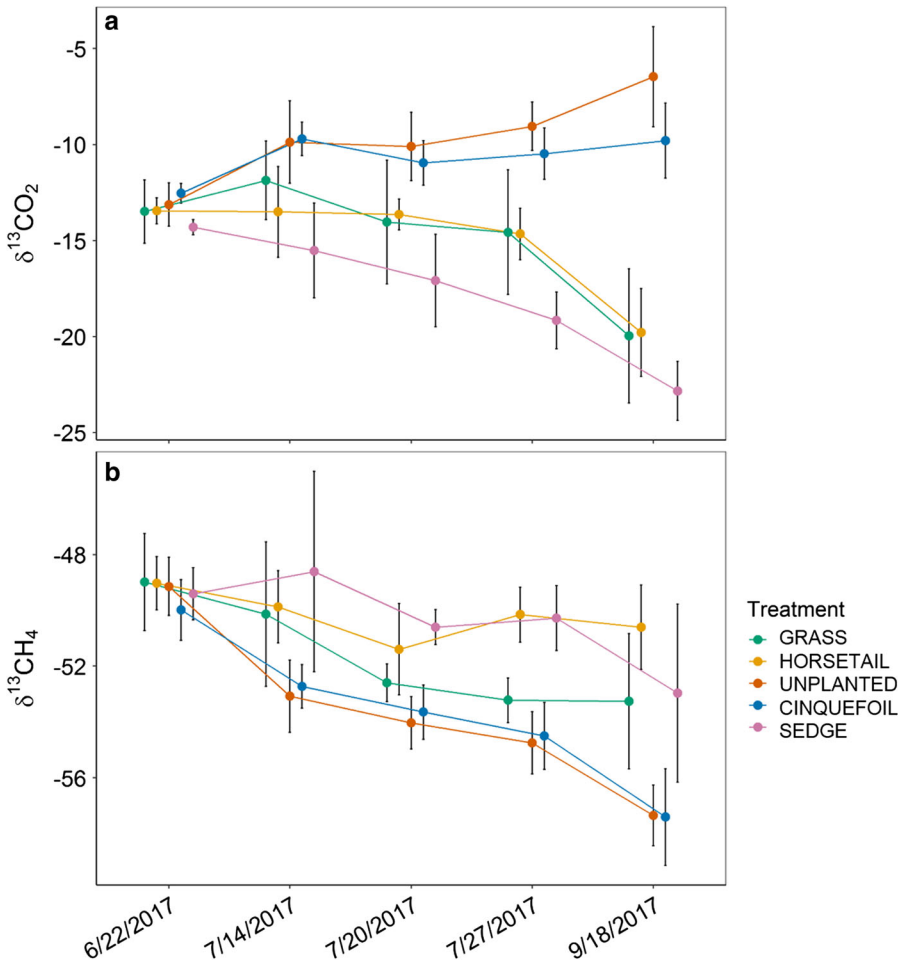

Fig. 3 ^{13}C natural abundance in pore water. **a** ^{13}C in methane was more enriched in the sedge, grass, and horsetail treatments than the cinquefoil and unplanted treatments ($p < 0.05$), suggesting selective methanotrophy. **b** Enrichment of $^{13}CO_2$ in the unplanted and cinquefoil treatment compared to the other plant treatments ($p < 0.05$) suggests more methanogenesis in these treatments, whereas the depletion of the sedge, grass, and horsetail further support the preferential conversion of light methane to carbon dioxide

carbon (Fig. 1, relationship between DOC and SUVA 254 by plant type). This was supported by humic index (HIX) (Ohno 2002) data showing low humification in sedges, mid-range values in the grass and horsetail, and high humification in the unplanted and cinquefoil treatments. Biological Index (BIX) and Freshness Index (Parlanti et al. 2000) values were significantly higher in the sedge, horsetail, and grass treatments than the cinquefoil and unplanted treatments, and the spectral ratio (Sr) (Helms et al. 2008) was significantly higher in sedges than in cinquefoil and unplanted treatments (Appendix Table 4). No significant differences by treatment were detected for the redox-related indices examined, e.g., the Ca:Cc (Kothawala et al. 2012) and Cory Index (Miller et al. 2006).

Dissolved Organic Carbon (DOC), Eh7, $\delta^{13}CO_2$ in pore water, and SUVA 254 were strongly correlated ($R^2 > 0.6$, $p < 0.01$), with variations among plant types in the slopes/intercepts of these relationships (Fig. 1). Belowground biomass also exhibited tight trends with these variables, separated by plant type. The leaf tissue extracts also exhibited significant differences between DOC character in the BIX, TI, and Freshness indices, which were higher in horsetail than in all other treatments. Leaf extract spectral ratio (Sr) was relatively low in the sedge (not significant)

Table 3 Dissolved organic carbon characterization of pore water carbon and dissolved carbon made from leaf extracts

Predicted variable	Late-season		Leaf teas	
	F-value	*p*-value	*F*-value	*p*-value
HIX	12.3074	**0.0018**		
	26.0482	< **0.0001**	2.435	0.0947
BIX	12.908	**0.0015**		
	12.223	< **0.0001**	14.029	< **0.0001**
Freshness	8.76	**0.0068**		
	9.624	**0.0001**	13.055	< **0.0001**
TI	3.9066	0.0597		
	2.8255	**0.0472**	11.591	< **0.0001**
Sr	9.207	**0.0057**		
	4.716	**0.006**	5.723	**0.0054**

Shown first for each variable is the response (F-value and p-value) to below-ground biomass; second is the response of the variable to the PFG treatment after accounting for below-ground biomass. Significant values are highlighted in bold text

and significantly lower in horsetail (p = 0.0054) compared to all other treatments (Table 3).

Solid phase peat used in this experiment exhibited polysaccharide:lignin (1060 cm^{-1}:1620 cm^{-1}) ratios from 1.807 to 2.495 (mean of 2.091) from FTIR analysis, and were not different between the treatments at the end of the experiment (p = 0.91). Electron shuttling assays of solid phase peat did not statistically change by treatment, but in July the lowest electron shuttling capacity (ESC) reflecting high oxidation was observed in the sedge treatment. Conversely, the unplanted treatment had the highest mean ESC, showing a more reduced character of the solid-phase peat in July (Appendix Table 4). Values from the September ESC assay were highly variable across all treatments (i.e., cinquefoil had mean 10 ± 10 µmol e^- g^{-1} and grass had mean 3 ± 3 µmol e^- g^{-1}) and there were no significant differences in electron shuttling capacity across treatments in the end-of season cores (p = 0.541, data not shown).

There were no significant variations among treatments regarding the decomposition of cellulose (F = 2.26, p = 0.09; Fig. 4). However, a marginal trend was driven by changes in cellulose mass loss between the unplanted (mean 92.71% mass loss) and cinquefoil treatments (mean 68.79% mass loss; p = 0.06 with Tukey post hoc comparison).

Discussion

Over the course of this four-month experiment, PFGs, including several understudied in peatlands, drove biogeochemistry in rich fen mesocosms. In particular, carbon cycling was highly influenced by the plant community's rhizosphere and functional traits—especially seen in changes in redox (Eh7). As we hypothesized, plants that had aerenchyma or hollow rhizomes (sedges, horsetail, grasses) tended to produce oxidized environments favorable for methanotrophy when we controlled for microtopographical effects. Sedges were particularly effective at oxidization of the belowground environment, followed by horsetails and grasses, as demonstrated by redox and isotope data (Table 2; Fig. 3; Appendix Fig. 6). Conversely, the non-aerechymal cinquefoil fostered a highly reduced belowground environment more suitable for methanogenesis, and showed signs of slowed decomposition (Fig. 4). Peat by itself produced conditions relatively more favorable for methanogenesis, yet showed a higher decomposition rate than plant treatments. In this study, it was apparent that PFG had significant or trending effects on redox, trace gas production, character of the dissolved belowground environment, and decomposition.

Rhizosphere biogeochemical effects of PFGs

Pore water gas concentrations and isotopes showed PFG effects on rhizosphere redox and C cycling. Sedges, for example, had a significant oxidizing effect on pore water CH_4. Although low concentrations of pore water methane under sedges could point to methane venting to the atmosphere (Strack et al. 2017), no increase in CH_4 efflux was detected. Furthermore, a depletion of pore water $\delta^{13}CO_2$ in the sedge, horsetail, and grass treatments points to an enhancement of CO_2 production in these treatments; in this case we suggest the conversion of CH_4 to CO_2 by means of methanotrophy (Fig. 3; Berger et al.

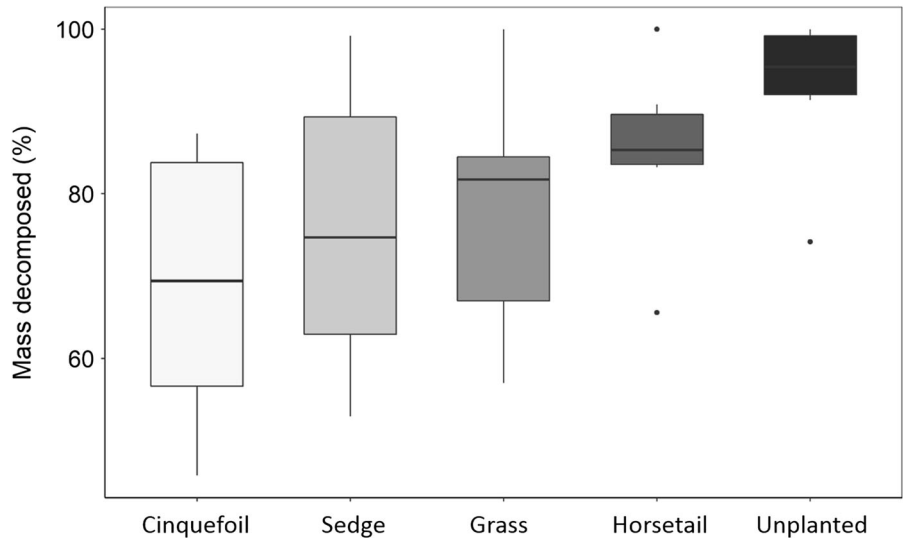

Fig. 4 Percent mass decomposed of a cellulose filter after 8 weeks of field incubation (F = 2.26, p = 0.09). Boxplot shows 25th and 75th percentiles and 95% confidence interval

2018). Methanotrophy produces CO_2, which would explain the isotopic evidence of enhanced CO_2 production (Chasar et al. 2000; Knorr et al. 2008; Throckmorton et al. 2015; Zalman et al. 2018). This observation was further supported by a corresponding $\delta^{13}CH_4$ enrichment indicative of preferential consumption of ^{13}C-depleted CH_4. Conversely, cinquefoil and the unplanted treatments exhibit depleted $\delta^{13}CH_4$ paired with enriched $\delta^{13}CO_2$, suggesting relatively higher rates of methanogenesis by conversion of CO_2 to CH_4 (Galand 2010). This finding is in agreement with Koelbener et al. (2009) who found that peat cores under cinquefoil (the shrub form) *Comarum palustre* L. produced higher CH_4 than other plant treatments (barring sedges, in their study). Therefore, it appears that in this mesocosm setting, either methanotrophy or a hindrance to methanogenesis is at play under sedges, horsetail, and possibly grasses, which possess aerenchyma or hollow rhizomes that allow air transfer deeper into the peat. These data suggest horsetails may have similar oxidizing effects as sedges in rich fens, though this plant functional group is relatively underrepresented in the literature (Marsh et al. 2000). Methanotrophy is very likely the driving force behind the observed trends in this study, which support observations by Agethen et al. (2018) and offer a partial explanation for the anomalous high CO_2:CH_4 ratios observed in northern boreal peatlands.

Dissolved organic matter responds faster to PFG-mediated changes in redox conditions than does solid phase organic matter. Dissolved and solid phase organic matter have been shown to transfer electrons in peatlands, with resulting consequences for redox-related reactions (Bauer et al. 2007; Heitmann et al. 2007; Blodau et al. 2009; Keller et al. 2009; Keller and Takagi 2013; Lau et al. 2015; Walpen et al. 2018). As variability in our solid-phase electron shuttling capacity assays was high, it may be that our treatments were too short in duration to manifest consistent changes in solid phase redox state. In contrast, pore water character responded to PFG and Eh7, and represented a rapid and non-destructive way to assess changes in redox conditions.

Contrary to expectation, all plant treatments tended towards slower cellulose decomposition rates than the unplanted treatment, suggesting that root priming effects either through plant-mediated oxygen delivery or through rhizodeposited carbon were not significant in the decomposition of the simple cellulose substrate. Because dissolved nitrogen concentrations were

significantly lower (and C:N ratios significantly higher; Appendix Table 4) in the plant treatments than the unplanted treatment, it is likely that the plants were taking up nitrogen at a rate that limited saprotrophic microorganisms, depressing decomposition (Kaye and Hart 1997; Cheng and Kuzyakov 2005). Interestingly, decomposition was the most suppressed within the cinquefoil treatment (Fig. 4), even though this plant group had the lowest root biomass, highest pore water dissolved nitrogen, and lowest pore water C:N ratio of the plant treatments by the end of the experiment. Paired with the observation that cinquefoil and unplanted treatments generally produced similar results except for in the decomposition assay (see Fig. 1), this suggests a departure from decomposition dynamics as observed in the other treatments. As a potential explanation, there are documented reports of the inhibition of free-floating saprotrophic decomposers by mycorrhizal communities (Gadgil and Gadgil 1971). Since mycorrhizal communities can obtain their carbon from host plants, it is thought that their enzyme systems focus more on nutrient mining rather than carbon uptake (Treseder et al. 2007; Hobbie et al. 2013; Lindahl and Tunlid 2015). Mycorrhizal associates of *Comarum palustris* have been documented (Schütte et al. 2019), along with several other plants of the family Rosaceae and genus *Comarum* (Kytoviita and Ruotsalainen 2007; Sudová and Vosátka 2008). If such mycorrhizal fungi were associated with the cinquefoil rhizospheres in this experiment, this may explain the slowed decomposition (Gadgil and Gadgil 1975; Wiedermann et al. 2017). Further investigation of the mycorrhizal effects on decomposition of this extensive rich fen shrub is warranted.

The findings of this experiment suggest that the sedge-dominated PFG resulted in DOM with higher redox potential and lower aromaticity than that of shrub dominated or bare peats, in agreement with Chanton et al. (2008), Elizabeth Corbett et al. (2013), and Dieleman et al. (2017). Taken together, our results indicate that increases in low-aromaticity DOC is likely driven by higher rhizodeposition in the sedge, grass and horsetail treatments than in the cinquefoil treatment. In contrast, the cinquefoil treatment DOM pool was dominated by large, aromatic compounds supported by high HIX and SUVA 254 indices (Appendix Table 4). While rhizodeposition has been reported to stimulate methanogenesis (Chanton et al. 1995), we suggest that rhizodeposition and rhizosphere oxidation capabilities belong to the same PFGs in this study, with the oxidizing effect likely outweighing methanogenesis stimulation in the mesocosms.

Aboveground C inputs

Dissolved organic carbon analyzed from leaf extracts suggests that water-soluble leachates from aboveground biomass of horsetail is different from the other plant treatments. First, horsetail leaf extracts demonstrated higher values in the BIX (Huguet et al. 2009), Freshness (Parlanti et al. 2000), and Tryptophan Indices than in other treatments (Table 3, Appendix Table 5). It is possible that horsetail possesses leaf traits that distinguish its chemical character in leaf extracts. For example, horsetail is known to be enriched in silica, calcium and potassium. One possibility could be that the additional base cations present preferentially adsorb to certain fractions of the DOM (Ali et al. 2014; Sowers et al. 2018); however, this is yet to be tested. The elevated indices could also speak to circumstances under which the aboveground biomass was harvested. In all of the horsetail treatment mesocosms, young shoots grew up around mid-season to replace the older shoots, producing younger, fresher tissue likely composed of relatively undamaged amino acids and proteins as opposed to the older, senescent leaves of the other treatments. Leaf nutrient content was not analyzed in this experiment, but this could be a possible explanation for the elevated Freshness and Tryptophan Index values for horsetail (Fellman et al. 2009). Horsetail has also been shown to act as a "nutrient pump" in Alaskan peatlands due to their deep rooting nature, bringing nutrients such as phosphorus to the surface in elevated concentrations within their tissue (Marsh et al. 2000). Although HIX, a measure of the degree of humification of DOM, was not significantly different between horsetail and other treatments, the spectral ratio (Sr) of the sedge and horsetail treatments was low compared with other treatments. This suggests higher molecular weight DOM derived from leaf litter of these species.

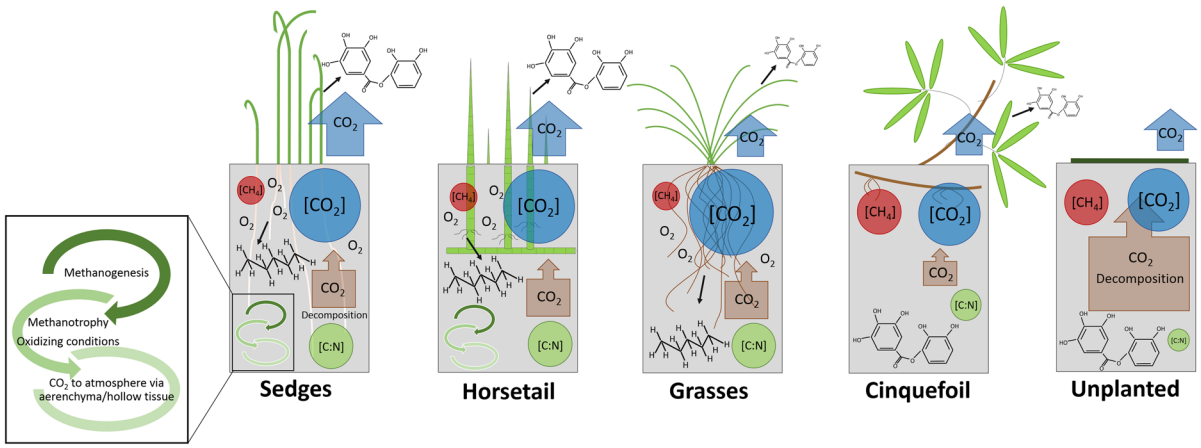

Fig. 5 Our conceptual understanding of C cycling in this rich fen as informed by mesocosm results. Sedges provided an oxidizing environment and root exudates (as represented by simple sugar in the diagram), but had recalcitrant above-ground inputs (as represented by aromatic compounds in the models). Horsetail acted like a sedge in the fen environment. Grasses were the hardest to predict when it came to carbon cycling, but for the most part acted like sedges and horsetail with respect to Eh7; this is likely due to their highly variable root mass and facultative aerenchymous rooting nature. Cinquefoil acted similarly to the unplanted control. This is likely due to its minimalist rooting structure; however, its association with mycorrhizae may slow decomposition in the rhizosphere (as represented by brown decomposition boxes in the diagram). In the unplanted treatment, microbes did not have to compete with plants for nitrogen (lower pore water C:N), enhancing the decomposition of organic matter and the model substrate cellulose; this resulted in poor quality (highly aromatic) carbon left behind

Interestingly, the belowground pore water DOM of sedge and horsetail showed the opposite trend, with a high spectral ratio (low molecular weight DOM), comparatively. The juxtaposition of more labile root-derived DOM with recalcitrant leaf litter inputs highlights the differences between surface and sub-surface carbon inputs to the system by the same plant. In the case of this short-term mesocosm experiment, plant litter did not have much time to accumulate on the surface of the peat. Based on this fact and the aforementioned C cycling effects, it appears that the belowground inputs had a greater impact on carbon cycling than aboveground inputs. Future work of interest could include a comparison of dissolved organic carbon in long-term horsetail peat versus sedge peat versus grass peat (cinquefoil does not usually form a litter-dominant peat).

Aboveground/belowground biogeochemical linkages

In conclusion, it is apparent that plant functional groups affect both above and belowground carbon quantity and quality, with resultant effects on our conceptual understanding of carbon cycling pathways in rich fen ecosystems (Fig. 5). Root structure, biomass, and chemical activity can impact how PFGs interact with and affect their environment. Root biomass in particular drove significant changes in trace gas concentrations and effluxes, and has the potential to affect ecosystem respiration. In this ecosystem, root respiration accounts for approximately 40% of soil respiration, with additional variation in ecosystem respiration being controlled by water table position and vegetation composition

(McConnell et al. 2013). Climate change could lead to higher precipitation and higher water tables in central Alaska, which would likely lead to higher abundances of gas-transporting PFGs such as sedge and horsetail (Churchill et al. 2014). While prior work suggests this could increase CH_4 efflux to the atmosphere (King et al. 1998; Strack et al. 2006b, 2017), we suggest that upon controlling for microform there may be an oxidizing effect of sedge/horsetail proliferation, which could attenuate CH_4 efflux, as was found in Strack et al. (2006a, b)'s drier sites (see also Dinsmore et al. 2009). These plants' ability to oxidize CH_4 under anaerobic conditions, in addition to their unique effects on pore water redox status, may explain in part the elevated CO_2:CH_4 ratios observed in central-Alaskan rich fens (Fan et al. 2013). As the landscape changes with the changing climate, vegetation community shifts will affect carbon cycling; whether it be oxidation of the belowground environment by hollow or aerenchymous plants like sedges, horsetail, and grasses, or via slowing of decomposition and lack of methanotrophy, as seen with obligate wetland shrubs such as marsh cinquefoil.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Appendix

See Fig. 6, Tables 4 and 5.

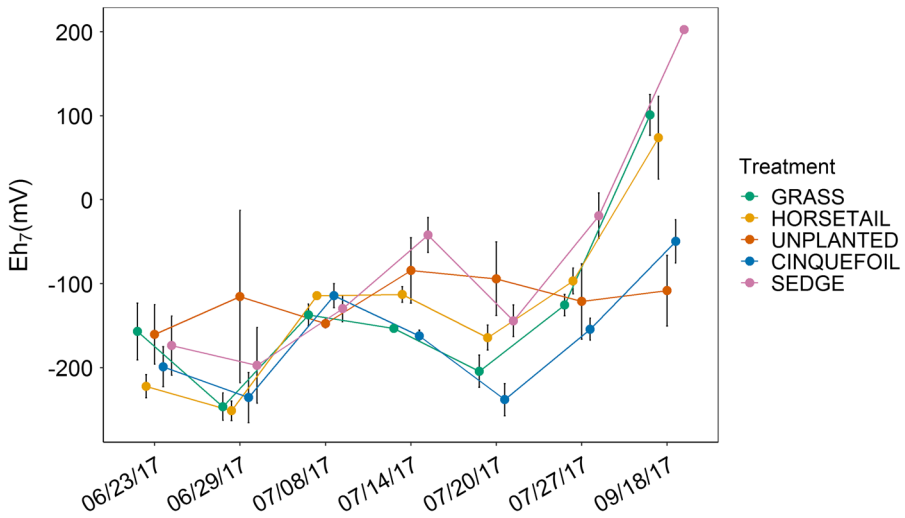

Fig. 6 Oxidation–reduction potential measured over the seven campaigns of the mesocosm experiment with standard error, demonstrating that the treatment effects did not equilibrate until early July, whereupon it was decided to use only data from campaigns 4–7 for statistical analysis and comparison

Table 4 Mean values of all measurements throughout the course of the experiment

Measurement	Mid-season (July)														
	Sedge			Grass			Horsetail			Cinquefoil			Unplanted		
	Mean	SD	Post-hoc	Mean	SD	Post-hoc	Mean	SD	Post-hoc	Mean	SD	Post-hoc	Mean	SD	Post-hoc
Temperature (C)	28.11	3.05	A	27.07	3.62	A	25.37	2.06	AB	28.04	2.84	A	24.04	3.39	B
CH_4 efflux	1.31	0.36	A	1.24	0.99	A	0.94	0.42	A	0.90	0.56	A	0.85	1.01	A
CO_2 efflux	5.07	2.03	A	4.12	3.67	AB	2.81	1.20	AB	2.45	1.56	B	1.65	0.98	B
CO_2:CH_4 efflux	4.23	1.94	A	9.17	13.87	A	3.33	1.78	A	3.84	3.82	A	6.94[a]	251.19	A
ppmv CH_4 in pore water	1352.97	895.63	A	2864.81	1223.13	B	2824.17	837.58	B	3209.46	817.28	B	3204.89	1341.33	B
ppmv CO_2 in pore water	28,069.89	12,408.52	AB	39,510.17	14,696.45	A	32,239.06	15,762.40	AB	22,008.94	13,640.95	B	22,233.61	13,054.91	B
CO_2:CH_4 in pore water	27.93	17.67	A	19.56	23.72	AB	11.66	5.22	B	7.12	4.26	B	8.40	5.92	B
$\delta^{13}CH_4$	− 49.83	2.17	A	− 51.98	1.99	B	− 50.47	1.37	AB	− 53.62	1.16	C	− 53.95	1.23	C
$\delta^{13}CO_2$	− 17.25	2.47	A	− 13.49	2.86	B	− 13.94	1.55	B	− 10.38	1.15	C	− 9.67	1.65	C
E2:E3 (A λ 250:365)	4.10	0.44	A	4.06	0.37	A	3.77	0.24	A	3.81	0.28	A	3.49	0.13	A
SUVA (λ 254)	3.52	0.24	A	3.68	0.50	AB	3.71	0.30	AB	3.68	0.53	AB	3.93	0.34	B
DOC (mg C/L)	72.35	10.09	A	77.92	12.54	AB	82.41	12.24	B	79.77	8.92	AB	80.96	8.42	AB
TDN (mg N/L)	2.16	0.50	A	2.88	1.09	A	2.50	0.55	A	2.78	0.42	A	4.84	1.36	B
C:N ratio (pore water)	34.21	3.98	A	28.94	5.66	B	33.53	3.42	A	29.14	4.18	B	17.65	3.88	C
Eh_7 (mV)	− 68.40	76.04	A	− 160.98	45.73	BC	− 124.52	42.82	ABC	− 184.76	50.38	C	− 99.77	99.43	AB
ESC (μmol e/gwd)	3.22	6.24	A	8.10	5.16	A	8.17	6.50	A	8.39	7.98	A	11.79	10.23	A
Sr (λ 275/295:350/400)	0.81	0.06	A	0.81	0.03	A	0.83	0.05	A	0.84	0.08	A	0.80	0.03	A
HIX	20.15	4.39	A	18.71	2.80	A	20.12	4.21	A	20.08	2.90	A	20.90	3.79	A
Freshness index	0.47	0.02	A	0.48	0.02	A	0.47	0.02	AB	0.46	0.01	B	0.45	0.01	B

Table 4 continued

Measurement	Mid-season (July)														
	Sedge			Grass			Horsetail			Cinquefoil			Unplanted		
	Mean	SD	Post-hoc	Mean	SD	Post-hoc	Mean	SD	Post-hoc	Mean	SD	Post-hoc	Mean	SD	Post-hoc
BIX	0.48	0.02	AB	0.48	0.02	A	0.48	0.02	ABC	0.46	0.02	BC	0.46	0.02	C
TI	1.46	0.16	A	1.88	0.40	B	1.62	0.25	AB	1.68	0.34	AB	1.77	0.28	B
Fluoride (ppm)	0.17	0.05	A	0.15	0.03	A	0.16	0.03	A	0.15	0.02	A	0.16	0.04	A
Chloride (ppm)	2.61	1.46	A	1.29	0.43	B	1.12	0.42	B	2.42	0.69	A	3.00	0.83	A
Sulphate (ppm)	0.14	0.04	A	0.13	0.04	A	0.16	0.04	A	0.15	0.04	A	0.14	0.03	A
Oxalate (ppm)	0.10	0.05	A	0.08	0.01	A	0.08	0.02	A	0.08	0.02	A	0.08	0.01	A
Nitrate (ppm)	0.06	0.03	A	0.08	0.04	A	0.08	0.05	A	0.07	0.04	A	0.08	0.04	A
Phosphate (ppm)	0.32	0.20	A	0.61	0.49	A	0.53	0.24	A	0.54	0.22	A	1.10	0.52	A
Formate (ppm)	0.11	0.05	A	0.14	0.07	A	0.11	0.05	A	0.12	0.04	A	0.10	0.04	A
Measurement	Late-season (September)														
	Sedge			Grass			Horsetail			Cinquefoil			Unplanted		
	Mean	SD	Post-hoc	Mean	SD	Post-hoc	Mean	SD	Post-hoc	Mean	SD	Post-hoc	Mean	SD	Post-hoc
Temperature (C)	12.73	0.54	B	18.03	1.91	A	10.87	1.69	BC	12.35	1.06	B	8.95	2.67	C
CH_4 efflux	0.13	0.05	A	0.72	1.10	A	0.06	0.04	A	1.67	2.48	A	0.23	0.20	A
CO_2 efflux	1.79	0.26	A	1.05	1.88	A	1.16	0.41	A	0.38	0.16	A	0.39	0.17	A
CO_2:CH_4 efflux	16.11	6.06	A	79.84[b]	138.28	A	23.95	13.97	A	1.01	0.90	A	648.61[b]	1122.07	A
ppmv CH_4 in pore water	247.63	248.75	A	1126.68	689.30	AB	938.43	878.77	AB	3784.82	2348.38	AB	4612.53	4579.04	B
ppmv CO_2 in pore water	30,822.33	15,908.23	A	34,501.83	11,592.57	A	25,325.67	6294.99	A	22,766.33	14,137.21	A	28,151.67	16,100.54	A
CO_2:CH_4 in pore water	218.78	236.92	A	38.07	19.14	AB	75.50	110.68	AB	6.99	3.17	B	9.86	4.95	B
δ^{13}CH4	− 52.96	3.04	A	− 53.26	2.31	A	− 50.60	1.44	A	− 57.41	1.65	B	− 57.35	1.04	B

Table 4 continued

Measurement	Late-season (September)														
	Sedge			Grass			Horsetail			Cinquefoil			Unplanted		
	Mean	SD	Post-hoc	Mean	SD	Post-hoc	Mean	SD	Post-hoc	Mean	SD	Post-hoc	Mean	SD	Post-hoc
$\delta^{13}CO2$	− 22.83	1.46	A	− 19.97	3.33	A	− 19.79	2.18	A	− 9.79	1.85	B	− 6.47	2.49	B
E2:E3	5.80	0.44	A	5.32	0.37	A	5.35	0.24	A	4.98	0.28	A	4.81	0.13	A
SUVA (254)	1.83	0.29	A	2.38	0.22	B	2.41	0.40	B	3.20	0.24	C	3.35	0.20	C
DOC (mg C/L)	31.93	4.56	A	41.13	6.58	A	38.82	6.55	A	59.13	8.79	B	63.85	6.49	B
TDN (mg N/L)	0.98	0.147	A	1.27	0.24	A	1.12	0.17	A	2.45	0.80	B	4.62	1.28	C
C:N ratio (pore water)	32.53	1.41	A	32.76	3.13	A	34.81	2.64	A	25.31	4.48	B	14.48	2.90	C
Eh_7 (mV)	202.37	7.28	A	101.06	59.83	A	73.85	120.93	AB	− 49.48	63.22	BC	− 108.31	103.26	C
ESC (μmol e/gwd)	6.79	7.14	A	3.44	7.51	A	13.89	14.95	A	10.49	21.44	A	3.72	4.86	A
Sr (λ 275/295:350/400)	0.94	0.06	A	0.85	0.03	AB	0.87	0.05	AB	0.80	0.08	B	0.80	0.03	B
HIX	12.42	1.27	A	16.13	3.10	B	14.53	1.98	AB	20.59	1.71	C	20.48	1.13	C
Freshness index	0.55	0.02	A	0.53	0.02	A	0.55	0.03	A	0.48	0.02	B	0.48	0.02	B
BIX	0.57	0.02	A	0.54	0.02	A	0.56	0.04	A	0.48	0.02	B	0.49	0.02	B
TI	0.82	0.13	A	0.89	0.08	AB	0.90	2.55	AB	1.08	0.23	AB	1.11	0.12	B

First section of table represents July measurements, whereas the second section of table represents measurements taken at the end of the experiment (September). E2:E3 and E4:E6 refer to pore water characterization ratios at given absorbance wavelengths. E2:E3 is inversely related to size of DOC (dissolved organic carbon). SUVA 254 is absorbance of DOC at λ 254 divided by the concentration of DOC in the sample. TDN is total dissolved nitrogen; Eh7 refers to oxidation–reduction potential (higher values more oxidized); ESC is electron shuttling capacity (lower values are more oxidized); Sr has an inverse relationship to molecular weight; HIX, or humification index, is directly related to humification, with higher values indicating more humified DOC. BIX, Freshnass index, and TI in this context refer to the freshness of the material (higher values = more recently produced)

[a]Outlier removed

[b]Large standard error due to 2 of 3 measurements being zero or very small, and the third being erratically large. Because so few measurements were taken, we decided to leave these values in to demonstrate the large variability in these treatments

Table 5 Mean values of post-experimental analysis, including leaf extracts

Measurement	Sedge			Grass			Horsetail			Cinquefoil			Unplanted		
	Mean	SD	Post-hoc	Mean	SD	Post-hoc	Mean	SD	Post-hoc	Mean	SD	Post-hoc	Mean	SD	Post-hoc
Decomposition (% mass loss)	75.78	18.54	A	77.98	15.74	A	85.04	11.32	A	68.79	17.16	A	92.71	9.70	A
Total biomass	21.08	7.45	AB	24.88	18.48	A	8.29	1.72	BC	6.52	2.26	BC	0.00	0.00	C
Above-ground biomass	4.76	1.63	A	4.90	2.48	A	0.96	0.27	BC	3.07	1.36	AB	0.00	0.00	C
Below-ground biomass	16.32	5.92	AB	19.98	16.16	A	7.33	1.51	ABC	3.45	1.02	BC	0.00	0.00	C
Cellulose in peat (FTIR λ 1160)	2.37	0.03	A	2.44	0.06	A	2.39	0.04	A	2.38	0.06	A	2.37	0.12	A
Lignin in peat (FTIR λ 1265)	1.51	0.04	A	1.49	0.10	A	1.51	0.04	A	1.51	0.02	A	1.50	0.09	A
Bulk density (g/cm^3)	0.43	0.11	AB	0.41	0.09	AB	0.51	0.05	A	0.35	0.03	B	0.41	0.08	AB
HIX (tea)	2.39	1.27	A	3.52	1.43	A	2.89	0.29	A	2.19	1.00	A	N/A	N/A	N/A
BIX (tea)	0.33	0.02	A	0.27	0.06	A	0.41	0.04	B	0.28	0.03	A	N/A	N/A	N/A
Freshness (tea)	0.33	0.02	A	0.26	0.06	A	0.40	0.03	B	0.27	0.03	A	N/A	N/A	N/A
TI (tea)	11.38	0.13	AB	9.46	2.64	BC	14.65	2.55	A	5.92	1.53	C	N/A	N/A	N/A
Sr (λ 275/295:350/400) (tea)	0.17	0.07	AB	0.28	0.20	B	0.09	0.08	A	0.34	0.07	B	N/A	N/A	N/A
Ca:Cc (tea)	1.20	0.06	A	1.07	0.33	A	1.34	0.50	A	1.20	0.37	A	N/A	N/A	N/A
RI (tea)	0.13	0.02	A	0.15	0.05	A	0.17	0.06	A	0.17	0.05	A	N/A	N/A	N/A
E2:E3 (tea)	7.61	0.44	A	8.06	1.86	A	7.56	0.92	A	6.32	0.85	A	N/A	N/A	N/A

Fourier-transform infrared spectroscopy (FTIR) was performed to ensure no significant differences between cellulose and lignin content in peat between treatments. HIX, or humification index, is directly related to humification, with higher values indicating more humified DOC. BIX, Freshness index, and TI in this context refer to the freshness of the material (higher values = more recently produced). Sr has an inverse relationship to molecular weight. In post-processing peat material from the mesocosms, leaf extracts were not significantly different according to fluorometric redox activity (Ca:Cc and RI indices). E2:E3 is inversely related to size of DOC (dissolved organic carbon)

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