

The effects of *Eriophorum vaginatum* on N₂O fluxes at a restored, extracted peatland

Martin E. Brummell^a, Cristina Lazcano^b, Maria Strack^a

^aDepartment of Geography and Environmental Management, University of Waterloo, Waterloo, N2L 3G1, Canada.

5 martinbrummell@gmail.com; mstrack@uwaterloo.ca

^bNatural Resources Management and Environmental Sciences Department, California Polytechnic State University, San Luis Obispo, California, 93405, USA. lazcano.cristina@gmail.com

Correspondence to: Martin E. Brummell (martinbrummell@gmail.com)

10 **Abstract.** Restoration of extracted horticultural peatlands commonly includes distribution of vegetation and propagules from nearby undisturbed sites over the recently-exposed surface. The resulting growth includes both mosses and vascular plants, which are important contributors to returning a peatland to a net carbon-storing ecosystem. Nitrous oxide (N₂O) flux has not been widely investigated in these restored ecosystems. We compared the N₂O flux from plots containing a vascular plant, *Eriophorum vaginatum*, to plots lacking vascular plant cover at a recently restored peatland. We hypothesized that *E. vaginatum* would result in decreased N₂O emissions compared to areas with only moss or bare peat due to rapid plant uptake of peat nitrogen. After an early-summer pulse of emitted N₂O, study plots containing *E. vaginatum* transitioned to net consumers of N₂O while bare plots remained sources as the summer progressed. Furthermore, *E. vaginatum* growing in the wettest parts of the study site also had significantly more extractable nitrogen in pore water collected from 75 cm below the surface, beyond the depth of most roots. We suggest the priming effect driven by the roots of this vascular plant, combined
15 with high water levels, frees some nitrogen from previously-inaccessible recalcitrant organic matter that then is taken up by plant roots and/or soil microorganisms, preventing its release as N₂O. Vascular plants may play important roles in both greenhouse gas processes and in the nutrient cycles of restored peatlands and these complex processes need further investigation to guide effective restoration efforts that aim to return these disturbed ecosystems to net greenhouse gas sinks.
20

25 Keywords: peatland; *Eriophorum vaginatum*; Nitrous oxide

Published in Ecological Engineering, 106: 287-295. 24-month Embargo before becoming Open Access,
Accepted 2 June 2017. Publisher's version on website 9 June 2017.

30 <http://dx.doi.org/10.1016/j.ecoleng.2017.06.006>

0925-8574/© 2017 Elsevier B.V. All rights reserved.

35 © 2017. This manuscript version is made available under the CC-BY-NC-ND 4.0 license
<http://creativecommons.org/licenses/by-nc-nd/4.0/>

1 Introduction

Commercial extraction of horticultural peat removes the living plants, the highly porous surface peat and some of the deeper, more decomposed peat layers, while compressing and drying the remaining material (Graf et al., 2012). Ecological restoration is an effort to return some or all of the functions of a degraded ecosystem to either an original, pre-disturbance state or to a state resembling that of a reference ecosystem. Restoration of extracted peatlands aims to recover a range of ecological functions, including hydrological conditions, plant diversity, and greenhouse gas exchange (Andersen et al., 2010a; Andersen et al., 2010b; Lucchese et al., 2010; Poulin et al., 2013; Price and Whitehead, 2001). Immediately prior to restoration, the recently-exposed surface of an extracted peatland is composed of relatively well-decomposed peat formed during earlier stages of peatland development that may have physical and chemical properties unlike those present prior to disturbance (Graf et al., 2008; Taylor and Price, 2015; Wind-Mulder et al., 1996; Wind-Mulder and Vitt, 2000). Restoration includes raising water tables by filling drainage ditches and spreading living material over the surface gathered at nearby undisturbed areas (González and Rochefort, 2014; Graf et al., 2012; Rochefort et al., 2003).

Prior to disturbance, bogs and some fens in Canada are dominated by bryophytes, particularly of the genus *Sphagnum*, with vascular plants such as the graminoids *Carex* spp., *Eriophorum* spp., and Ericaceous shrubs as well as trees such as *Picea mariana* and *Larix laricina* also present. Vascular plants such as *E. vaginatum* may spontaneously colonize post-extraction peatlands or establish during early stages of the restoration process (Graf et al., 2012; Graf et al., 2008; Mahmood and Strack, 2011) and can extend roots to the mineral soil underlying the peat, often 1 m or more (Adamson, 1918; Wein, 1973) to access water and nutrients that may be unavailable in the near-surface peat accessible to non-vascular bryophytes.

Roots change conditions for below-ground microorganisms by supplying more labile carbon through root exudates and the decomposition of dead root cells, and by providing routes for increased movement of oxygen, water, and dissolved materials (Bhullar et al., 2013; Crow and Wieder, 2005; Hardie et al., 2009; Tuittila et al., 2000). As roots grow deeper into the peat, the Priming Effect (Basiliko et al., 2012; Kuzyakov et al., 2000) increases microbial decomposition of relatively recalcitrant highly decomposed peat and leads to release of materials formerly bound to or included in peat such as nutrients (Dijkstra et al., 2013), including nitrogen (Kuzyakov and Xu, 2013).

Plants may affect soil GHG production, consumption, and movement through a range of mechanisms. Plant roots contribute directly to soil respiration and indirectly through microbial decomposition of root exudates and dead roots and root cells (Kuzyakov and Blagodatskaya, 2015). Peatland plants compete with each other (Kool and Heijmans, 2009) and with soil microorganisms for nutrients including nitrogen in mineral and organic forms (Chapin et al., 1993; Jonasson et al., 1999; Kuzyakov and Xu, 2013) and these interactions can lead to lowered emissions of N₂O (He et al., 2016). Emissions of N₂O and other gases may be increased where plants create a route between water-saturated below-ground areas and the atmosphere, especially through the aerenchymatous tissues of some graminoids (Chen et al., 2011; Jørgensen et al., 2012). Oxygen supplied to roots may link N₂O emissions to diurnal cycles (Jørgensen et al., 2012; Sheppard and Lloyd, 2002; Stewart et al., 2012).

Water plays a major role in peatland function and in structuring patterns of net GHG emissions, principally through the formation of restricted-oxygen zones in water-saturated soil (Groffman et al., 1998; Groffman and Tiedje, 1991; Haapalehto et al., 2014; Strack and Waddington, 2007). N₂O emissions from pristine peatlands have not been widely studied, but existing estimates suggest extremely low emissions, sometimes not distinguishable from zero, though disturbances such as 5 drainage and conversion to forestry or crop production can lead to increased N₂O emissions (Beyer and Höper, 2015; Frolking et al., 2011; Mustamo et al., 2016). During restoration of disturbed peatlands, water levels may fluctuate more than is typical in undisturbed peatlands (Holden et al., 2011; Price, 1997; Taylor and Price, 2015), potentially increasing N₂O emissions by generating conditions suitable for the production of N₂O by ammonia-oxidizing and denitrifying organisms (Andersen et al., 2013; Firestone et al., 1980; Richardson et al., 2009). However, to our knowledge, N₂O emissions from 10 restored peatlands in Canada have yet to be quantified.

N₂O is a potent greenhouse gas, with a CO₂-equivalence of 298 over a 100-year time horizon (IPCC, 2007) and accounts for a large fraction of the total GHG exchange of some ecosystems (Tian et al., 2012). In terrestrial ecosystems, N₂O is produced through ammonia oxidation, also known as nitrification, and through denitrification, which is also the only biological sink for N₂O, as the final step is the reduction of N₂O to N₂ (Firestone and Davidson, 1989). Most ammonia oxidizing bacteria are 15 active only under aerobic conditions, while denitrification occurs under anaerobic conditions; complete denitrification including the final reduction of N₂O to N₂ typically occurs only under conditions in which most other electron acceptors including O₂, Fe³⁺, and SO₄²⁻ are depleted or absent (Achtnich et al., 1995; Firestone and Davidson, 1989; Firestone et al., 1980; Gutknecht et al., 2006). As a result, reducing conditions generated by water-saturated soils often result in N₂O production that shifts to consumption only after redox conditions within the soil are further reduced by either biological 20 activity such as respiration or abiotic processes that remove or block the entry of O₂ and other materials (Schipper et al., 1993); net production of N₂O may be maximized at intermediate or fluctuating water levels (Jungkunst et al., 2008). Ammonia oxidation is inhibited by low pH, thus most N₂O production in acidic bogs is likely to be from denitrification 25 (Allison and Prosser, 1993; Maljanen et al., 2003).

In addition, in restored peatlands, increased microbial activity driven by the growth and presence of the roots of vascular 30 plants leads to increased rates of peat mineralization and greater availability of nitrogen (Kuzyakov and Xu, 2013) in forms microorganisms may convert to N₂O through either ammonia oxidation or denitrification (Conrad, 1996; Gutknecht et al., 2006). However, the role of vascular plants in N₂O emissions from restored peatlands has not been broadly investigated outside of Europe (Maljanen et al., 2012; Nykänen et al., 1995; Vanselow-Algan et al., 2015), and has not been previously measured in Canada. The primary objective of this study was to examine the effect of vascular plant colonization on net N₂O emissions of a restored, cutover peatland where the long-term goal of the restoration is a *Sphagnum*-dominated bog. We hypothesized that areas on a recently-restored peatland containing vascular plants would release lower amounts of N₂O to the atmosphere than comparable plots containing moss or bare peat without vascular plants, due to the ability of peatland vascular plants such as *E. vaginatum* to efficiently uptake mineral and organic N in soil (Gebauer et al., 1995; Silvan et al., 2005; Silvan et al., 2004). Furthermore, we hypothesized that high water levels in the wet part of the study site would

decrease N₂O emissions by restricting oxygen-dependent ammonia-oxidation, the major source of N₂O in other wetlands with low nitrate available for denitrification (Bayley et al., 2005; Verhoeven et al., 1990).

2 Methods

2.1 Experimental Site

5 Plots were established in two areas at a peat bog / fen complex near Seba Beach, Alberta, Canada (53° 27' 17" N, 114° 52' 50" W) where horticultural peat had been extracted, with restoration efforts commencing in late 2012. The site covers approximately 50 hectares across a gradient of peat depth and a bog / fen transition. From 1995 to 2010 the mean annual temperature was 3.5°C, with an average temperature of -11.3°C in January to 16.5°C in July, and an annual total precipitation average of 550 mm, of which approximately 125 mm falls as snow (Environment Canada, 2016); the nearest
10 reporting station is at Entwistle, Alberta, approximately 18 km northwest of the site. Extraction and restoration activities levelled the surface and peat depth now ranges from approximately 100 to 350 cm across the study area. Restoration activity in winter and spring 2013 included blocking and completely refilling ditches, leading to higher water levels to support the growth of transplanted materials collected in a nearby, undisturbed, ombrotrophic, treed bog following the moss layer transfer technique (Graf et al., 2012; Rochefort et al., 2003). After two full growing seasons, this site featured nearly
15 complete vegetation cover in most areas, with a clear water level gradient from a wet area in the centre to drier areas near the margins.

Plots consisting of steel collars 60 x 60 cm and adjacent pore water samplers, water-level wells and associated boardwalk were constructed in May 2015. Water-level wells consisted of a 150 cm long PVC plastic pipe with holes drilled approximately every 2 cm to allow water level in the pipe to equilibrate with soil water level; the outside of each well was
20 covered with nylon mesh and the pipe was inserted into a 1 m deep hole excavated with a hand auger.

Plots were established in pairs with at most 2 m between the members of each pair, with one plot encompassing either one large individual *E. vaginatum* tussock or several smaller tussocks covering more than 50% of the area of the plot, and the other plot containing no vascular plants at the time of establishment; each pair was considered a replicate for statistical analysis. Four pairs of plots were established near the middle of the field, in an area with some standing water and saturated
25 surface peat we designated “wet”; four pairs were established closer to the eastern edge and designated “dry”. Where vascular plants subsequently grew in bare plots they were clipped biweekly to the peat surface to limit below-ground inputs from roots; vascular plant cover in bare plots reached at most 20% (estimated visually) and a maximum height of 10 cm before clipping. Boardwalk constructed at the wet area included vertical supports driven into the peat to stabilize the platform and prevent movements by workers from releasing trapped gas bubbles from the water-saturated peat.

2.2 Greenhouse Gas Measurements

Nitrous oxide fluxes were measured at each plot approximately weekly from 11 May until 7 September 2015 (196 total N₂O flux measurements) using static chambers. An opaque plastic chamber containing a battery-driven fan was placed over the collar and 20 mL samples of internal air were withdrawn at 5 min, 15 min, 25 min, and 35 min using a syringe, and injected
5 into a previously-evacuated 12 mL Exetainer (LaboCo Ltd. Lampeter, UK). Filled Exetainers were sent to the laboratory at the University of Waterloo for analysis using a gas chromatograph (GC; Shimadzu GC2014, Shimadzu Scientific Instruments, Columbia, MD, USA) with an electron capture detector (ECD) and N₂O standards at 1.0 and 10.0 ppm. Air temperature was recorded at the same time as each gas sample withdrawal. Soil profile temperature from -2 cm to -30 cm
10 (every 5 cm from -5 cm to -30 cm) was recorded during each chamber measurement from nearby (approximately 20 cm away) and water level was recorded from each well.

We conducted measurements of net CO₂ exchange following the methods of Strack & Zuback (2013). Briefly, to measure total photosynthesis, a transparent acrylic chamber (60 x 60 x 30 cm) equipped with a battery-powered fan to mix the internal air was placed on to each collar and the concentration of CO₂ inside the chamber was recorded from the display of an EGM-4 infrared gas analyser (IRGA; PPSystems Amesbury, MA, USA) every 15 s over 2 minutes; photosynthetically
15 active radiation (PAR) and air temperature and humidity were also measured by the IRGA. Subsequent measurements with added shades over the chamber culminating with complete darkness were made after each measurement of total photosynthesis; the final measurement in the dark represents ecosystem respiration (ER). Estimates of ecosystem productivity based on these sets of measurements are part of a separate study (Lazcano et al. in prep).

Flux of each gas was calculated by the change in concentration over time within each chamber measurement period. A linear
20 regression was used to exclude flux estimates with $r^2 < 0.8$, that is, in these cases the flux was set to zero, and each estimate was inspected to correct errors associated with data-entry or other mistakes (e.g. outliers associated with poorly evacuated Exetainers). Apparent N₂O fluxes with a net change over the measurement period less than the precision of the GC,
25 approximately 0.02 ppm for repeated measurements, were also set to zero regardless of the r^2 of the regression; four estimates of non-zero N₂O flux were thus regarded as zero. Apparent CO₂ fluxes with a net change over the measurement period less than 5 ppmv, or 1% of the measured concentration, were regarded as zero flux because this is approximately equal to the measurement precision of the EGM-4; no estimates of total respiration fell below that threshold. Fluxes were collected weekly, but measurements were not collected during week 10, nor weeks 14-16, as efforts were focused on other projects at the site including vegetation surveys.

2.3 Pore Water Nitrogen

30 Pore water samplers were constructed of 30 cm long PVC pipe with holes at the middle 10 cm section. Each end was capped, the holes were covered with nylon mesh, and a 4 mm inside diameter Tygon tube was inserted; the other end of the tube was fitted with a 3-way stopcock and remained above the surface of the peat. Pore water samplers were buried at 20 cm and 75

cm depth near each plot. For plots containing *E. vaginatum*, pore water samplers were buried under the canopy of *E. vaginatum* tussocks, approximately 10 cm from its base, within 2 m of the plot and of a similar above-ground size rather than disturbing the plot itself; for bare plots, pore water samplers were buried in positions at least 30 cm from the nearest large vascular plant. Pore water was collected using a 60 mL syringe attached to the 3-way stopcock, and flushed three times with water from the sampler to ensure samples were from the indicated depth. Collections were made on 11 June, 23 June, 3 July, 15 July, 31 July, 10 August, 26 August, and 10 September. Low water levels, especially at the dry area, led to insufficient water in most samplers at 20 cm deep throughout the summer, but the deeper samplers at 75 cm were almost always below local water level as determined from well measurements and yielded at least 60 mL of water each. Pore water samples were acidified to pH < 2.0 with sulfuric acid for preservation within 48 hours of collection.

Pore water samples were shipped to the University of Waterloo and filtered using a syringe-mounted 0.45 μm cellulose acetate filter and diluted to 1/20 of original concentration in nitrogen-free solutions of sulphurous acid prepared in the laboratory. Total Kjeldahl Nitrogen (TKN) was determined using ammonium molybdate/ascorbic acid colorimetric methods (BranLuebbe AutoAnalyzer III system, Seal Analytical, Method G-188-097, detection limit 0.01mg L⁻¹ N).

2.4 Statistical Analysis

N_2O and CO_2 flux data were analysed in R and R Studio (R Development Core Team, 2013; R Studio Team, 2015) with regression against other measured variables including Total Kjeldahl Nitrogen, air temperature within the chamber at the time of gas measurement, soil profile temperature from -2 cm to -30 cm, depth to water table at the nearest well, vegetation cover type in each plot, and location in either the wet or dry areas of the site. Because measurements at each plot were conducted weekly but not necessarily in the same order or on the same day of each week, means were calculated for each week of measurements for each grouping of plots such as “Wet Moss” or “Dry *E. vaginatum*”. Each plot and pore water sampler was sampled repeatedly, and repeated measures analyses were included except where whole-summer means were used for each plot or pore water sampler. General linear models were constructed using the `glm` function to evaluate the correlations, if any, between these parameters. Analysis of Variance was conducted with the `anova` function to evaluate apparent differences among TKN contents. Orthogonal regression to analyse the relationship between N_2O and CO_2 fluxes was applied subsequent to a general linear model that suggested differences in the slope of that relationship for moss/bare and *E. vaginatum* plots; it was accomplished using the first Eigenvector generated by the Principal Components Analysis function `prcomp`. For all statistical analyses, the $\alpha=0.05$ was the threshold for differences or trends to be considered significant.

3 Results

Water table, but not air temperature at the time of measurement nor mean soil profile temperature, was significantly higher at the wet area than at the dry area (Fig. 1). There were no significant differences in these parameters between moss/bare plots and *E. vaginatum* plots. There was no significant correlation between temperature with either net flux of N₂O or TKN, or water table and N₂O flux. Water table was positively correlated ($r = 0.33, p = 0.089$) with TKN in pore water samplers at -75 cm below the ground surface (Table 1).

The flux of N₂O in chambers was most often not distinguishable from zero, although out of 196 total flux estimates we did observe 10 positive and 11 negative fluxes, a finding that is consistent with other studies of N₂O flux in terrestrial ecosystems (Chapuis-Lardy et al., 2007). As described in section 2.2, we evaluated apparent fluxes, that is, the accumulation or depletion of N₂O within a closed chamber over a 35 minute measurement period, using a simple linear regression of measured concentrations over time; fluxes with r^2 less than 0.80 were considered to be zero. Furthermore, the smallest magnitude accumulations or depletions we observed resulted in calculated daily fluxes equivalent to approximately 0.8 mg N₂O m⁻² d⁻¹, equivalent to an increase or decrease of greater than 0.020 ppm N₂O over 35 min within the approximately 100 L volume of the chamber. Smaller changes in N₂O concentration were observed but were set to zero because such small differences are within the precision of the GC and may represent measurement error. Means reported here include the large number of zero flux events observed at every plot.

The mean flux of N₂O for *E. vaginatum* plots over all measurements was -0.037 mg m⁻² d⁻¹, for moss/bare plots, the mean was 0.041 mg m⁻² d⁻¹. The mean flux of N₂O at the wet area was 0.0050 mg m⁻² d⁻¹ and -0.000023 mg m⁻² d⁻¹ at the dry area. Plots with *E. vaginatum* showed higher net emissions (i.e., movement from soil to atmosphere) than plots without vascular plants in the first week of measurement, but became consumers of N₂O by the late summer while moss/bare plots remained net producers (Fig. 2A). The rest of May and June showed gradually declining water levels and increasing temperatures (Fig. 1), and N₂O fluxes at all plots were close to zero (Fig. 2). In late July and August, however, moss/bare plots produced positive fluxes of N₂O while *E. vaginatum* plot fluxes were negative or zero. Concentrations of total dissolved nitrogen as TKN did not show a trend over the summer, and did not vary significantly between *E. vaginatum* and moss/bare plots (Fig. 2B). The general linear model of N₂O net fluxes indicated the interaction between time (as week of the year) and vegetation cover within plots was significant ($p < 0.01$; Table 2) while each of those factors did not significantly ($p > 0.05$) explain the variance in N₂O emissions in models that did not include a vegetation x day of year interaction term.

Plots in the wet area at the restored site with *E. vaginatum* had significantly higher TKN at -75 cm than plots in the dry area with either *E. vaginatum* or moss/bare cover inside the collar (Fig. 3). Pore water samples at -20 cm rarely contained water, but on three occasions at each of the *E. vaginatum* plots and at the moss/bare plots in the Dry area, and 21 occasions at the moss/bare plots in the Wet area there was sufficient water collected to show a general pattern of less TKN at shallow compared to deep pore water samplers (Fig. 3). There was no significant correlation between TKN at 75 cm and N₂O flux (Table 1).

Increasing total respiration in moss/bare plots was significantly ($p = 0.023$, $r = 0.78$) correlated with N₂O flux, but not in *E. vaginatum* plots; the slopes of these relationships are significantly different from each other when analysed by orthogonal regression (Fig. 4).

4 Discussion

5 The magnitude of N₂O net production we observed, considering single measurements of flux of approximately $\pm 3.0 \text{ mg m}^{-2} \text{ d}^{-1}$ was similar to some values reported for natural peatlands in Germany (Tauchnitz et al., 2015) and roughly half of maximum values reported from forests (Nicolini et al., 2013 and references therein), tropical peatlands (Hadi et al., 2000), or waterlogged rice fields in China (Chen et al., 1997). Our measurements are higher than for many temperate or boreal peatlands, with reports ranging from “very low” (Rückauf et al., 2004) to about $8.6 \text{ mg m}^{-2} \text{ d}^{-1}$ at a portion of a partially
10 drained peatland complex in Finland now used for crop production, though other parts of that peatland complex showed considerably less N₂O flux (Mustamo et al., 2016).

We expected the presence of *E. vaginatum* to decrease N₂O fluxes to atmosphere, but we did observe strong emissions in the early summer (Fig. 2A). The early high fluxes of N₂O from *E. vaginatum* plots may be the end of the often-observed “spike” of N₂O during or shortly after snowmelt in cold-temperate ecosystems, possibly caused by high N availability derived from
15 winter-killed cells, including the roots of sedges (Groffman et al., 1993; Maljanen et al., 2009; Mustamo et al., 2016; Rochette et al., 2008). Subsequent measurements over the rest of the growing season showed a sharp decline in N₂O flux from *E. vaginatum* plots to a level similar to moss/bare plots, and negative fluxes, indicating consumption of N₂O in peat, were a feature of *E. vaginatum* plots but not moss/bare plots after mid-July. Depth to water table and soil profile temperature to -30 cm did not differ between *E. vaginatum* plots and moss/bare plots within each of the Dry and Wet areas. The total
20 cumulative flux of N₂O was lower at *E. vaginatum* plots than at moss/bare plots, unlike some other studies of peatland N₂O emissions that have not observed differences between vegetation (e.g. Järveoja et al., 2016). Consumption of N₂O most likely indicates complete denitrification (Chapuis-Lardy et al., 2007), suggesting completely anaerobic conditions in peat that also includes sedge roots and aerenchymatous tissue that may lead to changes in CH₄ emissions depending on plant species and other factors (Cooper et al., 2014; Nielsen et al., 2016; Strööm et al., 2005).

25 Increasing total respiration in *E. vaginatum*, associated with plant growth and increasing total biomass over the summer, is associated with declining net N₂O emissions and the appearance of net sinks for N₂O, while increasing total respiration in moss/bare plots is associated with increasing net N₂O emissions (Fig. 4). The occurrence of sinks for N₂O where the gas is removed from the surface atmosphere is most likely caused by the activity of complete denitrifiers and other heterotrophs that remove enough O₂ and other electron acceptors from their local conditions to create the strongly reducing redox
30 conditions needed for complete denitrification (Ambus and Christensen, 1993; Butterbach-Bahl et al., 2013). However, the magnitude of N₂O consumption near aerenchymatous plant tissues such as are found in *E. vaginatum* maybe be reduced by oxygen supplied by the plant tissues, obscuring the relationship between respiration and denitrification as signalled by N₂O

consumption. The opposite relationship between N₂O and CO₂ at *E. vaginatum* vs. moss/bare sites provides indirect support for the hypothesis that plant-root-driven increased microbial activity leads to a net movement of soil organic matter-bound nitrogen to compounds other than N₂O.

Plots were established in early May, before most annual plants had emerged from the peat surface and before the presence of 5 moss rather than bare peat could be visually determined, but after established *E. vaginatum* individuals had begun producing new, green leaves. Roots were thus present, though possibly not as living tissue (Silvan et al., 2004), already in *E. vaginatum* plots but not in moss/bare plots, and it is most likely that the vascular plants grew new and longer roots over the growing season (Kummerow et al., 1988; Wein, 1973). As *E. vaginatum* plants grow, they extend roots (Saarnio et al., 2004) deeper 10 into the peat and stimulate greater activity by heterotrophic microorganisms through the Priming Effect (Kuzyakov and Xu, 2013). This leads to increased decomposition of relatively recalcitrant organic matter in the peat (Hardie et al., 2009; Leifeld et al., 2012) and the release of organic and / or mineral N that had been previously inaccessible as components of that 15 recalcitrant peat. *E. vaginatum* is an effective competitor for soil nutrients against soil microorganisms (Schimel and Chapin, 1996; Silvan et al., 2004) such that much of the released N would be quickly taken up by the plant roots (Chapin et al., 1993; Leadley et al., 1997). We found the largest individual *E. vaginatum* plants in the wet area, suggesting that this plant is able to 20 use increased available N even when roots are under severely anoxic conditions or that growth of this plant could be enhanced by patches of greater nitrogen availability (Gebauer et al., 1995; Shaver et al., 1986).

High levels of nitrogen were observed at plots in the wet area of the site at depths beyond the reach of nearly all roots (Fig. 25 3). We suggest that instead of release as N₂O, nitrogen liberated from decomposing peat is taken up by the plants (Thormann and Bayley, 1997), immobilized by soil microorganisms (Kuzyakov and Xu, 2013), or moves downwards as dissolved 20 compounds. This interaction between roots and water level is enhanced as the plants grow over the summer. Soluble nitrogen compounds that are not taken up by the plants or microbes leach downwards away from most of the populations of microorganisms and into a zone of reduced metabolic activity caused by poor conditions: low pH, little O₂, low porosity further slowing rates of nutrient and O₂ mixing and diffusion, and highly decomposed organic matter severely lacking in accessible carbon resources that microorganisms can rapidly metabolize (Artz et al., 2006; Binet et al., 2013; Graf et al., 2012).

The pore water samplers we used collect a sample of water that represents both water and dissolved materials from above and below the sampler's position, as well as laterally from approximately the same depth. Water level at both Dry and Wet sites was always above -75 cm (Fig. 1), but the amount of dissolved material that could be captured by a pore water sampler 30 may have varied due to the difference in potential supply from overlying saturated layers. There was not a significant difference in TKN contents of pore water samplers associated with *E. vaginatum* or moss/bare plots at -75 cm in the Dry area, suggesting the increased concentration of nitrogen under *E. vaginatum* at the Wet area results from both the plant roots and consistently higher water levels.

5 Conclusions

Vascular plants such as *E. vaginatum* are able to rapidly establish on disturbed peat when restoration efforts include the use of the moss layer transfer technique (González and Rochefort, 2014; Rochefort and Lode, 2006). As these plants extend roots into the underlying peat, the Priming Effect (Kuzyakov et al., 2000) helps drive increased mineralization of this recalcitrant organic matter and liberates nitrogen, which is taken up by the plants or immobilized by microbes rather than released as N₂O, or may be transported downwards in wetter areas of the peatland. Our results suggest restoration activities at disturbed peatlands that focus on re-establishment of mosses as ecologically dominant ground cover may release more N₂O to atmosphere than where restoration includes vascular plants such as *E. vaginatum*, a potentially important consideration where restoration goals include the establishment of a net-GHG-sink similar to undisturbed peatlands (Rochefort et al., 2003; Strack and Waddington, 2012); however, these vascular plants may also be associated with increased release of CH₄ (Cooper et al., 2014; Strack et al., 2017). The large potential effect of N₂O and the role of major groups of wetland plants in its emission from disturbed and restored peatlands deserves further consideration in the field of ecological restoration.

Acknowledgements

Sun Gro Horticulture Inc. graciously provided access to the study area and supplied in-kind support including assistance with disabled vehicles. Stephanie Singh, Ali Engering, and Sabrina Touchette assisted with data collection in the field and analysis by GC in the lab. This work was funded by an NSERC Collaborative Research and Development grant supported by the Canadian Sphagnum Peat Moss Association and its members.

References

- Achtnich, C., Bak, F., Conrad, R., 1995. Competition for electron donors among nitrate reducers, ferric iron reducers, sulfate reducers, and methanogens in anoxic paddy soil. *Biology and Fertility of Soils* 19, 65-72.
- Adamson, R.S., 1918. On the relationships of some associations of the Southern Pennines. *Journal of Ecology* 6, 97-109.
- Allison, S.M., Prosser, J.I., 1993. Ammonia oxidation at low pH by attached populations of nitrifying bacteria. *Soil Biology and Biochemistry* 25, 935-941.
- Ambus, P., Christensen, S., 1993. Denitrification variability and control in a riparian fen irrigated with agricultural drainage water. *Soil Biology and Biochemistry* 25, 915-923.
- Andersen, R., Chapman, S.J., Artz, R.R.E., 2013. Microbial communities in natural and disturbed peatlands: A review. *Soil Biology and Biochemistry* 57, 979-994.
- Andersen, R., Grasset, L., Thormann, M.N., Rochefort, L., Francez, A.-J., 2010a. Changes in microbial community structure and function following Sphagnum peatland restoration. *Soil Biology and Biochemistry* 42, 291-301.
- Andersen, R., Rochefort, L., Poulin, M., 2010b. Peat, Water and Plant Tissue Chemistry Monitoring: A Seven-Year Case-Study in a Restored Peatland. *Wetlands* 30, 159-170.
- Artz, R., Chapman, S., Campbell, C., 2006. Substrate utilisation profiles of microbial communities in peat are depth dependent and correlate with whole soil FTIR profiles. *Soil Biology and Biochemistry* 38, 2958-2962.

- Basiliko, N., Stewart, H., Roulet, N.T., Moore, T.R., 2012. Do Root Exudates Enhance Peat Decomposition? *Geomicrobiology Journal* 29, 374-378.
- Bayley, S.E., Thormann, M.N., Szumigalski, A.R., 2005. Nitrogen mineralization and decomposition in western boreal bog and fen peat. *Ecoscience* 12, 455-465.
- 5 Beyer, C., Höper, H., 2015. Greenhouse gas exchange of rewetted bog peat extraction sites and a *Sphagnum* cultivation site in northwest Germany. *Biogeosciences* 12, 2101-2117.
- Bhullar, G.S., Iravani, M., Edwards, P.J., Venterink, H.O., 2013. Methane transport and emissions from soil as affected by water table and vascular plants. *BMC Ecology* 13.
- 10 Binet, S., Gogo, S., Laggoun-Défarge, F., 2013. A water-table dependent reservoir model to investigate the effect of drought and vascular plant invasion on peatland hydrology. *Journal of Hydrology* 499, 132-139.
- Butterbach-Bahl, K., Baggs, E.M., Dannenmann, M., Kiese, R., Zechmeister-Boltenstern, S., 2013. Nitrous oxide emissions from soils: how well do we understand the processes and their controls? *Philosophical transactions of the Royal Society of London. Series B, Biological sciences* 368, 20130122.
- 15 Chapin, F.S., III, Moilanen, L., Kielland, K., 1993. Preferential use of organic nitrogen for growth by a non-mycorrhizal arctic sedge. *Nature* 361, 150-153.
- Chapuis-Lardy, L., Wrage, N., Metay, A., Chotte, J.-L., Bernoux, M., 2007. Soils, a sink for N₂O? A review. *Global Change Biology* 13, 1-17.
- Chen, G.X., Huang, G.H., Huang, B., Yu, K.W., Wu, J., Xu, H., 1997. Nitrous oxide and methane emissions from soil-plant systems. *Nutrient Cycling in Agroecosystems* 49, 41-45.
- 20 Chen, H., Wang, M., Wu, N., Wang, Y., Zhu, D., Gao, Y., Peng, C., 2011. Nitrous oxide fluxes from the littoral zone of a lake on the Qinghai-Tibetan Plateau. *Environmental Monitoring and Assessment* 182, 545-553.
- Conrad, R., 1996. Soil Microorganisms as Controllers of Atmospheric Trace Gases (H₂, CO, CH₄, OCS, N₂O, and NO). *Microbiological Reviews* 60, 609-640.
- 25 Cooper, M.D.A., Evans, C.D., Zielinski, P., Levy, P.E., Gray, A., Peacock, M., Norris, D., Fenner, N., Freeman, C., 2014. Infilled Ditches are Hotspots of Landscape Methane Flux Following Peatland Re-wetting. *Ecosystems* 17, 1227-1241.
- Crow, S.E., Wieder, R.K., 2005. Sources of CO₂ emission from a nothern peatland: Root respiration, exudation, and decomposition. *Ecology* 86, 1825-1834.
- Dijkstra, F.A., Carrillo, Y., Pendall, E., Morgan, J.A., 2013. Rhizosphere priming: a nutrient perspective. *Frontiers in microbiology* 4, 216.
- 30 Environment Canada, 2016. Climate Normals 1981-2010 Station Data Entwistle AB, In: Canada, E.a.N.R. (Ed.). Government of Canada, Ottawa, p. http://climate.weather.gc.ca/historical_data/search_historic_data_e.html.
- Firestone, M.K., Davidson, E.A., 1989. Microbiological Basis of NO and N₂O Production and Consumption in Soil, In: Andreae, M.O., Schimel, D.S. (Eds.), *Exchange of Trace Gases between Terrestrial Ecosystems and the Atmosphere*. Wiley-Interscience, Chichester, UK, pp. 7-21.
- 35 Firestone, M.K., Firestone, R.B., Tiedje, J.M., 1980. Nitrous Oxide from Soil Denitrification: Factors Controlling Its Biological Production. *Science* 208, 749-751.
- Frolking, S., Talbot, J., Jones, M.C., Treat, C.C., Kauffman, J.B., Tuittila, E.-S., Roulet, N., 2011. Peatlands in the Earth's 21st century climate system. *Environmental Reviews* 19, 371-396.
- 40 Gebauer, R.L.e., Reynolds, J.F., Tenhunen, J.D., 1995. Growth and allocation of the arctic sedges *Eriophorum angustifolium* and *E. vaginatum*: effects of variable soil oxygen and nutrient availability. *Oecologia* 104, 330-339.
- González, E., Rochefort, L., 2014. Drivers of success in 53 cutover bogs restored by a moss layer transfer technique. *Ecological Engineering* 68, 279-290.
- 45 Graf, M.D., Bérubé, V., Rochefort, L., 2012. Restoration of peatlands after peat extraction, In: Vitt, D., Bhatti, J. (Eds.), *Restoration and Reclamation of Boreal Ecosystems*. Cambridge University Press, New York, pp. 259-280.
- Graf, M.D., Rochefort, L., Poulin, M., 2008. Spontaneous revegetation of cutaway peatlands of North America. *Wetlands* 28, 28-39.
- Groffman, P.M., Gold, A.J., Jacinthe, P.-A., 1998. Nitrous oxide production in riparian zones and groundwater. *Nutrient Cycling in Agroecosystems* 52, 179-186.

- Groffman, P.M., Tiedje, J.M., 1991. Relationships between denitrification, CO₂ production and air-filled porosity in soils of different texture and drainage. *Soil Biology and Biochemistry* 23, 299-302.
- Groffman, P.M., Zak, D.R., Christensen, S., Mosier, A., Tiedje, J.M., 1993. Early spring nitrogen dynamics in a temperate forest landscape. *Ecology* 75, 1579-1585.
- 5 Gutknecht, J.L.M., Goodman, R.M., Balser, T.C., 2006. Linking soil process and microbial ecology in freshwater wetland ecosystems. *Plant and Soil* 289, 17-34.
- Haapalehto, T., Kotiaho, J.S., Matilainen, R., Tahvanainen, T., 2014. The effects of long-term drainage and subsequent restoration on water table level and pore water chemistry in boreal peatlands. *Journal of Hydrology* 519, 1493-1505.
- Hadi, A., Inubushi, K., Purnomo, E., Razie, F., Yamakawa, K., Tsuruta, H., 2000. Effect of land-use changes on nitrous oxide (N₂O) emission from tropical peatlands. *Chemosphere - Global Change Science* 2, 347-358.
- 10 Hardie, S.M.L., Garnett, M.H., Fallick, A.E., Ostle, N.J., Rowland, A.P., 2009. Bomb-¹⁴C analysis of ecosystem respiration reveals that peatland vegetation facilitates release of old carbon. *Geoderma* 153, 393-401.
- He, H., Jansson, P.-E., Svensson, M., Meyer, A., Klemedtsson, L., Kasimir, Å., 2016. Factors controlling Nitrous Oxide emission from a spruce forest ecosystem on drained organic soil, derived using the CoupModel. *Ecological Modelling* 321, 46-63.
- 15 Holden, J., Wallage, Z.E., Lane, S.N., McDonald, A.T., 2011. Water table dynamics in undisturbed, drained and restored blanket peat. *Journal of Hydrology* 402, 103-114.
- IPCC, 2007. Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.
- 20 Järveoja, J., Peichl, M., Maddison, M., Soosaar, K., Vellak, K., Karofeld, E., Teemusk, A., Mander, Ü., 2016. Impact of water table level on annual carbon and greenhouse gas balances of a restored peat extraction area. *Biogeosciences* 13, 2637-2651.
- Jonasson, S., Michelsen, A., Schmidt, I.K., 1999. Coupling of nutrient cycling and carbon dynamics in the Arctic, integration of soil microbial and plant processes. *Applied Soil Ecology* 11, 135-146.
- 25 Jørgensen, C.J., Struwe, S., Elberling, B., 2012. Temporal trends in N₂O flux dynamics in a Danish wetland - effects of plant-mediated gas transport of N₂O and O₂ following changes in water level and soil mineral-N availability. *Global Change Biology* 18, 210-222.
- Jungkunst, H., Flessa, H., Scherber, C., Fiedler, S., 2008. Groundwater level controls CO₂, N₂O and CH₄ fluxes of three different hydromorphic soil types of a temperate forest ecosystem. *Soil Biology and Biochemistry* 40, 2047-2054.
- 30 Kool, A., Heijmans, M.M.P.D., 2009. Dwarf shrubs are stronger competitors than graminoid species at high nutrient supply in peat bogs. *Plant Ecology* 204, 125-134.
- Kummerow, J., Mills, J.N., Ellis, B.A., Kummerow, A., 1988. Growth dynamics of cotton-grass (*Eriophorum vaginatum*). *Canadian Journal of Botany* 66, 253-256.
- Kuzyakov, Y., Blagodatskaya, E., 2015. Microbial hotspots and hot moments in soil: Concept & review. *Soil Biology and Biochemistry* 83, 184-199.
- 35 Kuzyakov, Y., Friedel, J.K., Stahr, K., 2000. Review of mechanisms and quantification of priming effects. *Soil Biology and Biochemistry* 32, 1485-1498.
- Kuzyakov, Y., Xu, X., 2013. Competition between roots and microorganisms for nitrogen: mechanisms and ecological relevance. *The New phytologist* 198, 656-669.
- 40 Leadley, P.W., Reynolds, J.F., Chapin, F.S., III, 1997. A model of nitrogen uptake by *Eriophorum vaginatum* roots in the field: Ecological implications. *Ecological Monographs* 67, 1-22.
- Leifeld, J., Steffens, M., Galego-Sala, A., 2012. Sensitivity of peatland carbon loss to organic matter quality. *Geophysical Research Letters* 39, n/a-n/a.
- Lucchese, M., Waddington, J.M., Poulin, M., Pouliot, R., Rochefort, L., Strack, M., 2010. Organic matter accumulation in a 45 restored peatland: Evaluating restoration success. *Ecological Engineering* 36, 482-488.
- Mahmood, M.S., Strack, M., 2011. Methane dynamics of recolonized cutover minerotrophic peatland: Implications for restoration. *Ecological Engineering* 37, 1859-1868.
- Maljanen, M., Liikanen, A., Silvola, J., Martikainen, P.J., 2003. Nitrous oxide emissions from boreal organic soil under different land-use. *Soil Biology and Biochemistry* 35, 689-700.

- Maljanen, M., Shurpali, N., Hytönen, J., Mäkiranta, P., Aro, L., Potila, H., Laine, J., Li, C., Martikainen, P.J., 2012. Afforestation does not necessarily reduce nitrous oxide emissions from managed boreal peat soils. *Biogeochemistry* 108, 199-218.
- 5 Maljanen, M., Virkajarvi, P., Hytönen, J., Öquist, M., Sparrman, T., Martikainen, P.J., 2009. Nitrous oxide production in boreal soils with variable organic matter content at low temperature - snow manipulation experiment. *Biogeosciences* 6, 2461-2493.
- Mustamo, P., Maljanen, M., Hyvärinen, M., Ronkanen, A.-K., Kløve, B., 2016. Respiration and emissions of methane and nitrous oxide from a boreal peatland complex comprising different land-use types. *Boreal Environment Research* 21, 405-426.
- 10 Nicolini, G., Castaldi, S., Fratini, G., Valentini, R., 2013. A literature overview of micrometeorological CH₄ and N₂O flux measurements in terrestrial ecosystems. *Atmospheric Environment* 81, 311-319.
- Nielsen, C.S., Michelsen, A., Ambus, P., Deepagoda, T.K.K.C., Elberling, B., 2016. Linking rhizospheric CH₄ oxidation and net CH₄ emissions in an arctic wetland based on ¹³CH₄ labeling of mesocosms. *Plant and Soil* 412, 201-213.
- 15 Nykänen, H., Alm, J., Lång, K., Silvola, J., Martikainen, P.J., 1995. Emissions of CH₄, N₂O and CO₂ from a virgin fen and a fen drained for grassland in Finland. *Journal of Biogeography* 22, 351-357.
- Poulin, M., Andersen, R., Rochefort, L., 2013. A New Approach for Tracking Vegetation Change after Restoration: A Case Study with Peatlands. *Restoration Ecology* 21, 363-371.
- Price, J., 1997. Soil moisture, water tension, and water table relationships in a managed cutover bog. *Journal of Hydrology* 202, 21-32.
- 20 Price, J.S., Whitehead, G.S., 2001. Developing hydrologic thresholds for *Sphagnum* recolonization on an abandoned cutover bog. *Wetlands* 21, 32-40.
- R Development Core Team, 2013. R: A language and environment for statistical computing. R foundation for statistical computing, Vienna, Austria.
- R Studio Team, 2015. RStudio: Integrated Development for R. RStudio, Inc., Boston, MA.
- 25 Richardson, D., Felgate, H., Watmough, N., Thomson, A., Baggs, E., 2009. Mitigating release of the potent greenhouse gas N₂O from the nitrogen cycle - could enzymic regulation hold the key? *Trends in biotechnology* 27, 388-397.
- Rochefort, L., Lode, E., 2006. Restoration of Degraded Boreal Peatlands, In: Wider, R.K., Vitt, D.H. (Eds.), *Boreal Peatland Ecosystems*. Springer-Verlag, Berlin, pp. 9-24.
- 30 Rochefort, L., Quinty, F., Campeau, S., Johnson, K., Malterer, T., 2003. North American approach to the restoration of *Sphagnum* dominated peatlands. *Wetlands Ecology and Management* 11, 3-20.
- Rochette, P., Worth, D.E., Lemke, R.L., McConkey, B.G., Pennock, D.J., Wagner-Riddle, C., Desjardins, R.L., 2008. Estimation of N₂O emissions from agricultural soils in Canada. I. Development of a country-specific methodology. *Canadian Journal of Soil Science* 88, 641-654.
- Rückauf, U., Augustin, J., Russow, R., Merbach, W., 2004. Nitrate removal from drained and reflooded fen soils affected by soil N transformation processes and plant uptake. *Soil Biology and Biochemistry* 36, 77-90.
- 35 Saarnio, S., Wittenmayer, L., Merbach, W., 2004. Rhizospheric exudation of *Eriophorum vaginatum* L. - Potential link to methanogenesis. *Plant and Soil* 267, 343-355.
- Schimel, J.P., Chapin, F.S.I., 1996. Tundra plant uptake of amino acid and NH₄⁺ nitrogen in situ: Plants compete well for amino acid N. *Ecology* 77, 2142-2147.
- 40 Schipper, L.A., Cooper, A.B., Harfoot, C.G., Dyck, W.J., 1993. Regulators of denitrification in an organic riparian soil. *Soil Biology and Biochemistry* 25, 925-933.
- Shaver, G.R., III, F.C., Gartner, B.L., 1986. Factors limiting seasonal growth and peak biomass accumulation in *Eriophorum vaginatum* in Alaskan tussock tundra. *Journal of Ecology* 74, 257-278.
- Sheppard, S.K., Lloyd, D., 2002. Diurnal Oscillations in Gas Production (O₂, CO₂, CH₄, and N₂) in Soil Monoliths. *Biological Rhythm Research* 33, 577-591.
- 45 Silvan, N., Tuittila, E.-S., Kitunen, V., Vasander, H., Laine, J., 2005. Nitrate uptake by *Eriophorum vaginatum* controls N₂O production in a restored peatland. *Soil Biology and Biochemistry* 37, 1519-1526.
- Silvan, N., Tuittila, E.-S., Vasander, H., Laine, J., 2004. *Eriophorum vaginatum* plays a major role in nutrient immobilisation in boreal peatlands. *Ann. Bot. Fennici* 41, 189-199.

- Stewart, K.J., Brummell, M.E., Farrell, R.E., Siciliano, S.D., 2012. N₂O flux from plant-soil systems in polar deserts switch between sources and sinks under different light conditions. *Soil Biology and Biochemistry* 48, 69-77.
- Strack, M., Mwakanyamale, K., Hassanpour Fard, G., Bird, M., Bérubé, V., Rochefort, L., 2017. Effect of plant functional type on methane dynamics in a restored minerotrophic peatland. *Plant and Soil* 410, 231-246.
- 5 Strack, M., Waddington, J.M., 2007. Response of peatland carbon dioxide and methane fluxes to a water table drawdown experiment. *Global Biogeochemical Cycles* 21, n/a-n/a.
- Strack, M., Waddington, J.M., 2012. Effects of peat extraction and restoration on greenhouse gas exchange from Canadian peatlands, In: Vitt, D., Bhatti, J. (Eds.), *Restoration and Reclamation of Boreal Ecosystems*. Cambridge University Press, New York, pp. 386-403.
- 10 Strack, M., Zuback, Y.C.A., 2013. Annual carbon balance of a peatland 10 yr following restoration. *Biogeosciences* 10, 2885-2896.
- Ström, L., Mastepanov, M., Christensen, T.R., 2005. Species-specific Effects of Vascular Plants on Carbon Turnover and Methane Emissions from Wetlands. *Biogeochemistry* 75, 65-82.
- 15 Tauchnitz, N., Spott, O., Russow, R., Bernsdorf, S., Glaser, B., Meissner, R., 2015. Release of nitrous oxide and dinitrogen from a transition bog under drained and rewetted conditions due to denitrification: results from a [¹⁵N]nitrate-bromide double-tracer study. *Isotopes in environmental and health studies* 51, 300-321.
- Taylor, N., Price, J., 2015. Soil water dynamics and hydrophysical properties of regenerating *Sphagnum* layers in a cutover peatland. *Hydrological Processes* 29, 3878-3892.
- 20 Thormann, M.N., Bayley, S.E., 1997. Aboveground plant production and nutrient content of the vegetation in six peatlands in Alberta, Canada. *Plant Ecology* 131, 1-16.
- Tian, H., Lu, C., Chen, G., Tao, B., Pan, S., Grosso, S.J.D., Xu, X., Bruhwiler, L., Wofsy, S.C., Kort, E.A., Prior, S.A., 2012. Contemporary and projected biogenic fluxes of methane and nitrous oxide in North American terrestrial ecosystems. *Frontiers in Ecology and the Environment* 10, 528-536.
- 25 Tuittila, E.-S., Komulainen, V.-M., Vasander, H., Nykänen, H., Martikainen, P.J., Laine, J., 2000. Methane dynamics of a restored cut-away peatland. *Global Change Biology* 6, 569-581.
- Vanselow-Algan, M., Schmidt, S.R., Greven, M., Fiencke, C., Kutzbach, L., Pfeiffer, E.M., 2015. High methane emissions dominated annual greenhouse gas balances 30 years after bog rewetting. *Biogeosciences* 12, 4361-4371.
- Verhoeven, J.T.A., Maltby, E., Schmitz, M.B., 1990. Nitrogen and phosphorus mineralization in fens and bogs. *Journal of Ecology* 78, 713-726.
- 30 Wein, R.W., 1973. *Eriophorum vaginatum* L. *Journal of Ecology* 61, 601-615.
- Wind-Mulder, H.L., Rochefort, L., Vitt, D.H., 1996. Water and peat chemistry comparisons of natural and post-harvested peatlands across Canada and their relevance to peatland restoration. *Ecological Engineering* 7, 161-181.
- Wind-Mulder, H.L., Vitt, D.H., 2000. Comparisons of water and peat chemistries of a post-harvested and undisturbed peatland with relevance to restoration. *Wetlands* 20, 616-628.

35

Table 1. Pearson's r (correlation) between examined variables

N₂O vs.	<i>r</i>	<i>p</i>
TKN @ -75 cm	0.03	0.83
Mean Air Temperature	0.02	0.86
Mean Soil Profile Temp.	-0.11	0.74
Water Table (below surface)	0.18	0.17
TKN vs.		
Mean Air Temperature	0.07	0.60
Mean Soil Profile Temp.	-0.03	0.93
Water Table (below surface)	0.33	0.0089

5

Table 2 N₂O flux depends on Vegetation cover, Day of Year, and the interaction term

Parameter	Estimate	Standard Error	T-value	<i>p</i>
(Intercept)	0.403	0.15	2.61	0.0099
Vegetation Cover	-0.485	0.22	-2.30	0.027
Week of Year	-0.0513	0.022	-3.19	0.0016
Vegetation x WoY (interaction)	0.0656	0.022	2.92	0.0039

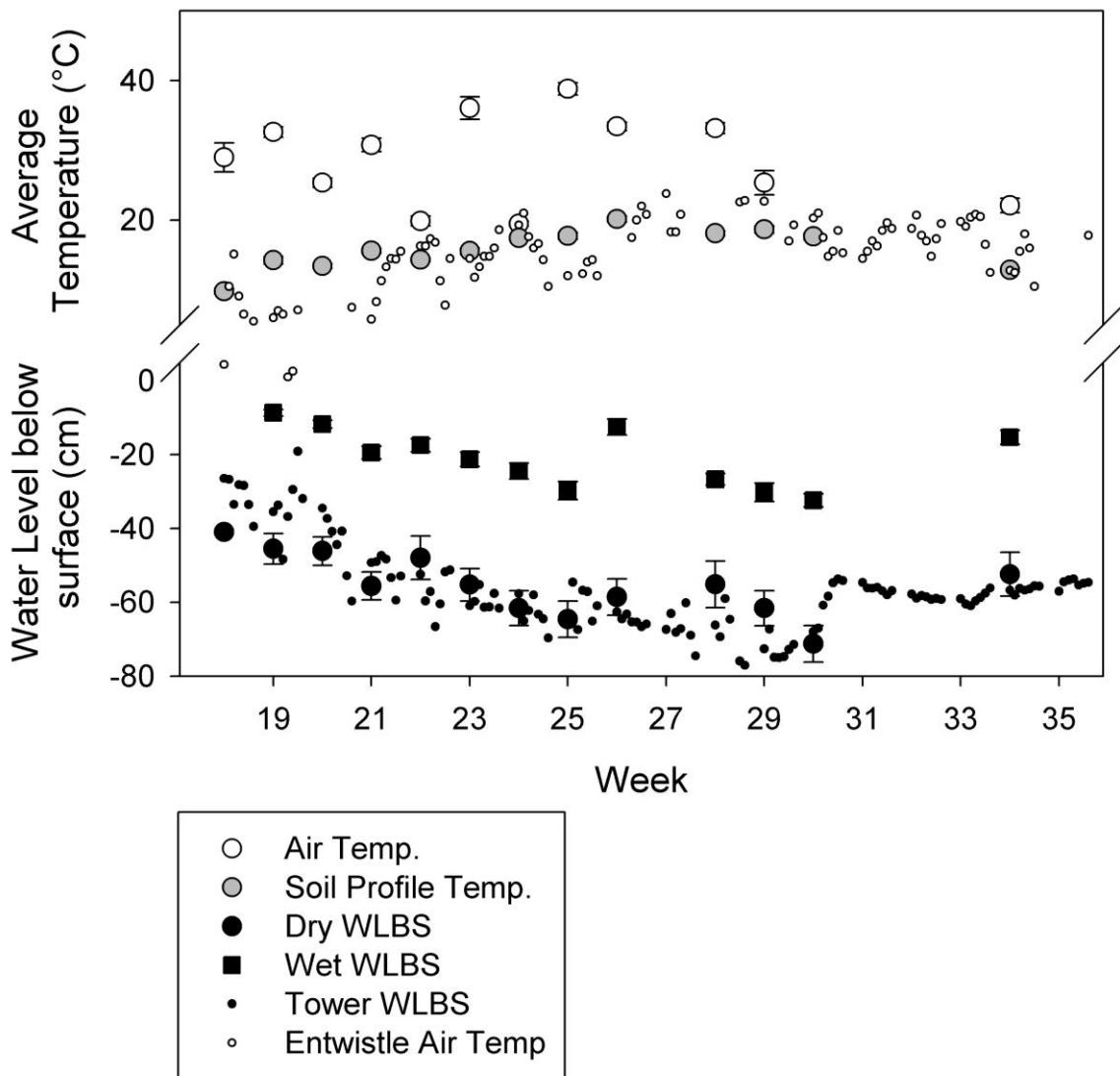


Figure 1. Water level in the dry (black circles) and wet (black squares) areas, mean air temperature (open circles), and mean soil profile temperature (-2 to -30 cm; grey circles) did not vary significantly between moss/bare and *E. vaginatum* plots; combined means \pm SE for all measurements at the study sites are presented here. The area designated as "Dry" at the beginning of the field season in early May had water levels significantly lower (t-test, $p < 0.01$) than at the area designated as "Wet" at the same time. No measurements of these parameters were made in week 10, 14, 15, or 16 (20 – 24 July, 17 August – 4 September). Small symbols show a daily record of air temperature from the Entwistle Environment Canada station, 18 km away (open circles) and water level below surface recorded by an automatic water depth logger installed in a well near a eddy-covariance tower located near the middle of the site (black circles).

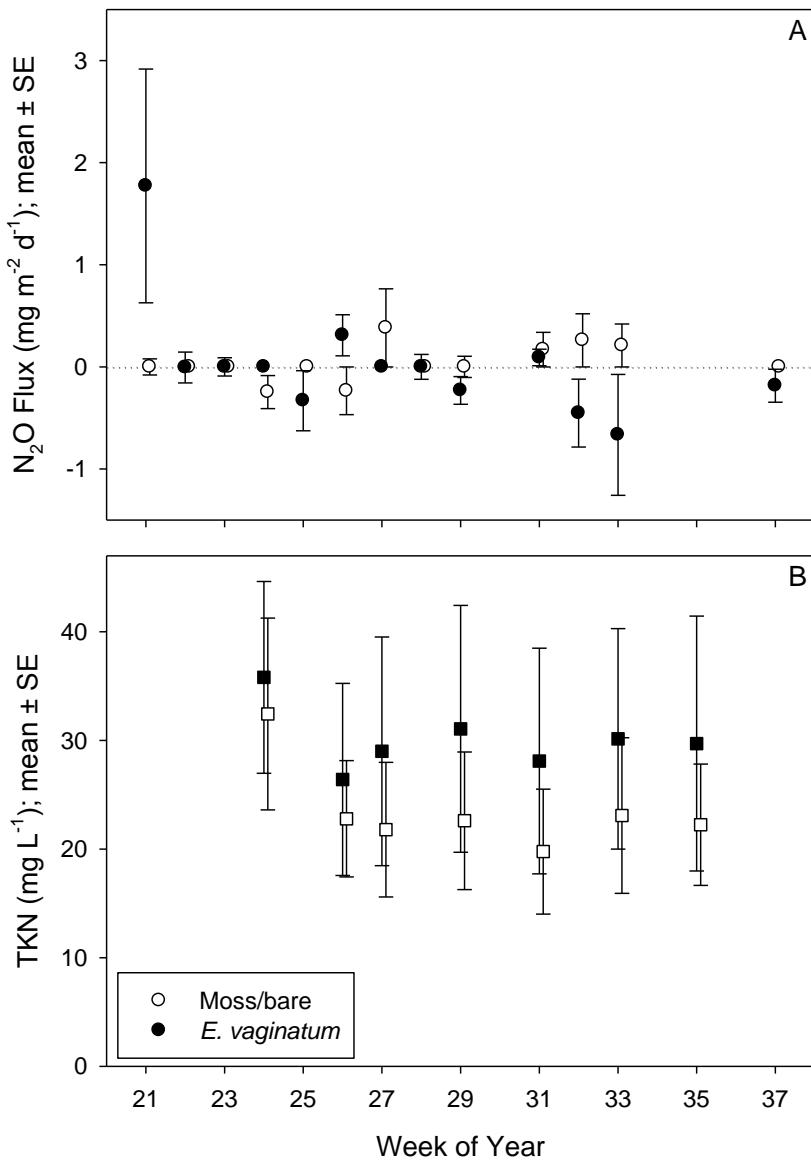


Figure 2. Flux of N_2O (A) from plots containing *E. vaginatum* (filled circles) declined over the course of the summer, but moss/bare plots without vascular plants (open circles) did not (GLM; $p < 0.01$ for interaction of vegetation cover and day of year). Total Kjeldahl Nitrogen (TKN; B) in pore water samplers at -75 cm below ground surface was high throughout the summer and was not significantly different between *E. vaginatum* and moss/bare plots (t-test, $p > 0.1$). Moss/bare symbols have been offset slightly to the right for clarity. No measurements of N_2O flux were made in week 10, 14, 15, or 16 (20 - 24 July, 17 August – 4 September).

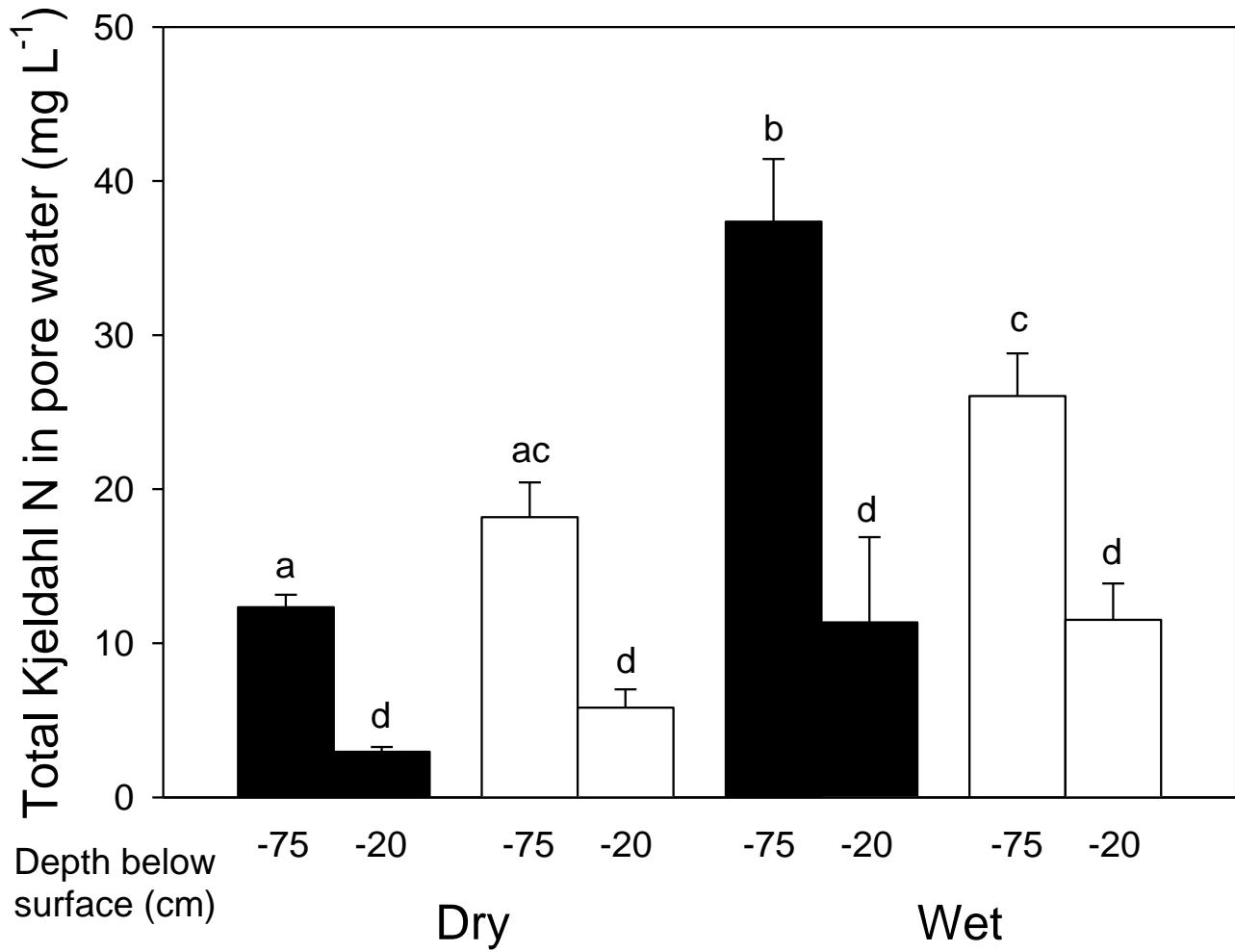


Figure 3. Total Kjeldahl nitrogen (TKN) concentrations in pore water collected from -75 cm below ground surface were significantly different, indicated by different letters (ANOVA, $p < 0.05$) among plots across the site. Light bars show mean \pm SE at moss/bare plots, dark bars show mean \pm SE at plots with *E. vaginatum*. Pore water collected from -20 cm below surface could not be collected in sufficient sample size for full analysis, with $n = 3$ for each site except Wet Moss ($n = 21$) compared to sample sizes of at least 22 for -75 cm pore water. However, t-tests indicate that shallow TKN concentrations were lower than deep TKN concentrations for each site ($p < 0.05$).

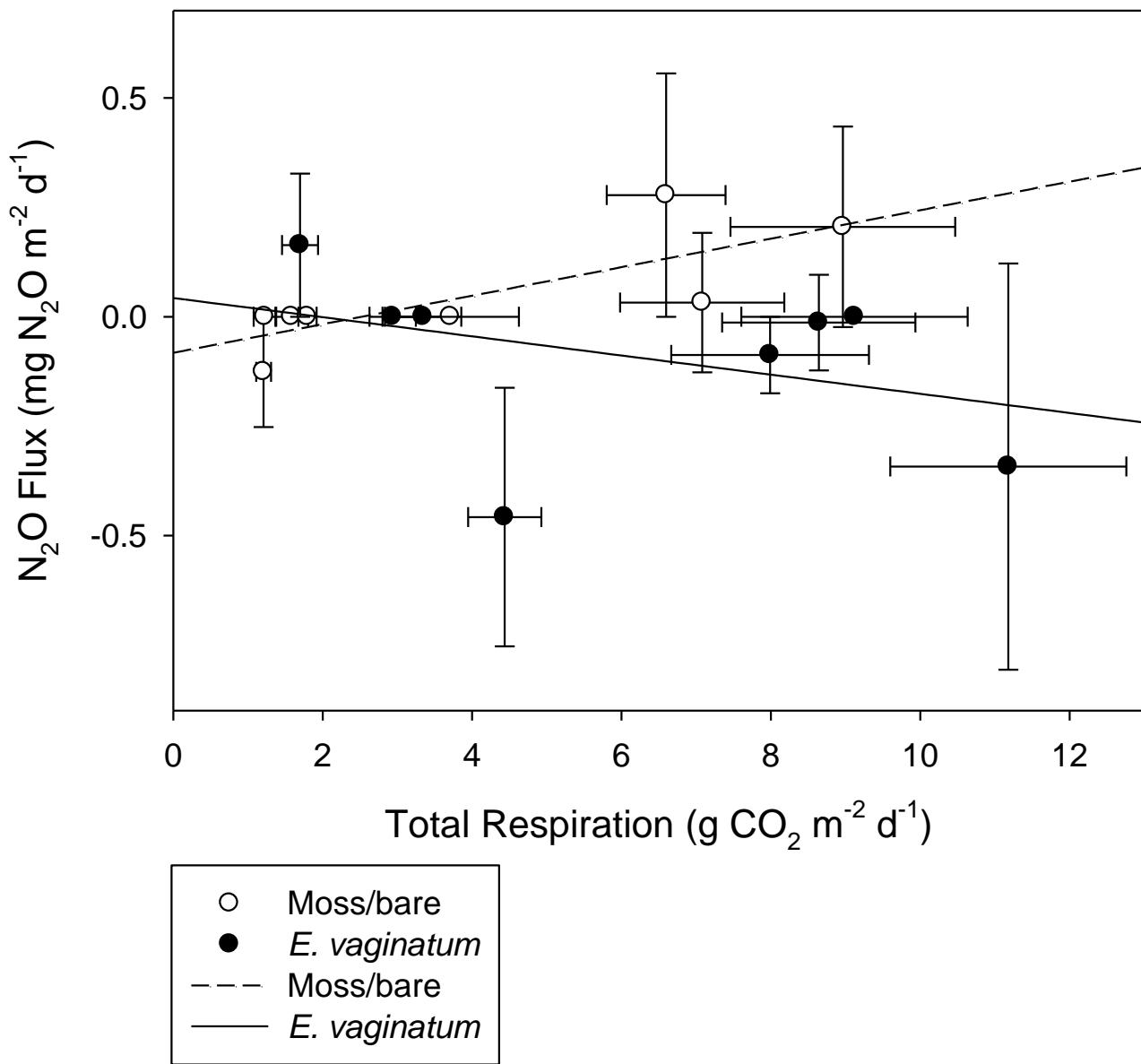


Figure 4. Net flux of N_2O increases with increasing total respiration in moss/bare plots, but the slope of that relationship is significantly less at plots containing *E. vaginatum*. The orthogonal regression of moss/bare plots is significantly different from zero ($p = 0.023$, $r = 0.78$) but is not significantly different from zero slope for *E. vaginatum* plots ($p = 0.37$, $r = -0.37$); a general linear model indicates the two slopes are significantly different from each other ($p = 0.023$). Mean \pm SE shown; some plots never showed non-zero flux of N_2O and thus have no vertical error bars.