Interactive effects of vegetation and water table depth on belowground C and N mobilization and greenhouse gas emissions in a restored peatland

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Abstract

Aims. This study assesses the relative effects of hydrology and colonization by vascular plants on belowground C and N mobilization, and emission of CO_2 and CH_4 in an extracted bog under restoration in Alberta (Canada).

Methods. A wet (high water table) and dry (low water table) area were identified at the site and plots with cottongrass (*Eriophorum vaginatum*) or bare peat were established in each area. Plant growth, peat and porewater dissolved C (DOC) and N (TDN), microbial biomass and the emissions of CO_2 and CH_4 were monitored at the plots throughout the growing season.

Results. The largest concentrations of DOC were measured in dry and bare sites. Lower E2:E3 ratios suggested a higher aromaticity of the DOC at these sites that were net sources of CO_2 and CH_4. The concentration of TDN was greater in plots with cottongrass and high water table, supporting a more abundant microbial biomass. Cottongrass dominated plots also had larger gas emissions as compared to bare plots even though they were net C sinks due to their high photosynthetic rates.

Conclusion. Maintaining a high water table is key to reducing peatland C losses. While vascular plant presence seems to prime the release of N and greenhouse gases, the inputs of C exceeded the losses and recovered the C sink function of the peatland ecosystem in the short term. Carbon inputs are maximized under high water table and plant presence.

Keywords: *Eriophorum vaginatum*, plant-soil interactions, ecosystem restoration, C cycling, N cycling, ecohydrology

Introduction

In northern peatlands interactions between plants and hydrological conditions are responsible for the long-term accumulation of large amounts of undecomposed organic matter. In this way, peatlands store one third (545 Gt) of the global soil C stock, despite representing only 3 % of the world's land area (Gorham 1991). Recent studies by Nichols and Peteet (2019) double this estimate to 1,055 Gt of C. Extraction of peat for horticultural purposes alters ecohydrological conditions through drainage and removes the vegetation cover and surface layers of peat. Exposure of peat to aerobic conditions after drainage triggers decomposition, increasing the concentration of dissolved organic C (DOC) and dissolved organic N (DON) in porewater (Frank et al. 2014; Peacock et al. 2015) thereby driving the loss of C through aquatic exports (Evans et al. 2016). Discharge of excess amounts of these compounds has a negative impact on aquatic ecosystems, as it increases microbial activity and oxygen consumption, affects metal mobility and availability (Porasso et al. 2002; Brooks et al. 2007), colours water, and results in the production of potentially carcinogenic compounds when drinking water is chlorinated (e.g.,Min and Min 2016). Furthermore, DOC is a substrate for methane (CH_4) formation and could lead to increased in situ emissions of this potent greenhouse gas. A large portion of the DOC might eventually be released to the atmosphere as carbon dioxide (CO_2) either within the peatland or in watercourses (Evans 2015). Thus, peat

extraction transforms peatlands from sinks into net sources of C, contributing to the increase in atmospheric greenhouse gases and potentially global warming (Strack and Waddington 2012; IPCC 2014).

Recovery of the peat accumulation and C sequestration function of these ecosystems could be achieved though the restoration of the initial conditions, that would slow down peat decomposition and increase C inputs (i.e., hydrology and vegetation cover). Peat rewetting alone, even if it allows for the restoration of anaerobic conditions, may not to be enough for the slowdown of decomposition rates and the recovery of the original peat accumulation and fluxes of greenhouse gases, at least in the short term (Jordan et al. 2016; Lazcano et al. 2018). A decrease in DOC and DON production after rewetting would be expected if decomposition rates decrease; yet, rewetting has contrasting effects on the quantity and quality of the dissolved organic matter (Urbanová et al. 2011; Frank et al. 2014; Strack et al. 2015), and some studies show a short-term increase in DOC concentration immediately after restoration (Wilson et al. 2011; Strack et al. 2011; Evans et al. 2018). Restoration effects on DOC production might depend on several factors such as the state of peat degradation, the magnitude of the fluctuations in the water table depth, or the type and abundance of the vegetation cover (Kalbitz and Geyer 2002; Zak and Gelbrecht 2007; Cabezas et al. 2012; Armstrong et al. 2012; Strack et al. 2015; Robroek et al. 2016; Del Giudice and Lindo 2017; Mastný et al. 2018).

The moss layer transfer technique of peatland restoration (Quinty and Rochefort 2003) incorporates the re-establishment of the original *Sphagnum*-dominated vegetation

88 cover as a way of promoting the peat accumulation and C sink function. This involves
89 the introduction of donor vegetation material from a nearby undisturbed site,
90 protection of the introduced moss propagules with straw mulch, fertilization, and
91 blocking of the drainage ditches in order to provide suitable ecohydrological conditions
92 for plant survival and establishment (Rochefort et al. 2003). In addition to *Sphagnum*
93 mosses, restoration typically encourages the establishment of naturally occurring
94 vascular plant species that regenerate from the local seed bank or are introduced with
95 the donor material. This includes a group of acidophilic plant species such as cottongrass
96 (*Eriophorum vaginatum*), one of the most commonly occurring vascular species in
97 extracted and restored peatlands (Waddington et al. 1996; Tuittila et al. 1999; Lavoie et
98 al. 2003, 2005; Silvan et al. 2004).

99 While vascular plant regrowth takes place relatively quickly (within months) after
100 restoration through the moss layer transfer technique, the establishment of a
101 *Sphagnum* moss carpet may take years (Rochefort et al. 2016). Therefore, this
102 restoration technique successfully recovers peatland hydrology while, at least in the
103 short term, vegetation cover differs substantially from what is expected for a peat-
104 accumulating ecosystem, potentially having unintended consequences for C and N
105 fluxes. In order to ensure the success of the restoration process, it is important to
106 determine the effects of vascular plants on the C accumulation potential of the restored
107 peatland.

108 Due to their fast growth, larger C assimilation rates and large aerial biomass as
109 compared to bryophytes (Ward et al. 2009), vascular plants could represent a valuable

alternative to increase peatland C inputs in the short term, through litter inputs, while the *Sphagnum* mosses become established (Graf and Rochefort 2009). Furthermore, observations suggest that plants like cottongrass may facilitate the growth of peat-forming *Sphagnum* mosses after restoration which drives peat and C accumulation (Tuittila et al. 2000), although some studies have found otherwise (Lavoie et al. 2005). Alternatively, other studies show that large C outputs and changes to short term C fluxes have also been associated with certain vascular plants via CO_2 and methane (CH_4) emissions or DOC exports (Crow and Wieder 2005; Mahmood and Strack 2011; Armstrong et al. 2012). These higher C outputs could be explained by differences in the quality of the C inputs, either through the higher decomposability of the fresh C inputs through vascular plant litter as compared to *Sphagnum* mosses (Del Giudice and Lindo 2017; Mastný et al. 2018), but also through the release of labile C compounds by root exudation. Peatland plants allocate a larger portion of the recently assimilated C to root exudation as a mechanism to increase nutrient uptake in these typically nutrient-poor environments (Trinder et al. 2008; Edwards et al. 2018).

The low molecular weight, labile C compounds found in root exudates are likely to have a direct effect on the soil microbial community, increasing microbial activity and triggering decomposition of the residual peat and further increasing the release of dissolved organic C and N (Basiliko et al. 2012; Robroek et al. 2016). Furthermore, the presence of vascular plants with aerenchyma, can also enhance CH_4 emissions by enhancing transport of this gas from anoxic layers to the atmosphere (Marinier et al. 2004; Bhullar et al. 2013).

While the effects of spontaneous colonization by *E. vaginatum* on the CO_2 and CH_4 emissions from restored peatlands are well studied (Tuittila et al. 1999; Marinier et al. 2004), it is not yet clear whether these emissions could be directly caused by belowground C and N mobilization. Previous studies show that cottongrass presence can lead to a significant change in C and N fluxes in peatlands restored through the moss layer transfer technique, yet these effects are usually confounded with the effects of water table depth (Järveoja et al. 2016). While water table depth and soil moisture can control above and belowground vascular plant growth (Murphy and Moore 2010), and consequently the quality and quantity of C inputs, it also strongly controls microbial activity and decomposition. Therefore it is important to understand to what extent water table depth has a role in modulating DOC, CO_2 and CH_4 emissions, or may be a stronger driver than the presence of *E. vaginatum*. Previous studies addressing this question have artificially manipulated plant cover by clipping and removing aboveground biomass (Waddington et al. 1996; Greenup 2000; Marinier et al. 2004; Ward et al. 2009; Kuiper et al. 2014; Gavazov et al. 2018) or studied the effects of water table depth in core mesocosms (Dinsmore et al. 2009). Here we took advantage of the field characteristics and sparsely distributed cottongrass tussocks to design a study that allowed us to separately observe the effects of cottongrass and water table depth on belowground peat decomposition using DON and DOC, without disturbing the ecosystem. We used DOC and DON in porewater and peat extracts to understand the drivers of CH_4 and CO_2 emissions under the different conditions. The aims of this study were (i) to determine the role of spontaneous colonization by the vascular plant *E.*

154 *vaginatum* on peat decomposition and belowground C and N mobilization two years
155 after restoration of a boreal bog, (ii) to determine the consequences of belowground C
156 and N mobilization for the fluxes of greenhouse gases and C sequestration potential,
157 and (iii) to study the relative importance of vascular plant presence versus hydrology as
158 controls of C and N dynamics post restoration. We hypothesized that the presence of *E.*
159 *vaginatum* would increase peat decomposition, microbial biomass and belowground
160 available C compounds, regardless of the water table depth, therefore leading to larger
161 CO_2 and CH_4 emissions and reducing the C accumulation potential of the restored
162 peatland.
163
164 **Material and Methods**
165 *Study site*
166 This study was carried out in a restored bog at Seba Beach, 100 km west of
167 Edmonton, Alberta, Canada (53° 33' N, 114° 44' W). This site was extracted for
168 horticultural purposes by Sungro Horticulture, Canada Ltd. for 12 years and restored
169 using the moss layer transfer technique (Quinty and Rochefort 2003). Briefly, the
170 surface was levelled and interior ditches completely filled with peat. *Sphagnum* and
171 other plant propagules were transferred from a nearby donor ombrotrophic bog and
172 spread at a 1:10 ratio of area, fertilized with phosphate rock (150 kg ha^{-1}) and covered
173 with straw mulch; finally, perimeter drainage ditches were blocked with peat dams to
174 recover original hydrological conditions. Restoration started in winter of 2012 with
175 completion in spring and early summer of 2013.

In 2015, two years after restoration, the site had abundant vegetation cover, including bryophytes such as *Sphagnum* mosses and *Polytrichum strictum*, and graminoids such as *E. vaginatum* (cottongrass), *Agrostis scabra* (tickle grass), *Calamagrostis canadensis* (blue-joint), and *Carex canescens* (silvery sedge). In addition, the site showed a concave profile which resulted in two distinct sites according to the prevailing water table depth: (i) a 'wet' site in the center of the peatland characterized by higher water table and therefore higher soil moisture and a (ii) a 'dry' site, towards the edge of the peatland characterized by lower average water table and therefore lower soil moisture. *E. vaginatum* was the only vascular plant species that was abundant in these two areas, and therefore it was considered as a good model to study the effects of vascular plants on peat and porewater biochemical properties across different soil moisture conditions.

Study design

We selected eight 60 x 60 cm plots with cottongrass and eight adjacent plots with no cottongrass or other vascular plants covering more than 1% of the surface at the time of plot establishment; in some bare plots, vascular plants did grow after plot establishment but were removed by clipping the shoots at the soil surface before reaching heights greater than 5 cm or coverage greater than 5% within the plot. Plots were distributed across the restored site, with four pairs in the 'wet' and four pairs in the 'dry' area. Boardwalks were installed next to each plot to reduce disturbance during measurements. While we do not have data on conditions in 'wet' and 'dry' areas prior to peat extraction, removal of vegetation and at least 50 cm of near surface peat likely

198 resulted in a similar substrate of highly decomposed Sphagnum peat prior to restoration
199 and the establishment of the present study.

200 Water samplers were installed at 75 cm depth next to each plot to study
201 porewater chemistry. Samplers were installed at this depth to ensure saturated
202 conditions throughout the summer period, even when water tables dropped in the dry
203 site, this depth was below the root zone for dry and wet plots (Figure S1). Porewater
204 samplers consisted of 30 cm length and 2.5 cm diameter PVC pipe perforated at regular
205 intervals for sample collection. Samplers were covered in mesh to prevent clogging and
206 sealed at both ends with stoppers. Tygon tubing was inserted at the top, fitted with a
207 three-way valve, and extended above the surface of the peat to enable collection of
208 water with a syringe (Mahmood and Strack 2011; Brummell et al. 2017). Porewater
209 samples were collected biweekly at 75 cm over the growing season (May-September). In
210 August 2015, we collected peat samples at each of the plots at three depth intervals (0-
211 5, 5-25 and 50-75 cm) with the use of a soil auger (AMS Inc., American Falls, ID, USA).

212 *Analysis of peat and porewater samples*

213 Water samples were stored on ice immediately after collection and transported
214 to the laboratory where they were filtered within 48 h through 0.4 μm borosilicate glass
215 fiber filters (Macherey-Nagel GmbH & Co. KG, Düren, Germany). Samples with high
216 particulate load were first pre-filtered using 1.5 μm borosilicate glass fiber filters and
217 then passed through the 0.4 μm filter.

218 Peat samples collected at the restored and unrestored sites were immediately
219 separated into subsamples for further analysis. Peat moisture content was determined

gravimetrically in a 20 g subsample. A 5 g (fresh weight) peat subsample was used to prepare water extracts that were used for the analysis of peat DOC and Total Dissolved N (TDN). Peat samples were shaken with 40 mL of deionized (DI) water for one hour at 120 rpm (Guigue et al. 2014), centrifuged and subsequently filtered through 0.4 µm borosilicate glass filters.

Dissolved organic C concentration of the peat water extracts and porewater samples was determined using a total carbon analyzer (Shimadzu 680) using the non-purgeable organic carbon method. Samples were diluted 1:10 with DI water prior to analysis. Absorbance at different wavelengths (250, 254, 365, 400, 465 and 665 nm) was measured on the peat water extracts and porewater samples using a UV–Vis Spectrophotometer (Perkin Elmer 3B Lambda). Samples were diluted 1:1 with DI water prior to spectrophotometric analysis. Spectrophotometric ratios were used as proxies of the molecular size and aromaticity of the C compounds present in the water samples (Peacock et al. 2014). The ratio between absorbance at 465 and 665 nm (E4:E6) is negatively correlated with DOC molecular size (Summers et al. 1987) and has been previously used to evaluate humification degree (Grayson and Holden 2012). The ratio between absorbance at 250 and 365 nm (E2:E3) is negatively correlated with aromaticity and molecular weight (Peuravuori and Pihlaja 1997; Helms et al. 2008). Specific ultraviolet absorbance at 254 nm ($SUVA_{254}$), was calculated as the ratio between absorbance at 254 nm and DOC concentration of the water samples and was used as a proxy for aromaticity of the C compounds (Peacock et al. 2014).

241 Total dissolved nitrogen concentration of pore water samples was determined
242 using standard methods based on EPA 351.1. Briefly, H_2SO_4 was added to subsamples of
243 collected pore water to adjust to pH < 2. Acidified samples were digested in
244 concentrated H_2SO_4 with $MgSO_4$ to reduce organic nitrogen species to ammonium; total
245 ammonium concentrations were determined colorimetrically. In peat samples, TDN was
246 determined in water extracts of the 5 g subsamples by using a Shimadzu 680 CN
247 analyzer.
248 Microbial biomass C (MB-C) was assessed in the fresh peat samples by using the
249 chloroform fumigation extraction method (Vance et al. 1987). Briefly, 5 g peat sub-
250 samples were fumigated with chloroform for 48 h to lyse the microbial cells and release
251 the C contained in them. Subsequently, fumigated and non-fumigated sub samples were
252 extracted with 40 mL of 0.5 M K_2SO_4, and filtered first through a 1.5 µm borosilicate
253 glass prefilter and then through a 0.4 µm borosilicate glass filter. Samples were diluted
254 to a 1:10 ratio with 18 mL of DI water and analyzed for TOC using the total carbon
255 analyzer (Shimadzu 680) as described above. Microbial biomass C was calculated as the
256 difference in TOC between fumigated and non-fumigated samples.
257
258 *Greenhouse gas measurements*
259 Fluxes of CH_4 and CO_2 were measured weekly at each plot from 11 May until 7
260 September 2015 using static chambers. Static chambers consisted of 60 x 60 cm steel
261 collars inserted 15-20 cm into the soil one week before the first sampling and left in
262 place throughout the study, plus an opaque or clear lid, depending on the gas sampled.

263 To measure CH_4 flux, an opaque plastic chamber (60 × 60 × 30 cm) containing a battery-
264 driven fan was placed over the collar and 20 mL samples of internal air were withdrawn
265 at regular time intervals (5 min, 15 min, 25 min, and 35 min) using a syringe, and
266 injected into a previously-evacuated 12 mL Exetainer (Labco Ltd. Lampeter, UK).
267 Chamber gas concentrations were converted to mass per volume units assuming ideal
268 gas relations using chamber air temperature values. Fluxes (mg CH_4 m^{-2} d^{-1}) were
269 calculated from the linear change in chamber CH_4 concentration over time, taking into
270 account chamber volume and soil surface area. If the pattern of concentration did not
271 consistently increase or decrease over time or jumped suddenly indicating potential
272 ebullition, the flux value was not used except in cases where the slope was not
273 significantly different from zero indicating a non-detectable, low flux. Other than these
274 low fluxes, values were accepted if the R^2 values of the linear regression between
275 sampling time and sample concentration were equal to or greater than 0.80. The
276 majority of fluxes (77%) were scored as net zero, with approximately 20% of
277 measurements showing significant positive or negative flux. Only 3% of the
278 measurements were discarded due to suspected ebullition or other problems during
279 chamber measurements. We conducted measurements of net CO_2 exchange following
280 the methods of Strack and Zuback (2013). To measure net ecosystem exchange of CO_2
281 (NEE), a transparent acrylic chamber (60 × 60 × 30 cm), equipped with a battery-
282 powered fan to mix the internal air, was placed on to each collar and the concentration
283 of CO_2 inside the chamber was recorded using an EGM-4 infrared gas analyser (IRGA; PP
284 Systems Amesbury, MA, USA) every 15 s over 2 min. Flux was determined as the linear

285 change in CO_2 concentration over time correcting for chamber volume and ambient
286 temperature as recorded with a thermocouple inserted into the chamber. Together with
287 flux measurement, photosynthetically active radiation (PAR) was measured with a
288 quantum sensor connected to the infrared gas analyzer. The chamber was subsequently
289 covered with a dark tarp to determine ecosystem respiration (ER) under complete
290 darkness. Gross ecosystem photosynthesis (GEP) was calculated from the difference
291 between NEE and ER.

292 *Assessment of ecohydrological characteristics*

293 Water table position was measured weekly between May and September in a
294 2.5 cm diameter standpipe with holes drilled approximately every 2 cm to allow water
295 level in the pipe to equilibrate with soil water level, inserted into the peat adjacent to
296 each plot to a depth of 1 m.

297 At the end of the growing season, in September 10th 2015, *E. vaginatum* shoots
298 adjacent to the gas sampling collars and close to the porewater samplers were clipped
299 at the soil surface and subsequently dried for one week at 60 °C for dry mass
300 determination. A significant quadratic relationship was found between shoot biomass
301 and tussock diameter (Figure S2, $R^2 = 0.95$, $p < 0.005$), and shoot biomass within the
302 collars was estimated non-destructively by measuring tussock diameter. Percentage
303 cover by other vascular plant species, mosses, bare peat and straw mulch was visually
304 estimated for each plot in August 2015. Root biomass density was determined by hand
305 sorting in peat subsamples collected at the different depth intervals used for soil
306 analysis (i.e., 0-5, 5-25 and 50-75 cm).

307 *Data analysis*

308 The effects of cottongrass presence, water table position (dry vs. wet plots) and
309 sampling depth on the biochemical properties of the peat and porewater samples were
310 analyzed through ANOVA and general linear mixed models. For those variables
311 measured multiple times over the growing season (porewater DOC concentration and
312 spectrophotometric ratios, CO_2 and CH_4 fluxes), repeated measures mixed models were
313 used with 'cottongrass presence' and 'moisture' as fixed factors, 'plot' as the main
314 subject and 'sampling date' as a within-subjects factor. Effect sizes are reported as Eta
315 Squared (η). Post-hoc comparisons were performed using Tukey HSD tests.
316 Relationships between porewater chemistry and gas fluxes or peat properties were
317 investigated using pairwise Pearson's correlations. A principal component analysis (PCA)
318 was carried out to summarize the results obtained in the analysis of belowground
319 biochemical variables, gas emissions and plant biomass. Two principal components (PC1
320 and PC2) were used for this analysis. Data was tested for normality by Kolmogorov
321 Smirnov criteria and transformed when necessary by using natural logarithm (ln) and
322 square root transformations to reach normality. Data analysis was carried out using SAS
323 (SAS Institute, Cary, NC, USA) and SPSS V 20.0 (IBM Corp., NY, USA) software programs.

324

325 **Results**

326 *Ecohydrological characteristics*

327 As predicted, average water table position throughout the season was
328 significantly lower for dry plots than for wet plots regardless of the presence of

cottongrass (Table 1, Moisture: $F = 173.27$, $p < 0.001$). In cottongrass plots, aboveground biomass was 1.5 times larger in the wet than in the dry plots, although these differences were not significant (Table 1, Moisture: $F = 3.9$, $p = 0.07$). Similarly, percent coverage by cottongrass was larger in plots with cottongrass although total cover depended on the soil moisture at the plots, with cottongrass in wet plots being twice as high as dry plots (Table 1, cottongrass*moisture: $F = 17.5$, $p = 0.0013$). Percent coverage by *Polytrichum* was similar across plots regardless of the cottongrass presence ($F = 0.45$, $p = 0.513$) or moisture ($F = 3.07$, $p = 0.105$), and the coverage by vascular species other than cottongrass was negligible across all plots except for wet plots with cottongrass, where they had to be manually removed through the study (Table 1, Moisture*cottongrass, $F = 33.68$, $p < 0.001$). Belowground root biomass density was larger in wet plots with cottongrass than in the rest of the plots (Table 1, Moisture*cottongrass: $F = 9.3$, $p = 0.003$) and plots with cottongrass (Table 1, $F = 10.8$, $p = 0.002$), irrespectively of the peat moisture.

Porewater chemistry

The concentration of total dissolved nitrogen (TDN) in porewater was significantly larger in wet plots with the presence of cottongrass plants (Figure 1, moisture $\times$ cottongrass, $F = 6.21$, $p = 0.014$) being three times larger than dry plots without cottongrass. The trend was the opposite for dissolved organic C (DOC, Figure 2a). The depth of the water table but not the presence of cottongrass had a significant effect on the concentration of DOC in porewater (Figure 2a). Dry plots had significantly higher concentrations of DOC in porewater (Moisture: $F = 7.16$, $p = 0.008$). Among dry

plots, those that did not have cottongrass growing on them and that were mostly bare had the highest DOC levels, particularly towards the end of the season (Figure 2a); however, this was not significant (moisture × cottongrass: $F = 3.58$, $p = 0.06$).

No significant differences were found in $SUVA_{254}$ across plots with different water table levels (Figure 2b, $F = 1.53$, $p = 0.21$) or cottongrass presence (Figure 2b, $F = 0.01$, $p = 0.89$), and similar results were observed for the E4:E6 ratio (Figure S3, Moisture: $F = 2.25$, $p = 0.13$; Cottongrass: $F = 0.32$, $p = 0.13$). The E2:E3 ratio was significantly lower in drier plots without cottongrass (Figure 2c, moisture × cottongrass: $F = 4.26$, $p = 0.041$) indicating a higher aromaticity as compared to the rest of the plots.

Peat chemistry

The biochemical properties of the C and N compounds in the peat water extracts showed significant changes with depth (Table 2). Similar to what was observed for porewater, the concentration of DOC in peat samples water extracts was significantly higher in dry plots with a deeper water table depth (moisture: $F = 7.57$, $p = 0.009$), but it was particularly higher in the top layer (0-5 cm) as compared to the deeper layers of the peat profile (Table 2; Depth: $F = 4.46$, $p = 0.018$). Differences in peat moisture and depth, accounted for 13.2% and 13.3% of the total sample variability respectively ($\eta = 0.132$ and $\eta = 0.133$).

Significant changes in quality of the DOC were also observed with peat depth, as shown by the spectrophotometric indexes although in most cases this depended on water table depth and cottongrass presence. For instance, the $SUVA_{254}$ was significantly higher at 75 cm than at 5 and 25 cm depth in wet plots with cottongrass presence,

indicating a higher recalcitrance of the organic compounds at depth (Table 2, depth x moisture x cottongrass: $F = 6.72$, $p = 0.003$, $\eta = 0.09$). In dry plots E4:E6 ratio decreased with depth (Table 2, depth x moisture: $F=8.25$, $p=0.001$, $\eta = 0.22$). Similarly, the E2:E3 ratio decreased with peat depth, although differences were stronger in plots with deeper water table or cottongrass presence (Table 2, depth x moisture x cottongrass: $F = 6.76$, $p = 0.003$, $\eta =0.045$). Larger concentrations of TDN in peat water extracts was measured in the deeper layers of the wet plots, regardless of the presence of cottongrass (Table 2, depth*moisture: $F = 4.10$, $p = 0.025$, $\eta = 0.096$).

Microbial biomass C in peat samples showed larger concentrations in the top layer (0-5 cm) as compared to the deeper layers of the peat profile. This change with depth was strongest in wet plots (Table 2, moisture x depth: $F = 4.56$, $p = 0.017$), which had the highest microbial biomass in the 0-5 cm peat layer. Changes in depth explained 64.5% ($\eta = 0.645$) of the variability in microbial biomass among the samples, while changes with depth and moisture explained only 5.3% ($\eta = 0.053$). Microbial biomass C was significantly and positively correlated to plant root density in the peat samples as well as to E2:E3 ratio (Table 3). Furthermore, higher microbial biomass was weakly associated to lower TDN concentration in the peat (Table 3).

Greenhouse gas exchange

The net ecosystem exchange of atmospheric CO_2 (NEE) was stronger (i.e., larger sink function) in wet plots with cottongrass presence (moisture x cottongrass: $F = 5.74$, $p = 0.0178$, Figure 3a), indicating higher assimilation of C. Carbon assimilation through photosynthesis (i.e., gross ecosystem productivity or GEP) peaked in early July and

decreased subsequently towards the end of the growing season (Figure 3b). Gross ecosystem productivity remained low (near zero C assimilation) in dry plots without cottongrass, but was stronger in wet plots without cottongrass, apparently due to the growth of moss and also other vascular plant species at this site, despite efforts to remove vascular plants from no-plant plots during the study period.

Overall, ecosystem respiration (ER) was higher in wet plots as compared to dry plots (Figure 3c; moisture, $F = 122.13$, $p < 0.001$), and in plots with cottongrass as compared to plots without cottongrass, irrespectively of the water table depth (cottongrass, $F = 10.52$, $p = 0.001$). No significant correlations were found between ecosystem respiration and water table position ($p = 0.07$) or porewater DOC ($p = 0.33$). Nevertheless, ER was significantly and positively correlated to TDN concentration in porewater ($p = 0.038$), although this correlation was weak (Figure S4; $R = 0.26$).

Emissions of CH_4 were significantly higher in the presence of cottongrass (cottongrass: $F = 6.43$, $p = 0.012$; Figure 4) and were not affected by the depth of the water table at the different sites (moisture: $F = 0.34$, $p = 0.56$). No significant correlations were found between the average daily flux of CH_4 and water table position ($p = 0.09$), porewater DOC ($p = 0.95$) or GEP ($p = 0.45$). However, CH_4 emissions were positively correlated to the aboveground cottongrass biomass (Figure S5, R= 0.0.56, $p = 0.0241$).

Summary of belowground available C and N and greenhouse gas emissions as affected by water table and plant presence

The principal component analysis (PCA) performed on the average seasonal values of the biochemical properties of porewater and peat water extracts, microbial biomass, plant biomass (above and belowground), and gas emissions (CO_2 and CH_4), explained 48.7% of the total sample variability (Figure 5). PC1 explained 31.2% of the sample variability and the main variables associated to the differences between samples along this component were NEE, GEP, ER, aboveground plant biomass, microbial biomass and $SUVA_{254}$ in peat water extracts. Plots with cottongrass presence and high water table separated clearly along PC1 and were characterized by higher plant biomass and lower (more negative) GEP and NEE, involving higher C inputs. These plots also had higher microbial biomass and $SUVA_{254}$ in peat water extracts. PC2 explained 17.5% of the sample variability and changes along this component were strongly associated to changes in DOC both in peat extracts and porewater, CH_4 fluxes and E4:E6 of the porewater samples. Differences between plots along this component were weaker, although peat and porewater DOC concentrations clearly differentiated dry from wet plots, and CH_4 emissions differentiated plots with cottongrass from plots without cottongrass.

Discussion

Two years after restoration through the moss layer transfer technique, the growth of *Sphagnum* mosses was minimal, with most of the peatland surface either being bare or covered by vascular plants, among which cottongrass dominated. We determined the effects of vascular plant cover and water table depth in belowground C

438 and N mobilization that could drive losses of C and N as water exports or GHG
439 emissions. For this, we analyzed the actual concentration in porewater and potential
440 release of DOC and TDN in peat water extracts. Porewater is influenced by peatland
441 hydrology and environmental factors, like rain events or the lack of thereof, thereby
442 resulting in dilutions, concentrations and transformations of the DOC in situ. On the
443 other hand, peat water extracts are a measure of peat degradability and show what
444 could potentially be released to the groundwater independently of dilution effects of
445 precipitation. We observed interactive effects of vegetation and hydrology in DOC, TDN
446 and GHG exchange (Figure 5). Vascular plant presence and aboveground biomass was
447 strongly associated with CH_4 and CO_2 fluxes (ER, GEP and NEE), while low peat moisture
448 (especially in the absence of plants) controlled belowground DOC mobilization.

449 Overall, DOC concentration in porewater at the restored site (60-245 mg L^{-1}) was
450 higher than previous studies in restored peatlands (23–150 mg L^{-1}; Strack et al. 2011,
451 2015; Lou et al. 2014). In particular, DOC concentrations in porewater were higher at
452 the dry sites irrespective of plant cover, suggesting greater peat degradation. This was
453 confirmed by the analysis of the DOC concentration in the peat samples collected at
454 different depths, which also had higher DOC in dry sites, particularly in the upper part of
455 the peat profile, where peat remained dry for the whole period. The higher E4:E6 of the
456 peat DOC suggests a lower molecular size of the C being released from the peat
457 suggesting that it could be further decomposed more easily; however, the observed
458 accumulation in situ, presumably indicates a decrease in microbial activity.

459 Increases in peat decomposition and porewater DOC concentration after water
460 table draw down have been previously observed across different natural and degraded
461 peatlands (Frank et al. 2014; Lou et al. 2014; Strack et al. 2015; Armstrong et al. 2015).
462 Higher temperature (Lou et al. 2014; Dieleman et al. 2016), exposure to light (Doane et
463 al. 2019), oxygen concentrations, enzyme production and overall microbial activity,
464 foster the increase in organic matter decomposition rates (Holden 2005), leading to
465 increased DOC production (Strack et al. 2011) and increased CO_2 efflux from soils
466 (Leiber-Sauheitl et al. 2014). Nevertheless, the lower microbial biomass and respiration
467 observed in dry bare plots as compared to wet bare plots, suggest that DOC
468 mineralization and CO_2 efflux could be limited, presumably by moisture availability. In
469 addition, the lower concentrations of available N in dry and bare plots indicate a
470 nutrient limitation that could reduce microbial growth and decomposition. Therefore,
471 higher concentration of DOC at these sites could be the result of accumulation due to
472 lower consumption rates as compared to wet plots, where conditions are favorable for
473 mineralization. In spite of the low ecosystem respiration, dry and bare plots still acted as
474 net sources of CO_2 due to the lack of vegetation cover, and hence low GEP.
475 The presence of cottongrass tussocks clearly contributed to increased C
476 sequestration, particularly in wet plots, as shown by greater CO_2 uptake as GEP and NEE.
477 Similar effects of vascular plants in NEE under varying peat moisture have been
478 observed previously in plant removal experiments (Kuiper et al. 2014). Part of the newly
479 sequestered C allocated belowground as root biomass and root exudates, could have
480 contributed to the DOC measured in the peat and porewater samples. This labile source

481 of C most likely fueled the increase in microbial biomass observed in wet plots with
482 cottongrass, as reflected in the positive correlation between microbial biomass C and
483 E2:E3 ratio, indicative of low molecular weight compounds. A more abundant and active
484 microbial community in plots with shallow water table and cottongrass presence, most
485 likely supported a rapid cycling of the newly fixed C, increasing the concentration of
486 available N that could be leached to 75 cm depth as sampled in the field and possibly
487 contributing to the production of CH_4 and CO_2 (Crow and Wieder 2005). Nevertheless,
488 the higher $SUVA_{254}$ of DOC at depth could indicate an accumulation of high molecular
489 weight peat C in plots with high water table and cottongrass presence, suggesting the
490 priming of microbial decomposition of peat C (Gavazov et al. 2018) or the consumption
491 of the lower molecular weight compounds in these areas of the peatland. In contrast,
492 the negative correlation between microbial biomass C and TDN from the peat samples
493 indicates N immobilization, particularly in the near-surface.

494 Cottongrass presence also played a clear role on the emissions of CH_4, which
495 were uniquely and strongly controlled by the presence of this vascular plant species.
496 Larger CH_4 emissions in the presence of cottongrass have been previously described in
497 restored peatlands (Marinier et al. 2004; Cooper et al. 2014), yet the relative
498 importance of peat moisture when cottongrass is present in the production and release
499 of this greenhouse gas has received little attention (Tuittila et al. 2000). In this study, we
500 observed that plots with this cottongrass presence had a CH_4 efflux that was 17% and
501 59% larger than plots without cottongrass in the dry and wet sites, respectively.
502 Therefore, even though the presence of this vascular plant seemed to be the main

503 driver of the emissions, moisture further stimulated the release of CH_4 (Tuittila et al.
504 2000).

505 Methane efflux is the result of the balance between production
506 (methanogenesis) and oxidation (methanotrophy) of this gas by soil microorganisms, as
507 well as the rate and mechanisms of transport to the atmosphere (Waddington et al.
508 1996; Segers 1998). Our results suggest that the increase in CH_4 emissions in the
509 presence of cottongrass was likely due to a higher transport of this gas through the
510 plant aerenchyma and a higher supply of organic substrates for methanogenesis, as
511 shown by the different DOC concentration and chemistry under the cottongrass
512 tussocks. Additionally, the greater microbial biomass in surface peat under cottongrass
513 in wet plots suggests also potential for higher consumption of CH_4 as substrate by the
514 microbial community, given the fact that the water table seldom reached the peat
515 surface in wet plots (Figure S6), allowing for the surface peat to be oxic. In spite of the
516 higher fluxes in wet plots with cottongrass, average seasonal CH_4 fluxes were lower than
517 those observed previously for undisturbed ombrotrophic peatlands (Waddington et al.
518 1996; Greenup 2000). Abdalla et al. (2016) reviewed a total of 87 studies that measured
519 CH_4 fluxes from peatlands, and concluded that undisturbed bogs emit an average of 7.1
520 g C m^{-2} y^{-1} as CH_4, which would be equivalent to 89.9 mg CH_4 m^{-2} day^{-1} during the three
521 months of the growing season (June- September, 85% of the annual emissions). In our
522 study, except for the peaks that reached exceptionally high daily fluxes in June and
523 August, the average daily emissions for the season in cottongrass plots were half of this.
524 This suggests the slow recovery of the ecosystem function in terms of C cycling, possibly

525 due to the lower substrate availability in the deep peat exposed after extraction (Glatzel
526 et al. 2004) and the presence of oxic conditions at the peat surface in wet plots, which
527 were probably dominated by methanotrophs rather than methanogens. Lower CH_4
528 emissions from restored peatland compared to undisturbed sites have also been
529 observed even 15 years post-restoration (Nugent et al. 2018). Accumulation of fresh
530 peat through the recovery of the peat forming vegetation, together with the
531 maintenance of high water tables may be essential to the recovery of pre-extraction CH_4
532 fluxes.

533 In spite of the belowground mobilization of C and N and higher efflux of CH_4, the
534 comparatively higher C uptake though photosynthesis turned the plots with cottongrass
535 into net sinks of CO_2; this C accumulation in the presence of cottongrass was stronger in
536 plots with higher water table, as previously observed by (Tuittila et al. 1999).

537

538 Conclusions

539 The processes governing C and N cycling post restoration were strongly
540 dependent on moisture and vegetation cover. Decomposition rates and C and N
541 turnover were limited by moisture and N availability in dry and bare sites, leading to the
542 accumulation of large amounts of available C as DOC. When the fluxes of C to the
543 atmosphere were considered, these sites acted as sources of C due to the lack of
544 photosynthetic C uptake.

545 Higher water table increased DOC turnover and ecosystem respiration rates
546 during the growing season, potentially increasing the loss of C. However, higher

547 moisture also promoted the increase of available N and the growth of vegetation that
548 could counteract the loss of C. When present, cottongrass contributed to increasing C
549 inputs into the ecosystem through photosynthesis, with the inputs of recently
550 assimilated C most likely contributing to the higher CO_2 and CH_4 efflux. However, no
551 evidence of increased peat C mobilization was found. Therefore, a higher water table
552 helped increase the C sink function of the peatland by promoting plant growth.
553 However, cottongrass presence was also a strong driver of C fluxes, turning dry areas
554 into C sinks. Thus, in addition to controlling hydrology, allowing for the colonization of
555 fast-growing vascular plant species recovers the C sink function of the ecosystem in the
556 short term while the *Sphagnum*-dominated vegetation slowly recovers.
557

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565

Table 1. Ecohydrological characteristics of the experimental plots with or without cottongrass presence at the dry and wet areas of the peatland.

	Dry		Wet	
	Cottongrass	No cottongrass	Cottongrass	No cottongrass
WT depth (cm)[1]	53.9 ± 2.81[a]	52.8 ± 3.33[a]	25.9 ± 1.15[b]	23.1 ± 1.46[b]
Aboveground cottongrass biomass (g)[2]	615.7 ± 135.8[a]	1.56 ± 1.7[b]	918.5 ± 67.3[a]	0 ± 0[b]
Belowground root density (mg dw root/ g dw peat) [2]	0.307 ± 0.1[b]	0.004 ± 0.0[b]	1.255 ± 0.37[a]	0.261 ± 0.09[b]
Cottongrass % cover[3]	43.7 ± 11	0 ± 0	90.0 ± 2.0	0 ± 0
Polytrichum % cover[3]	4.7 ± 1.8[a]	5.8 ± 2.5[a]	1.3 ± 1.3[a]	2.8 ± 1.6[a]
Other species % cover[3]	0 ± 0[b]	0 ± 0[b]	36 ± 0[a]	0 ± 0[b]

[1]WT: water table, average of values measured May-September 2015
[2]. Determined at the end of the growing season (September 2015)
[3]. Determined in August 2015

577 Table 2. Chemical properties of the water extracts of the peat samples collected at different depths (5, 25 and 75 cm) in the dry and
578 wet plots with or without cottongrass. Values are means ± standard error. Different letters within each column indicate significant
579 differences.

580

		Depth	DOC (mg kg^{-1})	TDN (mg kg^{-1})	SUVA 254 (mg L^{-1} m^{-1})	E4:E6	E2:E3	Microbial biomass C (mg kg^{-1})
Dry	No cottongrass	5 cm	1916 ± 179 a	114 ± 41 bc	3.75 ± 0.36 c	3.07 ± 0.2a	4.74 ± 0.2 a	985 ± 136 bc
		25 cm	941 ± 125 bc	79 ± 13 c	4.35 ± 0.33 c	2.28 ± 0.1 bc	4.36 ± 0.2 b	390 ± 146 de
		75 cm	1046 ± 209 abc	117 ± 39 bc	5.05 ± 0.73 bc	2.35 ± 0.1 bc	3.33 ± 0.1 d	478 ± 64 de
	Cottongrass	5 cm	1189 ± 376 ab	57 ± 9 c	4.44 ± 0.29 bc	2.62 ± 0.2 b	4.50 ± 0.1 ab	895 ± 131 bc
		25 cm	1037 ± 58 abc	50 ± 8 c	4.21 ± 0.14 c	2.28 ± 0.1 bc	4.50 ± 0.1 ab	554 ± 93 de
		75 cm	955 ± 212 ab	119 ± 31 bc	5.17 ± 0.52 bc	2.32 ± 0.1 bc	3.29 ± 0.1 d	385 ± 27 e
Wet	No cottongrass	5 cm	846 ± 93 bc	75 ± 13 c	5.00 ± 0.43 bc	2.29 ± 0.0 bc	3.92 ± 0.1 c	1166 ± 85 b
		25 cm	650 ± 97 c	55 ±8 c	6.32 ± 0.72 b	2.44 ± 0.1 bc	3.31 ± 0.1 d	492 ± 135 de
		75 cm	902 ± 172 bc	225 ± 27 a	6.19 ± 0.76 b	2.31 ± 0.2 bc	3.34 ± 0.1 d	438 ± 82 de
	Cottongrass	5 cm	1109 ± 102 abc	60 ± 5 c	3.87 ± 0.13 c	2.27 ± 0.1 bc	4.82 ± 0.1 a	1488 ± 47 a
		25 cm	785 ± 82 bc	58 ± 2 c	4.43 ± 0.09 c	2.19 ± 0.1 c	3.94 ± 0.1 c	692 ± 108 cd
		75 cm	816 ± 62 bc	158 ±44 ab	8.52 ± 0.71 a	2.60 ± 0.1 b	3.09 ± 0.1 d	323 ± 103 e

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585 Table 3. Pearson correlations between chemical properties, root density and microbial biomass carbon in the peat samples collected

586 at the field site.

	Root density (mg g^{-1})	TDN (mg kg^{-1})	Microbial biomass C (mg kg^{-1})
DOC (mg kg^{-1})	-0.004	0.207	0.237
$SUVA_{254}$ (mg L^{-1})	-0.270	0.437**	-0.389**
E4:E6	-0.233	0.256	0.096
E2:E3	0.352*	-0.429**	0.570**
Root density (mg g^{-1})	1	-0.245	0.576**
TDN (mg kg^{-1})	-0.245	1	-0.295*

587 **Correlation is significant at the 0.01 level.

588 *Correlation is significant at the 0.05 level.

Figure 1. Total dissolved N measured in the porewater collected at 75 cm depth in the dry and wet sites with or without cottongrass during the growing season. Values are means ± standard error. Different letters on the bars denote significant differences at α=0.05.

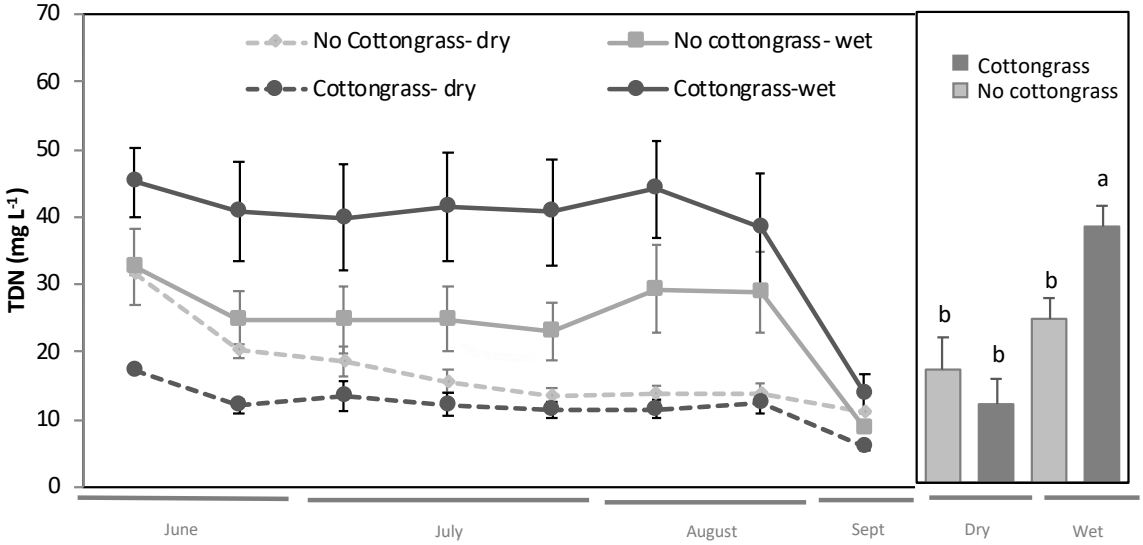
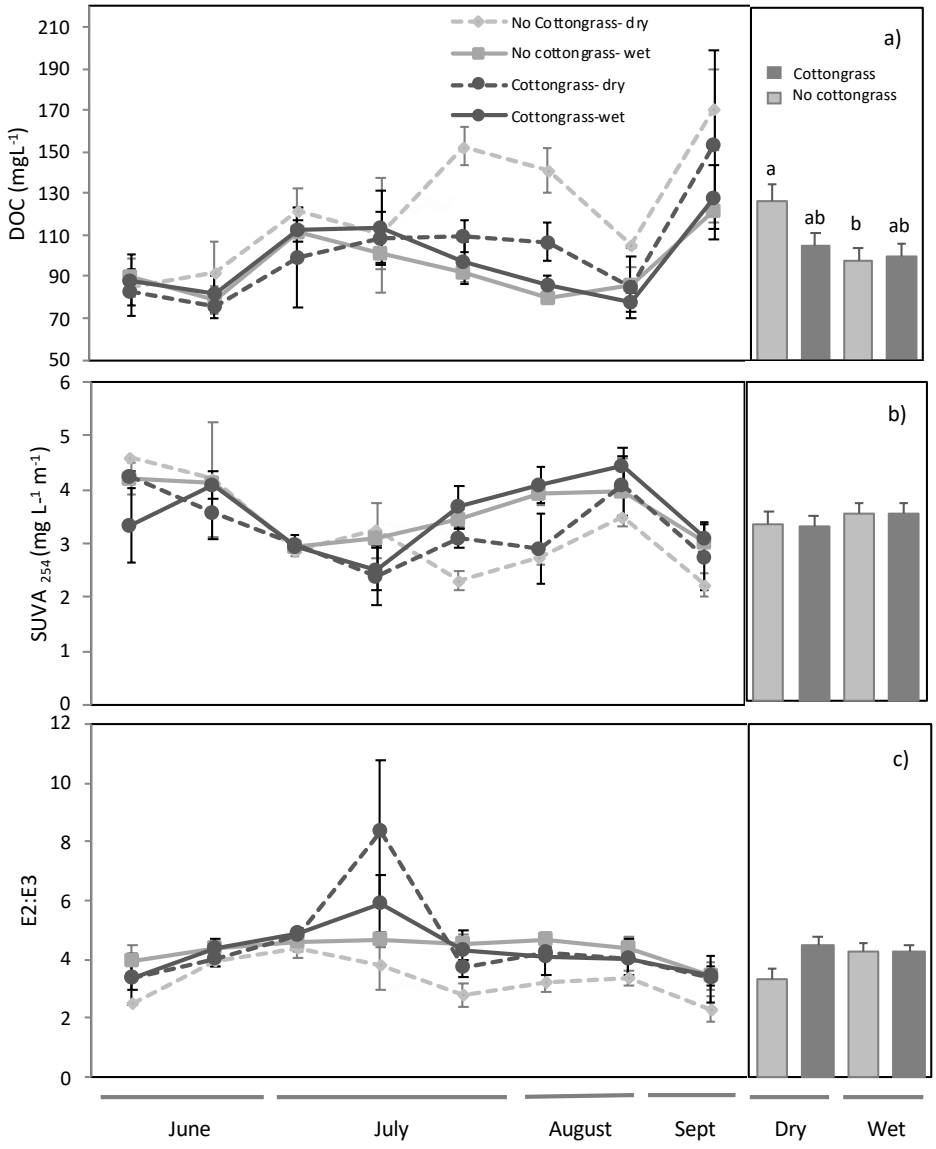
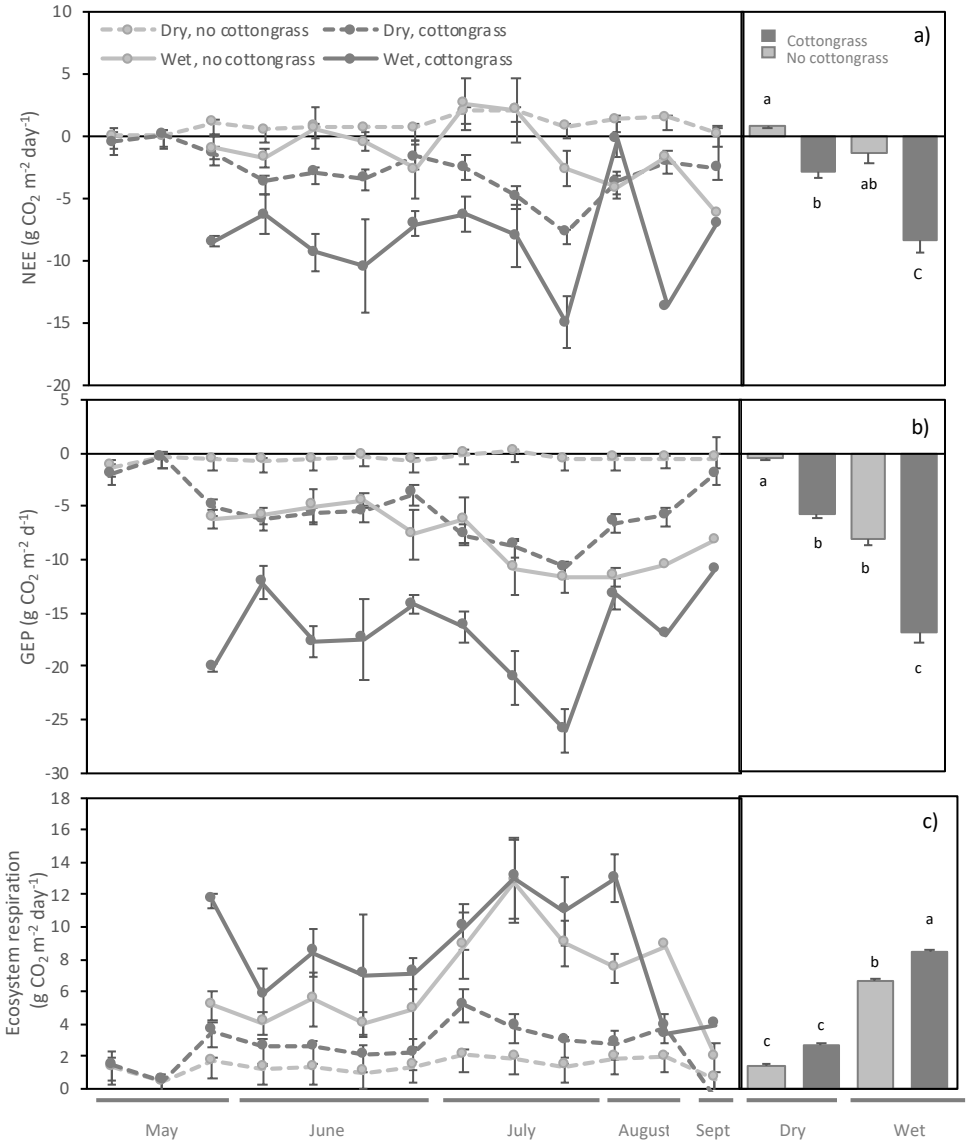


Figure 2. Dissolved organic C (DOC) concentration (a), $SUVA_{254}$ (b), and E2:E3 ratios (c) measured in the porewater collected at 75 cm depth in the dry and wet sites with or without cottongrass during the growing season. Values are means ± standard error. Different letters on the bars denote significant differences at α=0.05.

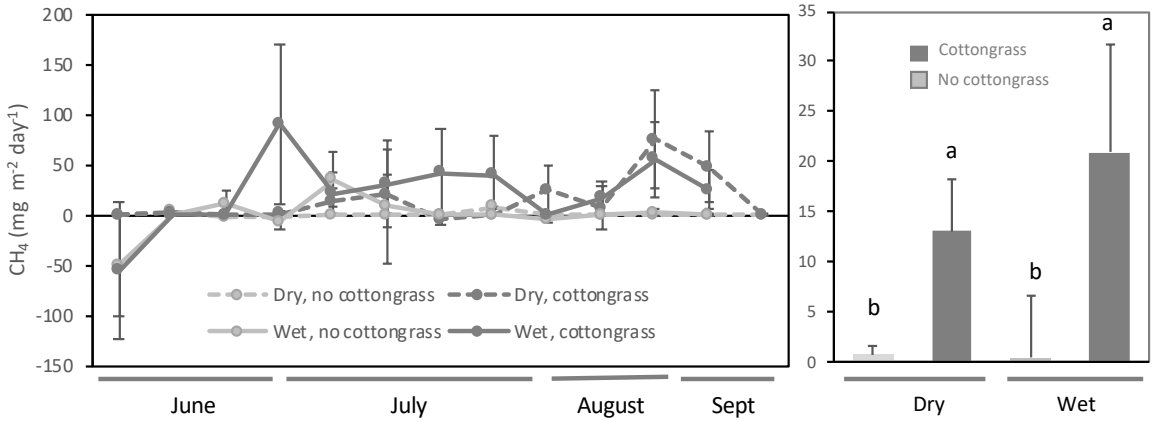


613 Figure 3. Seasonal dynamics (left chart) and average CO_2 fluxes (Net ecosystem
614 exchange or NEE (a), gross ecosystem productivity or GEP (b) and ecosystem Respiration
615 or ER (c)) measured in the wet and dry sites with (dark grey) and without cottongrass
616 presence (light grey). Values are means ± standard error. Different letters on the bars
617 denote significant differences at α=0.05.



618

620 Figure 4. Seasonal dynamics (left chart) and average daily methane fluxes measured in
621 the wet and dry sites with (dark grey) and without cottongrass presence (light grey).
622 Values are means ± standard error. Different letters on the bars denote significant
623 differences at α=0.05.



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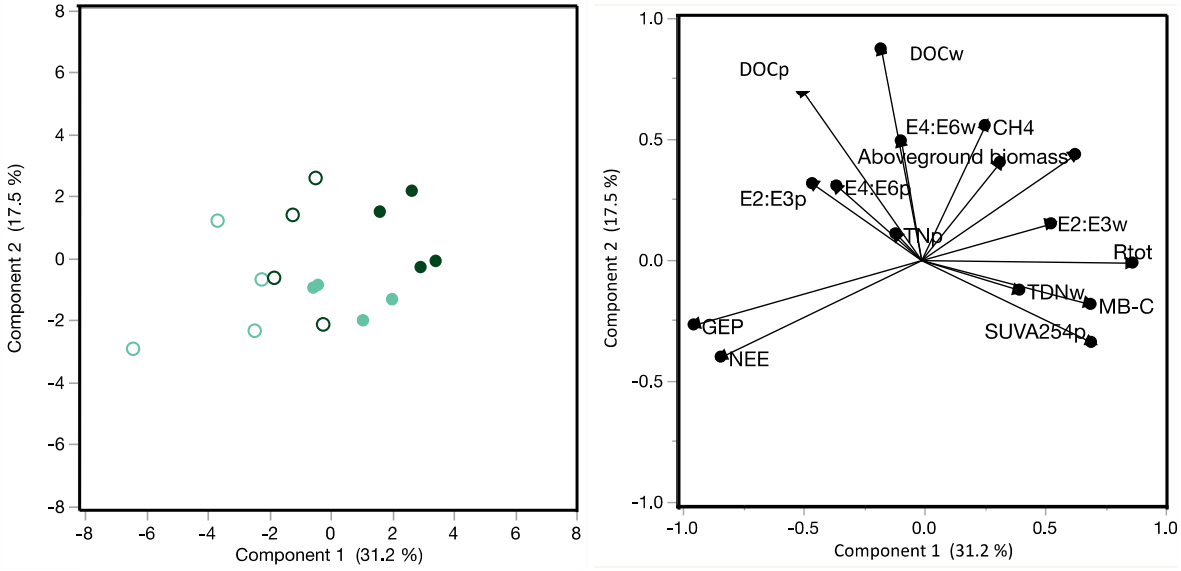
636 Figure 5. Principal component analysis (PCA) plots illustrating the difference between
637 the sampling locations or plots (left), and the contribution to the variables analyzed to
638 the two components (right). Full circles in the left depict high water table or 'wet' plots
639 whereas empty circles depict low water table or 'dry' plots. Dark green is used for plots
640 with cottongrass presence and light green for plots without cottongrass.



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