Influence of graminoid species identity on carbon exchange in a restored peatland in central Alberta, Canada

by

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Author's declaration

This thesis consists of material all of which I authored or co-authored: see Statement of Contributions included in the thesis. This is a true copy of the thesis, including any required final revisions, as accepted by my examiners.

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Statement of contribution

To reflect the result of this research, this thesis is written in manuscript format. Two independent manuscripts to be submitted for publication are presented as chapter 2 and 3 of this thesis. As a result, repeated information may be included.

Both manuscripts report on data collected at the SunGro Horticulture site near Entwistle for the 2016 growing season. All data was collected by S.Touchette with help from field assistants. M.Strack assisted with the design and planning of the study, and the development of each manuscript. I.B. Strachan assisted with the study design and the revisions of chapter 2. Each manuscript, including figures and tables, was written in its entirety by S. Touchette and reviewed by M. Strack.

Abstract

Peatlands are globally important ecosystems for carbon sequestration. Commercial extraction of peat layers alters the ecosystem services provided by pristine peatlands. One metric of peatland restoration is recovery of this carbon sink function. As peat extraction changes peat layer properties, the hydrology and nutrient availability are altered. Therefore, the new conditions on site may not be favourable to the establishment of mosses, responsible for slow peat accumulation, but more suitable for the establishment of vascular plants, such as graminoids. Graminoids are known to be strongly represented in the species pool of restored peatlands.

Land-atmosphere models have characterized the interaction between autogenic properties of natural peatlands and carbon accumulation processes. To represent the vegetation composition, the use of plant functional types (PFTs) grouping the main plant communities, according to their productivity characteristics, rooting characteristics and litter quality, is often used. In the case of restored peatlands, the species pool diversity, autogenic processes and carbon cycling are different than natural peatlands. Therefore, I questioned if the graminoid species are similar enough at the species level when evaluating their carbon dioxide (CO_2) and methane (CH_4) exchange to be grouped as a single PFT. As the peat hydrological functions are altered post-extraction, I also questioned how graminoid species distribution and carbon exchange function were affected by water table position. This study was conducted in a restored peatland in central Alberta, where five graminoid species were targeted: *Beckmannia syzigachne* (*B.syz*), *Calamagrostis canadensis* (*C.can*), *Carex canescens* (*Cx.can*), *Eriophorum vaginatum* (*E.vag*) and *Scirpus cyperinus* (*S.cyp*). All species were representative of the 'wet' section of the site, where they were compared at first within similar hydrologic conditions. To evaluate the impact of hydrologic heterogeneity on carbon exchange, species were also targeted in the 'dry' section of site, which includes *C.can*, *Cx.can* and *E.vag*. Quadruplicate plots were installed for the targeted species, and for both section. Both CO_2 and CH_4 flux measurements were conducted with the closed chamber technique during the growing season (May – September, 2016). A vegetation inventory, biomass production, and litter accumulation and decomposition rates were also measured to assess the species' plant productivity. A grid of wells and piezometers were installed and used to measure the hydrologic conditions.

When evaluating the correlation between the graminoid species distribution and the water table spatial variability, we found that presence of species was partly controlled by the water table position. The correlation between graminoid distribution and water table was greater for all graminoids combined and for *C.can* than for *E.vag* or *Cx.can*. The results show a significant difference between the graminoid species for their CO_2 exchange. *S.cyp* and *E.vag* were found to sequester the most CO_2 compared to *B.syz*, *C.can* and *Cx.can*. *S.cyp* and *E.vag* were also the species with the largest plant cover, which seems to relate to this higher carbon accumulation. Species CO_2 uptake differed also across the perennial stages of plants. When comparing the same species, but under different hydrologic conditions, species in the wet section were not significantly different from the dry. Methane flux was not found to be species controlled, but rather varied seasonally, where fluxes increased towards the end of the season with *E.vag* and *S.cyp* having significantly higher fluxes during this period. When considering the section of site, CH_4 emissions significantly increased under a shallow water table, with *E.vag* in the wet having the highest fluxes. Our results support the idea that graminoid species are abundant on restored peatlands under shallow water table positions and that species show enough difference in their CO_2 and CH_4 exchange that they should not be considered as a single PFT. However, more research is needed to assess the distribution and function of other graminoid species in restored peatland.

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Chapter 1: Introduction

With growing concern about the contribution of ecosystems to climate change, understanding land-atmosphere interactions is critical for climate models. Anthropogenic activities increase greenhouse gases (GHG) in the atmosphere, resulting in important changes in environmental conditions (e.g. precipitation regime, temperatures regime; IPCC, 2013). Ecosystems naturally control the climate locally and regionally. The ecosystems' species composition will affect its function, including GHG exchange (Hobbs et al., 2006). Additionally, some ecosystems are known to be important contributors to the global carbon budget. This is the case for wetlands, known to exchange great amounts of carbon dioxide (CO_2) and methane (CH_4) with the atmosphere (Loisel et al., 2014; Bridgham et al., 2013). Wetlands are also highly sensitive to climate variability, including precipitation and temperature anomalies (IPCC, 2013). This study investigates how species composition in a restored peatland ecosystem affects its GHG exchange.

The Canadian Wetland Classification System (NWWG, 1997) divides wetlands into two broad categories; either organic or mineral-soil based. Organic soil wetlands are known as peatlands and cover 3% of the world land area (Maltby and Immirzi, 1993) and represent 90% of Canadian wetlands (CSPMA, 2015). In Canada peatlands comprise 1.235 million km^2, making it the country with the second largest peatland cover after Russia (Vitt, 2013). They are well studied in the northern hemisphere, where they occur mainly between the 45 and 65°N latitudes (Price et al., 2003). Peatlands develop over thousands of years, with climate, geographic location, soil chemistry and hydrology as important controls on their development (Vitt, 2013). Four general types of peatlands are found based on water chemistry: ombrotrophic bogs, minerotrophic fens, intermediate or poor fens, and calcareous fens (Blodau, 2002). In general, peatlands are waterlogged systems and this results in anoxic soil conditions. Overall, they are characterized by production rates exceeding decomposition, resulting in accumulation of organic layers known as peat (Vitt, 2013). This slow decomposition rate is maintained through waterlogged conditions and non-vascular plants, such as bryophytes like *Sphagnum* mosses, that decompose slowly. To be classified as a peatland in Canada, a wetland must have at least 40 cm of incompletely decomposed organic matter (NWWG, 1997). Globally, peatlands store one third of soil terrestrial carbon with more than 400 GtC in northern peatlands (Loisel et al., 2014). In general, peatlands sequester CO_2, but also have a globally important release of CH_4. This important C cycling from peatlands is controlled by plant community structure, water table, soil temperature, and peat chemistry (Blodau, 2002; Bubier et al., 1995; Whiting and Chanton, 1993; Yavitt et al., 1997). As the C cycle is also subject to abiotic controls, CO_2 and CH_4 exchange will therefore vary spatially and seasonally within a peatland (Moore et al., 1998).

The peat vertical structure, based on the oxygen availability decreasing with depth, is mainly characterized with two distinct layers; the surface layer (acrotelm) and the deep layer (catotelm; Ingram, 1978). Natural peatland hydrology relies on the vertical structure of peat layers for water storage and discharge (Price et al., 2003). In the past century, these partially decomposed organic layers have been used for different purposes. In Canada, they are prized for their high porosity and water retention capacity and are extracted mainly for horticultural use (CSPMA, 2017a). To date, approximately 30,000 ha of peatlands have been extracted for horticulture, which represent 0.03% of the Canadian natural peatland area (CSPMA, 2015). The extraction of peat is conducted after removal of the surface vegetation and site drainage with ditches. Then the peat layers are extracted with heavy vacuum machinery. The extraction of peat releases the C that was stored in the system through oxidation (Cleary et al., 2005) and the remaining ecosystem no longer fulfills the functions of the natural system. Extraction of peat fields alone can increase CO_2 release by 400% compared to undisturbed sites (Waddington and Price, 2001). Moreover, peat extraction has a significant impact on hydrological and ecological functions, with a decrease in the specific yield of the remaining peat deposit and removal of plant communities (Price et al., 2003). Restoration of degraded peatlands is often undertaken with the development and management towards function very similar to pristine peatlands (Price et al., 2003), as restoration refers to the process of assisting to the recovery of an ecosystem degraded, damaged or destroyed (SER, 2004). As there is still an uncertainty in the ability of peatland restoration to return hydrology, ecology and the carbon storage functions (Price et al., 2003), additional studies are required on restored peatlands.

To promote the re-establishment of the ecosystem services on extracted peatlands, restoration processes are now part of the management of certain peatlands. Developed over the past decades, the Moss Layer Transfer Technique (MLTT) is often used in Canada for restoration and represents 16% of the post-extraction land restoration management projects (CSPMA, 2015; Graf and Rochefort, 2016). MLTT aims to establish mosses, essential for peat layer accumulation, and characteristic of peatlands. Restoration processes also take into consideration the substantial changes in the peatland structure and are designed to promote hydrological (Heathwaite, 1993) and ecological (Rochefort et al., 2003) conditions required for peat formation. However, the removal of the acrotelm affects the vertical soil profile important for hydrology by draining and exposing more decomposed layers, and through peat subsidence and peat oxidation (Heathwaite et al., 1993). The water storage capacity of the system is also altered with the removal of the surface layer (Price et al., 2003). With highly decomposed peat as the surface layer, large fluctuation in the water table is expected, with a decrease of shallow water table periods (Price, 1996; Lindsay, 1988). The removal of the acrotelm also results in exposed catotelm peat, available for plant colonization. With an important alteration of the hydrological conditions, the establishment of vascular plants is favoured at the expense of mosses (Graf et al., 2008; Poulin et al., 2012). Species of the Poaceae (Gramineae), Cyperaceae and Juncaceae families are successful in colonizing undrained extracted sites (Graf et al., 2008) and are representative of graminoids. As described by the National Wetlands Working Group (1997), graminoid is a wetland plant type dominated by undifferentiated grass-like plants, including grasses, low and tall rushes, reeds and sedges.

Despite a quick colonization by vascular plants in restored peatlands, the ecosystem services may not return to rates, at least in the short-term, similar to undisturbed peatland. As peat accumulation rate and the C exchange are important ecosystem functions in pristine peatland understanding the return of these functions with the different species pool present in restored sites is needed. Vascular plants will impact significantly the C storage, as they can be a strong determinant of C dynamics (Ward et al., 2015; Dieleman et al., 2014). Graminoid species increase respiration rates and soil organic C mineralization compared to moss (Blodau, 2002). Organic matter decomposition and CO_2 production is therefore stimulated by the readily-degradable litter of these species. Despite this, the gross ecosystem photosynthesis and the net ecosystem exchange of graminoids indicate higher CO_2 sequestration compared to mosses (Blodau, 2002). Despite an increase in the CO_2 sequestration potential from graminoid species, they also stimulate higher CH_4 emissions. Graminoids possess aerenchymatic tissues to aerate submerged roots, but these also provide a pathway for CH_4 emissions to the atmosphere (Whalen, 2005; Bhullar et al., 2013; Tuittila et al., 2000; Kao-Kniffin et al., 2010). In addition, graminoids alter the litter quality and therefore affect the microbial activity for CH_4 production and consumption (Kao-Kniffin et al., 2010; Bohdálková, 2013). Therefore, in a restored peatland colonized by graminoids, the CO_2 sequestration and CH_4 emissions will significantly increase compared to a natural site. However, the effect of individual graminoid species has not been quantified concerning their GHG exchange in restored peatlands.

Terrestrial models have been developed to assess terrestrial ecology in vegetation-soil relations, known as dynamic global vegetation models (DGVMs; Meir et al., 2006). Mainly, they are used to calculate the land-atmosphere fluxes of energy at different scales from past, present and future vegetation patterns and biogeochemical feedbacks (Meir et al., 2006). Global DGVMs are subject to the sensitivity of satellite resolution and generalized land cover within biomes, as land cover shows large variability from differences in data retrieval and no standard approach for vegetation classification (Poulter et al., 2001). By improving uncertainties in models for terrestrial ecosystem response to climate and CO_2 concentrations, we will have a better understanding of the impact of land-use change on the global carbon cycle (Meir et al., 2006; Sitch et al., 2005). By understanding the biogeochemical and biophysical processes affecting peatland C exchange, there is an opportunity to model and predict responses. In the case of peatlands, Frolking et al. (2010) have developed a model (Holocene Peatland Model, HPM) that investigates the climate-carbon-methane interactions at the local scale in pristine peatlands for the Holocene period. This one-dimensional model includes feedbacks among hydrology, plant communities and peat properties, that are dynamically integrated to model peatland development and its land-atmosphere interaction (Frolking et al., 2010). HPM was also a base model for dynamic multi-layer modelling approach applied for peatlands at the regional scale and across climatic gradients by Chaudhary et al. (2017).

As models improve the understanding of the long-term carbon dynamics of ecosystems at a given scale, modelling the ecosystem response post-restoration is imperative to quantify the time for the system to recover a carbon-sink function. Quillet et al. (in prep) have modified HPM for modelling the response of C cycling in extracted and restored peatlands. As the new conditions on site lead to different hydrological conditions and plant communities than a natural peatland, the biotic and abiotic feedbacks have to be redefined. With a better understanding of the controls on the GHG emissions from restored peatlands, modelling the systems could be used to characterize restoration success and enable peatland managers to make informed decisions on peatland after-use. To assess quantitatively the carbon dynamics and accumulation processes in relation with the vegetation composition, plant functional types (PFTs) has been a useful classification tool to describe the vegetation communities' interactions for HPM modelling (Laine et al., 2012).

PFTs aim to aggregate plant species into vegetation communities that distinguish themselves in productivity, rooting characteristics, and litter tissue quality (Frolking et al., 2010). HPM includes 12 PFTs based on their physiological process parameterization, with seven of these characteristic of vascular plants communities, responsible for peat growth over the Holocene time (Frolking et al., 2010; Laine et al., 2012; Tuittila et al., 2013). The use of PFTs is also useful for describing vegetation structure functions (Laine et al., 2012). The ecological niche optima along fertility and water table gradients guided plant species classification into PFTs for the HPM (Laine et al., 2012). The use of PFTs is not exclusive to modelling, but is also a simple classification tool used in other studies aimed at understanding how plant communities affect ecosystem function(e.g. Robroek et al., 2015; Adkinson et al., 2011; Glenn et al., 2006; Bhullar et al., 2013; Tuittila et al., 2013). The use of PFTs for modelling is a simplified quantitative method, as the species level is often too detailed and is too hard to model due to computational limits (Straková et al., 2010). Although PFTs have been successfully modelled and were closely linked to undisturbed peatland functions (Frolking et al., 2010; Laine et al., 2012; Chaudhary et al., 2017), the same PFTs may not be characteristic of restored peatlands.

Vegetation models that prescribe broad categories such as PFTs, group them by averaging attributes across many species and ecotypes (Weston et al., 2014). More precisely, PFTs are defined as species that have a similar response to a suite of environmental conditions, in attribution to their resource acquisition, growth, reproduction, dispersal and response to environmental stress (Smith et al., 1997). While graminoid species may be grouped as a PFT, it remains unclear if various graminoid species function similarly for GHG exchange, particularly in a disturbed ecosystem. However, as ecosystems are dynamic and the response to environment is species-dependent (Bret-Harte et al., 2008), model parameters do not quantify those shifts and community structure changes through PFTs and often over- or under-estimate parameters (Miller and Smith, 2012). Such averaging of ecosystem functions is known to contribute to important uncertainties in models (Zaehle et al., 2005; Kattge et al., 2009), as they are insensitive to changes in the community structure (Weston et al., 2014). PFTs and species response to change is also dynamic throughout the growing season and is often over-simplified with PFT categories (Khorsand Rosa et al., 2015; Arft et al., 1999; Starr et al., 2000). Considering the variation in plant growth form and carbon dynamics at the species level is imperative for land-atmosphere models. Graminoids are often categorized as a PFT in different models (e.g. Chaudhary et al., 2017; Frolking et al., 2010; Miller and Smith, 2012), and have been shown to be highly representative of the species pool in restored peatlands (Graf et al., 2008; Poulin et al., 2012). However, the implications of the presence of individual species and differentiation of function among species in peatlands post-restoration has not been quantified, particularly for peat accumulation processes and carbon exchange. Modellers have been challenged by Callaghan et al. (2011) to use findings to validate and improve models, and considering species level information in restored peatlands should improve model accuracy.

1.1 Objectives

When modelling ecosystem GHG exchange, taking into consideration the different controls on the systems' functions is crucial. Many peatland carbon models usually consider plant functional types (PFTs) and do not evaluate the effect of individual species (e.g. Frolking et al., 2010; Chaudhary et al., 2017). Graminoid species are highly productive and have a higher cover at restored peatlands than in natural bogs. Therefore it is important to evaluate species-specific effects for graminoids on C exchange in restored peatlands in order to evaluate how appropriate it is to group these species as a PFT. Additionally, as the hydrology is an important control on peatland ecology and GHG exchange, understanding how hydrology of a restored system interacts with the species distribution to influence C cycling is needed. Therefore the research questions are as follows:

1. To quantify the effect of graminoid species type for peatland CO_2 and CH_4 exchange post-restoration and define if graminoids should be grouped together as a plant functional type for restored peatland models,
2. To evaluate the impact of hydrological conditions on CO_2 and CH_4 exchange of graminoids and,
3. To determine the preferential distribution of different graminoid species according to the temporal and spatial variability of the water level in a restored peatland.

Preface to Chapter 2

The previous chapter highlights the effects of peat extraction and restoration on the species pool and biophysical conditions on site. As industries are interested in the impact of peatland restoration on short-term carbon exchange, there is a need to improve restored peatlands' model accuracy. Thus, Chapter 2 contributes to the literature by differentiating graminoid species (Poaceae, Cyperaceae and Juncaceae families), highly representative of restored sites, according to their plant growth form, CO_2 and CH_4 exchange in a restored peatland, four years post-restoration. The manuscript introduces the differentiation of graminoid at the species level according to their perennial stages. To that end, the chapter aims to characterize the graminoid species' function and evaluate if they should be considered as a plant functional type for a restored peatland model.

Chapter 2: Carbon dioxide and methane exchange from a restored peatland: evaluating graminoid species as a plant functional type

2.1 Outline

One metric of peatland restoration success is the re-establishment of a carbon sink. Conditions post-restoration may promote the establishment of vascular plants such as graminoids, often at greater density than would be found in undisturbed bogs. Although graminoid species are often considered as a plant functional type (PFT) in land-atmosphere models, the greenhouse gas (GHG) exchange of individual species in restored ecosystems is not well-quantified. I assessed the GHG exchange of different graminoid species in a restored peatland in central Alberta, Canada. Quadruplicate plots were installed on *Beckmannia syzigachne* (*B.syz*), *Calamagrostis canadensis* (*C.can*), *Carex canescens* (*Cx.can*), *Eriophorum vaginatum* (*E.vag*) and *Scirpus cyperinus* (*S.cyp*), where measurements were conducted from May-September 2016. The carbon dioxide (CO_2) flux of each species was measured with a clear chamber and an infrared gas analyzer. Methane (CH_4) fluxes were measured with the closed opaque chamber technique; CH_4 concentration was determined using a gas chromatograph in the laboratory. Results show a significant amount of variation in CO_2 exchange controlled by the species composition and the perennial stage (e.g. vegetative, elongation, reproductive, and dormant). *S.cyp* and *E.vag* had higher CO_2 sequestration during the study period, compared to the other species. It is likely that differences in the measured plant growth form of each species drove differences in species-level CO_2 uptake. The species also explained variation in CH_4 emissions, particularly during the dormant stage with *E.vag* and *S.cyp* having significantly higher fluxes. Our evidence suggests that graminoid species should not be considered as a single group in a restored peatland model, as *E.vag*, *S.cyp* demonstrated significantly greater CO_2 uptake and CH_4 emissions compared to the other species.

2.2 Introduction

Land-atmosphere interactions are greatly impacted by anthropogenic activities including climate change (Meir et al., 2006; IPCC, 2013). The ability of ecosystems to sequester and store carbon varies depending on the plant functional types (PFTs; Meir et al., 2006) present. These in turn lead to differences in biophysical and biogeochemical processes. Known to store one third of the world's terrestrial soil carbon with more than 400 GtC (Loisel et al., 2014), northern peatlands are important ecosystems for carbon sequestration. Peatlands are wetland ecosystems with at least 40 cm of organic matter, known as peat, accumulated through slowly decomposing organic material in anoxic waterlogged conditions (Vitt, 2013; Glaser, 1987). The accumulation of peat is subject to the plant species composition, where non-vascular plants such as *Sphagnum* moss enhance peat accumulation through their biochemical properties (van Breemen, 1995). More precisely, carbon sequestration occurs when plant net photosynthesis exceeds the carbon loss as CO_2, CH_4 and dissolved C arising from decomposition processes (Vitt, 2013). The fact that long-term CO_2 sequestration exceeds the emissions of CH_4, makes peatlands important net greenhouse gas sinks (Frolking et al., 2006). The rates of CO_2 sequestration and CH_4 emissions differ across peatland types. In North America, fens and bogs represent the two major classes of peatlands (Blodau, 2002). Rates of peatland CO_2 and CH_4 exchange are dependent on controls such as the plant community structure, peat chemistry and water table (Yavitt et al., 2000).

In Canada, peatlands cover 1.235 million km^2 of land surface; the second largest cover of peatlands in the world (Vitt, 2013). However, many peatlands have been disturbed because peat moss is valued for horticulture, fuel, oil absorbant and other uses (CSPMA, 2017a,b). To date, approximately 30,000 ha of peatlands have been extracted for horticultural purposes in Canada (Environment Canada, 2013). In western Canada, horticultural extraction of peatlands is expanding with Manitoba, Saskatchewan and Alberta accounting for 22% of the areas under production in Canada (CSPMA, 2015). With over 1,500 ha currently under extraction, Alberta accounts for 9% of the Canadian production (CSPMA, 2015). Horticultural peat extraction involves draining the site with ditches, removing the vegetation and extracting peat layers. Drainage increases the amount of oxygen input to the soil, thereby increasing the decomposition of peat and resulting in net CO_2 emissions (Cleary et al., 2005). The peatland therefore switches from being a net sink of GHG to a net source (Cleary et al, 2005).

Following peat extraction, restoration processes are undertaken to accelerate ecosystem recovery (Cleary et al., 2005). To promote the success of restoration after extraction, the Moss Layer Transfer Technique (MLTT) is commonly used to re-establish the ecosystem services from natural peatlands - among these is the return to a carbon sink (CSPMA, 2017a; Graf and Rochefort, 2016). This technique aims to create suitable conditions for the establishment of native peatland species, by: (1) levelling the peat to improve contact between substrate and diaspores; (2) creating peat berms to improve water distribution; (3) transferring plant donor material from a nearby site and spreading with a ratio of 1:10; (4) applying straw mulch on the donor material to create a suitable microclimate; (5) blocking the drainage ditches to promote a higher water table depth; and, (6) spreading phosphorus rock to fertilize the site (Rochefort et al., 2013).

While MLTT can successfully establish moss cover (Gonzalez et al., 2013), vascular plants have been found to be pioneer species post-restoration (Graf et al., 2008). Vascular plants, such as graminoids may alter rates of carbon cycling compared to natural sites (Dieleman et al., 2016) as they increase the ecosystem photosynthesis and respiration, as well as methanogenesis and release on site (Vitt, 2013). As plant litter is derived from the ecosystem photosynthesis (Keuskamp et al., 2013), the species composition also affects peat accumulation. Graminoids stimulate decomposition with readily-degradable litter (Bohdálkova et al., 2013) and low lignin (Straková et al., 2010), which impacts the carbon sequestration and peat accumulation potential. The volume of biomass and roots produced by graminoids is also proportional to CH_4 internal transport from plants (e.g. aerenchyma; Bhullar et al., 2013). Additionally, CH_4 emissions have been found to be species-dependent (Bhullar et al., 2013; Robroek et al., 2015), where the plants differentially increase the labile organic carbon deposition to the rhizosphere via root exudation processes (Lai et al., 2014). However, this process might be insufficient to explain the increase of CH_4 emissions in the presence of graminoids; additionally, plant effects through rhizosphere oxidation and internal transport (e.g. Bhullar et al., 2013) are important. Therefore, as graminoids will have an impact on the CO_2 and CH_4 exchange in restored peatlands, the species composition is an important factor to consider when modelling peatland C cycling post-restoration.

Empirically- and process-based models are used to describe the relationships between the environmental controls and the C cycle in natural peatlands, but differences in local conditions post-disturbance alter rates of C exchange. Accordingly, the Holocene peatland model (Frolking et al., 2010) has been modified in order to characterize carbon dynamics in post-restoration peatlands (Quillet et al., in prep) and can be used to evaluate the time needed for the restored system to become a C sink. In general, twelve PFTs are considered that combine species with a similar response, according to their peat growth over the Holocene time scale, quantitatively linking carbon accumulation with the vegetation composition and dynamics (Frolking et al., 2010; Laine et al., 2012). As vegetation species are assessed to a PFT, no studies to my knowledge, have evaluated the applicability of the Holocene peatland model PFTs to restored sites, or examined the relevance of any differences in PFT at the species level. More precisely, some PFTs, like graminoids, have been found to have species that differ in their carbon accumulation potential and their CH_4 emissions (Bhullar et al., 2013; Lai et al., 2014). Therefore, there is a need to evaluate the applicability of graminoids as a PFT or if species should be considered individually for a restored peatland model. This study evaluated the CO_2 and CH_4 exchange of five graminoid species (*Beckmannia syzigachne, Calamagrostis canadensis, Carex canescens, Eriophorum vaginutam* and *Scirpus cyperinus*), along with the biotic and abiotic factors known to control the fluxes, over a growing season in a restored peatland in central Alberta.

2.3 Methods

2.3.1 Study site

Field measurements were made from May 11–September 8, 2016 in a restored ombrotrophic bog located 17 km southeast of the town of Entwistle in central Alberta, Canada (53°27’26”N, 114°53’04”W; see also Appendix 1, Figures A1, A2). In Entwistle, the (1981-2010) mean annual air temperature is 3.5°C and mean annual total precipitation is 551 mm, of which 77% is rainfall (Environment Canada, 2017). From May to September, the (1981-2010) normal mean temperature and precipitation are 13.5 °C and 77.5 mm, respectively (Environment Canada, 2017). Peat was extracted for twelve years over the site and subsequently restored using MLTT in autumn and winter 2012. Prior to the installation of field equipment, a vegetation survey was conducted on site to determine the dominant graminoid species. The southwest portion of the restored area was selected for its accessibility and for the large representation and diversity of graminoid species. Quadruplicate aluminum collars (60 cm x 60 cm) were installed for each of the five dominant graminoid species selected: *Beckmannia syzigachne (B.syz), Calamagrostis canadensis (C.can), Carex canescens (Cx.can), Eriophorum vaginatum (E.vag)* and *Scirpus cyperinus (S.cyp)* and on bare soil for comparison.

2.3.2 Field Data Collection

2.3.2.1 Vegetation inventory

To assess the success of restoration and characterize the distribution of graminoid species across the site, a vegetation survey was conducted in August 2016, with 34 transects established east-west. Within the southcentral portion of the site, 15 transects were surveyed that were spaced 10 m apart. Quadrats were surveyed each 10 m along these transects. To the north and south of this section, four transects each were spaced 20 m apart with quadrats spaced at 20 m along each. Beyond this area, the remainder of the site was surveyed with transects and quadrats spaced at 30 m (Figure 2.1). Density of the survey was chosen to provide high density sampling in the area coincident with carbon measurements, while lower density outside this area allowed for broader comparison across the site while keeping the survey logistically feasible. At each point (quadrat) surveyed we determined the percentage cover of main plant groups on site (i.e. Sphagnum moss, other bryophytes, graminoid, herbaceous, deciduous trees, evergreen trees, and shrubs; Appendix 2). Vascular plant cover was evaluated within a 1 m x 1 m quadrat with moss percentage cover estimated in a 25 cm x 25 cm square located in the southwest corner of each 1 m x 1 m quadrat. In addition to the other plant functional type groups, the cover of the five targeted graminoid species was estimated. Cover of bare peat, straw mulch, litter and dead wood was also recorded. Surveyed points were recorded with a GPS (eTrex Venture HC, Garmin Ltd, USA; up to 3-5m horizontal accuracy) and geo-referenced and mapped with ArcGIS 10.5 (ESRI 2016, California, USA).

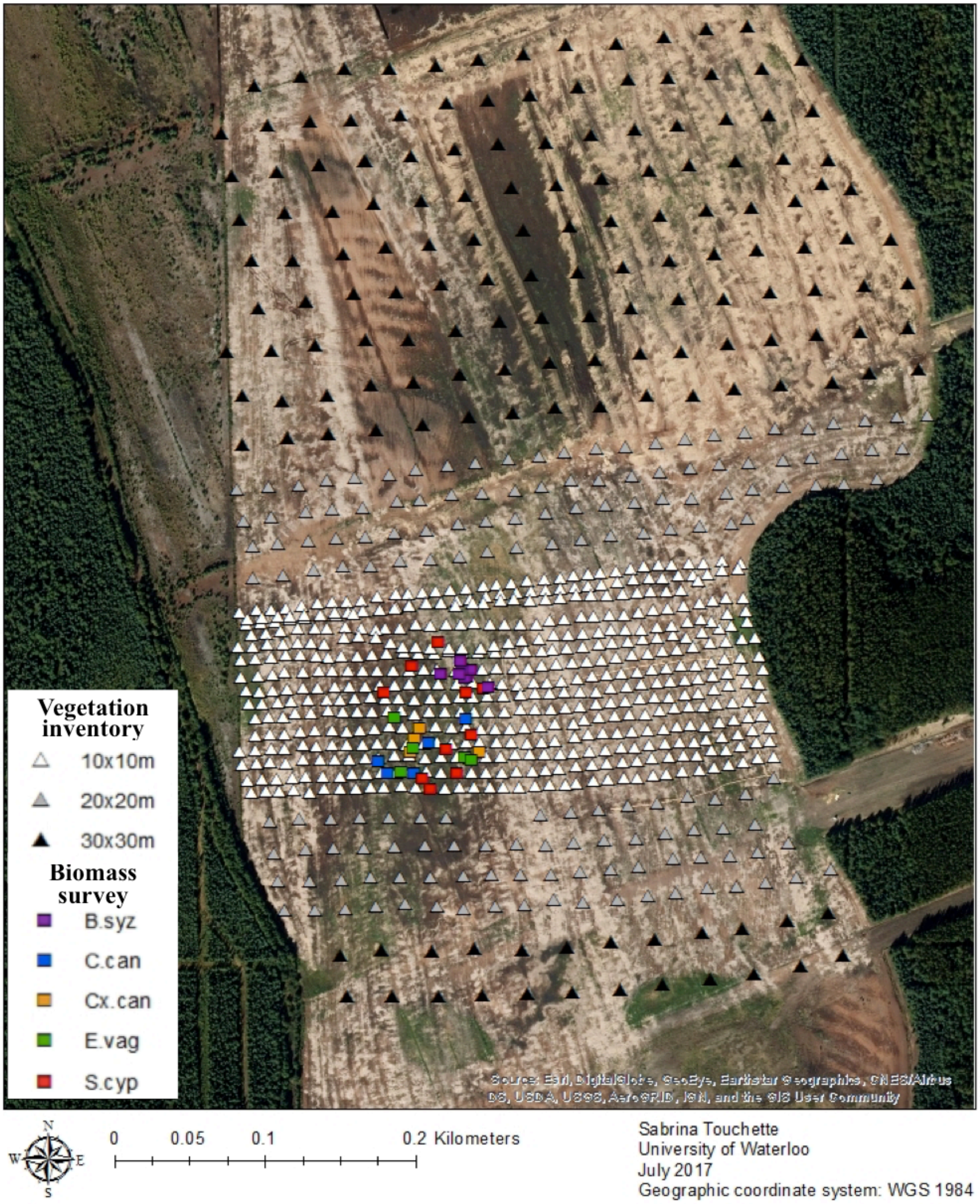

Figure 2.1: Location of the vegetation inventory points (triangles) and biomass survey (squares) over the study site. Section with biomass survey represents most of the study area.

2.3.2.2 Plant growth form

To determine the aboveground biomass of the graminoid species targeted, sampling was conducted on the site in August 2016, before the senescence period. Sampling was conducted randomly in the central portion of the site and considered the surface vegetation of the species targeted. A quadrat (0.25 m x 0.25 m) was placed on the ground within a plot dominated by one of the target graminoid species. All aboveground vegetation was clipped and divided into living biomass of the target species, litter, moss and other plant material (vascular plant species other than the one targeted in that quadrat). The set location was recorded using a handheld GPS (eTrex Venture HC, Garmin Ltd, USA; up to 3-5 m horizontal accuracy) to track the sampling and clusters of each species. In total, ten quadrats were sampled for each species and the biomass samples were transported to the Wetland Soils and Greenhouse Gas Exchange Lab at the University of Waterloo, Ontario for further analyses.

In the laboratory, aboveground vegetation biomass samples were dried individually in aluminum foil dishes for a minimum period of 48 hours at 60 °C in a mechanical convection oven (Heratherm OMS100, Thermo Scientific, Massachusetts, USA). Their final weight was measured using a balance with a 0.01 g precision and expressed as g m^{-2}. The carbon and nitrogen content in dry biomass of three samples for each species was determined by combustion (4010 Elemental Analyzer, Costech Instruments, Italy) in the Environmental Isotope Laboratory at the University of Waterloo and used to calculate C:N ratio.

To assess the difference in height for each graminoid species, plant height (m) was measured during the biomass sampling. Measurements were made from the ground surface to the highest part of the plant.

2.3.2.3 pH

Because peat extraction removes the upper peat layers, restoration occurs on the more decomposed layers of peat. The acidity of the lower layers presents different conditions for plants than an ombrotrophic bog surface. The water pH was measured throughout the 2016 growing season. From May to August, the pH (Lange Pocket Pro+ Multi 2, Hach, Colorado, USA) was measured once a month from a pore water sample from the standpipe next to each collar. In August, pH, conductivity, total dissolved solids (TDS) and salinity were measured from the same locations. In addition to the pore water pH, two peat cores were removed, where sampling was taken every 10 cm for a total of one meter. Peat pH was determined as detailed by Karla (1995) for pH measurement of organic soils. Each sample was air dried (~25 °C) for 96 h. Dried peat soil samples were passed through a 2 mm sieve and then 5 g of peat soil was put into a 50 mL beaker. Afterwards, 20 mL of distilled water (H_2O; mass ratio 1:4) was added to the soil sample with a pipet and the sample was mixed for 5 seconds with a glass rod. The soil-H_2O solution sat for 30 minutes before pH measurements. The pH measurements (pH, conductivity, TDS and salinity; Lange Pocket Pro+ Multi 2, Hach, Colorado, USA) were performed at ~22 °C on the solution suspension immediately after gently stirring. After removal, the electrodes of the pH meter were cleaned with distilled water to remove any peat soil material.

2.3.2.4 Carbon dioxide

To understand the carbon dioxide (CO_2) dynamics of the graminoid species, the net ecosystem exchange (NEE) was determined using the closed chamber technique (Alm et al., 2007; Appendix 1, Figure A3a). Measurements were conducted biweekly on the metal collars for a total of nine measurements per collar. A transparent acrylic chamber of 108 L (60 cm x 60 cm x 30 cm) with a cooling system was installed on the sampling plot and sealed with water poured on the collar edges. Two battery-operated fans circulated headspace air within the chamber, blowing past a copper coil containing cold water circulating from a cooler with ice to insure minimal heating during the measurements. For plants taller than 60 cm, an acrylic extension of 60 cm high (216 liters; Appendix 1, Figure A3b) with two additional battery-operated fans was added under the chamber to prevent damage to the stem of the plants. A portable infrared gas analyzer (IRGA; PPsystems EGM-4, Massachusetts, USA) connected to the chamber measured the CO_2 concentration with values recorded every 15 seconds for a period of 2 minutes following chamber closure. A thermocouple thermometer and a photosynthetically active radiation (PAR) sensor recorded environmental conditions within the chamber at the same time intervals. Measurements were repeated four times on the collars by simulating different light availability, from full light (no shades) to no light available (dark). The dark simulation was created with an opaque tarp covering the chamber and aimed to simulate conditions for measurement of the total autotrophic and heterotrophic respiration (Lovett et al., 2006), which represents the ecosystem respiration (ER, PAR=0 µmol m^{-2} s^{-1}). The difference between the NEE with full light (PAR> 1000 µmol m^{-2} s^{-1}) and ER was used to determine the gross ecosystem photosynthesis (GEP), which corresponds to the amount of organic carbon fixed by photosynthesis (Lovett et al., 2006). In addition to the fluxes, water table depth (WTD) was measured from a standpipe next to the collars and soil temperature was measured at 2, 5, 10, 15 and 20 cm below the surface with a thermocouple probe.

To estimate the CO_2 exchange from each sampling plot, the volume of the collars was added to the volume of the chamber. More precisely, twelve points systematically distributed across the collar were measured from the ground or the top of the vegetation, to the top of the collars. For any plants that were higher than the collars, negative values were considered. The mean value of the survey was considered as the adjustment of the volume.

Carbon fluxes from vascular plants have been found to vary temporally (Tuittila, 2000), thus the perennial stages were considered as a factor in the data analysis. Indeed, the carbohydrate reserve is species dependent and is subject to seasonal variation (White, 1973). In total, four stages were considered depending on the carbohydrate reserves (Guretzky et al., 2017): (1) vegetative, (2) elongation, (3) reproductive and (4) dormant. As perennial stage is species dependent, a middle line was found among the species according to time of year, and the variation of the fluxes in CO_2. As the sampling period falls mainly within the elongation and reproductive stages, they were represented by more measurements than the vegetative and dormant stages (Table 2.1).

Table 2.1 Perennial stages period of measurements and number of time measured. WOY is week of year.

Perennial stage	Month	WOY	Times measured
Vegetative	May	20-21	1
Elongation	Late May to mid-June	22-24	2 to 3
Reproductive	Late June to August	26-33	4
Dormant	September	35-36	1

2.3.2.5 Methane flux

To determine the methane (CH_4) emissions from graminoids, the closed chamber technique was used (Alm et al., 2007; Appendix 1, Figure A3c) with CH_4 measurements conducted biweekly on the metal collars, for a total of eight measurements per collar. An opaque square chamber of 108 liters (60cm x 60cm x 30cm) was installed on the sampling plot and sealed with water poured around the collar edges. A battery-powered fan in the chamber mixed the headspace air. As for CO_2 measurements, for plants with height exceeding 60 cm, a 60 cm high opaque extension was used. Following chamber closure, sampling was conducted at 5, 15, 25 and 35 minutes with 20 mL of headspace air extracted with a syringe from a tube inserted in the chamber and stored in a pre-evacuated sealed vial (Exetainer, Labco Ltd, UK). The temperature inside the chamber was monitored at the same intervals with a thermocouple inserted in the chamber. To determine the CH_4 concentration before chamber closure, samples from ambient air were taken during the first and before the last chamber measurements, twice a day.

The CH_4 concentrations were determined in the laboratory with a gas chromatograph (GC-2014 Gas Chromatograph, Shimadzu Scientific Instruments, Kyoto, Japan) with a flame ionization detector. The linear change in concentration determined the methane flux over time, which was corrected with the chamber volume and temperature inside the chamber. Before determining the CH_4 flux, data was quality controlled where measurements with concentrations at 5 minute higher than 5 ppm followed by a decline in concentration, or erratic concentration changes likely associated with ebullition events, removed from the data set. Cases where 5 minute concentration was less than 5 ppm and subsequent samples had concentrations that changed less than the precision of the gas chromatograph (10%) were assigned a value of 0 for flux. Accordingly, only those measurements assessed as zero flux or with a linear change with $R_2>0.70$ were kept in the data set, which resulted in the loss of 9.2% of the data set for the growing season. To meet normality and equal variance conditions, the CH_4 fluxes data were $\log(x+10)$ transformed. The perennial stages were also used for the methane fluxes according to the carbohydrate reserves. The same time periods as for the CO_2 measurements were considered (Table 2.1).

2.3.3 Data analysis

To determine the controls on variation in NEE, GEP, ER and CH_4 fluxes and WTD between plots, a linear mixed effect model comparison, considering the collars as the random effect to account for repeated measures, was conducted with graminoid species, WTD and soil temperature using a one-way analysis of variance (ANOVA) with repeated measures. A multi-way ANOVA, accounting for the collars, was used to compare individually the species with the stages, each stage and species, and the pore water pH with the species and stages. As for the peat pH measurements, a one-way ANOVA, accounting for the location of sampling, was used in comparison with the depth of sampling, the salinity, TDS and the conductivity. To assess the differences between the species and other controls, a two-way ANOVA was used where comparison between NEE, GEP, ER, CH_4 fluxes and pH were made with the species and the stages, WTD or soil temperature. Additionally, a two-way ANOVA was used for the peat pH, accounting for the depth of measurements in comparison with the pH and salinity, conductivity or TDS. Following significant pairs of the ANOVA analysis, the variance in components was estimated in models with random effect using a general linear hypothesis with Tukey pairwise test with multiple comparisons of means. All statistical analysis was conducted using the statistical program R (version 3.2.3, R Core Team 2013, Vienna, Austria; packages: 'TH.data' (Hothorn, 2017), 'survival' (Therneau, 2015), 'multcomp' (Hothorn et al., 2008)), and a significance of $\alpha=0.05$ was applied.

2.4 Results

2.4.1 Environmental conditions

Water table position varied between plot types with bare plots being significantly drier than all tested graminoid species that had similar water table positions ($F_{5,17}=5.1$, $p<0.01$; Figure 2.2a). All species had a similar pattern of water table change over the perennial stages. WTD position was significantly different across the perennial stages ($p<0.001$). As shown in Figure 2.2b, the WTD increased from the vegetative to the elongation stage, which was related to the intense rainfall received on site for June. A slight decrease is then observed from the elongation to the reproductive stage. The dormant stage was characterized with the shallowest WTD levels observed on site, coinciding with extreme rainfall events.

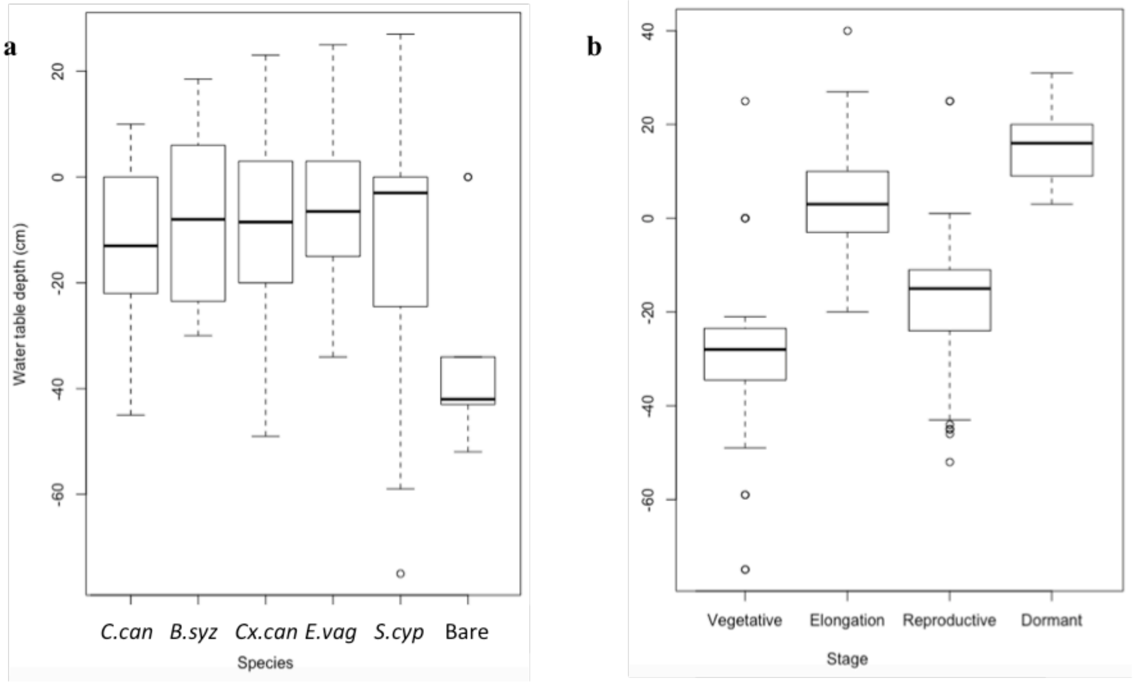

Figure 2.2 WTD variation according to plot types (a) and perennial stages (b).

The mean soil temperature at all depths measured during the CO_2 and CH_4 measurements did not vary between the graminoid species plots. However, bare plots had higher temperatures compared to those containing graminoid species. *S.cyp* had the lowest mean soil temperature at 2cm during the vegetative stage. The surface mean soil temperature at 5cm showed variation during the season (Figure 2.3). From the vegetative to the elongation stage, we observed a decrease in temperature followed by an increase during the reproductive stage and then a decrease during the dormant stage.

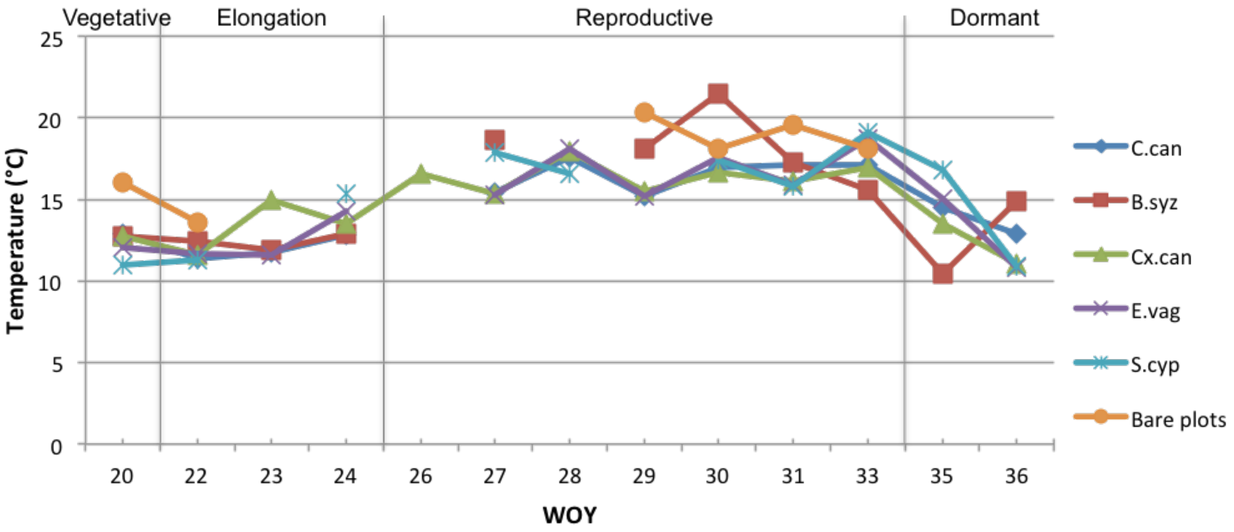

Figure 2.3 Soil temperature measured at 5cm deep throughout the season during CO_2 and CH_4 measurements and divided per perennial stages.

Pore water pH ($p=0.36$), conductivity ($p=0.25$), TDS ($p=0.23$) and salinity ($p=0.24$) did not vary between species. However, there was a significant relationship between the pH and conductivity ($F_{1,20}=31.2$, $p<0.001$), TDS ($F_{1,20}=27.9$, $p<0.001$) and salinity ($F_{1,20}=27.2$, $p<0.001$). *C.can* had the lowest pH, while *S.cyp* had the highest pH values observed (Figure 2.4a). The perennial stages were found to explain a significant variation in pore water pH ($p=0.02$) with the dormant stage having significantly higher values then the elongation stage. Peat pH was significantly related to depth ($F_{1,17}=108.7$, $p<0.001$) and increased with depth (Figure 2.4b), ranging from 3.95 on the surface to 5.07 in the deeper layers. However, peat conductivity, TDS and salinity were not related to peat depth.

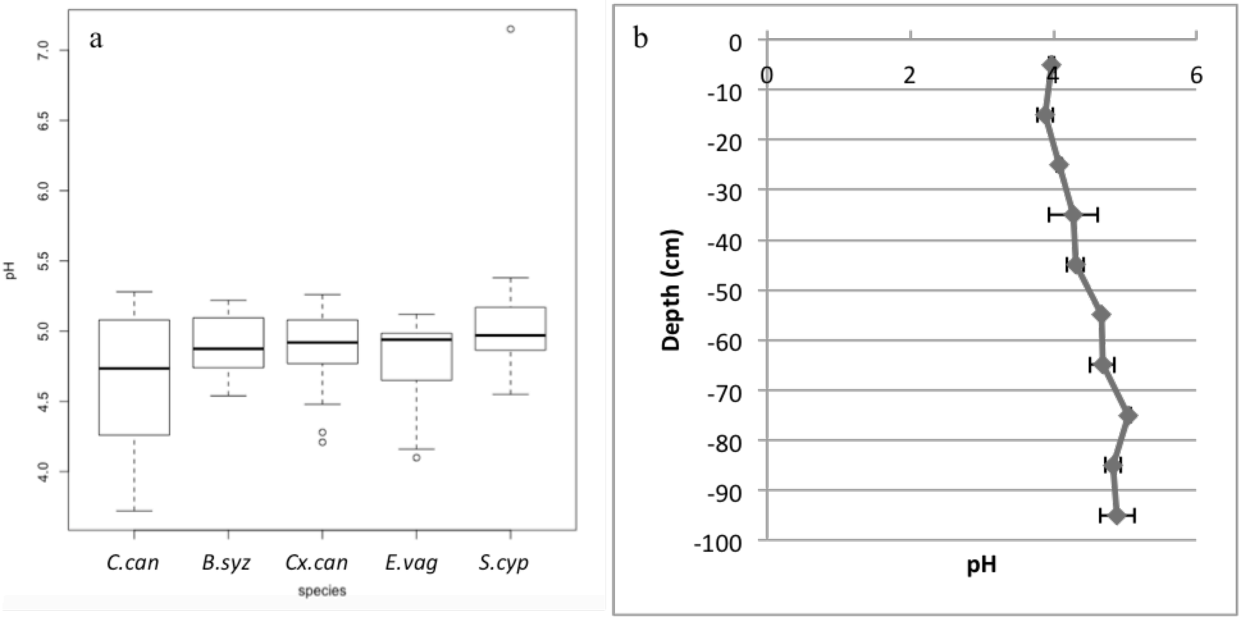

Figure 2.4 (a) Relation between the pore water pH according to the species; (b) Peat pH according to depth in August 2016, with standard deviation.

2.4.2 Carbon dioxide fluxes

Graminoid species type explained a significant amount of the variation in growing season respiration (ER; Table 2.2), with *B.syz* having the highest ER and *Cx.can* and bare plots having the lowest ER across all stages (Figure 2.5a). Considering ER, there was no significant interaction between species and perennial stage (Table 2.2). However, there were differences among species within the various stages. In the vegetative stage, *B.syz* had the highest respiration rate and *E.vag* the lowest; during the elongation stage, *E.vag* had the highest ER and *B.syz* and bare plots, the lowest; during the reproductive stage, *B.syz* respiration was significantly higher than most species (Figure 2.5a).

Graminoid species accounted for a significant amount of the variation in growing season GEP (Table 2.2), with *B.syz*, *E.vag* and *S.cyp* having the highest CO_2 uptake (Figure 2.5b). The perennial stages explained a significant amount of variation within the GEP fluxes (Table 2.2). The species and perennial stages interaction had no significant control on the variation in GEP (Table 2.2). The vegetative and elongation stages are characterized by more CO_2 uptake from the graminoid species compared to bare plots. However, within the reproductive stage, *B.syz, E.vag* and *S.cyp* had the highest CO_2 uptake. *E.vag* along with *C.can* and *S.cyp* showed greater CO_2 uptake compared to the other species during the dormant stage.

Variation in growing season net CO_2 sequestration fluxes was significantly explained by the graminoid species (NEE; Table 2.2), with *S.cyp* representing the greatest sequestration and bare plots representing the lowest. There was also a significant interaction between perennial stages and the species composition (Table 2.2, Figure 2.5c). Graminoid species showed greater CO_2 sequestration compared to bare plots during the vegetative and elongation stages. During the reproductive stage, *S.cyp* and *E.vag* showed greater CO_2 sequestration compared to other graminoid species and bare plots. The dormant stage was characterized by greater CO_2 sequestration from *E.vag, S.cyp* and *C.can*.

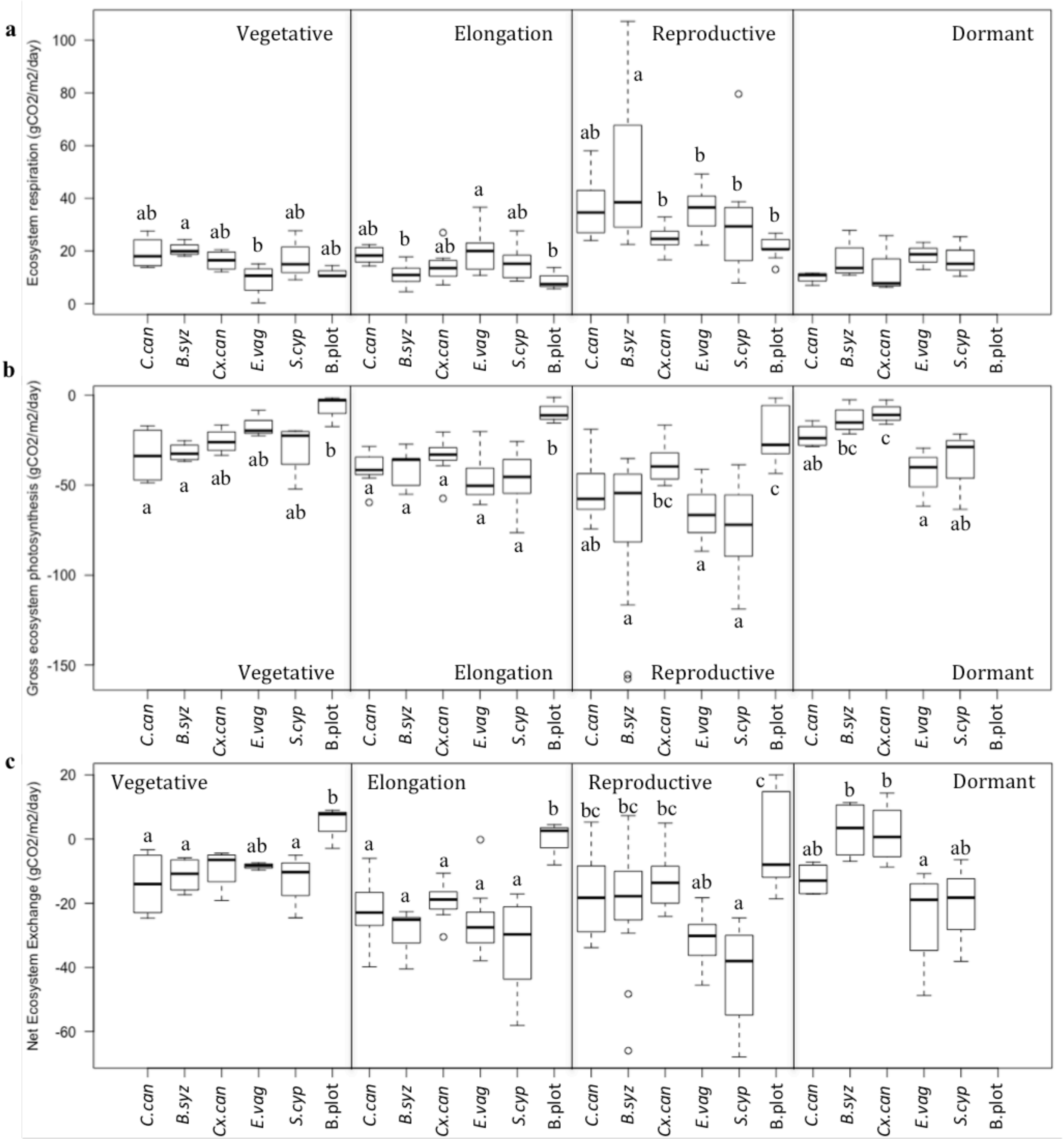

Figure 2.5 (a) Ecosystem respiration, (b) gross ecosystem photosynthesis, and (c) net ecosystem exchange per species according to the perennial stages. Gross ecosystem photosynthesis and net ecosystem exchange are based on measurements when the photosynthetically active radiation (PAR) is greater than 1000μmol m^{-2} s^{-1}. Median upper and lower quartile are shown with the boxes, error bars give standard error and points refers to outliers. Species are significantly different from each other when they do not share a common letter. Letters should only be compared within the same stage.

Table 2.2 Statistical analysis between the fluxes and the component measured using ANOVA and a pairwise comparison.

C-component	Factor	F value	p value
ER	species	$F_{5,17}=3.5$	0.02
	perennial stage	$F_{5,157}=15.3$	<0.001
	species*perennial stage	$F_{5,152}=0.8$	0.57
GEP	species	$F_{5,17}=8.9$	<0.001
	perennial stage	$F_{5,157}=8.2$	<0.01
	species*perennial stage	$F_{5,152}=1.5$	0.19
NEE	species	$F_{5,17}=9.3$	<0.001
	perennial stage	$F_{5,157}=0.2$	0.66
	species*perennial stage	$F_{5,152}=3.9$	<0.01
CH_4 flux	species	$F_{4,15}=0.95$	0.46
	perennial stage	$F_{3,113}=13.7$	<0.001
	species*perennial stage	$F_{12,101}=1.7$	0.09

2.4.3 Methane fluxes

Graminoid species was not found to be a controlling factor in CH_4 fluxes (Table 2.2). However, CH_4 emissions varied significantly between the perennial stages (Table 2.2, Figure 2.6). The dormant stage showed greater fluxes compared to every other stage and the reproductive stage had greater fluxes compared to the vegetative stage. Only within the dormant stage did graminoid species have varying CH_4 emissions with *E.vag* having significantly higher fluxes than all species except *S.cyp* (Figure 2.6), although the interaction between species and perennial stages was not statistically significant (Table 2.2).

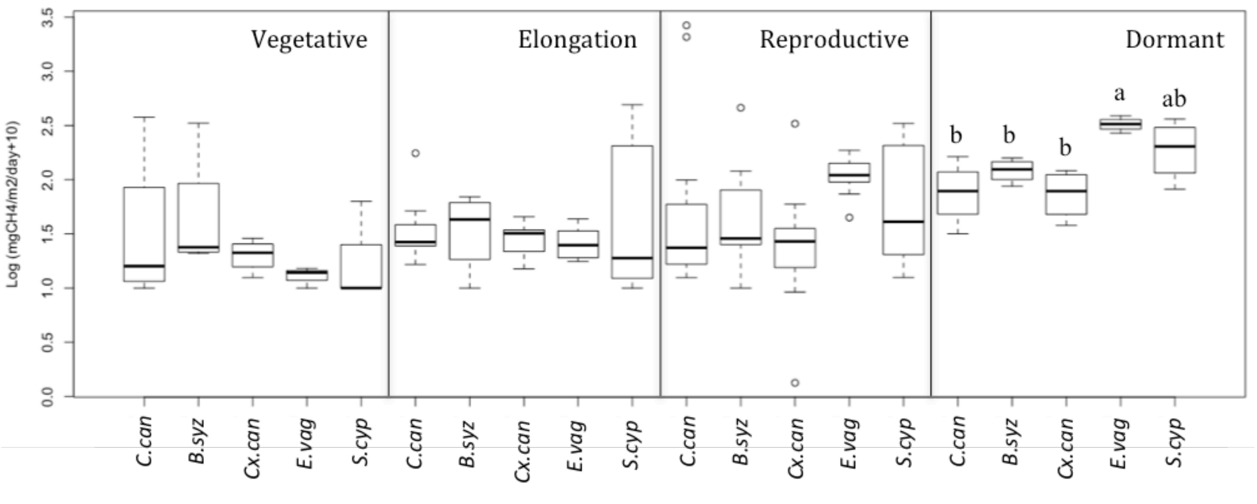

Figure 2.6 Log of methane fluxes per species according to the perennial stage. Median upper and lower quartile are shown with the boxes, error bars give the standard error and points refers to outliers. Species are significantly different from each other when they do not share a common letter. Letters should only be compared within the same stage.

2.4.4 Species distribution and biomass

In general, the species composition on site differed among locations. Graminoid species were recorded for 70.5% of the plots in the vegetation inventory. *B.syz, C.can, Cx.can, E.vag* and *S.cyp* were recorded, respectively for 2.9, 22.5, 37.1 57.9 and 10.2% of the total sample locations. Within the collars, the targeted species accounted for 30 to 100% of the cover within the plot. The plant height within the collars was found to be significantly different according to the species ($F_{4,15}$=22.1, p<0.001; Figure 2.7a) with *S.cyp* being the tallest. Similar observations were made across the site where the graminoid species explained the height of plants recorded ($F_{4.43}$=39.6, p<0.001; Figure 2.7b).

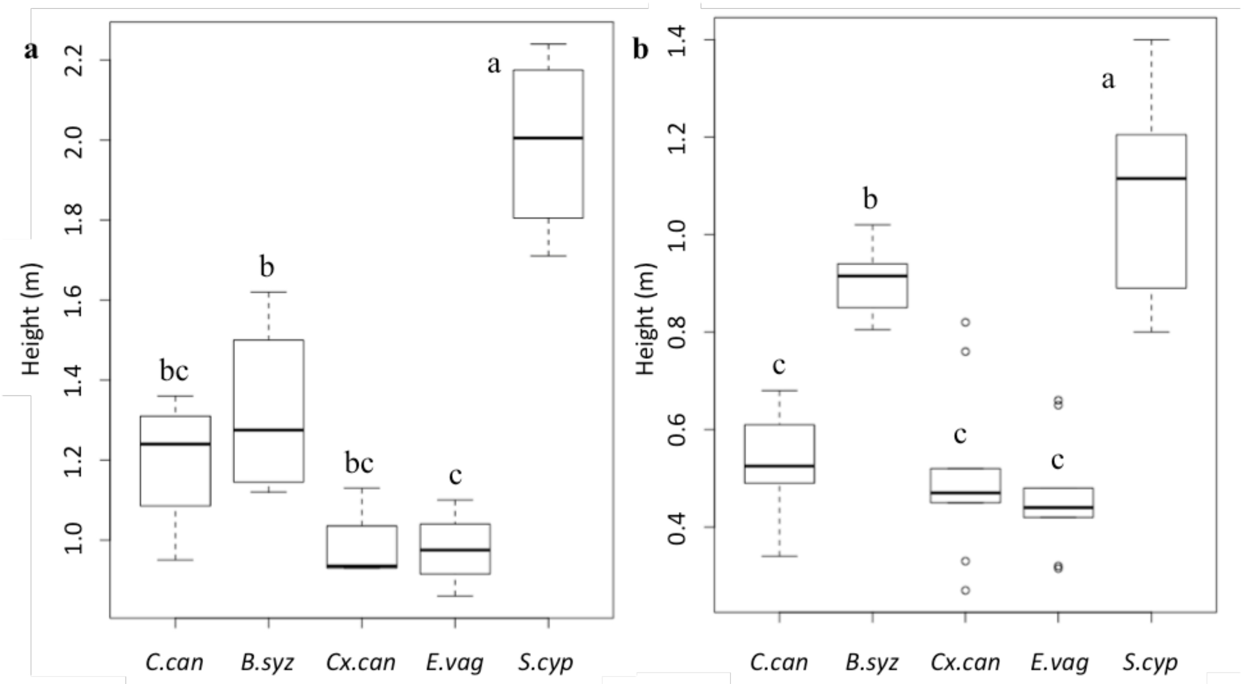

Figure 2.7 Plant height measured (a) in the collars and (b) on site. Median upper and lower quartile are shown with the boxes, error bars give standard error and points refers to outliers. Species are significantly different from each other when they do not share a common letter.

Plant aboveground biomass was significantly different among the species, with *S.cyp* and *E.vag* having the highest biomass (Figure 2.8a). Across the site, plant biomass was significantly related to plant height ($F_{1,43}=41.6$, $p<0.001$). Additionally, species type explained variation in the biomass of other species found within the sampling plots ($p=0.011$) with *B.syz* and *S.cyp* having the highest biomass of other species (Figure 2.8d). Also, plant biomass was significantly related to the litter biomass produced per species ($F_{1,44}=18.3$, $p<0.001$).

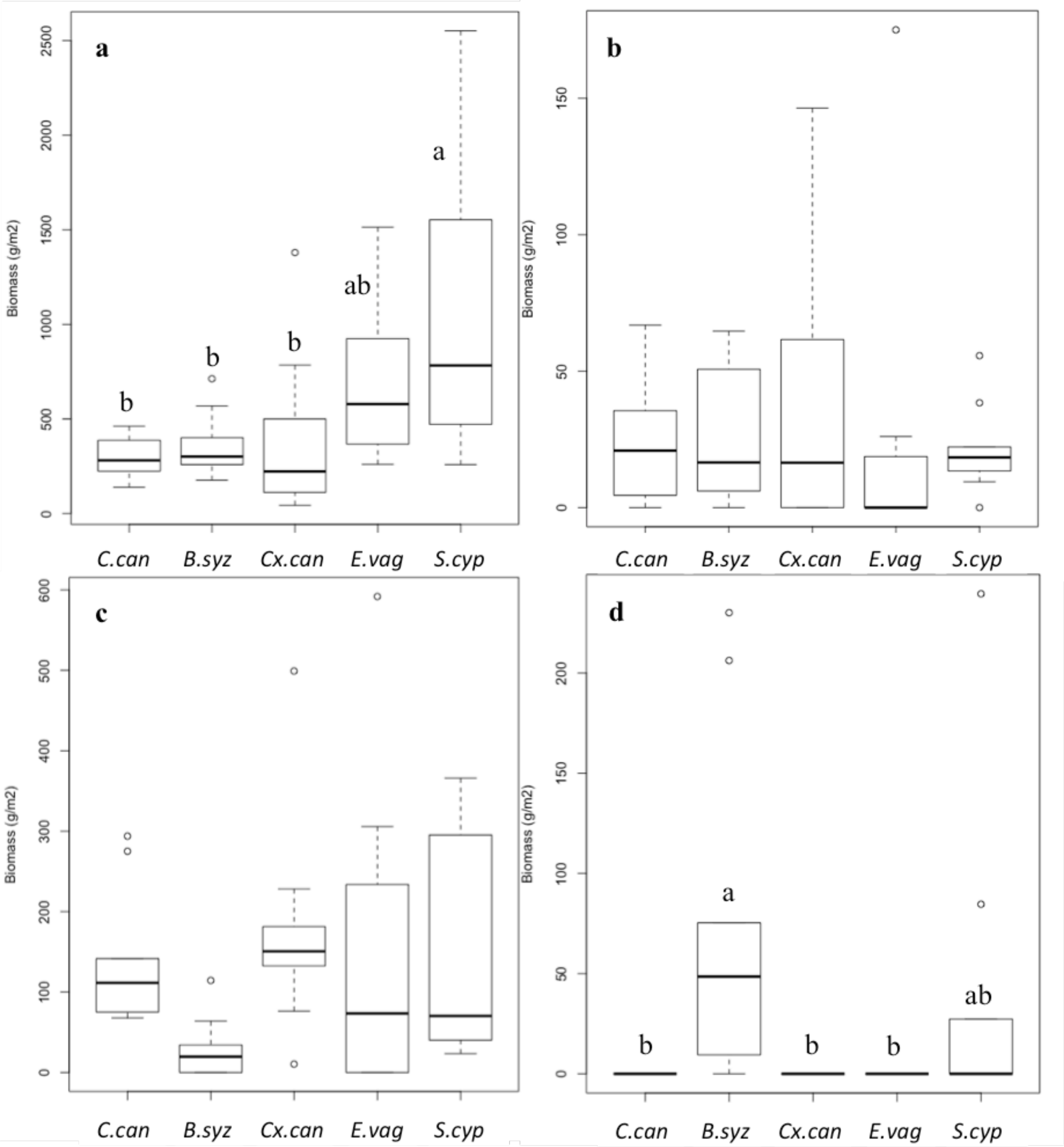

Figure 2.8 (a) Plant biomass, (b) moss biomass, (c) litter biomass, and (d) other species biomass according to species per species. Median upper and lower quartile are shown with the boxes, error bars give standard error and points refers to outliers. Species are significantly different from each other when they do not share a common letter.

The C:N in plant biomass was significantly different according to the species ($F_{7,9}$=13.5, p<0.001; Figure 2.9). *B.syz* had much higher ratios with a larger range compare to the other species. *C.can* showed the lowest ratios, while *Cx.can*, *E.vag* and *S.cyp* had ratios within a similar range.

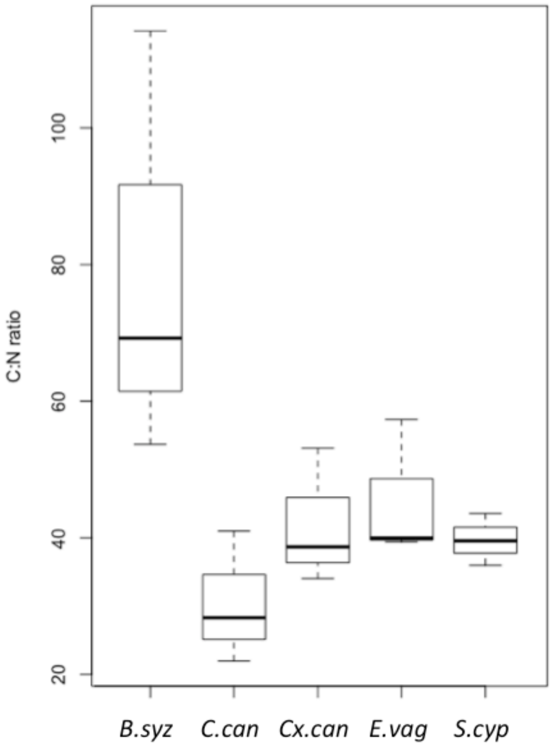

Figure 2.9 C:N ratio according to the species. Median upper and lower quartile are shown with the boxes, and error bars give standard error.

2.4.5 Controls on fluxes

The plant height explained a significant amount of variation in ER and GEP, when measured at the end of the growing season. As the plants increased in height, so did their CO_2 exchange (Table 2.3). Moss percentage cover within the collar was not a significant control on fluxes.

Soil temperature at each depth measured accounted for variability among the CO_2 fluxes (both ER and GEP). NEE was significantly related positively to the soil temperature at 15 and 20cm depth. Soil temperature at 20 and 25cm explained a significant amount of CH_4 fluxes variation (Table 2.3). Warmer temperatures stimulated higher ER, GEP, NEE and CH_4. The soil pH was a significant control on ER (Table 2.3).

Table 2.3 C-component fluxes controlling factors, including the plant growth form and the environmental conditions within the collars.

Factor	ER		GEP		NEE		Log CH_4	
	F value	p value	F value	p value	F value	p value	F value	p value
Plant productivity								
Plant cover	$F_{4.10}=0.6$	0.69	$F_{4.10}=2.3$	0.13	$F_{4,10}=1.1$	0.4	$F_{4,10}=1.5$	0.27
Moss cover	$F_{4.10}=0.9$	0.5	$F_{4,10}=1.9$	0.19	$F_{4.10}=0.5$	0.76	$F_{4,10}=2$	0.17
Plant height	$F_{4.15}=17.4$	<.001	$F_{4,15}=6.5$	0.0031	$F_{4,15}=2$	0.16	$F_{4,39}=1.4$	0.27
Soil temperature								
2cm	$F_{1,140}=35.3$	<.001	$F_{1,140}=20.4$	<.001	$F_{1,140}=0.5$	0.49	$F_{80,39}=1.2$	0.26
5 cm	$F_{1,140}=52.5$	<.001	$F_{1,140}=31.2$	<.001	$F_{1,140}=1.2$	0.27	$F_{74,45}=0.9$	0.73
10 cm	$F_{1,140}=57.4$	<.001	$F_{1,140}=40.3$	<.001	$F_{1,140}=3.5$	0.065	$F_{1,117}=1.7$	0.19
15 cm	$F_{1,140}=43.9$	<.001	$F_{1,140}=40.3$	<.001	$F_{1,140}=7.3$	0.008	$F_{1,117}=3.3$	0.07
20 cm	$F_{1,140}=36.6$	<.001	$F_{1,140}=36.5$	<.001	$F_{1,140}=7.9$	0.0055	$F_{1,117}=4.0$	0.048
25 cm							$F_{1,117}=4.5$	0.036
30 cm							$F_{65,54}=1.1$	0.35
Other controls								
WTD	$F_{1,147}=11.1$	0.0011	$F_{1,147}=0.9$	0.34	$F_{1,147}=4.9$	0.028	$F_{1,105}=12$	<.001
WTD*species	$F_{5,142}=1.5$	0.2	$F_{5,142}=0.9$	0.51	$F_{5,142}=0.3$	0.92	$F_{1,105}=12$	<.001
pH	$F_{1,145}=4.0$	0.047	$F_{1,145}=1.0$	0.31	$F_{1,145}=0.5$	0.47	$F_{1,115}=0.03$	0.86

2.5 Discussion

Plant functional types (PFTs) have been used to model vegetation feedbacks in ecosystem models, to reduce complexity (Laine et al., 2012; Chapin et al., 1996, Tuittila et al., 2013); however, our study supports the idea that graminoids differ enough at the species level to be considered individually, or within smaller groups, for restored peatland models. The five graminoid species evaluated in a restored peatland during the growing season had significantly different rates of CO_2 and CH_4 exchange, as well as variation in their height and biomass.

Restored peatlands are associated with higher species richness than natural sites, with a wider range of wetland species (Poulin et al., 2013). In general, with the exception of *Cx.can*, all species found within this study are commonly found in marshes of the Canadian prairie provinces (Lahring, 2003). *E.vag* and *S.cyp* were also recorded in bogs, while *C.can* and *Cx.can* were recorded in fens (Lahring, 2003). Despite the fact that plant colonization is often limited by resource availability, Cyperaceae and Gramineae species can successfully colonize undrained harvested sites (Graf et al., 2008; Strack et al., 2016). *B.syz* is sometimes used for wetland restoration and reclamation (e.g. Alaska; Wynia, 1983 and 2006), where it facilitates the transition of wetlands from mineral-based (marshes) to peat-based (fens) and provides a quick plant cover on site (Glaeser et al., 2015), as its germination is non-restrictive (Boe and Wynia, 1985). *C.can* thrives within saturated organic peat soils (Wynia, 2006) and is one of the species most associated with old successional sites for peatlands and marshes (Wilson and Keddy, 1985; Kellog and Brigham, 2002; Poulin et al., 2013). *Cx.can* is often recorded in the species pool within restored peatlands across Canada and abandoned peatlands in Europe (Strack et al., 2014; Graf et al. 2008; Salonen and Setälä, 1992) and proliferates within nutrient-poor systems (Graf et al., 2008). *E.vag,* widely distributed in North America (Aiken et al., 2007), is commonly found in restored peatlands (Poulin, 2013). *S.cyp* is largely found in undisturbed fens and abandoned extracted peatlands, such as undrained vacuum-harvested sites (Graf et al., 2008; Gagnon, 2017).

Despite their common colonization of extracted peatland sites, these species have significant differences in their plant growth form (e.g. biomass, plant height, C:N ratio). *S.cyp* was significantly taller than the other species recorded. *E.vag*, while not so different from *B.syz* and *Cx.can*, represented the shortest species. Despite differences in height, *S.cyp* and *E.vag* grew in dense tussocks, having higher coverage than the other species studied. Additionally, nutrient requirements and uptake may vary between graminoid species. The C:N ratio measured on site was much lower than the ratio of 92:1 reported from senescent tissue at Mer Bleue, a restored peatland in Quebec (Wang et al., 2014), except *B.syz* which had similar values. The *Cx.can*, *E.vag* and *S.cyp* C:N ratios were closer to the 50:1 reported for Arctic flora (Aerts et al., 2012), while for *C.can*, the C:N ratio falls into the range found for new plant material (Parton et al., 1988). This suggests that nutrient requirement varies between graminoid species, where *C.can* requires more nutrients and *B.syz,* the least.

Graminoids have been found to play an important role in carbon sequestration in restored peatlands (Strack and Zuback, 2013; Strack et al., 2016). Although the species studied had different plant growth forms, they all provided rapid plant colonization on the restored peatland and initiated the peat accumulating processes thus acting as an important control on the CO_2 and CH_4 exchange (Table 2.3). Species such as *E.vag*, are important for the initiation of carbon sequestration post-restoration (e.g. Tuittila et al., 1999). In contrast to previous studies (e.g. Strack et al., 2014; Strack et al., 2016), our study shows no relationship between the plant cover with NEE and ER. Our study supports the idea that graminoid species type is the main control on ER, GEP and NEE. Over the growing season, the highest ER mean was observed for *B.syz*, while *Cx.can* had the lowest CO_2 emissions observed. Similar observations were made with GEP, where *S.cyp*, along with *E.vag* and *B.syz*, had the greatest CO_2 uptake, while *Cx.can* had the lowest. However, the species effect was even more present when considering the net CO_2 sequestration for the growing season (NEE). *S.cyp* took up a significantly greater amount of CO_2 compared to the other species, along with *E.vag*. *C.can*, *Cx.can* and *B.syz* had similar CO_2 uptake, although *Cx.can* was not significantly different from plots with no vascular vegetation. Plant height explained a significant amount of variation in GEP and ER suggesting that the observed differences in growth form likely drive the species-level differences in CO_2 exchange.

The perennial stages were also an important indicator of changes in ER and GEP. Higher CO_2 sequestration and ER were found within the reproductive stage. The effect of the perennial stages combined with the species composition, controlled the net CO_2 sequestration from graminoids (NEE). ER increased under warm soil temperature and wet conditions; GEP increased with warm soil temperature and with tall and large plants, and NEE increased with warm soil temperature at depth, wet conditions and with tall and large plants. As WTD was correlated with ER and NEE and soil temperature with GEP, ER and NEE, local conditions under which species grow also affects differences in CO_2 exchange.

The vegetation community (Kao-Kniffin et al., 2010), soil temperature (Valentine et al., 1994) and the WTD (Tuittila et al., 2000; Strack and Zuback, 2013; Couwenberg and Fritz, 2012; Marinier et al., 2004) have been shown to control CH_4 fluxes in restored peatlands. In agreement with our findings, Tuittila et al. (2000) observed an increase in CH_4 emissions from *E.vag* when the WTD was raised. However, within our study, the WTD cannot alone explain the increase in methane emission since a shallow WTD during the elongation stage did not result in CH_4 fluxes as large as during the dormant stage. Soil temperature at depths of 20 and 25 cm were also found to explain a great amount of variation in CH_4 flux. It has been shown that within a habitat, plant biomass, soil temperature or WTD are not sufficient to explain the variation in CH_4 emissions, while species type can (Schimel, 1995; Kao-Kniffin et al., 2010; Bhullar et al., 2013). The aerenchymatic tissues within graminoids provide an internal CH_4 transport pathway from the rooting zone to the atmosphere (Whalen, 2005; Bhullar et al., 2013; Tuittila et al., 2000; Kao-Kniffin et al., 2010) with efficiency varying between species (Christensen et al., 2003). Root volume and surface biomass could also potentially explain CH_4 internal transport and high fluxes (Bhullar et al., 2013). As some species such as *E.vag* and *S.cyp* are known to be deep rooted (Marinier et al., 2004; GRET, 2016), and more likely to reach the anoxic zone, their high CH_4 emissions measured within our study could be related to the internal pathway for methane bypassing the oxidation zone (Bhullar et al., 2013).

Species physical traits can also influence soil microbial activity and metabolism for CH_4 production and consumption (Kao-Kniffin et al., 2010). The newly established graminoid species change the litter quality, which is easily degradable and is known to stimulate microbial activity through root exudates, enhancing CH_4 fluxes (Bohdálková, 2013). Species such as *Carex* spp. are a significant predictor of CH_4 emissions, where *Cx.can* would enhance CH_4 up to six times (Bohdálková, 2013). However, when comparing three wetland species, Strom et al. (2005) indicated that plant productivity did not predict fluxes, which does not agree with our results. Our results show that *E.vag* and *S.cyp* had the greatest above-ground biomass and the highest CH_4 emissions within the dormant stage (Figure 5 & 7). *B.syz*, *C.can* and *Cx.can* also shared a similar plant cover and CH_4 fluxes during the same period. This CH_4 flux increase towards the end of perennial stages also correlates with the CO_2 influx decrease from graminoids, which agrees with the findings of Tuittila et al. (2000) and Strack and Zuback (2013). As observed within this study, the high CO_2 uptake during the first perennial stages indicates carbon-rich soil levels for methanogenesis (Tuittila et al., 2000). However, as the plant's carbohydrate reserves are filled and irradiation decreases, the carbon fixed is then available for methanogenesis through senescence (Tuittila et al., 2000). Accordingly, many studies have shown that restored peatlands dominated with wetland species, such as graminoids, have large CH_4 fluxes (e.g. Strack and Zuback, 2013; Tuittila et al., 2000; Marinier et al., 2004; Kao-Kniffin et al., 2010; Bhullar et al., 2013).

As ombrotrophic systems were first minerotrophic systems, restoration including key minerotrophic species is a good indicator of a successful ecosystem rehabilitation (Graf et al., 2008). *Carex spp.* (including *Cx.can*) and *S.cyp* are good examples of proper conditions for the reintroduction of fen species (Graf et al., 2008). Although the species included in the present study had significant differences among themselves for CO_2 and CH_4 exchange, their establishment promotes rapid peat accumulating processes and promotes the reintroduction of important ecosystem services. Additionally, the mean pH observed from pore water under every graminoid species was $pH<5$, which is similar to a fen-bog transition and bog sites reported from Europe (Tuittila et al., 2013).

Although graminoid species are often considered as a single PFT (Frolking et al., 2010; Laine et al., 2012), my study shows that CO_2 and CH_4 exchange is species-specific. An increase in graminoid species cover resulted in an important increase in CO_2 sequestration and CH_4 emissions as shown by this study. Despite the idea that the species level is too detailed for Holocene peatland model (Tuittila et al., 2013), in the case of restored peatland, the species pool includes mainly the Cyperaceae and Gramineae families (Graf et al., 2008). This study shows how graminoid species should not be considered as a single PFT for restored peatland models, but species could be sub-grouped. We propose two main groups according to their biomass, plant cover and CO_2 sequestration during the season and CH_4 emissions towards the end of season: Highly Productive Species, including *S.cyp* and *E.vag*, and Moderately Productive Species, including *C.can*, *B.syz* and *Cx.can*. Although this study does not group all of the main graminoid species found in restored peatlands, it is a first guideline to model in detail the carbon balance of restored peatland in the first decades post-restoration.

2.6 Conclusions

I conducted measurements on five different graminoid species to evaluate if they should be considered as a plant functional type for vegetation-soil models. Graminoid species in a restored peatland were found to be significantly different from each other in their plant growth form, where *E.vag* and *S.cyp* had the largest plant cover. The species significantly controlled the CO_2 and CH_4 exchange during the study period, with *E.vag* and *S.cyp* sequestering higher rates of CO_2 sequestration and CH_4 emissions compared to *B.syz*, *C.can* and *Cx.can*. Therefore, graminoids should not be considered as a plant functional type in models. I propose two sub-groups of graminoids, according to their plant growth form and productivity. More research should be conducted on other graminoid species found in restored peatlands to evaluate the full range of CO_2 and CH_4 exchange.

Preface to Chapter 3

The previous chapter demonstrated the role of graminoid species for carbon uptake in a restored peatland, where species should be considered in smaller groups when identifying plant functional types for better carbon accumulation estimates in models within the years following restoration. This chapter introduces the novel combination of the hydrology gradient and graminoid species distribution within a restored peatland, to evaluate graminoid preferential ecological niche and evaluate whether carbon uptake differs under varying hydrological conditions. As some of the species were characteristic of different hydrological regimes, three species from the first manuscript were selected and also measured under drier conditions. Measurements were conducted over an area visibly different in species distribution and density. Therefore, this chapter seeks to determine the preferential water table for on graminoid distribution, and the implication of this spatial heterogeneity on the carbon exchange of different graminoid species.

Chapter 3: Influence of hydrologic conditions on carbon exchange from graminoid species in restored peatlands

3.1 Outline

Peatlands are ecosystems that are known to be net carbon sinks, the rate of which varies with the site's hydrology and plant community. Drainage and peat extraction alters elevation and peat properties and therefore has an impact on ecohydrological factors post-restoration. Spatial variability in water table position and chemistry could affect the vegetation distribution, and subsequently rates of carbon exchange. Graminoid species are known to be early colonizers post-restoration; however, individual species distribution and function on site according to water distribution is not well-quantified. Three graminoid species found under different water regimes were targeted in a restored peatland in central Alberta: *Calamagrostis canadensis* (*C.can*), *Carex canescens* (*Cx.can*) and *Eriophorum vaginatum* (*E.vag*). Quadruplicate plots were installed for each species in a 'wet' and 'dry' section of site. Carbon dioxide (CO_2) and methane (CH_4) exchange were measured biweekly from May to September, 2016. A vegetation inventory was conducted across the site. Within the south section of the site, a grid of wells and piezometers were installed and measured weekly to characterize the hydrology. Results indicate that the west section of site is characterized by a shallower water table position throughout the season. A shallower water table also promoted the establishment of graminoid species, particularly for total graminoid cover and *C.can*. The spatial variability of the water table position did not significantly control the CO_2 exchange from graminoids, but promoted the establishment of more species and thus more carbon sequestration overall. Methane emissions varied significantly between the sections of site and increased under the wet regime. The species controlled CO_2 exchange, but not CH_4. *E.vag* in the wet sequestered more CO_2 and emitted more CH_4. This preferential ecological niche for graminoid species impacts the CO_2 and CH_4 exchange in restored peatlands and should be considered when modeling land-atmosphere relations and carbon exchange.

3.2 Introduction

Species composition of a given ecosystem will drive plant-atmosphere interactions. However, the function of the plant community is subject to the physical and edaphic conditions of the given environment. By characterizing species composition and the environmental controls of ecosystem functions, it would be possible to better quantify the ecosystem services provided. As detailed in the literature, peatlands provide many important ecosystem services as they are important for climate regulation through carbon sequestration and storage, for water storage and filtration, and as habitats for wildlife (Bonn et al., 2014; Glenk et al., 2014; Joosten et al., 2012; D'Astous et al., 2013). Peatlands' species composition (e.g. *Sphagnum* spp.) and hydrological condition allows them to sequester a globally important amount of carbon dioxide (CO_2) and emit methane (CH_4) through slow decomposition processes resulting from saturated soils (Ward et al., 2013; Vitt, 2013). Over the Holocene period, peatland-atmosphere greenhouse gas exchanges have had a net cooling effect of ~0.5 W m^{-2}, according to paleoecological and biogeochemical estimates (Frolking and Roulet, 2007). By assessing the interactions between the inherent autogenic properties of peatlands, there is a possibility to model peatland growth and climate function (Frolking et al., 2010; Belyea and Baird, 2006; Dise, 2009). Frolking et al. (2010) have developed the Holocene peatland model (HPM) to investigate the climate ecosystem services from natural peatlands. HPM simulates northern peatland development by considering three major components for peat accumulation: hydrology, plant communities and peat properties (Frolking et al., 2010). The hydrology and peat properties are assumed to be the main control on vegetation composition and productivity (Frolking et al., 2010; Laine et al., 2012). As HPM simulates the long-term carbon and water dynamics of natural peatlands, it may need modification to account for the impact of disturbance on the driving controls for the peat accumulation processes.

Horticultural extraction of peatlands has been practiced over the past decades in Canada (CSPMA, 2017b). The removal of the vegetation layer and drainage of the site alters the ecological and physical conditions affecting ecosystem services. Peat extraction changes the hydrology of the site (Price et al., 2003), where the drainage and extraction of peat also affects nutrient dynamics and microbial communities (Andersen et al., 2013; Macrae et al., 2012). The resulting vegetative and hydrologic conditions are unsuitable for *Sphagnum* moss spontaneous regeneration (Price, 1996; Quinty and Rochefort, 2003). As degraded peatlands lack many functions of undisturbed peatlands, the Convention on Wetlands promotes peatland restoration with a goal to reach climate and biodiversity targets (Bonn et al., 2014; IPCC, 2013; Joosten, 2011).

To restore the ecosystem, the Moss Layer Transfer Technique (MLTT) is often used in post-production management (CSPMA, 2015). Developed to recover moss species and biophysical conditions, it promotes fast recovery. However, even following restoration, the effect of drainage and extraction on peatland hydrological function persists (e.g., McCarter and Price, 2015). By removing the surface layer (acrotelm) and exposing the more decomposed peat (catotelm; Ingram, 1978), peat extraction impacts widely the abiotic controls for restoration. Indeed, the capacity for water storage is significantly altered, as the more decomposed peat has smaller pores and a lower specific yield (Price et al., 2003). A lower specific yield also indicates a high water retention capacity, but results in greater water table (WT) fluctuations and a reduction in shallow WT frequency (Price et al., 2003; Lindsay, 1988). Therefore, plant colonisation will be favourable to species that are adapted to WT fluctuation, such as deep-rooted species (Schouwenaars, 1990; Lumiala, 1944; Välirante et al., 2007). Despite the effort of MLTT for quick moss establishment post-restoration, the new conditions on site are favourable to the establishment of vascular plants, including mainly graminoid species (Graf et al., 2008; Poulin et al., 2012). The graminoid species distribution across the restored site varies, as the optimal WT conditions vary among species (Lumiala, 1944).

An increase in vascular plant cover will also alter carbon accumulation processes compared to natural systems. Besides, extraction itself will also alter the CO_2 and CH_4 exchange across the site, largely due to drainage (e.g., Waddington and Price, 2000). Graminoid growth form and highly labile litter will impact the carbon uptake via photosynthesis, and indirectly, the release of carbon through decomposition (Dorrepaal, 2007; Del Giudice and Lindo, 2017; Bohdálkova et al., 2013). Therefore, graminoids are important for the initiation of CO_2 uptake following restoration and for CO_2 sequestration (Strack et al., 2014; Tuittila et al., 1999). However, the establishment of graminoids species can lead to important methane (CH_4) emissions, as graminoids provide a transport pathway from the anoxic zone (Marinier et al., 2004; Strack et al., 2014; Tuittila et al., 2000; Kao-Kniffin et al., 2010; Bhullar et al., 2013; Whalen, 2005).

Spatial variability in carbon exchange and plant community distribution in natural peatlands is mainly controlled by the water table position and the nutrient status (Laine et al., 2012; Frolking et al., 2010). While these same controls should also dominate in restored peatlands, plant species may occupy wider niches (e.g., *E.vag* in Campbell et al., 2003); defining the relationship between vegetation and productivity and hydrologic controls on this relationship can help modellers to characterize the carbon exchange within restored peatlands. Carbon modelling and measurements depend on the vegetation composition and its distribution, often related to the WT position (Bubier et al., 2006). Although graminoids are usually considered as a single plant functional type (PFT), they represent the main vegetation on site in most restored peatlands (Graf et al., 2008; Poulin et al., 2012) and individual species may respond differently to hydrologic conditions.

As individual graminoid species often grow under specific hydrologic conditions in undisturbed peatlands (Payette and Rochefort, 2001), determining hydrologic impacts on carbon exchange of individual species is difficult. Restored peatlands can provide this opportunity; however, we are not aware of any studies that have characterized the control exerted by the spatial variability of the hydrology on individual graminoid species distribution and their CO_2 and CH_4 exchange within restored peatlands. Therefore, this study aims to evaluate graminoid distribution and productivity relative to water table position in a restored peatland, and quantify the impact of different water levels regime on the CO_2 and CH_4 exchange of several graminoid species.

3.3 Methods

3.3.1 Study site

Data were collected in a restored ombrotrophic bog, 17 km southeast of the town of Entwistle in central Alberta, Canada (53°27’26”N, 114°53’04”W; Appendix 1, Figures A1 and A2). The study area was restored with the Moss Layer Transfer Technique in autumn and winter of 2012, after 12 years of active extraction. Data collection was conducted in August 2015 and from May to September 2016. Mean annual temperature and precipitation (1981-2010) for Entwistle are 3.5 °C and 550.6 mm (77% rainfall), respectively (Environment Canada, 2017). The normal mean temperature and precipitation from May to September is 13.5 °C and 77.5 mm (1981-2010 normal; Environment Canada, 2017).

In August 2015, the southern part of the study area was selected as it had a clear hydrologic gradient and suitable graminoid species diversity and density. More precisely, the study area was situated on the southern part of the site, between of two eddy covariance towers (seperated by 170m) already installed on site, which represented an area of 6 ha. In order to quantify the water distribution on site, standpipe wells were installed in a systematic grid and were measured weekly from May to September 2016. To quantify the species pool, a vegetation indentification was conducted in August 2015 to identify the graminoid species on site. Within the study area, three graminoid species were representative of the species pool and were present in both 'wet' and 'dry' sections of the site: *Calamagrostis canadensis* (*C.can*), *Carex canescens* (*Cx.can*) and *Eriophorum vaginatum* (*E.vag*). Quadruplet plots were installed in the same period for each graminoid species within each 'section' on the site.

3.3.2 Hydrology

Five transects of PVC standpipe wells (~1.5-2 m high and 2 cm diameter) were installed in the site to characterize the hydrology across the study area (Figure 3.1). A central transect (C) was first installed between two eddy covariance towers with the direction east-west for 360 m. Along this transect, 1.5 m PVC pipes were installed every 10 m, for a total of 36 wells. Four additional transects, parallel to the central one, were installed with two north (N1 and N2) and two south (S1 and S2). Wells were installed to make an equidistant grid according to transect C. Two transects were installed between the central transect and each of the eddy covariance towers (N1 and S1). Those transect of 1.5 m PVC pipes were installed every 20 m. N1 had a total of 17 wells, while S1 had a total of 18 wells. Two additional transects were installed 10 m outside the eddy covariance towers (N2 and S2), where the wells were distanced at 20 m. N2 had a total of 17 wells, while S2 only had 14 wells due to clay soil on the east part of the transect. The wells representing the start and end of the transects were recorded with a GPS (eTrex Venture HC, Garmin Ltd, USA; up to 3-5 m horizontal accuracy). The water table (WT) position was measured weekly. To measure the precipitation over the growing season, a tipping-bucket rain gauge (TE525M, Texas Instruments, Texas, USA) was on a meteorological station adjacent to the

SBW eddy covariance tower. Continuous measurements of the WT position were conducted with a levelogger (Levelogger Edge, Solinst, Ontario, Canada) installed in the standpipe adjacent to the SBR eddy covariance tower.

In addition to the wells, six piezometer nests were installed next to specific standpipes in order to estimate subsurface water flow. Each piezometer had a screen length of 20 cm and this opening was centred at depths of 0.5, 1.0 and 1.5 m at each nest. Satellite imagery suggested the presence of wetter conditions along a corridor running southwest to northeast through the study area. Two different 'lines' compromising three piezometers nest were installed to evaluate water movement across this feature (Figure 3.1). Each piezometer nest location was recorded with the handheld GPS (eTrex Venture HC, Garmin Ltd, USA; up to 3-5 m horizontal accuracy). Measurements were conducted at the same time as the WT.

Ground elevation was determined with a survey conducted in August 2016. The survey was conducted with a fully automatic self-levelling laser (Spectra Precision LL300, Trimble, California, USA) with a laser receiver (Spectra Precision HL450, Trimble, California, USA; numeric display of ±40 mm). The laser level was installed on site and set as the arbitrary datum and geolocated with the handled GPS (eTrex Venture HC, Garmin Ltd, USA; up to 3-5 m horizontal accuracy). From there, ground elevation at each installed well was measured. Elevation was then transformed according to sea level from the arbitrary datum position above sea level.

3.3.3 Vegetation distribution

In August 2016, a vegetation inventory was conducted across the study area to determine species distribution. To evaluate the species composition, a 1 m x 1 m quadrat was used to estimate vascular plant cover. Each plant group and graminoid species percentage cover was estimated visually and recorded. To estimate the moss cover establishment, 0.25 m x 0.25 m quadrats were used and sampled in the southwest corner of the main quadrat.

Vegetation cover was estimated along east-west transects, where quadrats were surveyed along these transects. To have intensive cover estimates of the study area, between the two eddy covariance towers, transects were laid out every 10 m and quadrats were surveyed every 10 m along these transects for high density (Figure 3.1). Two additional transects of 10 m were surveyed north of the northeast eddy covariance tower. Four transects, north and south of the initial grid, were distanced by 20 m and quadrats surveyed every 20 m. Outside of those transects, the rest of the site was surveyed with transects and quadrats every 30 m for general estimate of species establishment (Figure 3.1). For quality control, the first transect was conducted by all surveyor to agree on percentage estimation. Each point surveyed along transects were recorded with a GPS (eTrex Venture HC, Garmin Ltd, USA; up to 3-5 m horizontal accuracy) and associated to the survey data set for spatial analysis.

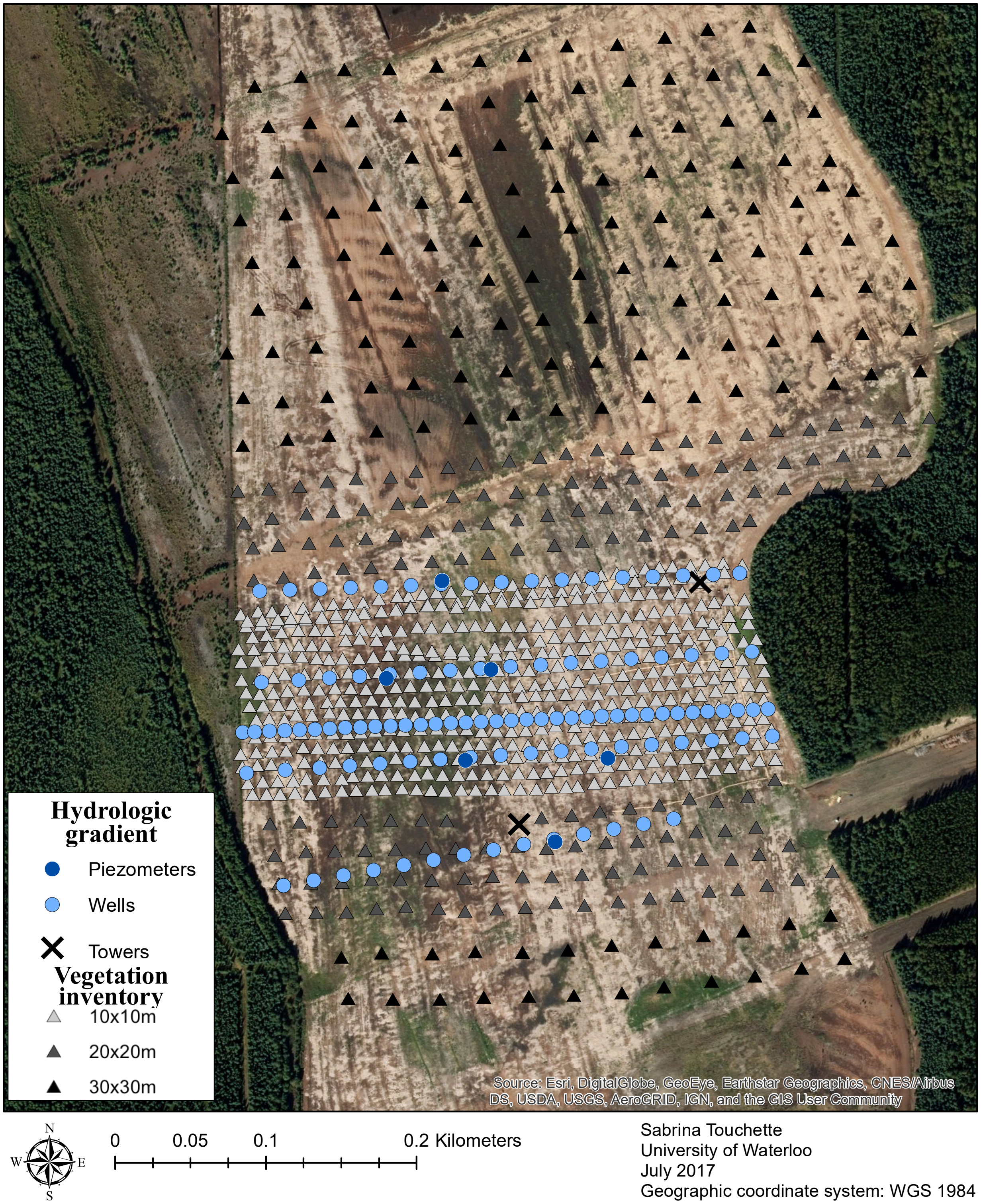

Figure 3.1 Map of the wells and piezometers distribution on site. Wells beginning and end of transect, and piezometers were taken with the GPS. Other points of the wells transect were estimated in GIS with constructed tool.

3.3.4 Plant biomass and litter decomposition

Aboveground biomass and litter decomposition were measured in wet and dry sections of the site. The biomass survey was conducted in August 2016. Biomass of target species was collected from specific sections of the site to assess the impact of the hydrology on the plant biomass. In both cases, aboveground biomass was collected from a 25 cm x 25 cm square placed on the target species. The surface plant material was cut to the ground surface and placed in labelled paper bags. Samples were sent to the Wetland Soils and Greenhouse Gas Exchange Lab at the University of Waterloo where they were individually dried in aluminum foil dishes for a period of 48 h at 60 °C. Their final weight was measured with a scale of 0.01 g precision and expressed as g m^{-2}. In total, the biomass survey of 2016 had a total of 10 samples per species, with five per section.

To determine the decomposition rates two different methods were used that could be later compared: litterbags and the tea bag index (TBI, Keuskamp et al., 2013). Using the three target species, *C.can, Cx.can and E.vag*, six litterbags were constructed from 1 mm mesh. At both the wet and dry locations, triplicate litterbags filled with litter from each species were buried horizontally around 5 to 8cm in the ground for a period of one year (365 days; August 22, 2015 – August 22, 2016). The Tea Bag Index (TBI) was measured at the same locations by burying commercially available Lipton Green tea and Rooibos tea pairs as representative of dead plant material (Keuskamp et al., 2013). The tea bags were buried for a period of 90 days (May 24 – August 22, 2016) at 8 cm deep, where environmental conditions are expected to be more stable (Keuskamp et al., 2013).

Plant material from the biomass and litterbag samples was used to estimate the carbon to nitrogen ratio for each species on triplicate samples. To remove any inorganic carbon contamination, litterbag plant material was acid washed with HCl 5% for 90 minutes at 50-60 °C and then rinsed four times with nano-pure water. All samples were dried for 48 hours at 60 °C in individual aluminum foil dishes in a mechanical convection oven (Heratherm OMS100, Thermo Scientific, Massachusetts, USA). Approximately 1.2 mg of plant material was extracted for each sample, on which the carbon and nitrogen content was determined by combustion (4010 Elemental Analyzer, Costech Instruments, Italy) in the Environmental Isotope Laboratory at the University of Waterloo and used to calculate C:N ratio.

3.3.5 Carbon gas exchange

Carbon dioxide and CH_4 measurements were conducted from May to September 2016. Both were measured with the closed vented chamber systems on collars extending below the rooting zone (~20cm; Alm, 2007; Appendix A1, Figure A3). Sampling was conducted once the chamber was placed on the groove of the collar and sealed with water. Measurements were conducted biweekly during the growing season of 2016, for a total of 8 measurements. For all measurements conducted during the sampling period, the WT position and the soil temperature profile to a depth of 20 cm for CO_2 and 30 cm for CH_4, at 5 cm intervals were recorded.

Plant-atmosphere CO_2 exchange was measured with a transparent chamber with dimensions of 60 cm x 60 cm x 30 cm (108 L). A cooling system was added in order to reduce fluctuations of temperatures inside the chamber. A cooler with ice was attached to the chamber and water was pumped through a copper coil installed along one side inside the chamber. Two battery-operated fans inside the chamber pushed the cold air from around the copper coil and mixed the chamber headspace air. Following chamber closure, the CO_2 concentration of the headspace was recorded every 15 seconds for 2 minutes with a portable infrared gas analyzer (IRGA; EGM-4 Environmental Gas Monitor, PP Systems, Massachusetts, USA) equipped with a sensor to measure photosynthetically active radiation and temperature inside the chamber. To estimate net ecosystem exchange (NEE), measurements were first conducted in prevailing light conditions and then under a series of shades. To simulate ecosystem respiration (ER) the chamber was covered with an opaque shroud. Gross ecosystem photosynthesis, representing the total amount of carbon fixed by vegetation (Lovett, 2006), was determined from the difference between NEE and ER. The flux of CO_2 was determined from the linear change in CO_2 concentration during chamber closure corrected for volume and temperature inside the chamber.

Plant-atmosphere CH_4 exchange was measured with an opaque chamber (108 L), with two battery-operated fans inside the chamber to mix headspace air. Following the chamber closure, four 20 mL samples of chamber headspace air were drawn in syringes at 5, 15, 25 and 35 minutes. Samples were stored in pre-evacuated sealed vials (Exetainers, Labco Ltd, UK). The temperature inside the chamber was also monitored during the sampling period with a thermocouple inserted inside the chamber. Ambient air samples were taken throughout the day and used to estimate CH_4 concentration at time of chamber closure. The CH_4 concentration was determined in the laboratory with a gas chromatograph (GC-2014 Gas Chromatograph, Shimadzu Scientific Instruments, Kyoto, Japan) equipped with a flame ionization detector. Methane flux was determined by the linear change in concentration over time and corrected with the volume and temperature of the chamber. Data were quality controlled considering that measurement of CH_4 concentration at 5 minutes post-closure higher than 5 ppm followed by a decline or erratic changes in concentration were likely associated with ebullition events and removed from the data set. In cases where the 5-minute concentration was less than 5 ppm and subsequent sample concentrations changed less than the precision of the gas chromatograph (~10%), a value of 0 for flux was assigned. Measurements assessed with a 0 or with a linear change with $R^2>0.70$ were kept in the data set, which resulted in the loss of 8.9% of data.

3.3.6 Data analysis

Using the elevation survey and weekly measured water table data, Surfer 14 (Golden Software, LLC, Colorado, USA) was used to produce ordinary Kriging interpolation of WT for each week. The grid data of the wells absolute WT position was used for an interpolation with Kriging linear variogram model with a default slope of 1, anisotropy ratio of 1 and anisotropy angle of 0. The same interpolation tool was used for piezometer data along the two piezometer lines.

A spatial analysis was conducted using ArcGIS 10.5 (ESRI 2016, California, USA) to compare vegetation inventory and hydrology data. First, a map of the wells along the transects was generated with the approximate distance between wells and points created through the construction tool, according to the accuracy of recorded points. Secondly, a multivariate interpolation of the WT position was conducted with inverse distance weighting (IDW) on the geolocated points, as the sampling was dense and for the simplicity of the tool. Interpolation using Kriging was also completed and gave nearly identical patterns to IDW. The seasonal average of the WT position relative to the surface was used in the interpolation. Third, the vegetation survey georeferenced points were overlayed on the IDW surface, where a new shapefile was created with the points covering only the area of the generated WT surface. The WT depth interpolation was spatially joined to the vegetation inventory, where a resulting estimated WT levels were given for each vegetation inventory plot and used for further statistical analysis. The association between the vegetation inventory and the mean WT depth was evaluated with a correlation analysis. The vegetation data was not normally distributed (Shapiro-Wilk test, $p<0.001$), due to the large number of zeros indicating absence of the target species. Therefore, Spearman correlation was used.

To meet normality and equal variance conditions, the CH_4 flux data was log(x+10) transformed for statistical analysis. Controls on variation in NEE, GEP, ER and CH_4 fluxes were determined with a linear mixed-effect model comparison, including collar as the random effect to account for repeated measures, where a one-way analysis of variance (ANOVA) was conducted with graminoid species and section of the site. To assess the control of species and section of site, a two-way ANOVA, including collar as a random effect, was used for NEE, GEP, ER and CH_4 fluxes. Similarly, a two-way ANOVA was used on biomass, litter accumulation and C:N ratios where comparisons were made with the species and section of site, accounting for the sampling location. When a significant effect was found with the ANOVA analysis, Tukey pairwise test for multiple comparisons was used (packages: 'TH.data' (Hothorn, 2017), 'survival' (Therneau, 2015), 'multcomp' (Hothorn et al., 2008), 'ggplot2' (Wickham, 2009), 'ggpubr' (Kassambara, 2017)). All statistical analysis was conducted using the statistical program R (version 3.2.3, R Core Team 2013, Vienna, Austria), with $\alpha=0.05$ used to evaluate significance.

3.4 Results

3.4.1 Hydrology

The water table measured throughout the summer varied across the site with up to 60 cm difference (relative to the surface) between the east and west parts of the site. The east end of the site was much drier than the west (Figure 3.2). Based on the WT position measured at each of the carbon gas flux collars WT in the dry section was -36.4(±20.7) cm and significantly drier ($F_{1,22}=140.8$, $p<0.001$) than the wet section of -8.1(±16.7) cm. However, all wells were highly responsive to rainfall events (Figure 3.2). On the contrary, when evaluating the absolute water level (AWL), wells in the dry section had a higher water level than the wet section. Accordingly, this difference between the sections indicates that the ground surface was not level and the east section of the site is more elevated than the west section. When interpolating the AWL position, it is possible to identify the surface water flow directions. As shown in Figure 3.2, the AWL position fluctuates across the season in response to rain events. For example, week 21 (Figures 3.2b and 3.3a) had high WT levels across the site with low variation between the contour lines. The south center section showed a much deeper AWL. During week 29 (Figures 3.2b and 3.3b), representative of a median AWL for the season, the east section of the site had AWL at least 50 cm higher than the west section. This difference between the sections of the site is even greater during week 33 (Figures 3.2 and 3.3c). For every week measured, the east part of the site had a higher AWL with a gradual decrease in level to the west end of the site indicating that water flows from east to west, further contributing to the shallow WT relative to the surface in the wet (west) section.

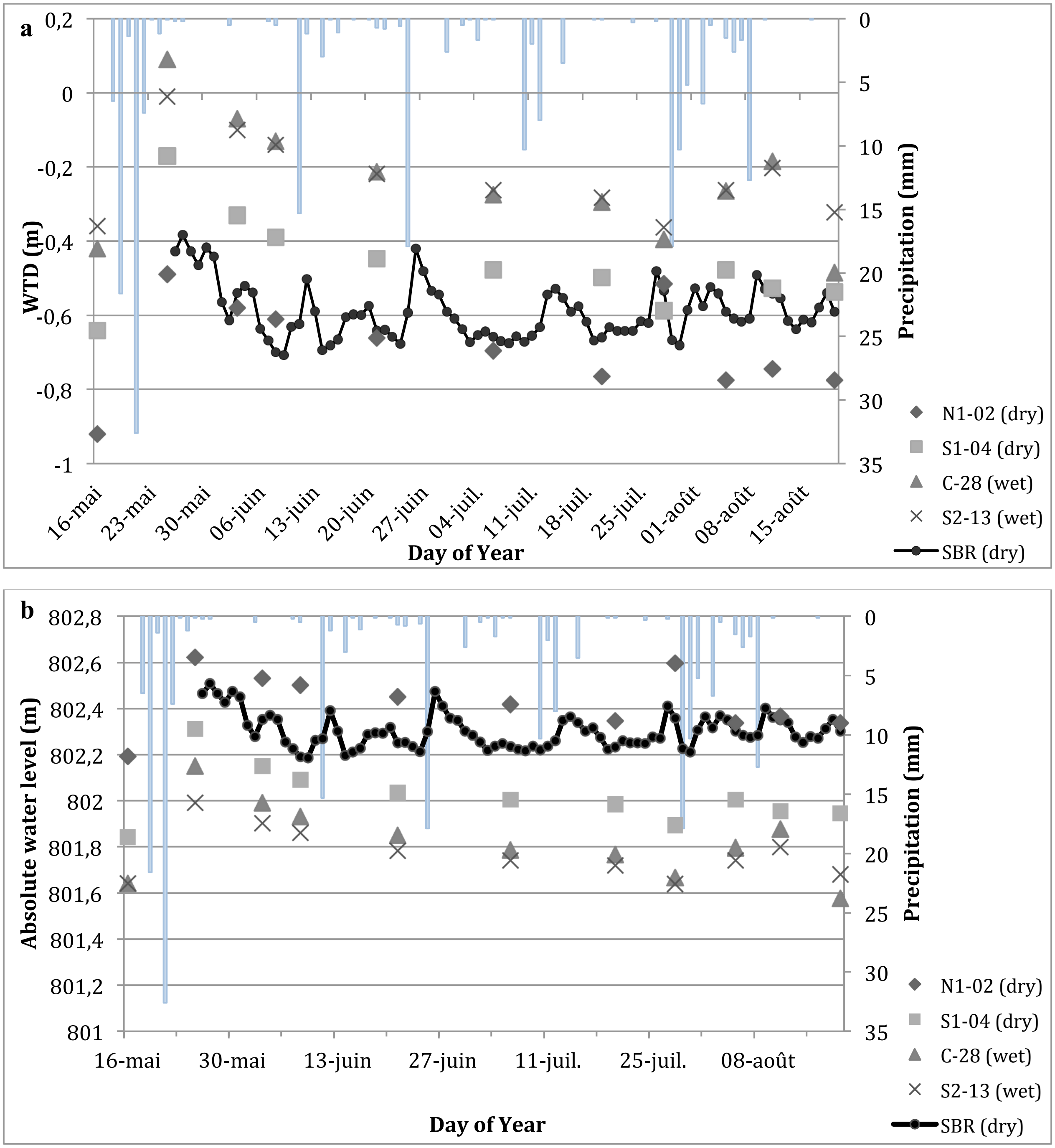

Figure 3.2 (a) WT position from the ground surface, and (b) Absolute water level (AWL) as a function of the week measured and the section measured. SBR represent the levelogger recording the mean WT position for each day measured. Precipitation and water levels are represented according to the day of year.

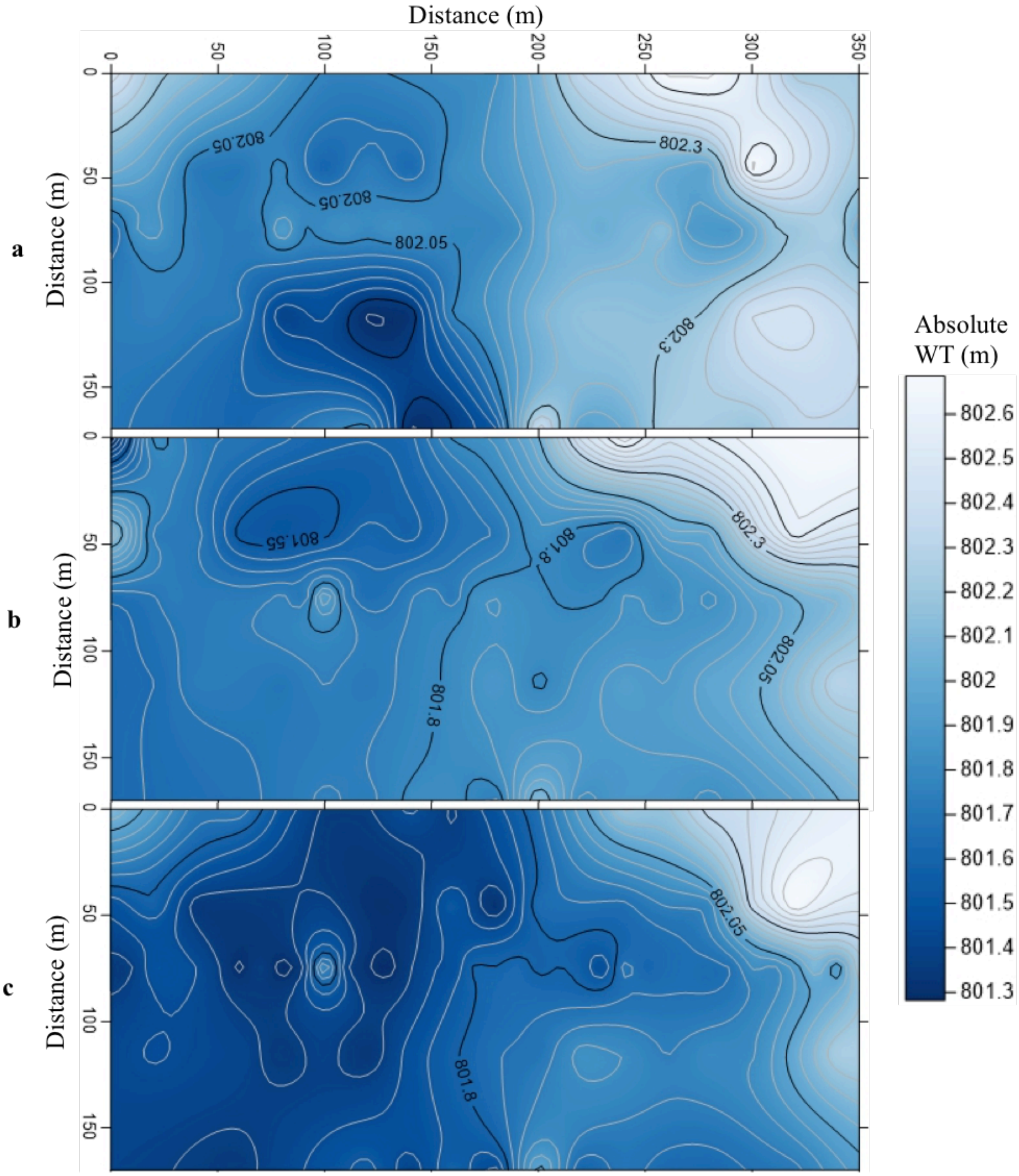

Figure 3.3 Absolute WT position interpolation across the study area for week 21 (a), 29 (b) and 33 (c). The interpolation takes into consideration the distance between wells along the x- and y-axis. The 0m on the x-axis represents the west, and 350m of the east; 0m on the y-axis is representative of the north and 170m of the south measurements.

The piezometer nests measurements from both 'lines' show water recharge in the profiles for all nests (Figure 3.4). The groundwater flow direction indicates a very slight lateral flow northwest-southeast, which is supported for every week measured and under different water regimes.

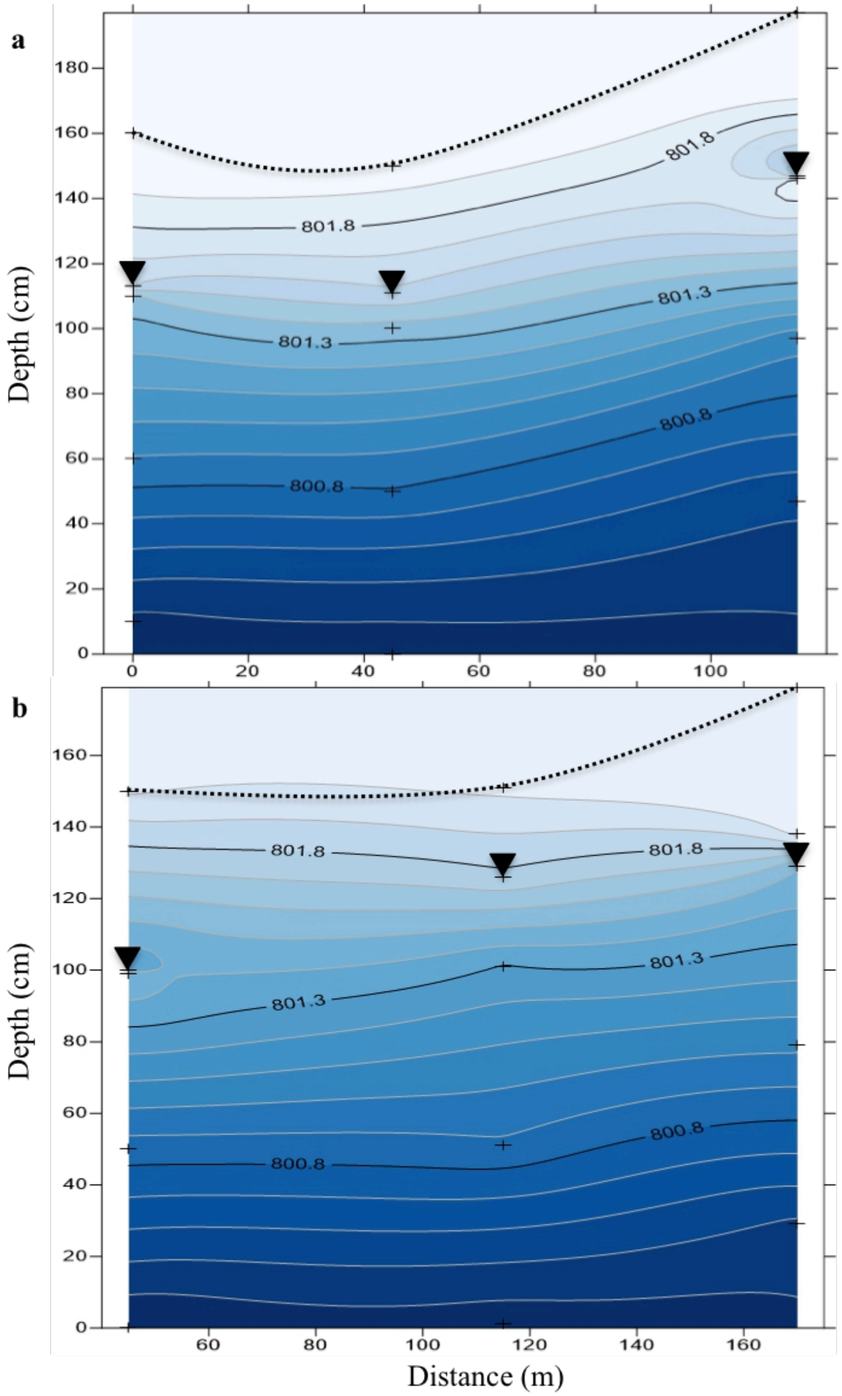

Figure 3.4 Piezometer nests (a=east; b=west) interpolation of the AWL during week 29. Each nest represents the soil profile over their distance on site. The 0m on the x-axis represents the northwest, and is directed to southeast. Each '+' sign represents a piezometer position along the depth profile. The dash line represents the soil surface.

3.4.2 Graminoid species distribution

The 2016 vegetation inventory indicates the establishment of tree, shrub, herbaceous and moss species. Herbaceous plants (largely graminoids) and mosses represented the groups with the most species found on site (Table 3.1).

Table 3.1 List of species observed on site during the 2016 vegetation inventory and classified with their main group.

Trees and shrubs	**Ericaceous shrubs**	**Herbaceous**	**Mosses**
Betula papyfera	*Andromeda glauca*	*Beckmannia syzigachne*	*Sphagnum angustifolium*
Populus tremuloides	*Rhododendron groenlandicum*	*Carex canescens*	*Sphagnum magellanicum*
Larix laricina		*Carex section ovales*	*Aulacomnium palustre*
Picea sp.		*Calamagrostis canadensis*	*Phytostochum creberrinum*
Salix spp.		*Poa palustris*	*Pleurozium schreberi*
Rubus idaeus		*Scirpus cyperinus*	*Leptobryum pyriforme*
		Eriophorum vaginatum	*Polytrichum strictum*
		Epilobium angustifolium	*Pohlia nutans*
		Ranunculus acris	*Mylia anomala*
		Trifolium sp.	*Marchantia polymorpha*

Graminoid cover varied across the study site increasing from 0-10% in the east (dry) section of the site to 90-100% to the west (wet) section (Figure 3.5a). *C.can* shows signs of establishment as a monoculture (Figure 3.5b). Its cover increased greatly in the center of the north part of the site and the west in the south part of the site. On the other hand, *Cx.can* was established across the site, with the exception of the southwest section, and its cover was generally between 0-20% across the whole site (Figure 5c). *E.vag* was also distributed across the site, with variable cover and limited presence in the dense graminoid pool in the southwest center section (Figure 3.5d).

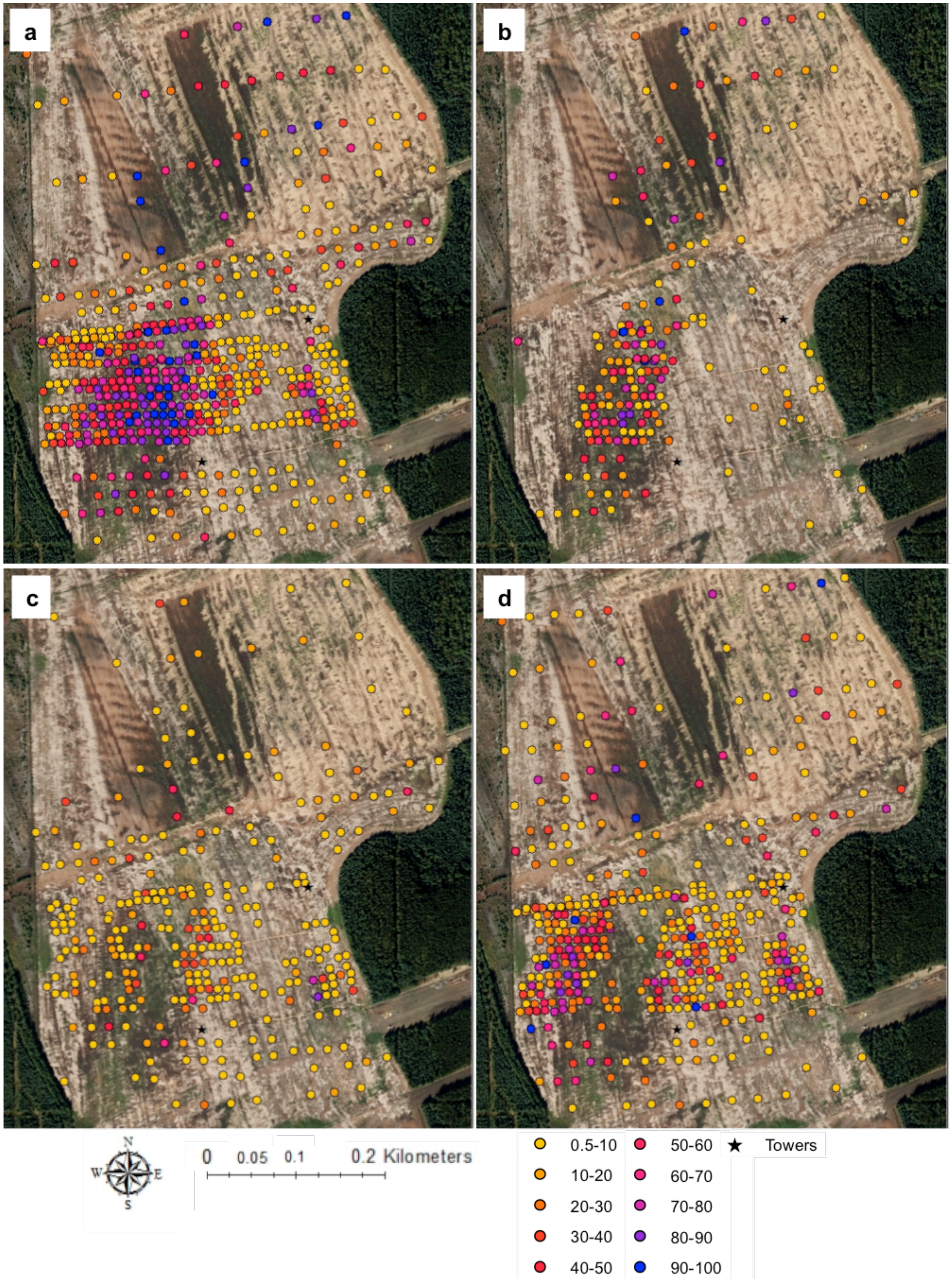

Figure 3.5 (a) Total graminoids, (b) *C.can*, (c) *Cx.can* and (d) *E.vag* spatial distribution and percentage cover across the site.

Overlaying the vegetation survey on the WT interpolation shows disparity in each species' coverage (Figure 3.6). Graminoid cover is highest in the wet section of the site. Similarly, *C.can* is mainly established on the west side of the site and its percentage increases in wet areas. Contrastingly, *E.vag* and *Cx.can* are absent in the wettest areas. The mean percentage cover of the studied species also varied across the site, with 40.9(±32.4)%, 33.2(±28.1)%, 27.0(±28.8)% and 11.2(±14.7)% for all graminoids, *C.can*, *E.vag* and *Cx.can,* respectively.

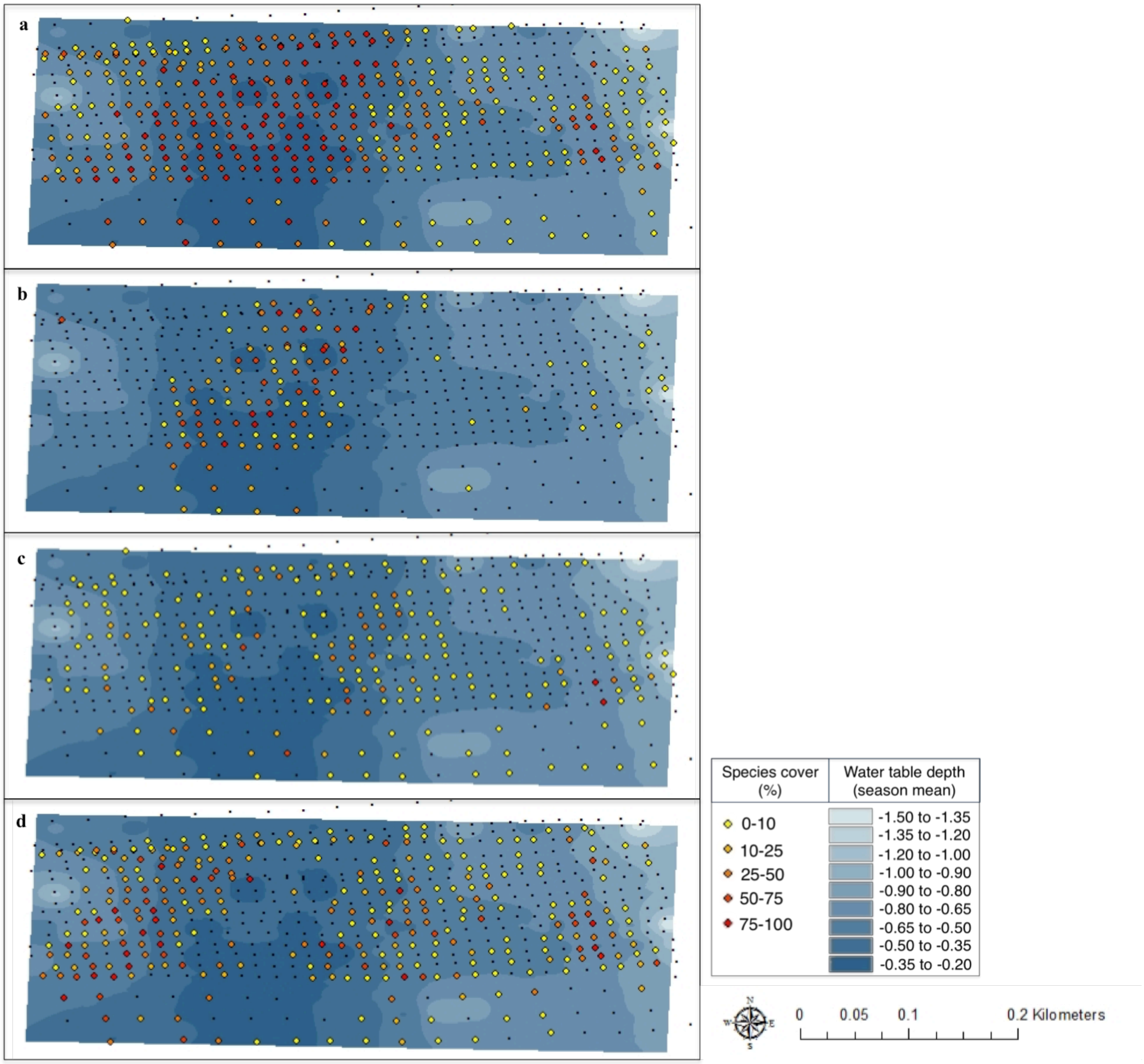

Figure 3.6 Graminoids distribution over the WT position interpolation. The bottom layer represents the WT position (m) seasonal mean. The surface layer represents the percentage cover for each group: total graminoids (a), *C.can* (b), *Cx.can* (c) and *E.vag* (d). Black dots represent survey points where the group evaluated was not found.

The WT means for each vegetation coverage survey points were also used to assess the correlation according to the species with the WT depth. Survey points representing a percentage cover equal or higher to 0.5% were defined as an occurrence within its category. The frequency of graminoid occurrence according to mean WT varied among species (Figure 3.7). *C.can* occurred mainly with a WT shallower than -0.5 cm. *Cx.can* occurred mainly with a mean WT of -0.75 cm or shallower, but was also present with deeper WT. *E.vag* was more frequent than the other species and occurred mainly with mean WT of -0.75 cm or shallower. The total graminoid species cover occurred mainly at depths shallower than -0.75 cm.

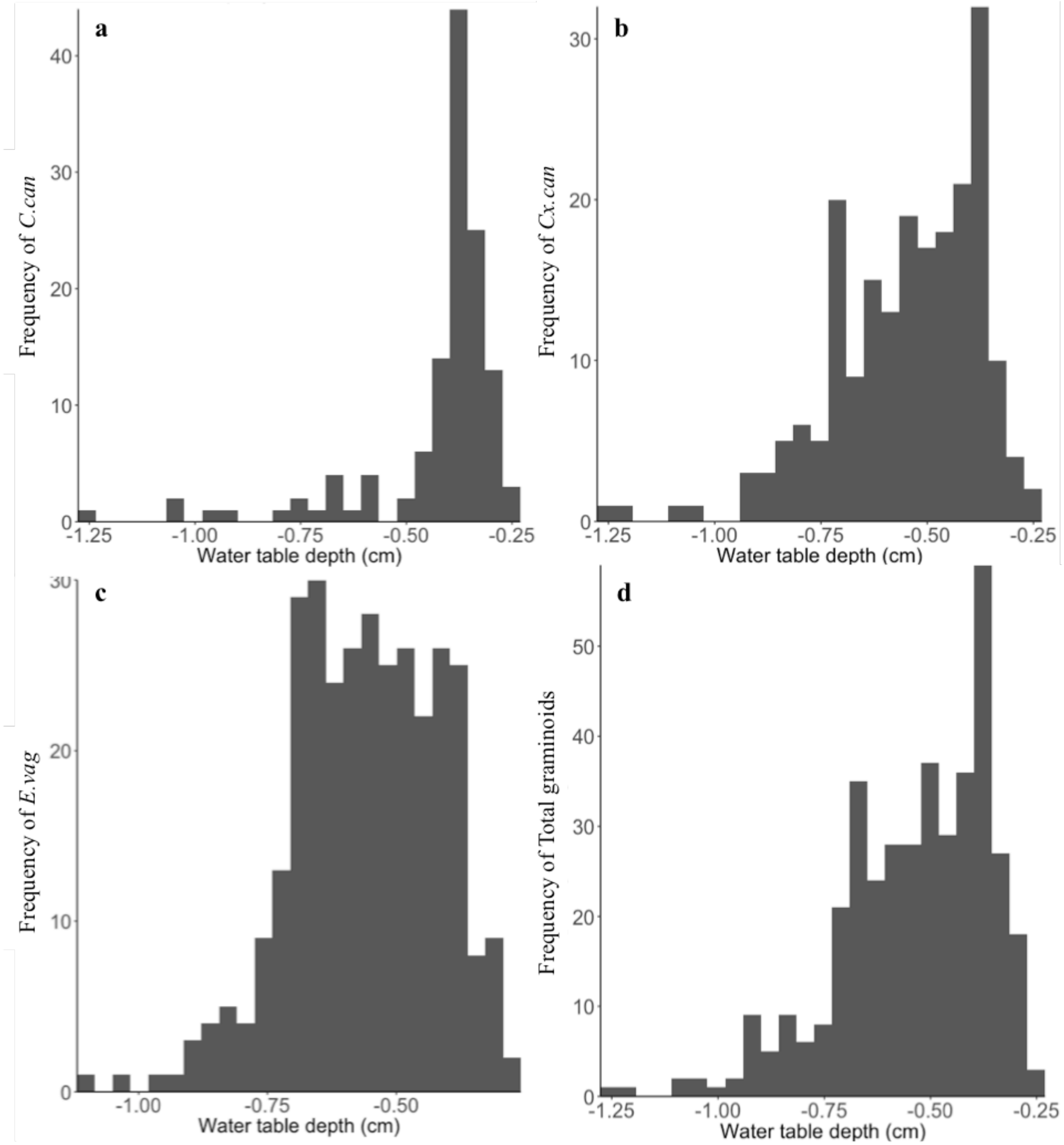

Figure 3.7 Histogram of the graminoids frequency recorded over the WT position interpolated and representative of each survey points.

The Spearman test shows a monotically increasing relationship for all targeted graminoid cover according to the water table depth. *E.vag* and *Cx.can* have a very weak correlation with the WT position (r_s=0.071 and r_s=0.146, respectively). *C.can* and the total graminoids cover were moderately correlated with the WT depth (r_s=0.52 and r_s=0.57, respectively).

3.4.3 Biomass, litter decomposition and C:N ratio

The species type (p=0.039) explained a significant amount of the variation in plant biomass, with *E.vag* having higher plant biomass compared to *C.can* (Figure 3.8a). The section (p=0.44) and the interaction of species and section (p=0.18) did not significantly explain variation in plant biomass. Similarly, species and section were not found to be a control (p=0.4) on litter mass either. *C.can* and *Cx.can* have comparable litter mass when compared between the sections, while *E.vag* had more litter in the wet section (Figure 3.8b). The interaction of species and the section of the site had a significant control on moss biomass (p=0.05), where *Cx.can* in the wet had significantly more moss than *Cx.can* and *E.vag* in the dry (Figure 3.8c). Moss biomass was also controlled by the section of site (p=0.0134), with the wet section significantly higher than the dry.

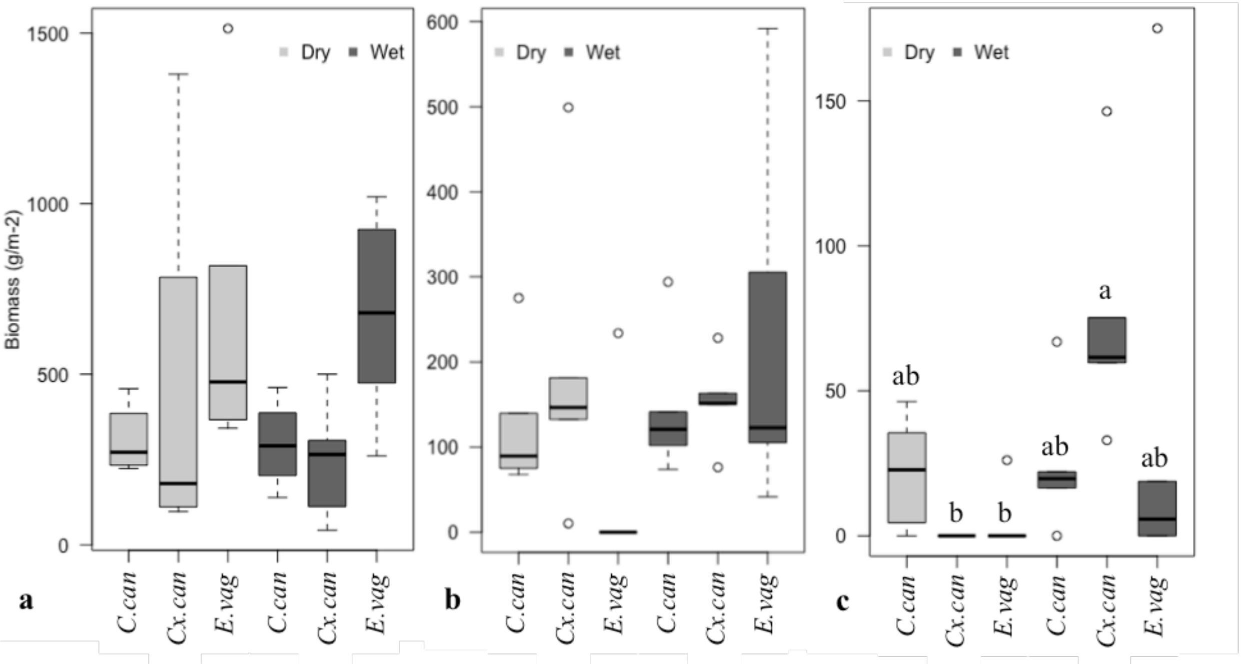

Figure 3.8 Biomass of plant (a), litter (b) and moss (c) according to species and section. Median upper and lower quartile are shown with the boxes, error bars give standard error and points refers to outliers. Species are significantly different from each other when they do not share a common letter.

The location of the tea bag (wet versus dry) burial was not a significant control on *k* (p=0.65; Table 3.2). Similarly, the burial location was not a control on litterbag *k* (p=0.12). The interaction of the species litter type with the section of the site explained a great amount (p=0.05) of variation in litterbag *k* (Table 3.2), with *C.can* had significantly greater k in the dry than wet, while the other species did not differ significantly between locations. The species composition alone was also not found to be a controlling factor for litterbags *k* (p=0.09). Even with a disparity in the WT position, the soil wetness was not found to be a significant control on tea bags or litterbags *k* (Macdonald et al., In Review).

Table 3.2 Minimum (min), mean and maximum (max) decomposition constant (*k*) of the litterbags and tea bags. Species litterbags are significantly different from each other when they do not share a common letter.

Litter type	Dry			Wet		
	Min	Mean	Max	Min	Mean	Max
C.can (g g^{-1} yr^{-1})	0.89	0.96a	1.05	0.48	0.59b	0.70
Cx.can (g g^{-1} yr^{-1})	0.63	0.77ab	0.85	0.66	0.77ab	0.95
E.vag (g g^{-1} yr^{-1})	0.52	0.64ab	0.71	0.32	0.49b	0.76
Tea bags (g g^{-1} d^{-1})	0.0048	0.0071	0.0089	0.0033	0.0062	0.0079

There was no difference in biomass C:N ratio among species, although *C.can* had a slightly lower ratio. Litterbag C:N ratios were controlled by species with *C.can* and *Cx.can* having a significantly higher ratio than *E.vag*. When comparing biomass and litterbag C:N ratios for each species, *C.can* and *Cx.can* ratios between biomass and litterbags were similar, while *E.vag* litterbag C:N ratio decreased compared to the biomass (Figure 3.9).

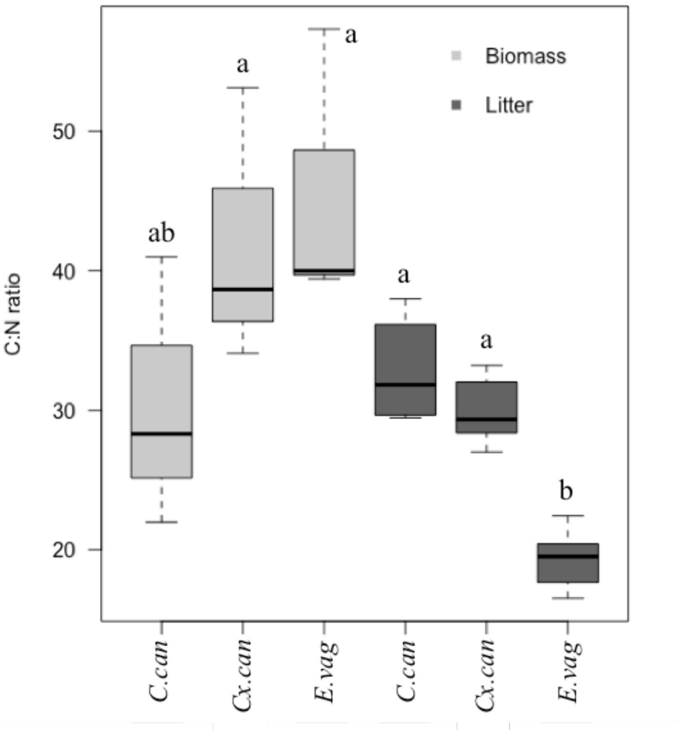

Figure 3.9 C:N ratio of biomass or litterbags plant material for each species. Median upper and lower quartile are shown with the boxes, error bars give standard error and points refers to outliers. Species plant material reference is significantly different from each other when they do not share a common letter.

3.4.4 Carbon gas exchange

Overall, graminoid species explained a significant amount of variation for all the CO_2 exchange components (Table 3.3), where *Cx.can* had significantly lower CO_2 uptake (GEP and NEE) and significantly lower ER compared to *C.can* over the growing season. The interaction of species with the section (wet versus dry) also significantly explained CO_2 exchange (Table 3.3; Figure 3.10). Over the growing season, *Cx.can* has the lowest CO_2 sequestration (GEP and NEE) within its section, while *E.vag* in the wet section had the highest (Figure 3.10-b and -c). Although the WT position measured at each of the carbon gas flux collars was different between the sections, as shown in the hydrology section, the section of the site alone was not a control on CO_2 exchange (ER, GEP and NEE).

Table 3.3 Statistical analysis between the fluxes and the component measured.

C-component	Factor	F value	p value
ER	species	$F_{2,21}=4.5$	0.024
	section	$F_{1,22}=0.24$	0.63
	species and section	$F_{5,18}=2.71$	0.053
GEP	species	$F_{2,21}=7.51$	0.0035
	section	$F_{1,22}=1.19$	0.29
	species and section	$F_{5,18}=4.35$	0.009
NEE	species	$F_{2,21}=9.88$	<.001
	section	$F_{1,22}=1.7$	0.21
	species and section	$F_{5,18}=6.12$	0.0018
Log CH_4	species	$F_{2,21}=1.83$	0.18
	section	$F_{1,22}=25.05$	<.001
	species and section	$F_{5,18}=8.19$	<.001

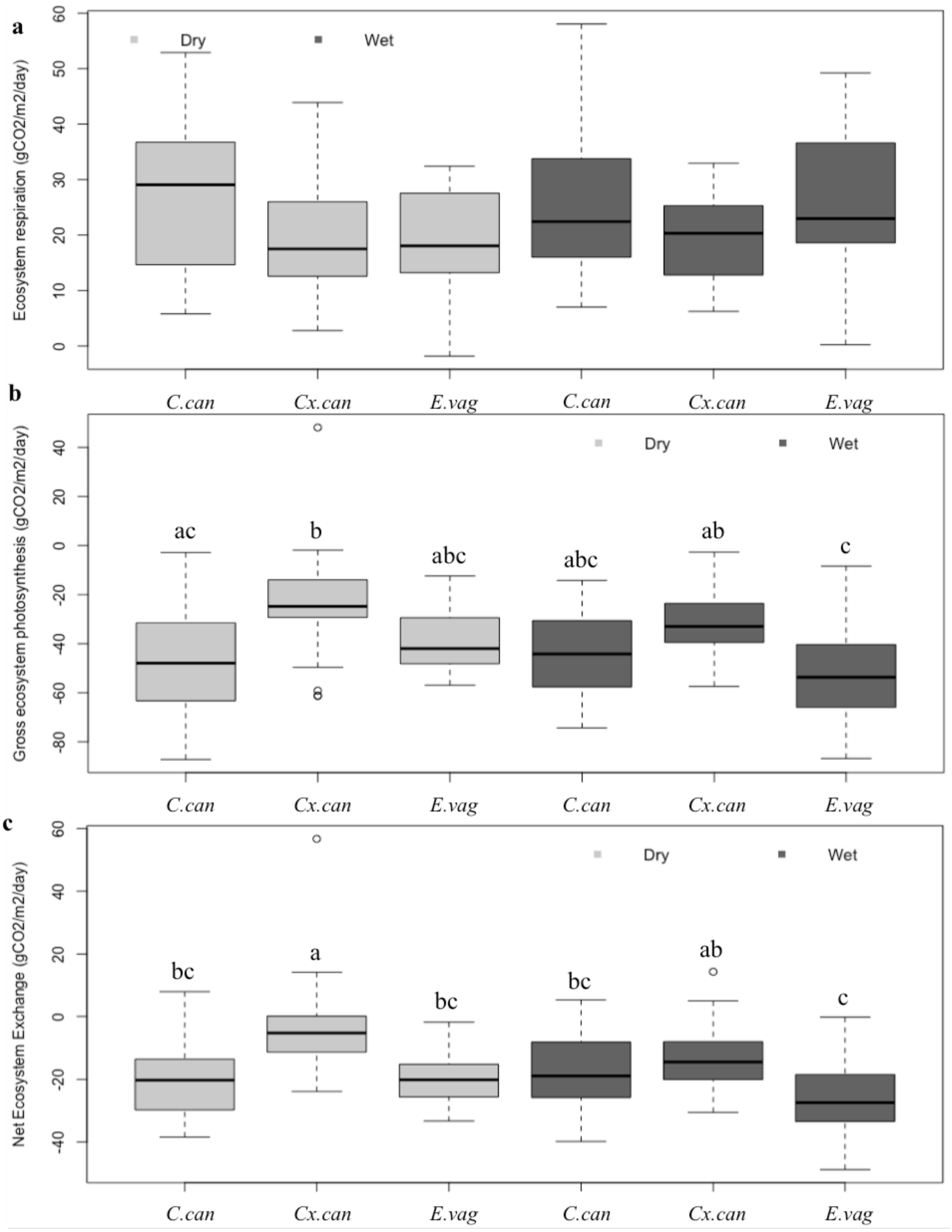

Figure 3.10 (a) ER, (b) GEP and (c) NEE according to the species and section of site. Median upper and lower quartile are shown with the boxes, error bars give standard error and points refers to outliers. Species are significantly different from each other when they do not share a common letter.

The species-section of site interaction explained a large extent of variation in CH_4 fluxes (Table 3.3). *C. can* and *E.vag* had significantly higher fluxes in the wet section compared to the dry, while there was no significant difference for *Cx.can* (Figure 3.11). The section of the site, with important variation in the WT position, also explained a significant amount of difference in CH_4 fluxes, with the wet section having significantly higher emissions than the dry. CH_4 fluxes were not significantly different between species considering all plots together (Figure 3.11).

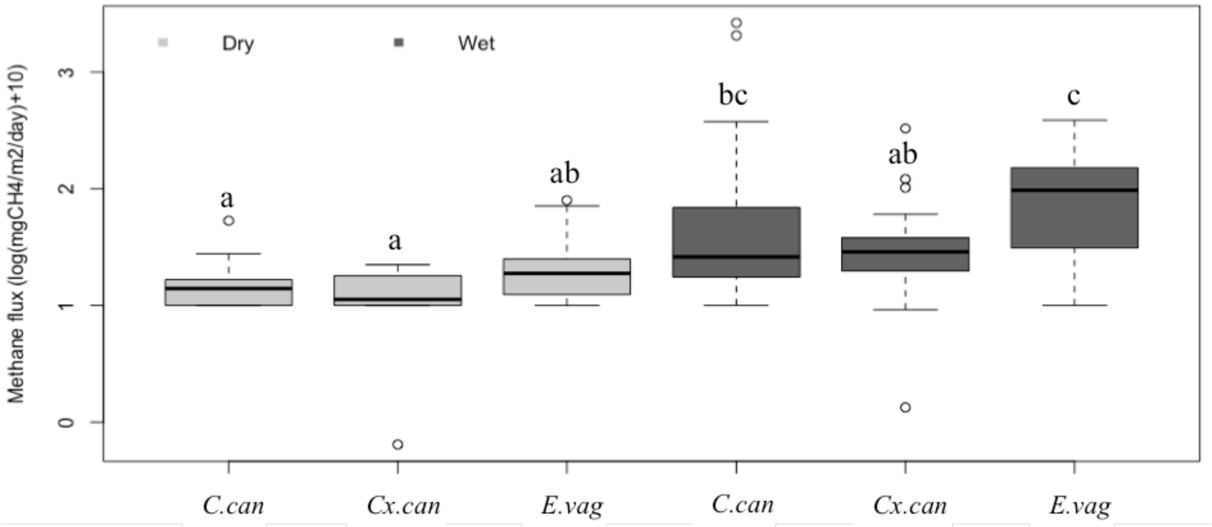

Figure 3.11 Log of methane fluxes per species and section according to the perennial stage. Median upper and lower quartile are shown with the boxes, error bars give standard error and points refers to outliers. Species are significantly different from each other when they do not share a common letter.

3.5 Discussion

The horticultural extraction and subsequent restoration of a peatland resulted in spatial heterogeneity of hydrology and vegetation distribution. In agreement with observations made by Poulin et al. (2012), the species richness was dependent on the habitat preferred by individual species. Graminoid establishment post-restoration showed a preferential habitat, partly in accordance to the WT position, with higher graminoid cover under wetter conditions.

The hydrology survey revealed important variation across the site. The eastern part of the site recharged the west central section of the site during all weeks of the sampling period. The western section is characterized with a shallow WT position relative to the peat surface, while its AWL is deeper than the east sections. Even with disparity between dry periods or after rain events, the WT position between the wet and dry section showed a mean difference of 65cm. This important difference across the study area can be explained by the higher ground elevation on the east side. Water table fluctuated by up to 40 cm during the study period. This WT fluctuation results from drainage and the extraction process that alters the peat structure and water storage capacity by decreasing the specific yield (Price et al., 2003; Price, 1996; Price, 1997; Money, 1995). An open drainage ditch remained at the western end of the site and this may have reduced the magnitude of WT response to precipitation events.

The high WT variability observed over the season shows that graminoid species have a high tolerance to water level fluctuation (Välirante et al., 2007) that will not affect the establishment of certain species even within the deep WT area. However, deep WT levels and a thick residual peat layer usually do not promote the establishment of plants, resulting in a post-extraction peatland dominated by bare peat surfaces (this study; Graf et al., 2008). The total graminoid cover was moderately related to the WT position, where a shallow WT increased their cover as has been observed in other restored peatlands (Tuittila et al., 2000; Strack and Zuback, 2013). Strack et al. (2014) also reported higher percentage cover among graminoid species at wetter sites following peatland restoration. However, individual graminoid species responded to WT position differently. *C.can* distribution was favoured with a higher water table, while *Cx.can* was favoured with a lower water table depth. *E.vag* distribution was independent of the water variability.

Although graminoid species distribution across the study site was linked to WT position, additional environmental gradients likely also contributed to these patterns. As mentioned previously, soil nutrient content is also an important control for graminoid establishment and performance. As *C.can* thrives within more nutrient rich soils (USDA, 1998), its establishment might be preferential within wet and high-nutrient soils. On the other hand, *Cx.can* has only been reported in a wetland along a small water course and in nutrient poor system (Schütz and Milberg, 1997). *E.vag* has been reported to be a deep-rooted species and can tolerate deep water levels (Marinier et al., 2004) and can effectively obtain nutrient in poor conditions (Siegenthaler et al., 2010). Given that water flows from the dry east section to the wetter west-central portion, chemistry may also vary between the sections. Indeed, pH was higher within the wet section of the site throughout the peat column (peat pH east = 3.45±0.33, west = 4.46±0.41) and this may also contribute to patterns of vegetation establishment post-restoration.

Differences in plant cover and WT position across restored peatlands have been observed and resulted in variable carbon fluxes (Strack et al., 2014; Tuittila et al., 1999; Strack et al., 2016). During the growing season, graminoid species controlled the CO_2 exchange (Chapter 2), where *E.vag* in the wet section was found to take up the most CO_2. Although the WT was significantly different between the wet and dry plots, with means of -35.6±20.8 and -8.4±16.0 respectively, the section of the site was not found to be a significant control on the CO_2 fluxes, which does not agree with the findings of Strack et al (2014). However, species with a shallow WT depth sequester carbon better throughout the season, while species, such as *C.can* and *Cx.can,* can emit CO_2 with a deeper WT position. In agreement with our findings, Strack et al. (2014) and Tuittila et al. (1999) also found more CO_2 sequestration with vascular plants in wetter sections. On the contrary, the species composition or the section of site was not found to be predictor of respiration rates. Shallow WT depths and species type also impacted the aboveground biomass production, where *E.vag* had the highest production, more particularly in the wet section, similar to the pattern of measured GEP and NEE. However, *Cx.can* had higher biomass production in the dry section an area with CO_2 emissions (release of CO_2 as NEE). This indicates that the biomass and the CO_2 uptake (GEP and NEE) are highly dependent on the species composition, and to a lesser extent on the WT position as long as the species is established. Although the WT position was not a significant control on CO_2 exchange, it was a strong predictor for species establishment, their cover, biomass and litter decomposition. As the wetter section of the site is covered by more graminoid species, a shallow WT position will drive higher C accumulation.

Sections of site characterized by deeper WT had higher litterbag decomposition rates (*k*). Despite this, no difference in ER was observed between the sections, likely because of the substantial contribution of plant respiration. As reported elsewhere (e.g. Bohdálková et al., 2013) graminoids had a high litter *k* indicating easily degradable litter. As the litter *k* differed among species, it also indicates different rates of C accumulation from different species. The litter C:N content was significantly lower for *E.vag* biomass compared to the other species. This indicates that *E.vag* has more recalcitrant material compared to other species, supported by the lower measured *k*. Bragazza et al. (2012) also observed lower C:N ratios for *E.vag* compared to *Sphagnum fuscum* and *Calluna vulgaris*. However, following one year of burial, *E.vag* litter C:N ratio was significantly lower than the other species, indicating microbial decomposition utilizing additional N sources. Brummell et al. (2017) reported higher total dissolved N pools underneath *E.vag* than areas without vascular plants providing evidence that this species enhanced soil N availability.

Species composition and the WT position, along with other environmental conditions (Whalen, 2005; Lai, 2009), are known to control the spatial variability of peatland CH_4 fluxes (Bohdálková et al., 2013). Our study shows that the WT position, and accordingly the section of the site, was a significant predictor of CH_4 fluxes, while the species composition alone was not sufficient to explain variation in fluxes. In accordance with our study, a shallow WT position has been found to increase significantly CH_4 fluxes compared to a deeper WT position (Strack et al., 2016; Couwenberg and Fritz, 2012; Strack et al., 2014). *E.vag* consistently had the highest fluxes among the graminoid species, regardless of wet or dry section. *E.vag* CH_4 flux in the dry section was also comparable to the fluxes of *C.can* and *Cx.can* in the wet. *E.vag* was also found within other studies to increase CH_4 fluxes under wet regimes or a rise in WT position (Tuittila et al., 2000; Strack et al., 2014; Marinier et al., 2004). Tuittila et al. (2000) reports $5.5 mgCH_4m^{-2}d^{-1}$ from *E.vag* tussocks, with an increase after rewetting. Marinier et al. (2004) also reports a coinciding increase in emissions with a rise in the water table, with a mean of $39 mgCH_4m^{-2}d^{-1}$ from *E.vag*. Although the species effect was not evaluated by Strack et al. (2014), when evaluating *Cx.can* and *E.vag*, they showed significantly difference in fluxes from wet and dry plots when grouped as a PFT (see also Chapter 2).

Our study shows that the WT position will drive graminoid species establishment to some extent four years post-restoration. The establishment of species will impact CO_2 and CH_4 exchange on site, where a shallow WT will drive more CH_4 emissions, but also will promote the establishment of more productive species for litter accumulation and slightly more CO_2 uptake. Bridgham et al.

(2013) state that biogeochemistry models need to take into consideration heterogeneous landscapes and the delimitation of species distribution has been found to be fundamental in conservation areas to better understand natural systems and guide decision-making (Mota-Vargas and Rojas-Soto, 2012). In the case of modelling carbon exchange in restored peatlands, it is also important to consider the chronological order of species appearance (Mota-Vargas and Rojas-Soto, 2012), which includes a large representation of graminoid species in the first few years post-restoration, as shown within the present study. More precisely, the area covered and the location of species varies spatially according to the WT position for most graminoids. As their ecological niche might differ at the species level, their spatial distributions will be subject to the conditions on site. By characterizing the availability of resources, it would be possible to define the graminoids' establishment preferences. Mota-Vargas and Rojas-Soto (2012) support that modeling the ecological niche of species provides better results of spatial sensitivity of a predicted area, more particularly for species with geographical restrictions. As this study focused on hydrological control on graminoid distribution and function, additional variables affecting graminoid species distribution were not determined; defining the hydrological niche of several common graminoid species in restored peatlands is a step towards modelling their interactions at these sites. By defining the species' ecological requirements at a finer scale, predicting the impact of land use change on the CO_2 and CH_4 exchange and the ecosystem response will improve model precision.

3.6 Conclusions

In this study, the water table position was an important control on graminoid establishment and on their CO_2 and CH_4 exchange. Although all wells were responsive to precipitation input, the site water table position varied consistently between the eastern and western end of the site, resulting in wetter and drier sections. The vegetation inventory also suggested an important variation in graminoid establishment and percentage cover across the site. The correlation between the water table position and the graminoid cover was supported for all species, particularly for all graminoids combined and for *C.can*. As the water distribution partly controlled the graminoids establishment, it also had an impact on the graminoid species CO_2 and CH_4 exchange over the growing season, where the species and the section of site were found to be controls. Although the section of site did not directly impact ER, GEP and NEE rates, the species controlled significantly the fluxes. As species distribution was correlated to water table, this indicates greater sequestration of CO_2 under wet regimes. Contrarily, the species did not directly control the CH_4 emissions, while the section of site did, resulting in higher fluxes under wet regimes, particularly for *C.can* and *E.vag*. However, *E.vag* had higher emissions, along with *C.can*, suggesting that the species composition impacted the CH_4 to some extent. The section and species were also important factors regarding the plant productivity (biomass) and decomposition, where decomposition decreased and productivity increased under wet regimes. These results correlated with higher GEP and NEE rates from species in the wet section of the site, indicating potential more carbon accumulation under wet conditions. This suggest that graminoid distribution and function are dependent on the WT position over the growing season, where wetter regimes will drive more CH_4 emissions, but also the establishment of more productive species that will result in carbon accumulation.

Chapter 4: Summary, limitations and recommendations

Peatland restoration results in the establishment of vascular plants, such as graminoid species. Four years post-restoration, a formerly extracted bog in central Alberta has flourishing graminoid cover, with graminoids recorded in 70.5% of the vegetation inventory plots with a mean of 37.4% cover. Their quick establishment promotes important CO_2 sequestration and CH_4 emissions post-restoration. Despite their readily degradable litter, high productivity contributes to peat accumulation processes quickly after disturbance and provides a fast recovery of ecosystem services. Although often grouped as one plant functional type (PFT), graminoids have a significant difference among species for plant growth forms, decomposition rates, and CO_2 and CH_4 exchange, as well as hydrological niche as shown within these studies (Chapter 2 and 3). As graminoids showed significant disparity at the species level, I support that they should not be considered as a PFT for restored peatland models. Besides, graminoids have been shown within my studies to represent the greatest cover of any plant group post-restoration and thus a very important contributor to peatland carbon exchange post-restoration. By characterizing them at the species level or grouping them within smaller groups, precision for CO_2 and CH_4 exchange prediction in restored peatlands will be increased. However, my studies include limitations that should be addressed in future studies.

The research site selected for this study was a bog restored with the MLTT (moss layer transfer technique) procedures. In general, peatland plant community structure within the first years post-restoration is unpredictable, even with the promotion of moss establishment via MLTT, as each site's environmental conditions are unique. However, the competition for resources is low and vascular plants such as graminoids usually establish quickly (Graf et al., 2008). In the case of these studies, three and four years post-restoration resulted in a significant cover of graminoid species. While I observed a correlation between graminoid distribution and WT (Chapter 3), in those two years, a succession in plant community structure was also observed, especially under wet conditions, indicating that these studies represent only a short period in the recovery of the ecosystem. Community succession is dependent on conditions on site and the species present. For our study site, we could potentially expect changes in the species composition, as competition for resources is dependent on the preferential ecological niche of each species. More precisely, *C.can* is often associated with *B.syz* in wetlands (Wynia, 2006) and in competition with *S.cyp* when water levels are controlled (Lajoie, 2015). However, *C.can* needs nutrient-rich conditions to proliferate and is not tolerant of competition for light (Lieffers et al., 1993; Powelson and Lieffers, 1992) and could potentially lose out to other more productive species with a large canopy. As *Cx.can* has a poor ability to compete with tall species (Schütz and Milberg, 1997), it could potentially only be found in sections with no competition and deeper WT levels. *E.vag* is often found in wet meadows with *Carex* spp. (Aiken et al., 2007) and we should also find this species in a similar ecological niche on site. However, each species' success on site is subject to their ability to compete with species of large canopy and extensive rooting system, such as *S.cyp* (GRET, 2016), as deep rooted species have the ability to use the nutrients from groundwater and therefore alter the nutrient content for other species (Tuittila et al., 2000; Marinier et al., 2004). Indeed, species such as *S.cyp* could result in mono-specific colonies at the expense of other species (GRET, 2016) that are less competitive such as *Cx.can* or *B.syz*. In the long term, this could be problematic for the site's biodiversity, but positively affect the total carbon fluxes. As ecological succession relies on the species' ability to compete, studying the species community structure over time would help models predict species cover and distribution, and improve carbon exchange estimates, since species were shown to differ in their CO_2 and CH_4 exchange within this study.

The study area selected was also mainly colonized by five different graminoid species whose carbon exchange function was compared within a similar ecological niche. Although they were representative of other post-restoration species pools, additional graminoid species have been recorded previously by other studies (e.g. *Eriophorum angustifolium, Carex aquatilis, Carex rostrata, Juncus effusus, Agrostis scabra*). Therefore, more research should be conducted at different sites to characterize the ecological niche, and CO_2 and CH_4 exchange of other graminoid species in order to associate them with a PFT sub-category. Based on the five species studied, we suggest grouping *E.vag* and *S.cyp* as highly productive, high CH_4 flux species and *C.can, Cx.can* and *B.syz* as moderate productivity and CH_4 flux (Chapter 2). As *S.cyp* has been reported to be only an intermediate CH_4 flux species in wetlands (Kao-Kniffin et al., 2010), new categories could be added for model precision (e.g., high productivity, low to moderate CH_4 flux).

The WT position was found to be an environmental condition partly controlling species distribution. However, our study only focused on the three graminoid species found within both dry and wet sections of the site (Chapter 3). This approach could be conducted with other graminoids representative of restored peatland, or that are representative within just a certain WT level. With more available data, predicting species establishment post-restoration would help models to predict the time for a site to become a carbon sink. Furthermore, other environmental conditions could be measured, such as the nutrient availability, which I hypothesized also explains graminoids' ecological niche preference.

My results become a challenge for modellers, as the parameters are more detailed for vegetation feedback. It becomes also a challenge for researchers to assess and measure species at the plot scale and not groups into plant functional types. However, this research provides an opportunity for models to improve the accuracy regarding plant-atmosphere interactions, and limit over- or under-estimation. This research also provides an opportunity for further work on various plant functional types, as graminoids have been shown to differ enough at the species level not be grouped. My results will help a restored peatland model to better assess the graminoids establishment and their impact on the carbon exchange according to a hydrologic gradient. By knowing species preferential hydrologic niche, it will be easier to estimate the carbon exchange over the site.

For the many reasons stated above, I recommend studying different graminoid species in restored peatlands and defining the category of graminoid PFT sub-group they would be best associated with. I recommend a long-term study (10-20 years) of the succession of the graminoid community structure, as restored peatland CO_2 uptake and CH_4 emissions will be dependent on the graminoids' species type, productivity and coverage. It is also the time period with more change noticeable, and a period that industries wish for successful restoration. I also recommend measuring the WT levels when studying graminoid species ecological niches, along with additional environmental conditions such as the nutrient content. As this study was conducted in central Alberta, I recommend future studies be conducted in other regions to establish if graminoid species carbon exchange and establishment differs under different climate regimes. Although the use of PFTs reduces complexity in ecosystem models, I believe that restored peatland models should take into consideration the heterogeneity between graminoid species and use sub-categories as an important factor when modelling restored peatland carbon exchange.

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Appendix 1: Photographs of the study site

Figure A1 Wet section of the site (west) represented by a high coverage of diverse graminoid species. This photo was taken on May 24 2016 by S.Touchette, when the water table position was above surface.

Figure A2 Dry section of the site (east) represented by some graminoid cover including mainly *C.can*, *Cx.can* and *E.vag* and bare peat with straw mulch. Photo taken on June 30 2016 by S.Touchette.

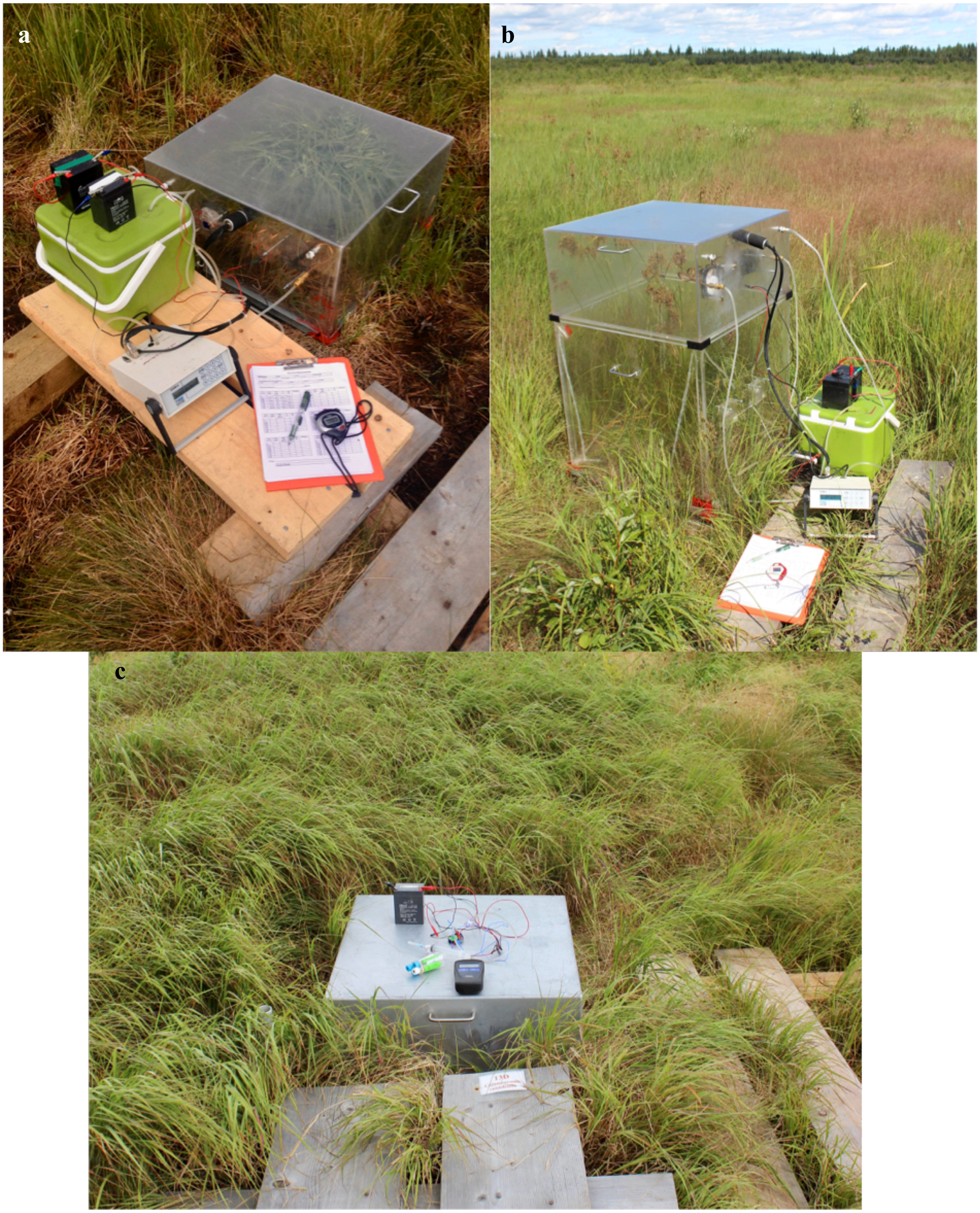

Figure A3 Chamber measurements of (a,b) CO_2 and (c) CH_4. These pictures represent measurements in the wet section, where species taller than the chamber (e.g. *S.cyp* and *B.syz*) used a clear extension (b), which was also adapted to CH_4 fluxes measurements.

Appendix 2: Vegetation inventory sample sheet

Vegetation inventory Seba Beach

Date:	Transect number:
Researchers:	GPS point:

☐ **Entered?**

Plot number:																	
Distance:																	
Total vegetation																	
Trees : deciduous																	
Trees : evergreen																	
Shrubs																	
Herbaceous : graminoids																	
Typha only																	
Herbaceous: broad leaf (without *Typha*)																	
Graminoids : total cover																	
Eriophorum vaginatum (cotton-grass)																	
Calamagrostis canadensis (blue-joint)																	
Carex canescens (clumpy Carex)																	
Agrostis scabra (purple, tickle-grass)																	
Scirpus cyperinus (tall, brown flowers)																	
Beckmannia syzigachne																	
Bare peat																	
Straw mulch																	
Litter (leaves, stems…)																	
Dead wood																	
Moss cover (25 cm x 25 cm)																	
Sphagnum section *Sphagnum*																	
Sphagnum section *Cuspidata*																	
Sphagnum section *Acutifolia*																	
Polytrichum																	
Other mosses																	
Lichen																	

Appendix 3: Light response curves