

Growing season carbon gas exchange from peatlands used as a source of vegetation donor material for restoration

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Abstract The moss layer transfer technique removes the top layer of vegetation from donor sites as a method to transfer propagules and restore degraded or reclaimed peatlands. As this technique is new, little is known about the impacts of moss layer transfer on vegetation and carbon fluxes following harvest. We monitored growing season carbon dioxide (CO₂) and methane (CH₄) fluxes as well as plant communities at donor sites and neighbouring natural peatland sites in an ombrotrophic bog and minerotrophic fen in Alberta, Canada from which material was harvested between 1 and 6 years prior to the study. Plant recovery at all donor sites was rapid with an average of 72% total plant cover one growing season after harvest at the fen and an average of 87% total plant cover two growing seasons after harvest at the bog. Moss cover also returned, averaging 84% 6 years after harvest at the bog. The majority of natural peatlands in western Canada are treed and tree recruitment at the donor sites was

limited. Methane emissions were higher from donor sites compared to natural sites due to the high water table and greater sedge cover. Carbon budgets suggested that the donor fen and bog sites released higher CO₂ and CH₄ over the growing season compared to adjacent natural sites. However, vegetation re-establishment on donor sites was rapid, and it is possible that these sites will return to their original carbon-cycle functioning after disturbance, suggesting that donor sites may recover naturally without implementing management strategies.

Keywords Bog · Carbon dioxide · Fen · Methane · Oil sands reclamation · Peat extraction · Wetland restoration

Introduction

Peatland ecosystems play an important role in the global carbon cycle and sequester large amounts of carbon (Loisel et al. 2014). It is estimated that 15–30% of the world's soil carbon is stored as organic matter in boreal peatlands (Limpens et al. 2008). Changes in the carbon stored in peatland soils result from changes in net ecosystem exchange of carbon dioxide (CO₂) and methane (CH₄), and the exchange of waterborne carbon, as dissolved organic carbon (DOC) (Strack et al. 2008).

Management activities, such as the restoration of peatlands that were previously harvested for

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horticultural purposes, can result in the removal of greenhouse gases (GHGs) from the atmosphere (Kimmel and Mander 2010; Joosten and Clarke 2002, etc.). In Canada, 28 150 ha of peatlands have been drained to facilitate the extraction of peat for horticultural uses (CSPMA 2014), an activity that can change peatlands from carbon sinks to sources (Waddington et al. 2010). Recently, construction of peatland ecosystems on land disturbed for resource extraction has been attempted (Daly et al. 2012; Vitt and Bhatti 2012). Peatland reclamation is particularly important in the Athabasca Oil Sands Region of northeastern Alberta where surface mining occurs, and 65% of the natural landscape is peatland (Price et al. 2010).

Peatlands that have been drained and used for horticultural peat harvesting are being restored in North America by establishing a plant cover of peatland species and raising the water table (Quinty and Rochefort 2003). Restoration in Canada typically includes the following steps: surface preparation, collection of donor plants, donor plant spreading, straw spreading, fertilization, and blocking drainage ditches. Donor plant collection involves collecting the top 5–10 cm of the living vegetation from an appropriate donor peatland. This donor plant material, including living mosses and vascular plants, is spread on the restoration site, typically in a ratio of 1:10, where 1 ha of donor material is used to restore 10 ha of disturbed peatland (Rochefort and Campeau 2002). This approach is known as the moss layer transfer technique (González et al. 2013). The moss layer transfer technique is also being tested in a constructed fen in Alberta's oil sands region in an effort to compensate for peatland lost due to mining activities (Price et al. 2010; Daly et al. 2012).

The collection of donor material from natural peatlands is an additional land disturbance that should be analyzed in peatland reclamation (Strack and Waddington 2012). As this is a relatively new method, there are few data on the recovery of donor sites, or the impact of donor plant collection on ecosystem GHG fluxes. In this study we analyzed growing season fluxes of CO₂ and CH₄ from donor sites in central and northeastern Alberta. Our goal was to evaluate vegetation recovery, determine differences in carbon gas emissions between donor sites and reference natural peatland sites, and investigate the dominant controls on gas fluxes. Rochefort and Campeau (2002) reported that donor site plant communities recovered in

3–5 years post-disturbance and a goal was to test this prediction. We hypothesized that: (1) sites where donor material had been collected more than 3 years prior to the study would have CO₂ flux values similar to undisturbed adjacent natural peatland sites, (2) CH₄ flux would be higher in the donor sites compared to natural sites due to a higher water table caused by the removal of surface material, and (3) vegetation composition and hydrologic regime would be critical controls on carbon gas fluxes.

Study sites

This study was conducted at two peatland types harvested for donor material used in the moss layer transfer technique, and reference sites near donor sites. The first peatland is an ombrotrophic bog located approximately 18 km southwest of Seba Beach, Alberta, Canada (53.285°N, 114.526°W). This peatland is located in the Dry Mixedwood Subregion of the Boreal Forest Natural Region in Alberta (Natural Regions Committee 2006). The 30-year mean (1980–2010) annual precipitation is 551 mm and the mean annual temperature is 3.49 °C (Government of Canada 2016). The recovery of two adjacent donor sites was evaluated at Seba Beach. One site was harvested in the winter of 2008 (bog-donor old), and a second in the winter of 2012 (bog-donor recent). Each donor site is ~1.8 hectares in size. Following tree removal with a forestry chipper, donor material was collected by a horticultural peat company using a mulcher that removed the top 10 cm of vegetation and snow cover, leaving a level low-decomposed peat surface with remaining plant fragments (C. Brown, personal communication). The collected donor material was windrowed with a bulldozer and later transported by wagon to restoration sites. An adjacent natural bog site (bog-natural) was analyzed as a reference site. Pore water samples taken in 2013 from ground water monitoring wells had a mean pH of 4.34 and mean corrected electrical conductivity (EC) (Sjörs 1950) of 73 µS/cm (with a range from 55 to 98 µS/cm).

Sample plots for carbon flux measurements were established along a 100 m long transect that ran north–south through all three study sites, including bog-donor old, bog-donor recent, and bog-natural. Stainless steel collars 0.60 m × 0.60 m, with an area of 0.36 m², were inserted ~0.20 m into the peat. The

collars were perforated to allow groundwater to move through and maintain natural water levels, and had grooves that the chamber was placed onto for gas flux measurements. Nine collars were established in 2013, three each in bog-donor old spaced ~10 m apart, bog-donor recent spaced ~15 m apart, and bog-natural, spaced ~5 m apart. Bog-natural had an overstory of black spruce (*Picea mariana* (Mill.) Britton, Sterns and Poggenb), and one plot in bog-natural had a small *Picea mariana* within the collar. In 2014 we added three collars near the transect in both bog-donor old and bog-donor recent to capture the full range of vegetation types present.

The second peatland is a rich-fen located approximately 25 km northwest of Fort McMurray, Alberta, Canada (56.939°N, 111.553°W) and about 10 km southwest of a constructed fen project that used the donor material for the moss layer transfer (Daly et al. 2012). The donor site was selected for the reclamation project based on accessibility, species composition, and proximity to the constructed fen. The rich-fen is in the Central Mixedwood Natural Subregion of Alberta's Boreal Forest Natural Region (Natural Regions Committee 2006) and receives 419 mm of precipitation per year with an average temperature of 0.96 °C, as indicated from a 30-year mean (1980–2010) (Government of Canada 2016). An area of ~0.5 hectares was harvested from the donor site by a consulting company in the spring of 2013 (fen-donor). Hardwood platforms were placed along an existing cleared path to allow heavy equipment access to the harvest site. After tree removal, a rototiller mounted on an excavator was used to shred the top 5–10 cm of vegetation, which was collected and placed into a dump truck for transport to the constructed fen. An undisturbed site in the adjacent moderate rich-fen (fen-natural 1) was also evaluated. Carbon flux measurements made at six additional plots in a similar fen located ~300 m northeast of the donor site were included as a second control to better represent variation (fen-natural 2). Overstory vegetation of fen-natural 1 and 2 was dominated by tamarack (*Larix laricina* (Du Roi) K.Koch) and *Picea mariana*, and one plot in fen-natural 1 had a small tree (*Larix laricina*) in the collar. Mean pH of shallow ground water at the fen was 6.66, and mean corrected EC was 253 $\mu\text{S}/\text{cm}$, ranging from 160 to 297 $\mu\text{S}/\text{cm}$.

Metal collars identical to those installed across the bog sites were also installed at the fen sites. In 2013,

carbon fluxes were measured in three collars ~3 m apart along a north–south transect in fen-donor and three collars ~5 m apart in dominant plant communities in fen-natural 1. In 2014 two more north–south transects of three collars each, also spaced ~5 m apart each were added to fen-donor. Fluxes were measured at the six plots in fen-natural 2 in both study years.

The study design at both study sites was developed to capture the spatial variability of vegetation and water table position while also allowing accessibility to the plots. The design resulted in replicates being within the donor sites. This study design was needed because few donor sites occur in the region. Additional sample plots were added in 2014 as the high sample variance in 2013 data indicated the need for more replicates to capture the range of vegetation and gradient of water table positions. Boardwalks were installed next to and between each plot to limit disturbance while measuring carbon fluxes.

Methods

Carbon flux measurements

Carbon flux measurements were made using the closed chamber method (Tuitilla et al. 1999). The height of each collar from the soil surface was measured to correct chamber headspace volume to calculate CO_2 and CH_4 flux rates. At the bog flux measurements were made 9–10 times at each plot from June 26–September 3, 2013 and 12–14 times from May 13–October 4, 2014. At the fen site, flux measurements were made only in the second half of the growing season in 2013, as donor material from this site was collected in the early growing season (June 19–26); 5–6 measurements were taken from July 25 to August 27. In 2014 at the fen, carbon flux was measured 8–10 times from May 13 to October 4, 2014. Our goal was to evaluate differences in carbon gas fluxes between the sites (donor, natural), and we did not compare means between the years. Also, comparisons were made separately across sites at the bog or fen, and the different lengths of study periods do not affect the interpretation of between site differences. Overall the collar data compared across sites (donor, natural) at the bog or fen had a similar number of replicates at each collar per month (within $n = 1$). At fen-donor the

six additional collars added in 2014 were not installed until the end of June due to ice. Flux data from the three collars measured in May and June at fen-donor were averaged and these values were used for the six additional plots so that the early growing season carbon fluxes were accurately represented.

To measure net ecosystem exchange (NEE) of CO₂ a clear chamber (0.6 m × 0.6 m × 0.3 m tall; with a volume of 0.108 m³) was placed on the collars and water was poured around the collar edge to create a gas tight seal. Battery-powered fans mixed the air inside the chamber during the measurement period. A portable infrared gas analyzer (EGM-4, PP Systems, Massachusetts, USA) connected to the chamber with tubing measured CO₂ concentration and relative humidity (RH). At the bog, measurements of photosynthetically active radiation (PAR; $\mu\text{mol m}^{-2} \text{s}^{-1}$) were obtained in 2013 with a quantum sensor attached to the EGM-4 and internal chamber temperature with a thermocouple inserted into the chamber and connected to a thermometer. All variables were manually recorded at 15 s intervals from 0 to 105 s. NEE measurements in 2013 at the fen and 2014 at both the bog and the fen included the use of an integrated temperature and PAR sensor connected to the EGM-4 and software that logged CO₂, PAR, RH and temperature in the chamber at 10-second intervals from 0 to 120 s at the fen site and at 27-second intervals from 0 to 243 s at the bog site. NEE flux was determined from the linear change in the CO₂ concentration over time, with corrections for temperature and chamber volume. For each CO₂ measurement date, NEE was measured in full light as well as at levels manually adjusted using one and two shade treatments, and in the dark using an opaque tarp to determine ecosystem respiration (ER). Gross ecosystem photosynthesis (GEP) was calculated as the difference between the NEE and ER. The convention that negative values indicate uptake of the carbon by the ecosystem was applied for this study (Chapin et al. 2006). Due to the short sampling time of CO₂ flux measurements, RH changes in the chamber that could influence flux were negligible, with an average change of 0.05% when considering all flux measurements taken at the fen in 2013 and 2014, and fluxes from the bog site in 2013.

Methane flux was measured using opaque chambers (0.6 m × 0.6 m × 0.3 m; 0.108 m³) placed on the collars. As with the CO₂ measurements, water was poured around the collar edge to seal the system, a

battery-powered fan mixed the chamber headspace, and a thermocouple and thermometer measured chamber temperature. The chamber had a plug with a tube equipped with a three-way valve that was inserted into a hole drilled in the chamber. Using a syringe, 20 mL gas samples were taken from the chamber at 7, 15, 25, and 35 min after closure and injected into pre-evacuated Exetainers (Labco, UK). A gas chromatograph (Varian 3800, Varian Canada) with a flame ionization detector was used to determine CH₄ concentrations of the field-collected gas samples, and the flux was determined from the linear change in concentration over time with corrections for temperature and volume of the chamber. Individual gas sample measurements that disrupted a linearly increasing or decreasing trend over time were removed to ensure an $R^2 \geq 0.50$, unless the change in a small concentration over time was low ($\pm 15\%$, overall concentration < 5 ppm), and the resultant low flux value was realistic. Due to the possibility of ebullition events inadvertently caused by chamber placement resulting in CH₄ consumption back into the soil, any CH₄ flux with a negative value greater than 1 was also removed. Together this resulted in removal of about 16% of the data from both the bog and the fen considering both sampling years (113 out of 712 gas samples at the fen and 181 out of 1121 at the bog).

Vegetation analysis

Vegetation composition was analyzed at the bog and fen in 2014 within the metal flux collars and at additional plots using a quadrat the same size as the collars (0.6 m × 0.6 m). A string grid in the quadrat was used to assist in determining species percent canopy cover that was visually estimated to the nearest 1%. At the bog the vegetation was analyzed along three transects that ran perpendicular to the collar transect. Along each transect vegetation was analyzed in six plots ~20 m apart in bog-donor old and bog-donor recent and six plots randomly chosen within a 10 m radius of bog-natural collars. This resulted in 12 plots analyzed for vegetation at bog-donor old and bog-donor recent, and 9 plots at bog-natural, including the surveys in the flux collars. At the fen site, vegetation was analyzed in August 2014 at fen-donor in three plots (with the 0.6 m × 0.6 m wooden quadrat) spaced ~8 m apart along two transects that ran parallel to the collar transects. Fifteen plots were

analyzed at the fen-donor site, including the flux collars. At fen-natural 1, three transects of three plots ~ 10 m apart parallel to the collars were analyzed for vegetation composition for a total of 12 plots. Vegetation was not sampled at fen-natural 2.

To calculate the growing season carbon budget, tree biomass was determined for the natural sites in 2014 by analyzing trees in $10 \text{ m} \times 10 \text{ m}$ quadrats. The survey quadrats were randomly chosen near the plots in the bog and fen natural sites. Three quadrats were sampled near bog-natural and fen-natural 1, while an additional quadrat was sampled at fen-natural 2. Trees > 137 cm tall (Munir et al. 2014) were measured for diameter at breast height (DBH) at bog-natural and fen-natural 1. At fen-natural 2 the height of tall trees was calculated using an equation generated from preliminary sampling where height was determined using a clinometer and related to DBH ($\text{Height} = 148.88 + 37.98 (\text{DBH}), n = 24, R^2 = 0.97$). We measured both height and leader length (terminal shoot) of small trees in the survey quadrats at bog-natural in 2014. At fen-natural 1 and 2, basal diameter and height of small trees were measured in quadrats. Eight *Larix laricina* tree samples taken from fen-natural 2 in the summer of 2013 were used for growth increment analysis to calculate fen tree NPP (see “Data analysis” section).

Environmental variables

Water table was measured in ~ 1 m deep fully slotted groundwater monitoring wells, installed by hand (PVC diameter 0.05 m) adjacent to all flux collars. Soil temperature at 5 cm depth was measured with a thermocouple probe inserted into the peat at the time of all gas flux measurements. At fen-donor the water table was corrected for local topography in 2014 as only one well was used to represent the three collars in each transect.

A meteorological tower located ~ 1.5 km from the bog continuously measured PAR (LICOR quantum sensor, USA) and soil temperature at 5 cm depth (T_5) with Type T thermocouple (Omega, Canada) connected to a data logger (Campbell Scientific CR1000, Canada). A PVC ground water monitoring well with a levellogger (Model 3001) and barologger to correct for barometric pressure (Solinst, USA) was located ~ 2.4 km from the bog and provided a continuous measure of water table. At the fen, similar instrumentation measured PAR at a site ~ 35 km from the site,

while T_5 and water table were measured at fen-natural 2. T_5 was measured in a similar manner as at the bog, while water table fluctuations were recorded with a capacitance water level logger (Odyssey, New Zealand). These meteorological stations measured PAR and T_5 every 2 s and averaged the data every 30 min. The levelloggers recorded water table every half hour. Values of T_5 and water table were adjusted to account for spatial variability by generating a monthly quotient between each plot and time period using T_5 and water table values measured at the study sites during flux sampling and the T_5 and water table values from the meteorological stations.

Data analysis

All analyses were performed using R 3.0.2. (R Core Team 2013). To understand the recovery of donor site vegetation and carbon gas fluxes post-harvest, the data for each year and at each peatland (bog or fen) were analyzed separately. To ensure normality and equal variance of the residuals from ANOVA and regression models the Shapiro-Wilks and Levene tests were applied. To meet normality and variance conditions some data were log transformed, including CH_4 fluxes from both years at the bog and fen, and NEE_{max} flux values (see description of NEE_{max} below) at the bog in 2013. As the CH_4 fluxes contained small negative values, +1 was added to each flux prior to log transformation. For all inferential statistics a significance of $\alpha = 0.05$ was used.

A one-way ANOVA with repeated measures was used to compare differences in flux values between donor and natural sites at the bog or fen for each year of sampling. Data from fen-natural 1 and 2 were analyzed together, and the data from both sites are reported together (as fen-natural) unless stated otherwise. To evaluate NEE and GEP, values at full light conditions measured when PAR photon flux density exceeded $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$ were used and will be referred to as NEE_{max} and GEP_{max} (Bubier et al. 2003). A pairwise *t* test with adjusted *p* values using the Holm method (Holm 1979) was applied to determine which sites were different when the ANOVA results were significant.

Species percent cover data were organized into functional groups (moss, shrub, sedge, and total) by adding percent cover of each constituent. Small trees found in survey plots were considered in the shrub

functional group. A one-way ANOVA and pairwise *t* test with adjusted *p* values using the Holm method was applied to the percent cover of moss, shrub, sedge, total plant cover, as well as water table values, to compare between donor and natural sites at the bog or fen.

Linear regression was used to determine the controls on carbon flux at the bog or fen sites using seasonal averages from each plot for both years with water table data, and for 2014 only, vegetation cover data included as variables in the models. As vegetation was not analyzed at fen-natural 2, vegetation regression models for fen-natural only include data from fen-natural 1. Multiple linear regression was used where appropriate.

A growing season carbon budget was calculated only for the 2014 growing season when flux measurements were consistently made over similar time periods spanning from early May to early October at the bog and fen. The following equation was used to determine NEE:

$$NEE = NEE_{ff} + NPP_{tree} + L - R_r \quad (1)$$

where NEE_{ff} refers to net ecosystem exchange at the forest floor, NPP_{tree} is the net primary productivity of the trees, L represents tree litter fall, and R_r is tree root respiration. To calculate NEE_{ff} chamber flux data was used at each plot with empirical models relating GEP and ER to environmental variables that had been continuously measured near the two sites during the 140 days (May 13–September 30, 2014) over which flux measurements were taken. This period was considered to be the growing season for the purposes of the carbon budget. A rectangular hyperbola related to PAR was used to estimate GEP:

$$GEP = \frac{PAR \times Q \times GP_{max}}{PAR \times Q + GP_{max}} \quad (2)$$

where Q , the quantum efficiency, corresponds to the initial slope, and GP_{max} , the theoretical maximum GEP value, is the asymptote of the hyperbole (Strack et al. 2014). Separate empirical equations were created for GEP at two different periods during the growing season at the bog based on PAR and NEE differences that resulted in higher R^2 values of the hyperbola within a given period (Schreader et al. 1998). Period one was from May 13 to June 6 while period two lasted from June 7 to September 30. The fen plots were only modelled with one GEP period. ER was modelled using multiple linear regression:

$$ER = aT_5 + bWT + c \quad (3)$$

where T_5 is temperature at 5 cm depth ($^{\circ}C$), WT is water table position in cm, and a , b , and c are fit by least squares regression (Strack et al. 2014). Plot GEP and ER values were summed to determine NEE_{ff} , and averaged across plots within each donor or natural site at the bog and fen. As tree productivity at the bog and fen donor sites was negligible, CO_2 exchange from these sites was equivalent to NEE_{ff} .

To estimate carbon balance for bog-natural and fen-natural, aboveground tree NPP (NPP_{tree}) and litter fall, L , was added to NEE_{ff} estimated with the chamber fluxes (Eq. 1). NPP_{tree} is the difference between annual tree gross primary production (GPP) and annual respiration of aboveground and belowground biomass components (Munir et al. 2014). NEE_{ff} included the addition of GPP at the forest floor and ER_{ff} , the understory biomass respiration, heterotrophic soil respiration and tree root respiration (Munir et al. 2014). The ER_{ff} value ignores respiration of aboveground tree biomass but takes into account tree root respiration. To avoid accounting for tree root respiration twice in natural site productivity calculations, values calculated from 2012 for an ombrotrophic bog near Wandering River, Alberta by Munir et al. (2014) using a trenching method were correlated to aboveground NPP [$12.76 + 0.57 (NPP_{tree})$, $R^2 = 0.77$] to determine R_r and subtracted from the natural site NEE balance for the bog and fen site in this study.

The dominant tree at bog-natural was *Picea mariana*. Tall tree total biomass was calculated using an allometric equation from Grigal and Kernik (1984) (dry biomass = $0.153 (\text{tree DBH})^{2.248}$), and total biomass of short trees was estimated using an allometric equation by Munir et al. (2014) (dry biomass = $0.0085 (\text{tree height})^{2.2088}$). NPP of tall trees was then calculated using the dry biomass and average values determined by Munir et al. (2014) of the 2011 and 2012 growing season of tree ring widths using DendroScan (Varem-Sanders and Campbell 1996). For short trees we used leader length to estimate annual change in height and estimated NPP based on differences in total biomass due to height changes. Belowground annual biomass was determined following Li et al. (2003) (tree root biomass = $0.222 \times \text{tree aboveground biomass}$). Annual litterfall was calculated with reference to Szumigalski and Bayley (1996) who found stand litter production to be 17% of annual biomass for *Picea mariana*.

The dominant tree at fen-natural was *Larix laricina*. Total tree biomass was determined using regression equations by Lavigne (1982) (tall tree dry biomass = $584.910 + 32.612 \text{ (DBH} \times \text{height)}$) and Szumigalski and Bayley (1996) (small tree dry biomass = $10.744 + 24.200 \text{ (basal diameter squared} \times \text{height)}$). NPP of tall trees was calculated using growing season tree ring widths measured using DendroScan (Varem-Sanders and Campbell 1996) on tree wood samples collected at fen-natural 2 in 2013, and an equation by Szumigalski and Bayley (1996) was used to estimate NPP of small trees (log increment = $-0.922 + 0.885 \text{ (log biomass)}$). Below-ground annual biomass was also calculated using the equation of Li et al. (2003). Finally, litterfall was calculated using findings from Szumigalski and Bayley (1996) where litter was 144% of total incremental biomass at a moderate-rich fen.

Model error (ME) was calculated for the NEE_{ff} variable in the CO_2 budget across fen and bog sites following Adkinson et al. (2011):

$$ME = 1 - \frac{\sum_{i=1}^n (NEE_{flux} - NEE_{mod})^2}{\sum_{i=1}^n (NEE_{flux} - NEE_{flux})^2} \quad (4)$$

where NEE_{flux} represents NEE values measured in the field using the chamber method, and NEE_{mod} represents the modelled NEE values generated using Eqs. (2) and (3) for each flux measurement. ME was calculated at each plot and multiplied by 140 to understand the growing season error. Plot ME values were then averaged across sites. A 50% error was assumed for the tree productivity variables NPP_{tree} , L , and R_r (Eq. 1).

Regression between weekly CH_4 flux and environmental variables at each plot in 2014 was not significant at the bog or fen. Therefore, instead of modelling a seasonal CH_4 balance per plot similar to the CO_2 budget, the seasonal CH_4 balance was calculated by multiplying the mean flux at each plot by the 140 days in the growing season.

Results

Vegetation and hydrology

Moss cover was higher at bog-donor old and bog-natural compared to bog-donor recent in 2014

(Table 1). Of the three bog sites, shrub cover was highest at bog-natural. Bog-donor old and bog-donor recent both had higher sedge cover than bog-natural. Total plant cover was lower at bog-donor recent compared to bog-natural, similar between bog-donor recent and bog-donor old, and similar between bog-donor old and bog-natural. At the fen in 2014, fen-natural 1 had a significantly higher cover of moss, shrubs, and total vegetation. However, fen-donor had higher sedge cover.

The bog and fen natural sites had deeper mean water tables than the donor sites in both years, and were closer to the surface in 2014 at natural sites (Table 1). In 2013 water levels from bog-donor recent and bog-donor old were significantly shallower than bog-natural, while in 2014 the water table position between sites was not significantly different. In general, the water table was shallowest early in the growing season and declined until August. At the fen, the water table position at fen-donor was slightly lower in 2014 than in 2013. In both years the difference in the mean water table position between fen-donor and fen-natural was not statistically significant.

Carbon dioxide flux

Mean GEP_{max} was significantly different among all three bog sites in 2013, with a value indicating highest carbon uptake at bog-donor old and the lowest at bog-donor recent ($F_{2,16} = 106.9$, $p = 0.002$; Fig. 1). In 2014 GEP_{max} had a similar pattern but was not significantly different between sites. ER was similar across all three sites in 2013 while bog-natural and bog-donor old had significantly higher ER values than bog-donor recent in 2014 ($F_{2,136} = 15.6$, $p < 0.001$). Bog-donor old had significantly higher uptake of carbon as indicated by NEE_{max} in 2013 compared to the other sites ($F_{2,16} = 17.5$, $p = 0.01$). In 2014 no statistically significant differences in NEE_{max} were found between sites.

Mean GEP_{max} was not significantly different between fen-donor and fen-natural in either year (Fig. 1). ER was lower at fen-donor in both years compared to fen-natural (2013: $F_{1,41} = 128.6$, $p = 0.001$; 2014: $F_{1,56} = 142.0$, $p < 0.001$) while NEE_{max} was not statistically different between sites in either year.

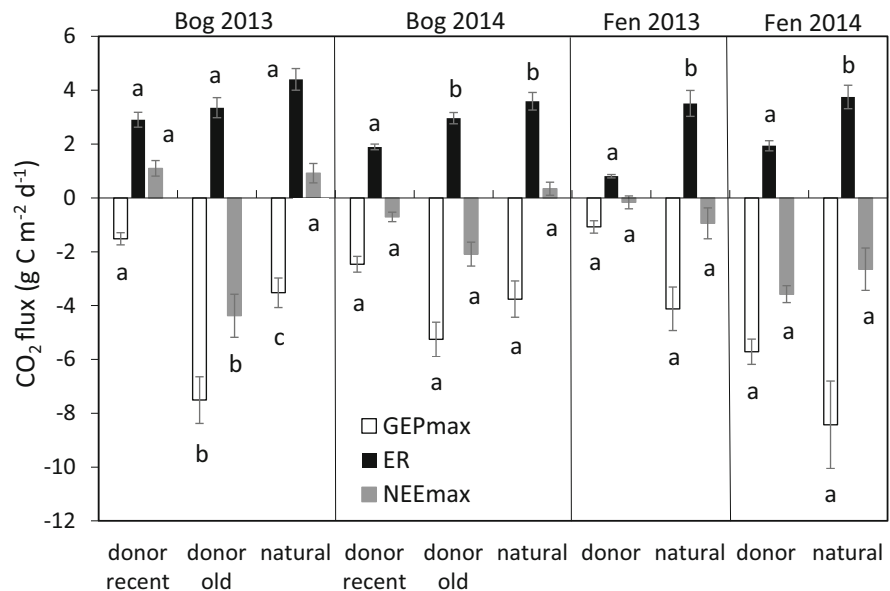
Table 1 Average water table (WT) and vegetation percent cover results \pm standard error of the mean

Variable	Bog-donor recent	Bog-donor old	Bog-donor natural	Fen-donor	Fen-natural*
WT (2013)	$-15.2 \pm 1.44a$	$-18.7 \pm 1.95a$	$-37.4 \pm 3.39b$	$-2.5 \pm 0.73a$	$-11.8 \pm 2.72a$
WT (2014)	$-17.7 \pm 1.73a$	$-18.7 \pm 2.00a$	$-21.9 \pm 3.02a$	$-2.7 \pm 0.28a$	$-2.9 \pm 1.19a$
Moss cover	$48.3 \pm 0.09b$	$83.5 \pm 0.09a$	$88.6 \pm 0.07a$	$13.3 \pm 0.03a$	$88.2 \pm 0.07b$
Shrub cover	$16.6 \pm 0.05a$	$14.4 \pm 0.06a$	$66.8 \pm 0.12b$	$13.7 \pm 0.03a$	$33.5 \pm 0.03b$
Sedge cover	$22.0 \pm 0.05a$	$20.9 \pm 0.04a$	$3.4 \pm 0.02b$	$45.1 \pm 0.07a$	$9.9 \pm 0.05b$
Total cover	$86.8 \pm 0.04a$	$118.8 \pm 0.06ab$	$158.8 \pm 0.08b$	$71.5 \pm 0.08a$	$132.0 \pm 0.05b$
Dominant species	<i>Eriophorum vaginatum</i> , <i>S. magellanicum</i> , <i>Politrichum strictum</i> , <i>Ledum groenlandicum</i> , <i>S. angustifolium</i>	<i>S. angustifolium</i> , <i>S. magellanicum</i> , <i>S. rubellum</i> , <i>Eriophorum vaginatum</i> , <i>Politrichum strictum</i> , <i>Andromeda polifolia</i>	<i>Ledum groenlandicum</i> , <i>S. fuscum</i> , <i>S. angustifolium</i> , <i>Ptilium crista-castrensis</i> , <i>S. magellanicum</i> , <i>Picea mariana</i> , <i>Politrichum strictum</i> , <i>Eriophorum vaginatum</i>	<i>C. diandra</i> , <i>Smilacina trifolium</i> , <i>C. disperma</i>	<i>S. angustifolium</i> , <i>Tomentypnum nitens</i> , <i>S. warnstorffii</i> , <i>Larix laricina</i> , <i>C. disperma</i>

Letters indicate significant differences in a variable (WT or one vegetation functional group) and should be compared only within a given year between the sites (donor, natural) across the bog or fen separately. All cover values are in percent. WT position is in cm with negative values indicating a depth below the ground surface. Dominant species include species with an average cover of $> 10\%$ and found in more than 1 vegetation survey plot, listed in order of declining coverage

* WT is averaged from fen-natural 1 and 2, while vegetation was just sampled in fen-natural 1

Fig. 1 Mean CO_2 fluxes including maximum gross ecosystem productivity (GEP_{max}), ecosystem respiration (ER), and maximum net ecosystem exchange (NEE_{max}) \pm standard error of the mean bars at bog-donor old, bog-donor recent, bog-natural, fen-donor and fen-natural in 2013 and 2014. Letters indicate significant differences in a variable (GEP_{max} , ER, NEE_{max}) and should be compared only within a given year between the sites (donor, natural) across the bog or fen separately



Methane flux

For all sites at the bog and fen mean CH_4 flux was positive, indicating a net release to the atmosphere (Fig. 2). Methane flux was significantly higher at bog-

donor old compared to the other bog sites in 2013 ($F_{2,48} = 37.5$, $p < 0.001$), while both bog-donor old and bog-donor recent had higher CH_4 flux than bog-natural in 2014 ($F_{2,118} = 14.9$, $p < 0.001$). Methane flux was not significantly different between

fen-donor and fen-natural in 2013 but was statistically higher in 2014 at fen-donor than fen-natural ($F_{1,101} = 30.1, p = 0.001$).

Controls on carbon flux

GEP_{max} became more negative (greater CO_2 uptake) in plots with higher moss cover across the bog sites ($F_{1,13} = 9.8, p = 0.008, R^2(adj) = 0.39$). At both the bog and fen GEP_{max} became more negative with increasing total plant cover (bog: $F_{1,13} = 6.2, p = 0.03, R^2(adj) = 0.5$; fen: $F_{1,10} = 6.9, p = 0.03, R^2(adj) = 0.41$; Fig. 3c). Multiple linear regression models that included ER and the independent variables GEP_{max} , water table position, and moss cover were significant at the bog ($F_{3,11} = 11.5, p = 0.001, R^2(adj) = 0.69$) and fen ($F_{3,8} = 17.4, p < 0.001, R^2(adj) = 0.82$). For both sites ER increased as GEP_{max} became more negative, ER was correlated positively with moss cover, and decreasing ER occurred in plots with shallower water tables. ER significantly increased with total vegetation cover at both sites (bog: $F_{1,13} = 9.9, p = 0.007, R^2(adj) = 0.29$; fen: $F_{1,10} = 6.9, p = 0.03, R^2(adj) = 0.33$; Fig. 3d). The fen site also had a significant positive relationship between ER and shrub cover ($F_{1,10} = 7.0, p = 0.03, R^2(adj) = 0.35$). Higher sedge cover resulted in more negative NEE_{max} values (greater CO_2 uptake) across the fen ($F_{1,10} = 5.5, p = 0.04, R^2(adj) = 0.36$; Fig. 3a). At the bog, multiple linear regression indicated greater CO_2 uptake through NEE_{max} with a higher percent cover of sedge, moss and total vegetation, along

with higher soil temperature at 5 cm ($F_{4,10} = 5.5, p = 0.01, R^2(adj) = 0.56$).

Methane flux was related to water table position at both sites, with the flux increasing with shallower water table (bog: $F_{1,22} = 10.1, p = 0.04, R^2(adj) = 0.31$; fen: $F_{1,28} = 7.6, p = 0.003, R^2(adj) = 0.27$; Fig. 3b). Methane flux increased with increasing sedge cover at the bog site ($F_{1,13} = 8.1, p = 0.01, R^2(adj) = 0.34$), but decreased with increasing shrub cover ($F_{1,16} = 21.8, p < 0.001, R^2(adj) = 0.55$), moss cover ($F_{1,16} = 11.2, p = 0.004, R^2(adj) = 0.38$), and total cover ($F_{1,16} = 12.5, p = 0.003, R^2(adj) = 0.40$) at the fen site.

Growing season carbon balance 2014

At both the bog and fen donor and natural sites the mean growing season NEE_{ff} was positive, indicating higher ER than GEP modelled values at most measurement plots and suggesting a net flux of carbon to the atmosphere (Table 2). At fen-natural, the calculated tree productivity resulted in NEE indicating a carbon sink, although high NEE error at fen-natural and bog-natural was calculated. Average seasonal NEE and CH_4 values at fen-donor were the highest of all sites analyzed. GEP and ER models for each site were suitable for characterizing the data over the 140 day growing season of 2014 for most of the flux measurement plots (Supplemental material, Tables S1, S2). Standard error (SE) of the GEP parameters (Eq. 1) at the bog site ranged between 0.8 and 9.6, while SE of the ER parameter (Eq. 2) a ranged from 1.1 to 4.8 while b was between 1.1 and 8.5. The fen site SE of the GEP parameters was between 4.0 and 14.3 and for ER the SE of a was between 1.6 and 22.1 while b was between 2.9 and 21.9.

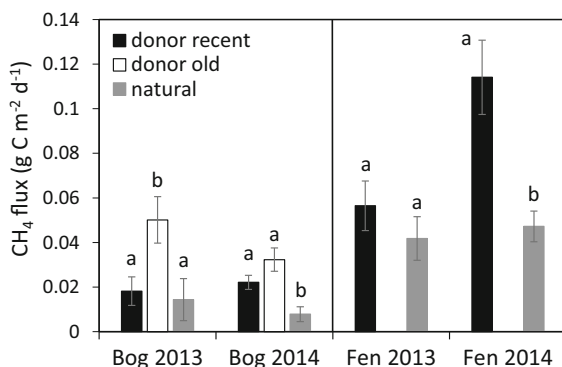


Fig. 2 Mean CH_4 flux \pm standard error of the mean bars at bog-donor old, bog-donor recent, and bog-natural and fen-donor (represented as donor recent) and fen-natural 1 and 2 in 2013 and 2014. Letters should be compared only within 1 year between fen and bog sites separately

Discussion

A goal of peatland restoration is to convert disturbed ecosystems from carbon sources to sinks at rates that would be similar to naturally functioning reference peatlands (Waddington et al. 2010). Natural peatlands are used as vegetation donors for many restoration projects that use the moss layer transfer technique (Quinty and Rochefort 2003). We found that moss and

Fig. 3 Relationship of NEE_{max} and sedge cover (a), $\log CH_4$ flux and water table position (b), GEP_{max} and total vegetation cover (c) and ER and total vegetation cover (d) at the fen and bog donor and natural sites. *Panels a, c, and d* include data from 2014, while *panel b* includes data from both 2013 and 2014. *Panels a, c, and d* include data from fen-natural 1 only, while *panel b* includes data from fen-natural 1 and 2. Error bars are omitted for clarity

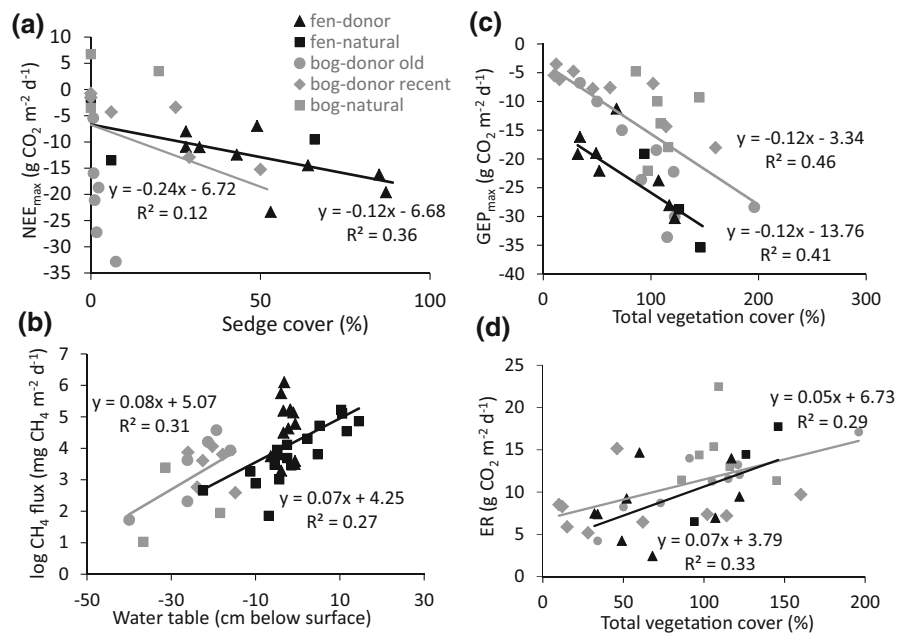


Table 2 Average 2014 growing season carbon balance from bog-donor old, bog-donor recent, and bog-natural, and fen-donor and fen-natural

Site	NEE_{ff}	NPP_{tree}	L	R_r	NEE	CH_4
Bog						
Donor recent	76.8 ± 28.1				76.8 ± 28.1	3.8 ± 0.8
Donor old	75.0 ± 29.6				75.0 ± 29.6	4.7 ± 1.5
Natural	189.0 ± 73.9	-77.7 ± 38.9	-10.9 ± 5.5	63.0 ± 31.5	37.4 ± 149.8	1.4 ± 0.9
Fen						
Donor	175.0 ± 26.6				175.0 ± 26.6	17.4 ± 4.9
Natural	143.8 ± 22.9	-101.7 ± 50.09	-119.8 ± 59.9	138.5 ± 69.3	-216.2 ± 202.2	6.6 ± 1.7

For all variables the unit is $g C m^{-2}$

For natural sites, values for net ecosystem exchange at the forest floor (NEE_{ff}), net primary productivity of trees (NPP_{tree}), litter productivity (L) and tree root respiration (R_r) used to calculate NEE are included (Eq. 1). R_r was subtracted to avoid accounting for root respiration twice. Due to little tree growth at donor sites only NEE_{ff} contributed to NEE. For NEE_{ff} model error was calculated according to Eq. 4. A 50% error was assumed for NPP_{tree} , L , and R_r . Standard error of the mean was calculated for CH_4

total vegetation cover, water table position, NEE_{max} , GEP_{max} , and ER of a bog donor site 6 years post-harvest was similar to an adjacent natural reference bog, while a fen donor site had similar water table position, NEE_{max} , and GEP_{max} 1 year following harvest (Table 1; Fig. 1).

Rapid vegetation recovery was observed at bog donor sites in Québec, Canada that recovered with no management practices, such as spreading straw mulch,

or reintroducing *Sphagnum* species, after harvest, with species composition and cover similar to natural sites after 3–5 years (Rocheffort and Campeau 2002). Several dominant species at bog-donor old and bog-donor recent were also found at bog-natural, and one dominant species (*Carex disperma* Dewey) was found at both fen-donor and fen-natural 1 (Table 1). Similar species between donor and natural sites and the quick recovery of vegetation indicates that propagules

remained at the donor sites following harvest. All plant species found at bog-donor old, bog-donor recent, and fen-donor were species that commonly inhabit peatlands (Vitt 2006). Differences in the cover of plant functional groups at bog-donor recent and bog-donor old varied depending on time since harvest, providing evidence for vegetation change over time as sedges dominated soon after harvest with moss cover increasing years later (Table 1). Similar vegetation change has been described in spontaneously revegetated post-vacuum-harvested sites as well as restored sites across North America and Europe, associated with functional group attributes created by different establishment rates (Lavoie et al. 2003; Rochefort et al. 2013; Chimner et al. 2016; Cooper et al. 2017). Lack of shading due to the absence of an established tree canopy at donor sites likely contributed to initial high sedge cover as light availability has been found to increase the productivity of vascular plant species in fens (Kotowski et al. 2001). *Eriophorum vaginatum* L. comprised the majority of sedge cover at bog-donor old 2 years after harvest, likely because it can colonize bare ground and has good seed dispersal (Rochefort and Campeau 2002). High cover of *E. vaginatum* was found by Rochefort and Campeau (2002) at donor sites harvested in Québec, and other post-restoration bog sites (e.g. Tuitilla et al. 1999; Marinier et al. 2004; Silvan et al. 2005). At the fen a few *Carex* spp. especially contributed to the high sedge cover 1 year post-harvest. This further supports a pattern of vegetation succession of donor sites that begins with sedge dominance immediately following harvest.

Picea mariana and *Larix laricina* are abundant in many North America bogs and fens (Vitt 2006). While a few *Picea mariana* seedlings were observed at bog-donor old and bog-donor recent in 2014 (results not shown), tree colonization at donor sites was not common. Limited tree recovery at donor sites could be associated with the higher water table (Lieffers and Rothwell 1987), but may also reflect the longer period required for establishment of woody plants compared to herbs (González et al. 2013). Wieder et al. (2009) found that it took decades after wildfire disturbance in Alberta bogs for *Picea mariana* stands to store carbon. Maximum accumulation rates occurred 34 years after wildfire for fine root biomass and 74 years' post-wildfire for aboveground and coarse root biomass (Wieder et al. 2009). This indicates that decades will be required for donor sites to store substantial carbon

through tree productivity in western Canada. When considering the results of the carbon budget determined for the natural sites in this study, we emphasize that the NPP_{tree} , L , and R_f calculations (Eq. 1) for tree productivity incorporate work by other researchers. While care should be taken in interpretation of the final carbon balance value of bog-natural and fen-natural, tree productivity was found to contribute substantially to the total carbon budget of these natural sites in this study (Table 2). Planting trees on donor sites post-harvest may be a strategy to improve tree establishment, although NPP_{tree} may be limited by wet conditions. Studies considering tree recruitment and NPP over time at donor sites where tree removal occurred would be beneficial. Further research is necessary to understand differences in carbon exchange between peatland donor and natural sites in locations where trees are not abundant and will not contribute to total carbon uptake, for instance at non-forested northern or maritime bogs in eastern Canada, or sedge fens (Glaser and Janssens 1986).

In 2013 the water table at bog-donor recent and bog-donor old was closer to the surface than bog-natural. This is due to removal of the top layer of vegetation in the donor sites that results in a reduced depth to the water table. Similar mean growing season water table position between bog-donor recent, bog-donor old, and bog-natural may be related to wetter conditions in 2014, but also suggests that the hydrologic disturbance at donor sites is not permanent, and the recovery of water table position similar to natural sites is possible post-disturbance.

Results from the 2014 growing season carbon budget indicated that there was less CO_2 release as NEE_{ff} at bog-donor recent and bog-donor old compared to bog-natural (Table 2). This was related to higher sedge cover at these sites (Table 1; Fig. 3a), as sedge establishment is known to correlate with initial high rates of carbon sequestration following disturbance (Strack et al. 2014). The higher NEE_{ff} values from bog-natural may be associated with the low number of collars that may not have captured the full range and distribution of microtopography. This could have resulted in understory productivity being underestimated. High understory CO_2 release as NEE_{ff} at bog-natural also is related to tree root respiration (Hanson et al. 2000; Valentini et al. 2000). Specifically, R_f at bog-natural was estimated to be 63.0 g C m^{-2} , or 33% of the modelled growing season NEE_{ff}

value of 189.0 g C m^{-2} . Across the fen, fen-natural had a lower NEE_{ff} value, indicating less CO_2 release, compared to fen-donor (Table 2), associated with higher productivity related to greater vegetation cover at fen-natural (Fig. 3c). We calculated a growing season CO_2 balance of $-216.2 \text{ g C m}^{-2}$ at fen-natural, which is in a similar range compared to other studies of natural treed peatlands in Alberta and almost identical to natural sedge-dominated fens in Colorado (Chimner and Cooper 2003). Wieder et al. (2009) reported annual CO_2 fluxes ranging from -120 to -220 g C m^{-2} in an Alberta bog complex while Adkinson et al. (2011) reported a growing season CO_2 flux value for a *Sphagnum* dominated poor fen in Alberta of $-110.1 \text{ g C m}^{-2}$.

We expected higher CH_4 fluxes from donor sites compared to the natural sites due to the shallower post-harvest water tables and a smaller oxic zone for CH_4 oxidation and a larger anoxic zone where methanogens could be active (Lai 2009). Increasing CH_4 flux with shallower water table was observed across bog and fen sites in this study (Fig. 3b), as well as in other studies of peatlands (e.g. Couwenberg and Fritz 2012). CH_4 fluxes increased with increasing sedge cover at the bog due to abundant aerenchyma that allowed CH_4 transport from the anoxic peat to the atmosphere and bypassing the oxic soil zone (Whalen 2005). Likely insufficient vascular plant cover occurred at fen-donor to produce higher CH_4 flux compared to fen-natural in 2013, while increased vascular plant cover at fen-donor in 2014 resulted in higher CH_4 emissions than at fen-natural (Fig. 2). Higher CH_4 flux from the donor sites compared to natural sites at the bog and fen is important to consider when evaluating the recovery of donor sites, as CH_4 has a global warming potential of 28 on a 100-year time scale (IPCC 2013). Mean daily CH_4 flux rates from bog-natural were 13.3 to $28.1 \text{ mg CH}_4 \text{ m}^{-2} \text{ day}^{-1}$ similar to that reported by Olefeldt et al. (2013) of $23.0 \text{ mg CH}_4 \text{ m}^{-2} \text{ day}^{-1}$ from non-permafrost northern bogs. In contrast, fen-natural had higher average growing season CH_4 fluxes (63.0 – $65.7 \text{ mg CH}_4 \text{ m}^{-2} \text{ day}^{-1}$) than median reported value $37.1 \text{ mg CH}_4 \text{ m}^{-2} \text{ day}^{-1}$ (Olefeldt et al. 2013). Higher mean CH_4 flux compared to values found at bog-donor recent (30.0 – $32.7 \text{ mg CH}_4 \text{ m}^{-2} \text{ day}^{-1}$), bog-donor old (72.8 – $48.2 \text{ mg CH}_4 \text{ m}^{-2} \text{ day}^{-1}$), and fen-donor (75.3 – $170.9 \text{ mg CH}_4 \text{ m}^{-2} \text{ day}^{-1}$) have been reported from other natural peatlands (Crill et al. 1988, Moosavi et al. 1996, etc.). For example, Sebacher et al.

(1986) found a mean flux of $289.0 \text{ mg CH}_4 \text{ m}^{-2} \text{ day}^{-1}$ from a waterlogged alpine fen which had vegetation including *Carex* sedge species.

It is also important to consider how the moss-layer transfer technique contributes to recovery of the carbon sink function of sites being restored. Our 2014 modelled carbon balance, specifically from bog-donor old, indicated that it would likely take longer than 6 years for donor sites to have similar carbon fluxes as natural sites. However, projects that have used moss layer transfer in the restoration process have measured reduced GHG emissions in restored sites (Waddington et al. 2010). For instance, Strack et al. (2014) reported that a restored bog in northern Alberta functioned as a total growing season carbon sink just 3 years' post-restoration. Studies of cutover peatland sites that were not restored report high CO_2 emissions for many years, associated with lower water table position causing increased respiration, along with lower vegetation productivity (Waddington and McNeil 2002). Strack et al. (2014) found that unrestored sites released $1386 \text{ g CO}_2 \text{ m}^{-2}$ over a single growing season at an Alberta bog 3 years post disturbance, while Waddington and McNeil (2002) reported growing season releases of 323 and $1331 \text{ g CO}_2 \text{ m}^{-2}$ from an abandoned cutover peatland in Québec 2 and 3 years after disturbance. We assume that over time emissions to the atmosphere from donor sites will decrease, and overall the benefit to the GHG functioning of the restoration projects offsets the increase in GHG release from donor sites in the short-term. The alteration of peatlands by oils sands mining in Alberta creates a large GHG emission (Turetsky et al. 2002), and the use of small donor sites that function in the short term as a source of carbon to the atmosphere is justifiable when it facilitates the creation of much larger restoration or reclamation peatlands and the ecosystem services they provide.

Conclusions and recommendations

Our results show that bog and fen donor sites that were harvested 1–6 years previously for moss layer transfer have been naturally recovering since harvest. Sedges rapidly revegetated the donor sites, however, tree recruitment was limited. While donor sites could be

left to recover without management practices, tree planting may be beneficial to speed up overstory recovery. Quick vegetation recovery at the bog and fen donor sites indicates that propagules remained at these sites following harvest. Recovery of donor sites would likely take longer if a greater moss layer depth was harvested. Considering the rapid moss recovery at bog-donor old it may be possible to re-use the same donor site for moss layer transfer to other disturbed sites once its vegetation has recovered, ~5 years post-harvest, as suggested by Rochefort and Campeau (2002). Similarly, peatlands that have been disturbed by prior uses and are not treed, such as cut lines or winter roads, may be suitable donor sites if their vegetation cover includes species needed for restoration/reclamation sites. This could reduce impacts to natural peatlands.

In this study NEE_{max} ($PAR > 1000 \mu\text{mol m}^{-2} \text{s}^{-1}$) was similar between all donor sites and adjacent natural sites in 2014, one to 6 years following donor harvest. This finding did support our hypothesis about donor site CO_2 flux being similar to natural sites. However, the 2014 carbon budget results indicated a higher release of CO_2 through NEE at donor sites. Methane fluxes were higher than the natural sites as expected. We had further hypothesized that vegetation and hydrology would act as controls on carbon gas exchange from study sites, and total vegetation cover, functional group (i.e. shrub, moss or sedge) cover, and water table position did explain variation in CO_2 and CH_4 flux variables. Continued research at these and other donor sites is required to further our understanding of long term growing season carbon budgets. Trees played an important role in the bog-natural and fen-natural carbon budgets and future monitoring of donor sites is needed to determine the trajectory of tree colonization and its impact on carbon storage. Additional monitoring of donor sites will also be beneficial to determine when CH_4 flux decreases to levels comparable to natural peatlands. We suggest that emissions from donor sites be included in estimates of carbon exchange related to restoration, particularly in scenarios of donor harvest where tree removal occurs. However, the release is small compared to the carbon emission prevented from extracted sites through peatland restoration using the donor material, suggesting that the long-term benefit of including donor material in restoration and reclamation projects offsets this release.

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