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Carbon Dynamics in Extracted Minerotrophic Peatlands: An Analysis of the Effect of Plant Biodiversity

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Carbon Dynamics in Extracted Minerotrophic Peatlands:

An Analysis of the Effect of Plant Biodiversity

by

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ABSTRACT

Recent experiments have shown that biodiversity loss can impair natural ecosystem functioning. Extraction of horticultural peat is known to alter the diversity of vegetation and convert peatlands from net sinks to persistent sources of carbon to the atmosphere. Peatland restoration has been shown to re-establish the natural carbon sink function, however, current restoration techniques could be refined with more knowledge of the role of plant biodiversity. In a controlled field study, I tested the effect of plant biodiversity on carbon sequestration in an extracted peatland in Quebec, Canada. Closed-chamber method was used to measure the flux of carbon between the peatland and the atmosphere in fourteen treatments planted with different numbers of species. Species richness was not found to have a significant impact on carbon sequestration and no overyielding was detected in polycultures. Species identity was important with *Carex aquatilis* having a significantly positive impact on carbon sequestration.

UNIVERSITY OF CALGARY

FACULTY OF GRADUATE STUDIES

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies for acceptance, a thesis entitled "Carbon Dynamics in Extracted Minerotrophic Peatlands: An Analysis of the Effect of Plant Biodiversity" submitted by GOLNOUSH HASSANPOUR FARD in partial fulfillment of the requirements for the degree of MASTER OF SCIENCE.

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LIST OF ABBREVIATIONS

BEF – Biodiversity Ecosystem Function

C – Carbon

CH_4 – Methane

CO_2 – Carbon Dioxide

GEP – Gross Ecosystem Photosynthesis

N – Nitrogen

NEE – Net Ecosystem Exchange

PAR – Photosynthetically Active Radiation

PRS™ – Plant Root Simulator

RESP – Respiration

T2 – Soil Surface Temperature

Ta – Air Temperature

WL – Water Level

CHAPTER 1: INTRODUCTION AND RESEARCH GOALS

1.1 Overview

Human activities have transformed substantial portions of the Earth's surface, causing adverse modifications in the number and types of organisms that appear in ecosystems (Vitousek *et al.*, 1997; Millennium Ecosystem Assessment, 2005). Increased awareness of these changes has triggered major research initiatives by the international scientific community, particularly after the 1992 Earth Summit in Rio de Janeiro (Cardinale et al., 2012). In the two decades that followed the Summit, hundreds of research experiments were carried out globally with the aim of understanding how biodiversity loss affects natural ecosystem dynamics and functions (Cardinale *et al.*, 2012). This has led to the emergence of a field called Biodiversity-Ecosystem Function (BEF) (Loreau, 2000). There has been extensive development in BEF research over the past twenty years, with early debates and controversies giving way to consensus formed around key findings and themes (Cardinale *et al.*, 2012). While early research was inconclusive in resolving the effect of biodiversity (Waide *et al.*, 1999), it is now accepted that biodiversity loss reduces the efficiency by which ecological communities capture resources, produce biomass, decompose, and recycle essential nutrients (Cardinale *et al.*, 2012).

Two mechanisms are accepted to be equally important drivers of a biodiversity effect on ecosystem functions (Cardinale *et al.*, 2012). In diverse communities, trait variations between species allow for access to a greater proportion of available resources than in less diverse communities, leading to greater efficiency and overall productivity (Hooper and Vitousek, 1997). Furthermore, positive interactions between species increase the overall functional capacity of the community. These mechanisms are together referred to as complementarity. In addition, diverse communities are more likely to contain key species with a disproportionate or dominant influence on ecosystem functions (Tilman *et al.*, 1997). This is referred to as sampling effect.

As researchers strive to manage and mitigate the consequences of diversity loss effectively, unexplored areas of knowledge still remain. Until a decade ago, a large volume of BEF studies had been conducted in grasslands to examine the biomass production function (Naeem and Wright, 2003). So far, few such studies have been done in wetland ecosystems, particularly peatlands (Riutta *et al.*, 2007; Kivimaki *et al.*, 2008; Ward *et al.*, 2009), and have not extensively examined the uptake and storage of carbon (C) in the context of biodiversity. To address this gap in BEF research, this study focuses on C sequestration function in peatlands.

Peatlands are highly valued as substantial sinks of C from the atmosphere (Gorham, 1991; Turunen *et al.*, 2002). The degradation of natural peatland functions after industrial extraction of peat for horticulture converts them to a persistent source of C to the atmosphere (Waddington *et al.*, 2002) that contributes to climate change (Cleary *et al.*, 2004). Extraction also modifies the diversity of plant assemblages that occur in pristine peatlands. Although restoration is practiced as a post-extraction management strategy, current restoration planning in North America does not specifically consider the role of biodiversity in restoring natural C sink function of peatlands (Rochefort *et al.*, 2003). There is, however, reason to believe that biodiversity changes could play an important role in re-establishing the natural C sink function of peatlands. The purpose of this study is to determine the effect of plant biodiversity on peatland C dynamics.

1.2 Peatlands

Peatlands are the most common type of wetland in the world, representing 50-70% of global wetlands (Chapman *et al.*, 2003). They are predominantly found in the northern cold-temperate boreal climate that is characterized by short summers and long winters (Vitt, 2006), though tropical peatlands in Southeast Asia also comprise an important portion of global peatland resources (Page *et al.*, 2011). The most extensive deposits of peat reside in Canada, USA, Fennoscandinavia, and the former

USSR (Chapman *et al.*, 2003; Vitt, 2006). Canada is well endowed with 1.24 x 10^6 km^2 of peatlands (Vitt, 2006) expanding across 12% of its land area.

Peatlands are characterized by persistently high water levels (Vitt, 2006; Kivimaki *et al.*, 2008). This feature strongly shapes the form and function of peatlands. The waterlogged environment creates anoxic conditions that significantly reduce the decomposition rate and contribute to the important function of peat accumulation. Peat is partially decomposed organic matter, produced when the accumulation of C in the ecosystem through net primary productivity (NPP) exceeds the release of C to the atmosphere through decomposition (Vitt, 2006; Vasander and Kettunen, 2006). Carbon-rich organic matter accumulates and is stored over time. Based on the Canadian Wetland Classification System, peatlands are characterized as having greater than 40 cm of accumulated peat (National Wetlands Working Group, 1997).

Hydrology is responsible for characterizing the soil, vegetation, and ecological structures that differentiate peatlands into bogs and fens. Peatlands that are removed from the influence of groundwater and that are fed largely by precipitation are called bogs and are characterized by lower concentrations of dissolved cations and anions (Vitt, 2006). Fens on the other hand receive a large part of their water from minerotrophic groundwater and contain more dissolved cations and anions (Vitt, 2006). For the purposes of this study I will focus on a former bog that has been extracted down to its minerotrophic peat level. While research on restoring bogs is abundant (e.g. Price *et al.*, 1998; Rochefort, 2000; Rochefort *et al.*, 2003; Campeau *et al.*, 2004; Chirino *et al.*, 2006), fen research has received considerably less attention, although experimentation is ongoing (e.g. Cooper & MacDonald, 2000; Cobbaert *et al.*, 2004; Graf and Rochefort, 2008).

1.3 Peatland Carbon Dynamics

Peatlands act as long-term net sinks of C, storing 23-28 g C m^{-2} yr^{-1} (Gorham, 1991; Vasander and Kettunen, 2006), and over thousands of years have accumulated

approximately one-third of the world's terrestrial soil C (Gorham, 1991). Literature estimates of the net C stored in soil are highly varied. A recent review by Page *et al.* (2011) suggested that with a mean thickness of 1.3 m, the best estimate for net C trapped and accumulated in peatlands worldwide could be updated to 480 Pg (and 610 Pg with thickness of 2.3 m where 1 Pg = 10^{15} g). This makes peatlands highly valued for their important role in the global C cycle (Gorham, 1991).

Carbon enters the peatland system through photosynthesis (gross ecosystem photosynthesis, GEP) when growing plants fix atmospheric CO_2 during the growing season to maintain their tissue. The rate of photosynthesis in boreal peatland ecosystems is comparatively low and is a function of plant species, biomass, temperature, carbon dioxide (CO_2) concentration, water/nutrient availability, and light level (Vasander and Kettunen, 2006).

A portion of this photosynthesized C is returned to the atmosphere by autotrophic respiration of the plants ($RESP_a$). The rate of $RESP_a$ is regulated by photosynthesis, temperature, and water and nutrient availability (Vasander and Kettunen, 2006). Plant roots can contribute 10-45% of CO_2 respiration through exudation and turnover of fine roots (Silvola *et al.*, 1996). As plants die, senescing biomass is deposited on the soil as litter and left to decay. Heterotrophic soil organisms consume litter and respire CO_2 back to the atmosphere ($RESP_h$). This is called aerobic decomposition and is a function of soil temperature, oxic peat layer volume, nutrient availability, soil pH, and quality and quantity of decomposable material (Vasander and Kettunen, 2006). In boreal peatlands, heterotrophic respiration can occur outside the growing season, releasing significant portions of the photosynthesized CO_2 back to the atmosphere (Roehm and Roulet, 2003).

GEP, $RESP_a$, and $RESP_h$ comprise the exchange routes of CO_2 in the system. It is said that CO_2 exchange is the dominant pathway of C movement into and out of the system; however, the balance between them is often close to zero (Waddington and

Roulet, 2000). Accurate measurements of CO_2 exchange are thus necessary for estimates of C accumulation.

As litter continues to be deposited, previous layers get buried in the waterlogged peat profile. In this environment most decomposition occurs very slowly through anaerobic processes, releasing some C in the form of methane (CH_4). The CH_4 flux from peatlands to the atmosphere depends on three processes: production, transport, and oxidation. Methane production is called methanogenesis and is facilitated by methanogenic archaea (Vasander and Kettunen, 2006). The rate of methanogenesis depends on the quantity and quality of substrate, microbial population, and temperature (Vasander and Kettunen, 2006). Old peat and certain types of vegetation (e.g. bryophytes) are recalcitrant or resistant to decomposition, whereas many vascular plants can provide fresh and easily decomposable (labile) litter (Graf and Rochefort, 2009) for methanogenesis. As CH_4 forms deep in the anoxic portion of the peat profile, it travels upwards through diffusion in the peat matrix, ebullition (bubbling), and passage through plant gas exchange tissue called aerenchyma. It has been shown that an abundance of herbaceous vegetation enhances CH_4 production by providing a labile C source such as easily degradable root exudates directly in the anoxic zone where methanogenesis occurs (Saarnio and Silvola, 1999; Ström *et al.,* 2003). Some vascular plant species also have the ability to provide an escape route for CH_4 formed deep in the peat profile through their porous aerenchyma (Schimel, 1995). Methane transport via the plant matrix reduces exposure to methanotrophic bacteria that feed on and re-oxidize CH_4 to CO_2 (Blodau, 2002). Plant aerenchyma can also transport oxygen from the air down to the anoxic peat layer, where higher root density may cause local oxidation of CH_4 to CO_2 (Arah and Stephen, 1998; Dannenberg and Conrad, 1999; Vasander and Kettunen, 2006). Plant-mediated CH_4 transport depends on the relative contribution of each of these processes. Ebullition or bubbling is another means of CH_4 transport. Ebullition can release large amounts of CH_4 to the atmosphere (Glaser *et al.*, 2004).

Every year, northern peatlands fix approximately 0.096 Pg C and release roughly 0.046 Pg of CH_4-C (Gorham, 1991). Since both CO_2 and CH_4 are contributors to climate change, natural peatland functioning can contribute to net climate cooling when long-term effects are considered (Frolking and Roulet, 2007). Any disturbance that upsets the balance in C dynamics can convert peatlands to large, persistent sources of C. Dissolved organic C (DOC) and C leaching are also important components of the C budget in peatlands (Gorham *et al.*, 1991; Billett *et al.*, 2004; Roulet *et al.*, 2007; Waddington *et al.*, 2008) that fall outside the scope of this project and are not discussed in this section.

1.4 Peatland Disturbance

The last century has witnessed considerable global losses of peatlands to various sectors competing for its valuable resources including forestry, energy, agriculture, and horticulture (Waddington *et al.*, 2002; Chapman *et al.*, 2003). In Canada, where peatlands are estimated to cover 139 million ha of the land surface, about 24,000 ha have been disturbed for horticultural peat extraction (with 14,000 ha under active extraction) (Environment Canada, 2010). This amounts to only about 0.02% of the extent of Canadian peatlands, which is not considered substantial. However, in some regions such as the St. Lawrence lowlands, horticultural peat extraction has disturbed over 70% of the peatland area (Lavoie and Rochefort, 1996). With increasing human disturbance to Canada's boreal peatland region, for example through oil and gas development (Turetsky and St. Louis, 2006), the need for restoration and reclamation research is ever increasing.

In this research project, extraction for horticultural purposes will be the point of focus. The current vacuum-extraction method (Crum, 1988) involves drainage by large ditches on the periphery and throughout the extraction site to lower the water level, allowing the peat to dry. The vegetation on the surface is removed in preparation for extraction. Following drainage and extraction, the natural functioning of peatlands is severely altered. This occurs primarily due to removal of

photosynthesizing vegetation and elimination of the waterlogged hydrology. These, in turn, alter the normal C dynamics and convert peatlands from long term net sinks to net sources of atmospheric C (Loreau, 2000; Waddington *et al.*, 2002; Kivimaki *et al.*, 2008).

Extraction also reduces CH_4 emissions due to changes in hydrology. Waddington and Price (2000) found that CH_4 flux at a cutover peatland was decreased to 12-50% of the adjacent natural site following drainage.

1.5 Peatland Restoration

Extraction often leaves peatlands bare and hostile to re-vegetation even after decades of abandonment (Desrochers *et al.*, 1998). This is in part due to the harsh microclimatic conditions (i.e. dry and prone to large fluctuations), and in part due to the lack of a viable seed bank (Campbell *et al.*, 2003). In order to re-establish functionality of disturbed sites, particularly to reduce C emissions, human-assisted restoration is suggested as a post-harvest management practice to accelerate recovery (Rochefort *et al.*, 2003). Although restored areas are usually small and do not make a noticeable contribution to C storage on a global scale, they prevent further oxidation of residual peat and re-establish photosynthesis (Kivimaki *et al.*, 2008; Tuittila *et al.*, 1999; Waddington *et al.*, 2001).

Strategies for restoration vary based on the specific project goals, desired end-states, and restoration challenges (Graf and Rochefort, 2008). In Canada, the short-term goals usually include establishing a plant cover composed of peatland species and restoring a water regime characteristic of peatland ecosystems (Rochefort *et al.*, 2003). The long-term objective is to return cutover areas to functional peat accumulating ecosystems (Rochefort *et al.*, 2003). This strategy is often different than the European strategy, which focuses primarily on biodiversity and rare species as the target of restoration (Graf and Rochefort, 2008).

The peatland type focused on in this study is a cutover bog, also called an extracted fen. Cutover bog refers to a raised bog that was extracted down to its minerotrophic peat layer. Restoration of a cutover bog differs from that of a typical bog because residual environmental conditions differ from the original, natural surface. Wind-Mulder *et al.* (1996) reported that the post-extraction peat chemistry in four sites under study were richer in minerals and higher in pH, similar to earlier successional fen stages. Bog plants will not be successful in these conditions, and thus the system should be restored using fen species instead (Wind-Mulder *et al.*, 1996; Graf and Rochefort, 2008). Although many fens are able to spontaneously recolonize following extraction, species are sometimes not representative of natural fens (Graf and Rochefort, 2008). While research on restoration of bogs is abundant in North America (Price *et al.*, 1998; Rochefort *et al.*, 2003; Campeau *et al.,* 2004; Chirino *et al.*, 2006), there is a lack of sufficient knowledge on restoration of cutover fens and how they may differ from bogs.

The traditional North American restoration method that has successfully been applied in bogs is referred to as the *Sphagnum*-transfer method (Graf and Rochefort, 2008). Ditches are blocked to raise the water level (Waddington and Day, 2007). Donor material composed of near surface moss, including rhizomes and seeds of vascular plants is then transferred from a pristine site and distributed on the extracted site. Straw mulch and a light dose of fertilizer are applied to ameliorate the harsh microclimate (Rochefort *et al.*, 2003). Evidence shows that active restoration can significantly reduce C release to the atmosphere and ultimately return peatlands to C accumulating ecosystems (Waddington *et al.,* 2002; Bortoluzzi *et al.,* 2006). The restoration of C sink function has been reported to occur in as little as two years (Tuitilla *et al.*, 1999).

There are, however, several shortcomings in the traditional restoration strategy. For one, species that are not initially planted and those that do not readily recruit from propagules cannot re-establish unless they are specifically targeted for planting, and any positive contributions they could make to achieve the restoration

goals are not realized. The unvegetated sites might never achieve the functional level of species-rich sites. Even where traditional restoration sites contain greater species number than natural sites (e.g. Poulin *et al.*, 2013), there is no knowledge of how the C storage function of that assemblage of species compares to C storage of peatlands with a natural diversity of vegetation species. In addition, initiatives targeting C storage typically view species diversity as desirable but not instrumental in achieving the main goals of the project. Biodiversity concerns receive only marginal attention, often merely as having side benefit (Diaz *et al.*, 2009).

This leads to one question: can plant biodiversity be manipulated and used as a tool to enhance the North American goals for restoration, such as to increase C storage capacity? To answer this question, it is necessary to understand the roles of different plant species in ecosystem C dynamics and the conditions favouring their establishment and growth. This knowledge would allow restoration project managers to use active, targeted planting to manipulate projects towards a desired species richness and composition that serve to enhance C accumulation capacity.

1.6 Biodiversity

The term biodiversity is a complex and multi-dimensional term, with great ambiguity (Hamilton, 2005). In this project, biodiversity refers to species richness (i.e. number of species), species identity (i.e. presence of particular species), species composition (i.e. assemblage), functional identity (i.e. presence of particular functional types), and functional richness (i.e. number of functional types) of the plants involved. The past two decades have witnessed a surge of research interest in biodiversity loss (Tilman *et al.*, 2001; Loreau and Hector, 2001; van Ruijven and Berendse, 2005; Hooper *et al.*, 2005; Cardinale *et al.*, 2007; Reiss *et al.*, 2009; Cardinale *et al.*, 2012; Maestre *et al.*, 2012), brought about by the realization that human activities are causing serious and often irreversible modifications to ecosystems (Vitousek *et al.*, 1997; Millennium Ecosystem Assessment, 2005). Among the many potential consequences of species loss that are relevant to this

project, it is thought that a reduction in diverse species traits and interactions can alter how efficiently solar energy and matter are captured, ultimately affecting the productivity, functioning, and stability of various ecosystems (Chapin *et al.*, 2000; Cardinale *et al.*, 2002).

An attempt to address these concerns has resulted in an emerging scientific topic. Biodiversity-Ecosystem Function (BEF) research, as the name implies, aims to investigate the mechanisms that link biodiversity and ecosystem functioning (Loreau, 2000). In a typical BEF research experiment, combinations of species ranging from high to low species richness are selected to measure how ecosystem functions respond to variation in biodiversity (Naeem and Wright, 2003). In the past two decades, a vast body of work has been conducted (>600 experiments since 1990, Cardinale *et al.*, 2012) with the general hypothesis that changes in species richness have measurable effects on ecosystem functioning (Drake, 2003). With many of the initial debates regarding interpretation of BEF experiments now resolved, Cardinale *et al.* (2012) determined that there is conclusive evidence that biodiversity loss reduces the efficiency by which ecological communities capture biologically essential resources, produce biomass, decompose, and recycle nutrients. These findings are consistent across different organisms, trophic levels, and ecosystems (Naeem *et al.*, 1994; Tilman *et al.*, 1996; Tilman 1997a, 1999, 2001; Hector *et al.*, 1999; Schlapfer and Schmid, 1999; Schwartz *et al.*, 2000; Schmid *et al.*, 2002; Callaway *et al.*, 2003; Roscher *et al.*, 2004; Cardinale *et al.*, 2004; Hooper *et al.*, 2005; Balvanera *et al.*, 2006; Cardinale *et al.*, 2007; Cardinale *et al.*, 2011), suggesting that unique underlying principles dictate the relationship between biodiversity and ecosystem functions (Cardinale *et al.*, 2012). Contrasting results also exist and there is some experimental evidence that not all ecosystem functions are improved by enhanced species richness (Naeem *et al.*, 1994, 1995; Wardle *et al.*, 1997; Tilman *et al.,* 1997).

The ecosystem function that will be examined in this study is C sequestration. Carbon sequestration refers to the process of capture and storage of carbon from

the atmosphere to build C stocks in peatlands and is also commonly referred to as C fixation, C accumulation, and C assimilation. In this study, C sequestration function is measured using the variable net seasonal C flux, where the word flux refers to CO_2, CH_4, or net C flowing between the peatland and the atmosphere. Net seasonal C flux is the sum of all CH_4 and CO_2 fluxes between the peatland and the atmosphere during the length of the growing season. A negative C flux indicates that C was added to the peatland, and a positive flux indicates C was lost to the atmosphere. To clarify, C flux and sequestration describe movement in opposite directions. Carbon sequestration has gained interest in an era when mitigating climate change has become a global challenge (Diaz *et al.*, 2009). There is evidence to believe that C sequestration is influenced by the number, identity, relative abundance, and spatial arrangement of plant species in ecological treatments (Diaz *et al.*, 2009).

Few C sequestration publications to date have addressed the effect of plant biodiversity (e.g. Catovsky, 2002 theoretical review; Fornara and Tillman, 2008 in grassland; De Deyn *et al.*, 2008 theoretical review; Diaz *et al.*, 2009 in forest) and even fewer have done so in peatland ecosystems (e.g. Riutta *et al.*, 2007 in peatland under climate change scenario; Kivimaki *et al*., 2008 in restored peatland; Ward *et al.*, 2009 in boreal bog). Kivimaki *et al.* (2008) studied CO_2 exchange in monocultures and polycultures of different plants in a restored peatland over two growing seasons to quantify their ability to form a C sink. Using the closed chamber technique, they measured GEP and RESP and reconstructed the NEE of the various stands. Their study found that enhanced functional diversity led to increased C accumulation per vegetated green area (VGA). Riutta *et al.* (2007) examined changes in C sequestration of fen species belonging to three different functional groups (moss, sedge, and shrub) following a drawdown in water level to simulate climate change. The study reported that changes in water level did not alter the overall CO_2 exchange of diverse vascular plant communities; however, sedges became the dominant contributors to gas exchange under wetter conditions and in drier conditions the shrubs were dominant in C exchange. They reasoned that plant

functional biodiversity could potentially act as a buffer against environmental variability and is a valuable feature of an ecosystem.

Biodiversity considerations are not simply a side issue in peatland restoration projects aiming to re-establish natural C sequestration function. Biodiversity has important consequences for long-term C sequestration, and thus warrants more detailed research in order to incorporate this knowledge into the guidelines and planning of restoration initiatives.

1.6.1 Debates in Biodiversity-Ecosystem Function Studies

While researchers have established that changes in biodiversity indeed impact the way ecosystems operate, there has been controversy in analyzing the mechanisms that cause this effect. Two common debates in the field of BEF have centred on interpretation of which aspect of biodiversity is responsible for this effect: 1) the number of species or the presence of particular species; 2) the number of species or of functional groups.

Many early BEF experiments confounded species richness and identity, and thus found it challenging to understand the result of their study (Drake, 2003). The case in favour of species richness is that in more diverse plantings, species can provide mutual benefits to one another and/or exploid a more diverse set of resources as a result of differential preference and access to resources, leading to increased productivity. The argument for species identity is that particular species with unique functional abilities can enhance the functionality of ecosystems. Research over the past decade has made it clear that this is a false dichotomy; there is evidence to show that both the number and the types of species in an ecosystem impact the rate of processes at work (Cardinale *et al.*, 2012).

As BEF research has evolved, its focus has shifted from taxonomic diversity toward a functional, trait-based perspective. Researchers believe that functional richness is

a greater determinant of ecosystem processes than taxonomic (species) richness (Reiss *et al.*, 2009). Functional groups consist of member species with similar physiological, structural, or behavioural traits that respond similarly to the environment and have similar effects on the functioning of the ecosystems (Diaz *et al.*, 2007). A measure of functional diversity requires the classification of individual species into groups based on an assessment of their properties. Three methods are most commonly applied: 1) Grouping species into discrete bundles based on previous knowledge; 2) Creating dendrograms based on determined distance between species in continuous trait space and finding clusters, where traits may include canopy height, structure, root depth, leaf morphology, etc. (Diaz *et al.*, 2009; Roscher *et al.*, 2004); 3) Assignment of *a priori* functional groups (e.g. grasses, forbes, legumes) (Reiss *et al.*, 2009; Roscher *et al.*, 2004). The present study applies the last method mentioned. This method is appropriate for this project because it allows restoration practitioners to group species that likely contribute to similar C dynamics in a simple, cost-effective, and time-efficient manner.

Several studies have attempted to test the relative importance of species versus functional groups. Tilman *et al.* (1997) monitored six ecosystem functions in 289 plots planted with 0-32 savannah-grassland species representing between 0-5 functional groups. The study found that while each of species richness, functional richness, and functional identity had a significant effect on ecosystem processes, functional group richness and identity were the principal determinants of ecosystem processes. They suggested that it is more important to have functionally different roles represented in an ecosystem than to control the total number of species. Another study by Fornara and Tilman (2008) addressed the effect of plant functional diversity on rates of soil C and N accumulated in N-limited grasslands. The study found that the presence of specific functional groups made a significant impact in soil C and N accumulation at both higher and lower species richness. The study concluded that specific functional group identities greatly increase ecosystem services such as soil C accumulation and biomass production regardless of species richness.

The concept of functional groups has led to new questions in BEF research. If species can be grouped based on similarity of functional roles, are species within each functional group ecologically equivalent to each other in functional terms? Functional redundancy refers to species that perform the same functional roles in ecosystems so that the loss of like species does not alter ecosystem functioning (Gitay *et al.*, 1996; Loreau, 2004). The addition of species with redundant functions may have only a limited effect on ecosystem properties (Waide *et al.*, 1999; Drake, 2003; Reiss *et al.*, 2009). This has been found to be the case for some processes and systems (e.g. for leaf breakdown by stream fungi or invertebrates, Reiss *et al.*, 2009). On the contrary, some studies have found that increasing species richness while keeping functional group composition constant actually has a positive effect on biomass production, suggesting that species within functional groups are not completely redundant in their functions (Reich *et al.*, 2004; Lanta and Leps, 2007). Marquard *et al.* (2009) found that for treatments with the same number of functional groups, the production of biomass was significantly affected by the identity of the functional groups present.

1.6.2 Mechanisms Controlling Biodiversity Effect

Much of the historical controversy in BEF involved the underlying mechanisms controlling the biodiversity effect. There are two general hypotheses in the literature: the selection effect (also called sampling) and complementarity (Loreau and Hector, 2001; Cardinale *et al.*, 2012).

The selection effect suggests that as the number of species in a mixture increases, so does the probability of including one or more species with extreme traits that may be dominant, high-biomass-producing, or better adapted to particular habitats that eventually causes greater yield (Aarsen, 1997; Huston, 1997; Tilman *et al.*, 1997; Hector *et al.*, 2002; Callaway *et al.*, 2003; Fridley, 2002; Drake, 2003; Roscher *et al.*, 2004, Fargione *et al.*, 2007; Reiss *et al.*, 2009).

The complementarity effect results from either resource partitioning or facilitation (Loreau and Hector, 2001; Drake, 2003; Roscher *et al.*, 2004). Resource partitioning occurs due to niche differences; more species are able to utilize a greater portion of the available resources due to inter-species differences in spatial and temporal resource use, ultimately allowing greater productivity (Hooper and Vitousek, 1997; Loreau, 1998; Tilman, 1999; Hector *et al.*, 2002). For example, the different canopy structures of plants increases interception of available sunlight, and differential rooting depths allow increased access to water and nutrients at various depths (Vitousek and Hooper, 1993; Hooper, 1998). Resource partitioning also occurs temporally as the period of maximum growth, productivity, and resource uptake varies for different species (Sanderson *et al.*, 2004; van Ruijven and Berendse, 2005; Van Ruijven and Berendse, 2005; Fargione *et al.*, 2007; Roscher *et al.*, 2008; Frankow-Lindberg *et al.*, 2009). A BEF study by Kivimaki *et al.* (2008) in a restored peatland found that when stands of *Carex* and *Eriophorum spp*. were planted in combination with *Sphagnum*, they were able to increase the seasonal rates of C fixation since each species was efficient at different times of the growing season.

Complementarity can also occur due to facilitation, in which some species create favourable environmental amendments for the growth of other species, for example by providing shade, increasing moisture, improving soil properties, or moderating temperature (Callaway 1997, 2007; Hooper, 1998; van Ruijven and Berendse, 2005; DaBler *et al.*, 2008). Cardinale *et al.* (2002) describes this phenomenon as individual species facilitating vertical and horizontal flux of resources to neighbours through biophysical interactions and delivery of gases, water, and nutrients. In a peatland study, McNeil and Waddington (2003) found that the presence of vascular companion species led to a doubling in the photosynthesis rate of *Sphagnum* species due to creation of a more favourable microclimate. However, facilitation is most commonly seen in legumes, which can fix nitrogen from the air and increase its availability for other species (Vitousek and Walker, 1989; Vandermeet, 1990).

Distinguishing the effect of niche differentiation from facilitation is difficult in practice; therefore, these mechanisms are referred to collectively as complementarity (Loreau and Hector, 2001). Research and syntheses over the past ten years have established that selection and complementarity often simultaneously account for the effect on ecosystem function (Cardinale *et al.*, 2012). An overview of >200 studies found that each mechanism contributed roughly equally to the net biodiversity effect (Cardinale *et al.*, 2011). Some studies have attempted to statistically differentiate between these two mechanisms (Caldeira *et al.*, 2001; Mulder *et al.*, 2001; Callaway, 2007) though no C flux studies that I am aware of have made such an attempt.

The sum of the complementarity and sampling effect is referred to as the biodiversity effect or net effect. The biodiversity effect measures the deviation of the mixture yield from its expected value on the basis of monoculture yields and the relative abundance of the species in the mixtures (Loreau and Hector, 2001). The biodiversity effect, as well as both complementarity and sampling effect can be positive or negative, and there is a potential for complementarity and sampling effects to cancel each other out, resulting in a zero net effect (Loreau and Hector, 2001). The biodiversity effect is equal to zero under the null hypothesis of no net biodiversity effect.

1.6.3 Overyielding

A typical hypothesis for the existence of the biodiversity effect is that the yield in a mixed plot of two or more species exceeds the production that would have been obtained by growing the same quantity of species alone in monoculture (Drake, 2003). This phenomenon is called 'overyielding' and results from positive interactions between species. Overyielding represents a positive deviation from the expected yield (Drake, 2003). There are two main ways in which overyielding is determined. Non-transgressive overyielding occurs when the observed yield of a mixture is greater than the weighted average of the monoculture yields of the

component species (Hector *et al.*, 2002). Transgressive overyielding occurs when mixtures produce more biomass than the most productive monoculture of the mixture's constituent species (Frankow-Lindberg *et al.*, 2009). The relationship between overyielding and causative mechanisms remains vague in the literature (Drake, 2003). It is commonly cited that complementarity (i.e. resource partitioning and facilitation) generates transgressive overyielding (Hector *et al.*, 1999; Fargione *et al.*, 2007). The sampling effect alone cannot result in mixtures producing more biomass than the most competitive component monocultures (Huston *et al.*, 2000; Tilman *et al.*, 2001).

One method of measuring overyielding and determining its causative mechanisms is the relative yield total (RYT). The relative yield for each species in a mixture is calculated by dividing its biomass in the mixture by its monoculture biomass (Hector, 1998). The sum of all relative yields for a mixture produces the relative yield total (Harper, 1977). A RYT > 1 indicates overyielding has occurred due to positive interactions between species (i.e. complementarity). A RYT of < 1 indicates underyielding has occurred due to negative interactions between species (i.e. competitive interference) (Hooper, 1998).

Review of agricultural and ecological experiments has shown that non-transgressive overyielding occurred in 53% of cases and transgressive overyielding in 24% of the data (Hector *et al.*, 2002). Although transgressive overyielding was not of wide occurrence, it is known that it requires years to develop, thus non-detection may be due to difficulty in its assessment (Frankow-Lindberg *et al.*, 2009). In many cases, the primary cause of overyielding is not the number of species, but the fertilization effect of nitrogen-fixing legumes (Loreau and Hector, 2001).

1.6.4 Limitations of Biodiversity-Ecosystem Function Studies

One of the many concerns in BEF research is the limited length of experimentation. Reviews of BEF research have revealed the median length of BEF study to be 730

days (Cardinale *et al.*, 2007) and sometimes as short as a single growing season (van Ruijven and Berendse, 2005). There is justified concern that short-term research projects do not capture a true and complete picture of the dynamics at work.

Increasingly, studies are finding that the diversity-productivity relationships and their underlying mechanisms are temporally dynamic, often growing stronger through time (Cardinale *et al.*, 2004, 2007). Cardinale *et al.* (2007) estimated that it takes approximately 1750 days or 2-5 growing seasons before we can reliably observe the effect of overyielding in multi-species treatments.

Another limitation in BEF studies is that in order to correctly detect and separate the mechanisms behind the effect of biodiversity on ecosystem function, relevant environmental conditions must be tightly controlled (Loreau, 1998). This is a very difficult task, particularly in field conditions. Relevant environmental conditions generally include drivers of ecosystem processes such as resource supply for productivity. Otherwise, the effect of environmental parameters may mask a biodiversity effect. Hector *et al.* (1999) suggested that the effect of environmental factors on productivity is, at a minimum, nearly twice as that of species diversity. In relevance to this study, environmental effects that may mask a biodiversity effect on C sequestration include water level, peat depth, peat age, and nutrient availability.

1.6.5 Peatland Plant Functional Types and Carbon Dynamics

Peatland plants generally fall into three categories: ericaceous shrubs, graminoids, and bryophytes (Ward *et al.*, 2009), which are considered as functional groups in this study. Each functional group has distinct traits that influence the rate of C input, output, and its residence time in the ecosystem (De Deyn *et al.*, 2008; Ward *et al.*, 2009).

Fast-growing plant species, such as graminoids and to a lesser extent shrubs, have much higher rates of C input to peatlands through photosynthesis than slow-

growing bryophytes, although this trades off with shorter lifespan and lower tissue C concentration (Aerts and Chapin, 2000). In boreal peatlands where the growing season is relatively short, vascular plants reach their optimal temperature for cell division and shoot elongation only during the peak of the short growing season when temperature is around 15-30 ^{o}C (Larcher, 1995), and bryophytes accumulate C more efficiently at lower temperatures (Silvola and Hanski, 1979; Harley *et al.*, 1989). Peatland sedges and ericaceous shrubs allocate most of their C resources to production of aboveground tissues, although a considerable amount can also be translocated to root biomass (Crow and Weider, 2005).

Interactions among plant species can influence C input in highly complex and context-dependent ways (Gartner and Cardon, 2004; Hooper *et al.*, 2005). For example, ericaceous shrubs tend to live in association with N-fixing bacteria that can facilitate growth of other plants by nutrient transfer and contribute to increasing community soil C input (Hooper *et al*., 2005; Ward *et al*., 2009). The canopy of vascular plants can alter photosynthesis by shading other plants (Grace and Marks, 1978), and it can also alter abiotic conditions such as temperature and moisture that ultimately influence the rate of C input (Chapin, 2003) in unpredictable ways. The myriad of complex interactions that can occur between plants have either positive or negative influence on C dynamics of plant communities, which makes it difficult to make predictions about the response of C sequestration.

In boreal peatlands, the rate of C sequestration is largely a result of slow plant litter decomposition and C loss through respiration. Fast-growing plant species have high metabolic rates, which leads to higher rates of respiration (De Deyn *et al.*, 2009). Graminoids allocate C to photosynthetic structures with low density and high nitrogen content, producing easily decomposable litter (Ward *et al.*, 2009). They also produce dense clumps of roots and rhizomes that have lower litter quality than shoots, and contribute to soil C storage potential (Craine *et al.*, 2005; Tjoelker *et al.,* 2005). However, Crow and Weider (2005) reported finding higher turnover rate of C in roots of graminoids and shrubs compared to aboveground C pools of these

groups. Shrubs retain high proportion of C in long-lived dense woody branches that is slow-cycling (Ward *et al.*, 2009) and produce litter that is rich in phenolics, which can potentially inhibit decomposition (Read *et al.*, 2004). On the other hand, low C to N ratio of shrub litter may be conducive to increased activity of decomposing bacteria and enhanced C loss. Bryophytes produce small but long-lived biomass that is C-rich, nutrient-poor, and recalcitrant (Aerts and Chapin, 2000). *Sphagnum* biomass is rich in phenolic compounds, tannins, and lipids coating cell wall polysaccharides that render its litter recalcitrant or poor quality for bacterial consumption (Karunen and Ekman, 1982). As a result, *Sphagnum* decomposes much more slowly (10-20% mass loss yr^{-1}) than leaves of most other plants in their natural habitat (40-80% mass loss yr^{-1}) and can potentially enhance C storage (Rochefort *et al.*, 1990; Johnson and Damman, 1991). In a litter decomposition study of various plant materials in fens, Graf and Rochefort (2009) reported finding the highest decay rate in aboveground tissue of vascular species and the lowest decay rate in bryophyte species, with root material having intermediate decay rate. Fine roots have been found to play an important role in C accumulations in fens (Scheffer and Aerts, 2000; Chimner *et al*., 2002), constituting 10-40% of net primary production (Graf and Rochefort, 2009). Litter mixing can cause interactions that either speed up or retard activity of decomposers through influences on temperature, moisture, and nutrients (Hättenschwiler *et al*., 2005, Cornelissen *et al.*, 2007). The complexity of possible interactions in mixed litter hampers predictability of the net effect on decomposition and C loss (Bardgett *et al.*, 2008; Ward *et al.*, 2009).

There is little agreement over which species contribute most to peat accumulation and C storage (Graf and Rochefort, 2009). *Sphagnum* is believed to be the main peat forming species (van Breemen, 1995), at least in bogs, which is the basis of the *Sphagnum*-transfer restoration method under practice in extracted peatlands (Rochefort, 2000). Vitt (2000) has found that among 341 peat cores from across North America, *Sphagnum* was the dominant material in poor fens and brown moss was dominant in rich fens. However, some paleontological studies have found

approximately half of residual peat to consist of root and other materials from vascular species (e.g. Kubiw *et al.*, 1989; Nicholson and Vitt, 1990; Chimner *et al.*, 2002), and yet others have determined vascular species to be dominant in peat formation (e.g. Warner *et al.*, 1991; Hu and David, 1995; Griffin, 1997). Several fen restoration projects in the past have focused on establishing vascular species for restoration of peat accumulation in disturbed peatlands (e.g. Roth, 1999; Wheeler and Shaw, 1999; Cooper and MacDonald, 2000; Lamers *et al.*, 2002).

1.7 Research Goals and Objectives

1.7.1 Research Motivations

The loss of peatlands due to peat extraction creates a measurable release of greenhouse gases to the atmosphere. In addition, extraction leads to loss of the original species diversity, which has the potential to impair ecosystem functioning (Marquard *et al.*, 2009). Restoration is an attempt to prevent these effects. There is reason to believe that the manipulation of biodiversity is effective and desirable for achieving and enhancing restoration objectives (Diaz *et al.*, 2009). Biodiversity can have important consequences on long-term C storage by modifying the rates of C gain and loss, as well as the size and permanence of C stocks (Vitt, 2006; Diaz *et al.*, 2009).

The primary purpose of this BEF project is to investigate the effect of biodiversity on the ability of minerotrophic peatlands to sequester C as well as to distinguishing between the underlying mechanisms that control this biodiversity effect.

The effect of biodiversity on C dynamics has only been examined in a few studies (Fornara and Tillman, 2008; Diaz *et al.*, 2009), and although C sequestration has been extensively studied in peatlands, it is rarely examined from a BEF perspective (Riutta *et al.*, 2007; Kivimaki *et al.*, 2008). Studies that examine C focus mostly on aboveground net primary production (ANPP), which is a relatively straightforward

ecosystem parameter to measure (Catovsky *et al.*, 2002). However, ANPP only provides a measure of the amount of C accumulating in aboveground plant biomass, but does not account for the total amount of C being stored in the ecosystem including belowground biomass and soil organic matter. Understanding the impact of biodiversity on total ecosystem C retention could have important benefits in efforts to mitigate climate change (Diaz *et al.*, 2009; Catovsky *et al.*, 2002). This is particularly important in peatlands, where the majority of the C is stored in soil organic matter (Gorham, 1991; Vitt, 2000).

The majority of peatland restoration research in Canada has focused on ombrotrophic type of peatlands. Considering that fens comprise approximately 65% of North America's peatlands (Vitt *et al.*, 2000) and that the use of peatlands as a natural resource is increasing, it is important to develop the scientific tools that can be used in the restoration of minerotrophic type of peatlands. Reliable knowledge of the impact of biodiversity on C dynamics could inform guidelines and policies for post-extraction management of peatlands by the peat industry.

1.7.2 Research Questions

This project attempts to answer four main questions:

1) Functional Groups: Can reasonable generalizations be made about the C sequestration capacity of species by organizing them into functional group? In other words, are species in the bryophyte functional group and graminoid functional group redundant in C sequestration ability?

2) Richness: Does increased species/functional richness (i.e. number) provide a C sequestration advantage in a restored peatland?

3) Identity: Which key species and functional groups are most efficient at C sequestration?

4) Composition and Interactions: How do inter-species interactions in polyculture treatments influence C sequestration? What are the dominant inter-species interactive mechanisms (e.g. competition, complementarity) that control this effect? How does species richness/identity affect the interaction between species?

The answers to these questions will allow me to consider ways in which biodiversity can be incorporated into the framework of restoration projects in such a way to maximize the C sequestration capacity of the restored peatland and contribute to mitigation of climate change at a regional scale.

1.7.3 Hypotheses

I intend to test four main hypotheses to address the research questions above. My general hypothesis is that changes in biodiversity result in a response in the C sequestration capacity of a restored peatland. My specific hypotheses are listed below and summarized in Table 1.1.

1) Functional Groups: My first hypothesis is that there is a relationship between species within the same functional group in terms of C sequestration capacity. To test this hypothesis I will compare the net seasonal C flux of monoculture treatments in the bryophyte and graminoid functional groups using mixed model ANOVAs.

2) Richness: My second hypothesis is that changes in species/functional richness will result in a significant response in C sequestration. To test this hypothesis, regressions and mixed model ANOVAs will be employed. Mixed model ANOVAs of net seasonal C fluxes at different species/functional richness level (i.e. number) will be used to determine if C sequestration is similar or different at various richness levels. R-squared (R^2) value and significance (p) of regression testing will indicate which of type of response (e.g. linear, exponential, or unimodal) best describes the

form of the relationship between net seasonal C flux and species/functional richness.

3) Identity: My third hypothesis is that the presence of particular species/functional groups will have a measurable effect on C sequestration. Regressions and mixed model ANOVAs will be used to test this hypothesis. If this hypothesis holds true, multiple regression testing should show a significant relationship between net seasonal C flux and changes in biomass of specific species/functional groups. In addition, mixed model ANOVAs should show significant variation in net seasonal C flux with and without the presence of specific species/functional groups.

4) Composition and Interactions: My fourth hypothesis consists of two components, both related to the interactions between species composing polyculture treatments. First, I hypothesize that interactions between species within polycultures will have a measurable effect on the C sequestration as opposed to when there is no interaction between species in monocultures. To test this hypothesis, I will conduct paired-sample T-test between expected and observed C flux of polycultures, where expected C flux represents the case *without* species interactions and observed C flux represents the case *with* species interactions. Expected C flux is determined as 1) the biomass-weighted sum of polyculture components in monoculture (non-transgressive), 2) the maximum C sequestering monoculture component (transgressive). Second, I hypothesize that species richness and identity will cause a response in overyielding. Regressions and mixed model ANOVAs will be used to determine if species richness and identity are significant predictors of overyielding.

1.7.4 Predictions

1) Functional Groups: I predict that species of the same functional group will have comparable C sequestration ability. Since functional groups consist of species with similar physiological, structural, or behavioural traits, they are expected to respond similarly to the environment and have similar effects on the functioning of the

ecosystem (Diaz *et al.*, 2007). Therefore, generalization of C sequestration function at the functional group level may be more appropriate than at the species level.

2) Richness: I expect that as species/functional richness increase, so will C sequestion, therefore, I expect to observe a reduction in net seasonal C flux. I predict that the form of the relationship between species/functional richness and C sequestration can be described by one of linear, saturating, or unimodal fits (e.g. as found in a review of BEF studies by Waide *et al.*, 1999).

3) Identity: My prediction is that the presence of graminoid and bryophyte species/functional groups, particularly *Sphagnum*, will result in a significant positive response in net seasonal C flux. *Sphagnum* is believed to be the main peat forming species (van Breemen, 1995), however, sedges and grasses (graminoids) are also known to be important contributors to peat accumulation, particularly in fens (Kuhry and Nicholson, 1993). Therefore, I predict that the presence and increased biomass of these species will be positively linked to C sequestration.

4) Composition and Interactions: I predict that polycultures will sequester more C than expected as a result of positive interactions between species compared to monocultures where there is no interaction between species. In other words, I expect to see an overall overyielding effect in polycultures. Increased species richness and the presence of unique species may have a positive control on overyielding.

1.7.5 Implications

1) Functional Groups: If species that have been classified under the same functional group are found to have comparable functional capacity, we can say that they are redundant in C sequestration function. In that case, the loss of one species can be functionally compensated by the presence of species from the same functional group without significant affect on the C sequestration ability of the community.

Redundancy will allow restoration planners to make reasonable generalizations about the C sequestration capacity of a restored site.

Any significant difference in C sequestration between species of the same functional group indicates that species within that functional group are not redundant in C sequestration function. This would suggest that diversity at the species level is more important than the functional group level and that the absence of one species cannot be functionally replaced by the presence of other species from the same functional group. The implication of this for restoration would be that evaluating the progress of restoration could not be simplified by monitoring at the functional group level.

2) Richness: The relationship between species/functional richness and C sequestration can have important implications for restoration planning, monitoring, and policy, as well as climate change mitigation. Restoration projects aiming to return the natural C dynamics of peatlands with climate change mitigation objectives would benefit from encouraging increased species/functional richness if a positive relationship between richness and C sequestration is found. In the absence of a positive relationship between C sequestration and richness, the time, effort, and cost of promoting increased species/functional number in restoration projects cannot be justified.

3) Identity: Species with a positive influence on C sequestration are desirable for integration into restoration planning. Increased C sequestration capacity in peatland restoration projects is valuable to return the natural functioning of the system. On a regional scale, increased C sequestration will contribute to reduction of greenhouse gases that affect climate change.

4) Composition and Interactions: Evidence of transgressive/non-transgressive overyielding in polycultures indicates that when several plant species grow together and interact, they sequester C more efficiently than their individual parts without

interaction. This is evidence for facilitation. Transgressive overyielding indicates that polycultures sequester C even more efficiently than the most efficient component monoculture and is very strong evidence for facilitation. Underyielding (less C sequestration than expected) will be considered evidence for negative interactions between species such as competition. If there is no significant evidence of either over- or underyielding, one of two phenomena could be the reason: either resource partitioning was dominant, allowing polycultures to sequester C similar to the sum of the weighted individual parts in monoculture or that facilitation was in balance with competition, preventing any net overyielding effect (Drake, 2003). In the case that key species or increased species richness are observed to contribute to an overyielding effect, these factors can be incorporated into restoration planning to increase C sequestration capacity of the restored site with climate change mitigation objectives.

1.7.6 Assumptions of Inquiry

Several assumptions are required to accept the logic of this research inquiry.

First, it is assumed that seasonal findings are representative of the relative C sequestration capacity of each treatment through time. Realistically, treatments will respond differently to temporally changing environmental factors, which may alter the functional capacity of each species and the interaction between species. However, for the purposes of this project, it is assumed that the relative C sequestration between treatments will remain comparable through time. For example, it is assumed that if the C sequestration in one treatment increases, the C sequestration in other treatments will increase proportionally.

Second, it is assumed that the treatments and their pseudo-replicates will have similar C sequestration capacity if planted in other minerotrophic peatlands under comparable abiotic conditions (e.g. water level, climate, fertility). This study design including the number of treatments and use of pseudo-replicates were suitable for

the scope of this project. In order to accept the implications of these findings, it is assumed that the study can be repeated on other sites and yield comparable results.

Lastly, it is assumed that the response of the selected individual species to abiotic conditions is representative of the greater population of that species and a repetition of the experiment with the same treatments would yield the same results, given that all other factors are equal.

Table 1.1: Summary of hypotheses and predictions to be tested. [C=carbon]

Hypothesis	Prediction	Implications	Test	Variables
1) A relationship between species within a *functional group* in C sequest-ration capacity	Species in functional groups have statistically similar C sequestration capacity	-Restoration monitoring -Redundancy, insurance for species loss	Mixed model ANOVA	Net seasonal C flux vs. bryophyte species, block Net seasonal C flux vs. graminoid species, block
2) C sequestration responds to changes in species/functional *richness*	Increased species/ functional richness results in increased C sequestration with one of linear, unimodal, or exponential relationships	-Restoration planning -Climate change mitigation	Linear and non-Linear Regression	Net seasonal C flux vs. species richness
			Mixed model ANOVA	Net seasonal C flux vs. species richness, block
3) C sequestration responds to the presence of key species/functional groups (i.e. *Identity*)	Presence of graminoids and/or bryophyte species/functional groups increases C sequestration capacity	-Restoration planning -Climate change mitigation	Multiple Linear Regression	Net seasonal C flux vs. biomass of each species Net seasonal C flux vs. biomass of each functional group
			Mixed model ANOVA	Net seasonal C flux vs. presence of species, block Net seasonal C flux vs. presence of functional group, block

Hypothesis	Prediction	Implications	Test	Variables
4) -Species interactions (i.e. *composition*) will result in overyielding response -Overyielding responds to changes in species richness and identity	-Species interactions in polycultures will result in negative overyielding values -Overyielding increases with species richness -Overyielding increases with presence of key species	-Restoration planning -Climate change mitigation	Paired–samples T Test	Expected 1 vs. observed net seasonal C flux Expected 2 vs. observed net seasonal C flux
			Multiple Linear Regression	Non-transgressive overyielding vs. species biomass
				Non-transgressive overyielding vs. species richness
			Mixed model ANOVA	Non-transgressive overyielding vs. presence of species, block

CHAPTER 2: METHODS

2.1 Study Site

The study was conducted at Bic Saint-Fabien (BSF) peatland (48° 18′ N, 68° 52′ W), which is located in the St. Lawrence Lowlands, approximately 25 km west of Rimouski, Quebec (Figure 2.1). Mean annual precipitation based on 1971-2000 measurements from the Rimouski meteorological station is 915 mm, 30% of which falls as snow (Environment Canada, 2013). The growing season between May-August receives on average 336 mm of rain. Average daily temperatures are -12 °C and 18 °C in January and July, respectively (Environment Canada, 2013).

The peatland complex consists of undisturbed and disturbed sites. The undisturbed part of the peatland, a 6.8 ha forested moderately rich fen with an average peat depth of 4.5 m, is dominated by Eastern White Cedar (*Thuja occidentalis*), Black Spruce (*Picea mariana*), and Tamarack (*Larix laricina*) in the overstory, with the lower moss layer dominated by brown mosses including *Campylium stellatum*, *Drepanocladus spp*., and *Tomenthypnum nitens*. A variety of species of *Sphagnum* moss, shrubs, and graminoids occur across microhabitats at the site. This natural site, is generally used as a reference for restoration targets.

The extracted portion of the peatland consists of 22 ha, which was extracted for horticultural peat between 1946-2000. This portion was initially a raised bog, which was harvested down to its minerotrophic peat layer and residual peat conditions of the site now resemble that of a fen. Since the site was extracted in parts, most of the site has now been abandoned for the last few decades. Peat thickness varies between 1.6 and 3.5 m (Ketcheson *et al.*, 2012). This section of the BSF peatland is characterized by a well-decomposed and compacted peat substrate, with very limited spontaneous recolonization of mosses in some sections, and ruderal non-fen species such as cattails (*Typha* spp.) in former ditches. The vast majority of the eastern-most part of the site remained bare until 2010 when

assortments of restoration methods were implemented following preliminary research. Traditional *Sphagnum*-transfer method with donor material from a local fen has been applied for restoration on the eastern-most section. The central section has been restored using a biodiversity-control method. This is the main site for this study. Figure 2.1 shows an aerial view of the natural and extracted portions of the peatland.

The restoration project is a collaborative effort between three universities: University of Laval (responsible for ecological studies), University of Calgary (responsible for C flux studies), and University of Waterloo (responsible for hydrological studies).

2.2 Plots

The biodiversity-control plots were planted by Vicky Bérubé (PhD Candidate – University of Laval) during summer of 2009. The planted species were selected following an inventory of three moderately rich fens near Rimouski, QC. Common boreal fen species of bryophytes, graminoids (sedges and grasses), and shrubs were chosen based on regional frequency and abundance. Each of the aforementioned species types is treated as a functional group in this study as a means of simplifying the understanding of results and forming appropriate generalizations and theories regarding species that have similar responses to environmental factors. This method of designating functional groups is common in the literature (e.g.Riutta *et al.*, 2007; De Deyn *et al*., 2008; and Ward *et al.,* 2009).

To maintain reasonable simplicity for practical and statistical purposes, the number of selected species of bryophytes, graminoids, and shrubs were limited to eight for the study of carbon (C) sequestration. The summary of species characteristics is shown in Table 2.1.

Fourteen treatment combinations of 1, 2, 3, and 6 species were selected for this study (Table 2.2) out of 24 treatments originally planted by Vicky Bérubé. Treatments were planted using randomized block design. Each treatment was replicated in four blocks arranged along a hydrological gradient, of which three blocks were monitored for this study (i.e. three pseudo-replicates in block 1, 3, and 4). Block 1 was planted in field 6 and was generally drier than the other blocks. Block 4 was planted in fields 8 and 7 and was wetter than the other blocks. Block 3 was planted in field 7 and had intermediate wetness. Details of the site and block layouts are provided in Appendix A. Four bare unplanted peat plots, six plots with traditional *Sphagnum*-transfer restoration, and six plots from the natural sites were also monitored for comparison. The natural and traditional restoration sites will not be directly used in this study and only serve as a reference for comparison. The biodiversity plots were planted on a 3 m x 3 m area and collars of 60 cm x 60 cm were inserted for gas flux measurements (Figure 2.3A). The natural and traditional restoration collars measure the same dimensions. The bare peat collars were smaller and circular with a diameter of 30 cm (Figure 2.3B). The small collars are appropriate for non-vegetated peat as they allow for detection of small changes in gas concentrations. All collars were grooved, so as to ensure sealing with water. The collars extended 20 cm into the soil, which is usually below the rooting zone (Laiho and Finér, 1996; Mahmood and Strack, 2011).

2.3 Data Collection

Field measurements were conducted during the growing seasons of 2011 (May-August) and 2012 (May-September). Only five treatments were measured in 2011 as part of a preliminary investigation. This was expanded to 14 treatments in 2012. Closed chamber measurements of gas fluxes were collected weekly in 2011. Methane (CH_4) fluxes during the 2012 growing season were measured (Figure 2.2A) weekly on plots that had been monitored in 2011, and monthly on the remaining plots. During the 2012 growing season, carbon dioxide (CO_2) flux measurements (Figure 2.2B) were conducted weekly on all plots, except for six weeks in July and

August when they were done biweekly due to instrumental malfunctions. Vegetation volume measurements (Figure 2.2C) were conducted weekly during both growing seasons. Nutrient probes (Plant Root Simulator (PRS™), Western Ag innovations) were inserted in late July 2012 and removed eight weeks later in September. Vegetation harvesting (Figure 2.2D) was completed at the end of the 2012 field season. Details of all methods are given below.

A meteorological station located on the extracted site continuously recorded Photosynthetically Active Radiation (PAR), precipitation, water level position, soil surface temperature, and air temperature throughout the growing season. Measurements were taken each minute and averaged at 30 min intervals in 2011 and 20 min intervals in 2012. Additionally, three probes recorded soil surface temperature at three locations (one in each block) at half-hour intervals in 2012.

2.4 Carbon Dioxide Flux Field Measurements

The CO_2 exchange measurements were made using a transparent plastic chamber (60 cm x 60 cm x 30 cm) and a portable Infra-Red Gas Analyzer (IRGA; PP systems EGM 4) (Alm *et al.*, 2007). The chamber was equipped with two fans to mix the air in the headspace. In the case that the chamber was too short for the height of vegetation in a plot, a 60 cm high extension, equipped with two additional fans, was attached to lengthen the chamber. Before a measurement, the groove in the collar was filled with water to ensure airtight seal between the collar and the chamber. The chamber was then placed on the collar and CO_2 gas concentrations in the headspace were recorded every 15 s with the IRGA for a period of 2 min. Air temperature of the headspace of the chamber, PAR (μmol/m^2/s), and relative humidity (%) were also recorded concurrently with CO_2 measurements. This was repeated with two shade levels by covering the chamber with plastic netting that reduced PAR by approximately 50% and 75%. These measurements provide an estimate of net ecosystem exchange (NEE). A dark measurement using an opaque tarp was done to estimate ecosystem respiration (RESP). Gross ecosystem

photosynthesis (GEP) was calculated as the difference between NEE and RESP. Between measurements, the chamber was vented to allow equilibration of the air in the headspace with ambient air. In addition, water level and temperature of the peat profile at depths 2, 5, 10, 15, and 20 cm below the bare peat/moss layer were also recorded.

Instantaneous CO_2 fluxes were calculated as the linear change of CO_2 concentration over time, where positive values indicate the ecosystem is losing C to the atmosphere and negative values indicate C sequestration to the peatland.

2.5 Methane Flux Field Measurements

The closed chamber method was applied for CH_4 flux measurements (Alm *et al.*, 2007). Opaque metal chambers (60 cm x 60 cm x 30 cm) were placed on top of collars to create a closed system, and the grooves of the collar were filled with water to ensure an airtight seal. Each chamber was equipped with two battery-operated fans to ensure proper mixing of the air in the headspace. Four 20 mL gas samples were taken from the internal headspace at regular intervals after chamber closure (7, 15, 25, 35 min) using a syringe equipped with a three-way stopcock. Samples were transferred to evacuated Exetainers (Labco Ltd., UK) and sent to the Department of Geography, University of Calgary for analysis. The gas samples were analyzed for CH_4 concentration using a Varian Gas Chromatograph 3800 (GC) with flame ionization detector. The GC was calibrated with standards after every eight samples. The instantaneous flux was calculated as the linear change in CH_4 concentration in the headspace over time. Significant outliers were identified by constructing boxplots with outliers and removed from seasonal flux calculation.

Environmental variables that were monitored during CH_4 flux measurements included air temperature inside the chamber using a thermocouple thermometer (VWR int., USA), water level in a well adjacent to each collar, and soil temperature at 2, 5, 10, 15, 20, 25, and 30 cm depths using thermocouple thermometers.

2.6 Vegetation Volume Field Measurements

The 'Fuel Rule' is a simple, fast, and non-destructive method of estimating aboveground biomass in the form of vegetation volume. In this method, visual obstruction of a banded measurement stick was used to estimate vegetation volume based on a combination of the height of the vegetation and its density (Davies *et al.*, 2008). It has previously been found that there is a statistically significant relationship between vegetation volume determined with this method and destructively harvested biomass for the BSF peatland (Strack and Srivastava, 2010).

The Fuel Rule is a 2-m measuring stick that is 2.5 cm wide and painted with alternating white and red bands. One face has bands 10 cm wide whereas the reverse has two bandwidths of 2 and 5 cm starting at opposite ends and running half its length. Each set of bands is labeled with numbers. The bandwidth used for each survey depends on the vegetation height. Generally, it is desirable to have at least five bands obstructed to some degree.

To take a reading, the Fuel Rule was placed vertically in the middle of a collar and pressed down through the moss and litter layer until it reached the more compact horizon below. The user, while standing at arm's length, visually estimated the percentage of each band obscured by vegetation. The data were entered into the PObscured computer program to determine vegetation volume as described by Davies *et al.* (2008).

Vegetation volume data were used in combination with harvested biomass data to produce and simulate models for seasonal C sequestration.

2.7 Nutrient Content Measurements

In order to have an idea of how fertility differed among the collars, Plant Root Simulators (PRS™ Probe, Western Ag Innovators) were installed. PRS probes utilize

ion exchange resin membranes to estimate ion flux in soil. The chemically pre-treated anion and cation exchange resin membranes act similar to plant root surfaces in nutrient sorption and surface characteristic. When buried in soil, the probes assessed nutrient supply rates by continuously adsorbing charged ionic species over the burial period.

Four sets of probes (four anions and four cations) were inserted into the peat at each sampling plot on July 24, 2012 and removed on September 10, 2012. Three sets were inserted directly outside the flux collar at the top, left, and right sides of the collar. One set was inserted in the center of the collar. Following removal, the probes were washed with deionized water and excess dirt was removed with a scrub brush. The probes were sent to Western Ag Innovators for analysis. The results were determined as an average of the four probe sets.

2.8 Biomass Harvesting

At the end of the 2012 field season, shoots from the 60 cm x 60 cm biodiversity-controlled plots were harvested in order to aid in the estimation of overyielding. Aboveground biomass, including all stems, leaves, and reproductive parts, were clipped at the surface, sorted by species, and bagged. The full collar biomass of all vascular species, and only a quarter of the ground layer of bryophytes were collected. To determine the total bryophyte biomass in each collar, the collected bryophyte biomass of the quarter collar was multiplied by four. Any remaining plant litter on the soil surface and fragments that could not be identified by species were bagged separately as litter. These were sent to the laboratory at the Department of Geography, University of Calgary. Plant tissues were refrigerated in the laboratory prior to analysis. Each separate specie was then weighed, oven dried at 80^{o}C for 48h, and weighed again, in order to estimate aboveground dry biomass.

2.9 Modelling and Model Simulations

Models of the individual components of C flux (GEP, RESP, and CH_4) were parameterized for the combined pseudo-replicates of each treatment and simulated using measured control variables for each season to determine the net seasonal C flux. Net seasonal C flux is a measure of the seasonal C sequestration and was used to analyze and interpret the role of plant biodiversity. Parameterization of the three C models was performed using SPSS statistical software, Version 21.0.0.0 for Mac.

2.9.1 Vegetation Volume Model

Vegetation volume (VV) for each of the plots with vascular species was modeled by applying Gaussian curve-fitting (Riutta *et al.*, 2007) using MATLAB's (R2012a Student version) curve-fitting tool. This allowed for incorporation of the VV parameter into the seasonal C flux models. Since the VV in bryophytes did not vary significantly over the season, the harvested biomass (g) of the moss was substituted as a single fixed value for each replicate of a treatment.

$$VV = VVmax * \exp[(\frac{JD-JDmax}{b})]^2 \qquad \text{Equation 2.1}$$

(From Riutta *et al.,* 2007)

Where, *VV* is the vegetation volume calculated by the PObscured software from field readings, *VVmax* is the maximum *VV* during the season, *JD* is the Julian day (days of a year numbered from 1 to 365), *JDmax* is the timing of *VVmax* and *b* is the width of the Gaussian curve.

2.9.2 Carbon Dioxide Exchange Models

The form of the photosynthesis (GEP) model was adapted and altered from Riutta *et al.* (2007). The model describes daily photosynthesis (g CO_2 m^{-2} d^{-1}) as a non-linear

multivariate function of vegetation volume, PAR, air temperature, and water level. The model defines the response of photosynthesis to PAR as saturating, to vegetation volume as either linear (for mosses) or saturating (for vascular plants), and to air temperature and water level as Gaussian.

$$GEP = \frac{GEPmax*PAR*VV}{k+PAR} * e^{\frac{-0.5*(Ta-Topt)^2}{Ttol}} * e^{\frac{-0.5*(WL-WLopt)^2}{WLtol}} + constant \quad \text{Equation 2.2}$$

$$GEP = \frac{GEPmax*PAR*(1-\exp(-a*VV))}{k+PAR} * e^{\frac{-0.5*(Ta-Topt)^2}{Ttol}} * e^{\frac{-0.5*(WL-WLopt)^2}{WLtol}} + constant$$

Equation 2.3

(Modified from Riutta *et al.,* 2007)

In Equations 2.2 and 2.3 *PAR* is the measured photosynthetically active radiation (µmol m^{-2} s^{-1}), *Ta* is the average air temperature (°C) in the headspace of the chamber during the run, and *WL* is the water level position (cm) below the surface of the bare peat or moss layer (whichever is higher). *GEPmax* is the maximum potential photosynthesis rate (g CO_2 m^{-2} d^{-1}) per one gram of vegetation for bryophyte treatments or per one vegetation volume unit for vascular collars, when PAR, Ta, and WL are non-limiting. Parameter *k* (umol m^{-2} s^{-1}) is the level of PAR at which half of the maximum photosynthesis rate is reached; parameter *Topt* (°C) denotes the optimal Ta for GEP; parameter *Ttol* (°C) denotes the Ta tolerance (deviation from the optimum at which GEP is 61% of its maximum); parameter *WLopt* (cm) denotes the optimal WL for GEP and parameter *WLtol* (cm) denotes the WL tolerance. Parameter *a* denotes the initial slope of the saturating VV response function (per VV unit) and is useful in describing the decrease in the GEP rate of collars with vascular species caused by self-shading. Equation 2.2 was parameterized for bryophyte-only collars and equation 2.3 for collars containing at least one vascular species.

Since *PAR* measurements from the meteorological station were in volts, a calibration was completed with the EGM-4 PAR sensor to obtain the linear regression equation used to convert these values into μmol m^{-2} s^{-1}.

Total respiration (RESP, g CO_2 m^{-2} d^{-1}) was modeled as a multivariate non-linear function of *Ta*, and *VV*, with *WL* included as an extra parameter in bare peat and bryophyte-only collars (Equations 2.4, 2.5, and 2.6). Total respiration represents the combination of autotrophic and heterotrophic respiration and was modeled separately for each treatment type. Respiration was modeled as having a sigmoidal response to *WL* and *Ta* and a linear response to *VV*. Equation 2.4 was used to model respiration in treatments with only bryophytes to account for the strong influence of *WL* fluctuations on non-vascular species, Equation 2.5 was applied to treatments with vascular species present, and Equation 2.6 was used for bare peat sites to represent cases where vegetation is absent.

$$RESP = \frac{b1}{1+\exp(-b2*(Ta-b3))} + \frac{b4}{1+\exp(-b5*(WL-b6))} + b7 * VV + constant \quad \text{Equation 2.4}$$

$$RESP = \frac{b1}{1+\exp(-b2*(Ta-b3))} + b7 * VV + constant \quad \text{Equation 2.5}$$

$$RESP = \frac{b1}{1+\exp(-b2*(Ta-b3))} + \frac{b4}{1+\exp(-b5*(WL-b6))} + constant \quad \text{Equation 2.6}$$

(Modified from Riutta *et al.,* 2007)

In Equations 2.4 to 2.6, *b1* is the amplitude of the response of respiration to *Ta* (g CO_2 m^{-2} d^{-1}), *b2* ($^oC^{-1}$) is the slope determining the speed and direction of change in respiration along the *Ta* range and *b3* denotes the *Ta* (^oC) at the centre of the fastest change along the *Ta* range. Similarly, *b4* is the amplitude of the response of respiration to *WL* (g CO_2 m^{-2} d^{-1}), parameter *b5* (cm^{-1}) is the slope determining the speed and direction of change in respiration along the *WL* range and *b6* denotes the

WL (cm) at the centre of the fastest change along the *WL* range. Parameter *b7* (g CO_2 m^{-2} d^{-1} VV $unit^{-1}$) denotes the change in respiration per *VV* unit.

2.9.3 Methane Flux Models

Methane (CH_4, mg CH_4 m^{-2} d^{-1}) flux was modelled with a multivariate non-linear model with *VV*, soil surface temperature (*T2*), and *WL* as control variables (Equations 2.7 and 2.8). The model predicts flux as having a linear response to *T2* and *VV*, and a Gaussian response to *WL* position. Models used for estimating flux of bryophyte-only collars and bare peat collars did not include the *VV* variable.

$$CH4 = b1 * T2 + b2 * VV + b6 * \mathrm{e}\left(\frac{-0.5(WL-WLopt)}{WLtol}^{2}\right) + constant \qquad \text{Equation 2.7}$$

$$CH4 = b1 * T2 + b6 * \mathrm{e}\left(\frac{-0.5(WL-WLopt)}{WLtol}^{2}\right) + constant \qquad \text{Equation 2.8}$$

In Equations 2.7 and 2.8 *T2* is the soil temperature (^oC) at 2 cm depth from either the bare peat surface or the top of the moss layer, *b1* ($^oC^{-1}$) is the slope determining the speed and direction of change in flux along the *Ta* range, *VV* is the vegetation volume, *b2* is slope and direction of change in flux along the *VV* range (VV $unit^{-1}$), *WL* is the water level depth (cm), *WLopt* denotes the optimal *WL* for CH_4 production (cm) and parameter *WLtol* denotes the WL tolerance (cm).

2.9.4 Flux Simulations

Carbon sequestration was estimated for each collar for the growing seasons of 2011 (May-August) and 2012 (May-September). The variable net seasonal C flux is an estimate of seasonal C sequestration that is obtained from the sum of simulation results of the GEP, RESP, and CH_4 models. Since C sequestration and net seasonal C flux have reversed signs, a negative net seasonal C flux indicates net sequestration of C to the peatland and a positive net seasonal C flux indicates a net release of C to the

atmosphere. Each model was simulated in two ways: 1) under the existing environmental conditions of each plot, 2) under a standard condition with three moisture scenarios: dry, moderate, and wet.

Each of the C component models (GEP, RESP, and CH4) was calculated for half-hourly time steps in 2011 and 20-min time steps in 2012. The values of the control variables (i.e. T2, Ta, and WL) for each collar were interpolated as a linear regression between the weather station measurements and measurements taken at each plot location. The VV value of each collar was interpolated from the Gaussian fit for each day of the year (Equation 2.1).

To standardize the net seasonal C flux for each treatment, each of the three models (GEP, RESP, and CH4) was run under three standard wetness scenarios. The WL fluctuations for each wetness scenario were taken from three plots that were good representations of the dry, moderate, and wet conditions for each season. The results from these three standardized simulations allow for comparison between the treatments without concern for inter-plot variation in C flux caused by differences in WL. T2, Ta, and PAR fluctuations were taken from a single plot and kept the same under all scenarios.

To assess the reliability of the model estimates, the model simulation results for each plot were compared with the average instantaneous field measurements for that plot.

2.9.5 Testing the Biodiversity Effect

The main purpose of this study was to understand the effect of changes in biodiversity on the capacity of a restored peatland to sequester C. Four main inquiries were made:

1) Functional Groups: I compared C sequestration potential of species within each

graminoid and bryophyte functional groups to determine if reasonable assumptions about C sequestration could be made at the functional group level. Mixed model ANOVA in IBM SPSS (Version 21.0.0.0) was used to compare the net seasonal C flux of monoculture treatments within each of the bryophyte and graminoid functional groups with species as a fixed factor and block as a random factor, in 2012 only (in 2011, only one species within each functional group was tested). For example, I tested for differences in net seasonal C flux between Tn, Cs, and Sw within the bryophyte functional group and Ca, Tc, Ta, and Cc within the graminoid functional group.

Interpretation: If species within functional groups are comparable net seasonal C flux, classifying of species into *a priori* functional groups can be used to make effective generalizations about C sequestration capacity of species. This can have important implications for planning and monitoring of restoration projects. Evaluating the progress of restoration can be simplified by monitoring at the functional group level rather than at the species level. If species within the same functional group are redundant in functional capacity, the loss of one species can be compensated by the presence of another. Any differences between species of the same functional group can be understood as a sign that the species within that functional group are not redundant in nature. In this case, it would be reasonable to monitor restoration progress at the species level.

Richness: The influence of species richness on C sequestration was tested for 2012 using regression and mixed model ANOVA tests. Linear, quadratic, and exponential regressions were used to find the form that best describes the relationship between net seasonal C flux and species/functional number (e.g. as found in a review of BEF studies by Waide *et al.*, 1999). Net seasonal C flux was transformed by addition of a constant to avoid negative values, which would have prevented exponential regression testing. This was achieved by adding a value of 321 to the 2012 net seasonal C flux for each plot. To be consistent, all regressions were completed using the transformed data. Any significant regression between net seasonal C flux and

species/functional number was interpreted based on the direction and significance of the relationship. The largest R^2 of linear, quadratic, or exponential regressions was assumed to best describe the form of the relationship. Mixed model ANOVA was used to determine any significant difference in net seasonal C flux due to richness with each species/functional number as fixed factor (separately) and block as a random factor.

Interpretation: Understanding the relationship between richness and C sequestration can be valuable in restoration planning. The above tests can determine whether there is an ideal level of species richness that can maximize C sequestration. Increased C sequestration is advantageous from a climate change perspective by reducing the C in the atmosphere.

Identity: The impact of species identity on C sequestration was initially tested using multiple linear regression applied between the dependent factor, net seasonal C flux and 1) the biomass of each species as a variable in multiple regression, and 2) the biomass of each functional group as a variable in multiple regression. Any species/functional groups that had a statistically significance effect on net seasonal C flux were further tested using a mixed model ANOVA, with the presence of significant species/functional groups as a fixed factor and block as a random factor. If more than one test was conducted, the significance factor was adjusted by applying Bonferroni adjustment. Using both regression and ANOVA was useful to determine whether the presence or the increased appearance of a species/functional group was important for C sequestration.

Interpretation: Key species/functional groups with a positive influence on C sequestration (i.e. negative correlation with C flux) were identified for integration into restoration planning. Species that increase the C sequestration capacity of a restored peatland at a regional scale are advantageous from a climate change perspective.

Composition: Lastly, I compared the *expected* net seasonal C flux with the *observed* net seasonal C flux in 2012, to test the overall influence of interactions between plant species. The expected values were calculated from net seasonal C flux of monocultures and represented the scenario *without* species interactions, while the observed net seasonal C flux represented the scenario *with* species interactions. The direction of deviation of the observed from the expected net seasonal C flux was indicative of the overall species composition effect and contributed to understanding the impact of species interactions on C dynamics. The expected net seasonal C flux was calculated in two ways. In the first method ($C\ flux_{E1}$), expected net seasonal C flux for each polyculture was calculated as the biomass-weighted average net seasonal C flux of its components in monoculture. In other words, the biomass of each species in a polyculture (B_p) was divided by its biomass in monoculture (B_m) and multiplied by its net seasonal C flux in monoculture ($C\ Flux_m$) under the same wetness scenario (Equation 2.9). In the second method ($C\ flux_{E2}$), expected net seasonal C flux of each polyculture was equal to the largest C sequestering component monoculture (i.e. lowest net seasonal C flux) under the same wetness scenario (Equation 2.10). Paired-samples T-test was used to determine significant difference between the expected and observed net seasonal C fluxes.

$$C\ flux_{E1} = \Sigma \left(\frac{Bp}{Bm} * C\ Flux_m\right) \qquad \text{Equation 2.9}$$

$$C\ flux_{E2} = \min (C\ Flux_m) \qquad \text{Equation 2.10}$$

Overyielding in C sequestration was determined as the deviation of the expected from the observed net seasonal C fluxes (Equation 2.11), and was used to further understand the nature of the interactions between species. Non-transgressive overyielding was calculated in relation to the first expected net seasonal C flux (Equation 2.9, $C\ flux_{E1}$). Transgressive overyielding was calculated as the difference between the observed net seasonal C flux and the second expected net seasonal C flux (Equation 2.10, $C\ flux_{E2}$). A negative overyielding value was indication that

mixtures sequestered more C than expected. A positive value (also referred to as underyielding) was indication that mixtures sequestered less C than expected. The unintuitive sign convention relates back to the fact that C sequestration function is measured as negative net seasonal C flux.

$$\text{Overyielding} = \text{C Flux}_{O} - \text{C Flux}_{E} \qquad \text{Equation 2.11}$$

The impact of species richness and identity on overyielding were tested using multiple regression testing between non-transgressive overyielding and 1) the biomass of each species as a variable in multiple regression, 2) the species richness. Any variables that were significant in regression were tested again using mixed model ANOVA, with block as a random factor. If more than one test was conducted, the significance factor was adjusted by applying Bonferroni adjustment. The overyielding results of each treatment were also qualitatively compared to make inferences about inter-species interactions (i.e. complementarity vs. competition) between plant species.

Interpretation: Results of the paired-samples T-test, multiple linear regression, and mixed model ANOVA were used to draw conclusions about the interaction between species. The method used in this study for differentiating between interaction mechanisms is adapted and modified from Drake (2003). In this method, negative overyielding values (i.e. where more C was sequestered than expected) were interpreted as resulting from interactions that led to more efficient C sequestration than expected. It was assumed that in such cases inter-species facilitation outweighed competitive interference, creating suitable conditions for additional C sequestration. On the contrary, positive overyielding values (i.e. underyielding) were interpreted as resulting from interactions that were not conducive to efficient C sequestration. It was assumed that in such cases inter-species competition for limited common resources was strong enough to reduce the C sequestration capacity of one or more species. Zero overyielding was considered as evidence for one of two phenomena: either resource partitioning was dominant, allowing

polycultures to sequester C similar to the sum of the weighted individual parts in monoculture or that facilitation was in balance with competition, preventing any net overyielding effect. Transgressive overyielding was considered as more conservative evidence for facilitation than non-transgressive overyielding. Results of multiple linear regression and mixed model ANOVA were interpreted to detect any effect of species richness or identity on overyielding. Any significant negative relationships between overyielding and species richness/identity were deemed important for providing a C sequestration advantage, which was valuable from a climate change perspective.

Abiotic Factors: In order to investigate possible abiotic influences on biodiversity effect, Pearson's correlation test was applied to detect any relationships between species/functional group richness and each of 1) average seasonal soil moisture, 2) average seasonal soil temperature, and 3) nutrient content. Pearson's correlation test was applied on the biomass of each species/functional group present and the abovementioned abiotic factors. The correlation between net seasonal CH_4/C flux and nutrient content was also tested.

The results were used to understand the ways in which plant biodiversity could either promote or diminish C sequestration through effects on soil moisture, soil temperature, and nutrient content. Any significant correlations were interpreted in terms of the direction of correlation and the variables involved

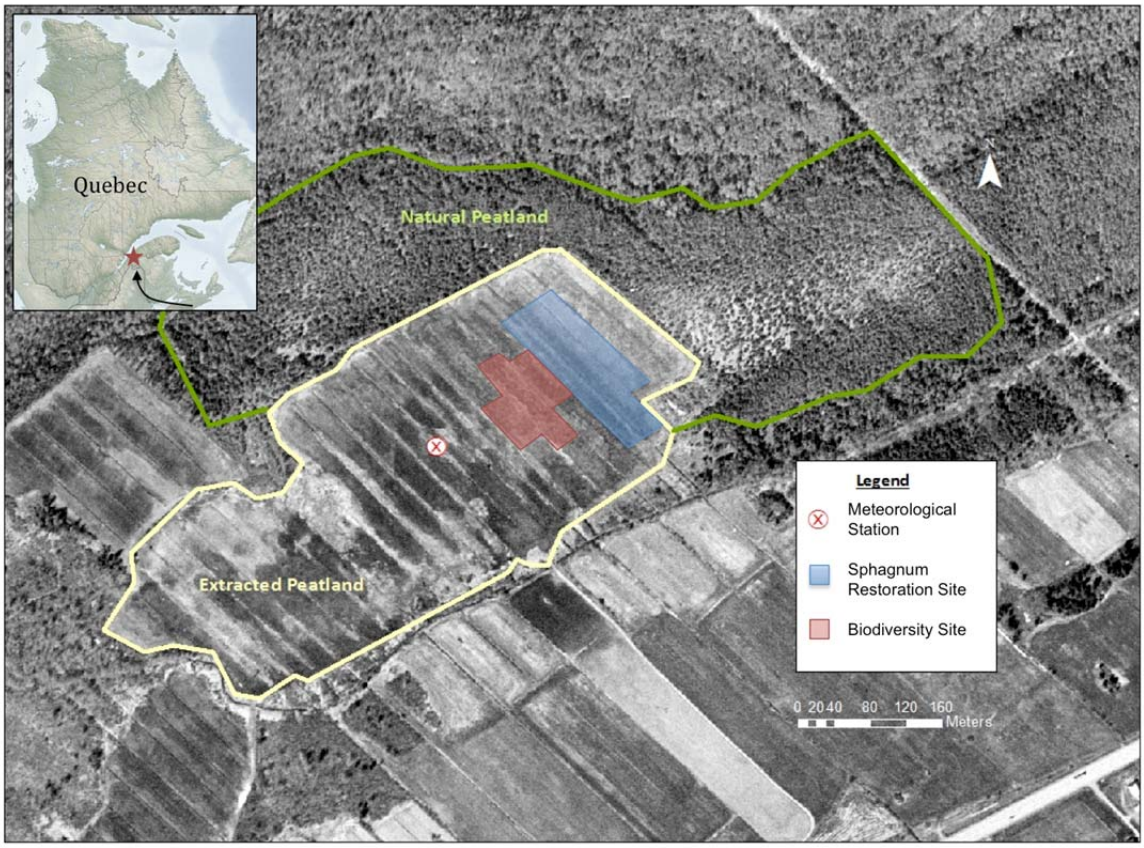

Figure 2.1: Aerial view of Bic Saint-Fabien Peatland.

Source: Marie-Claire LeBlanc

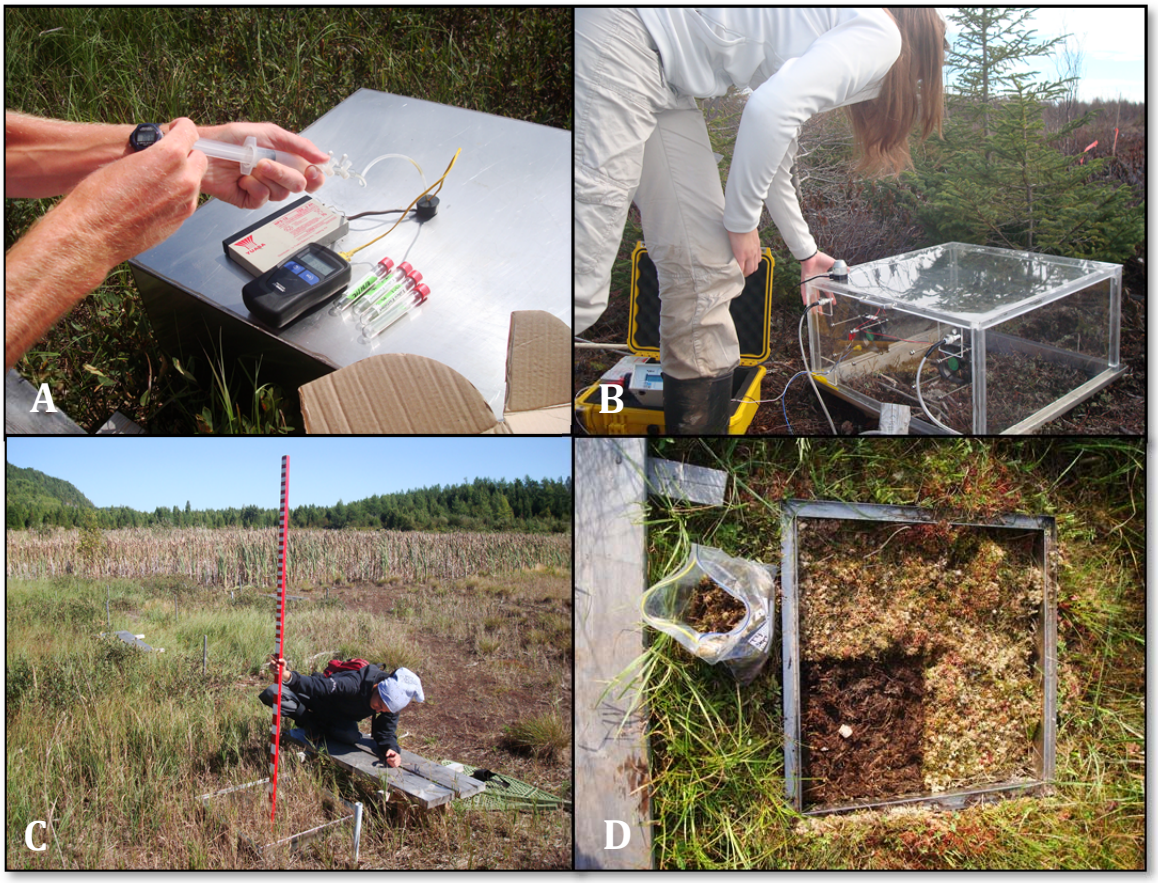

Figure 2.2: A) Opaque chamber used to take methane flux measurements. B) Transparent chamber used to make carbon dioxide flux measurements. C) Non-destructive 'Fuel Rule' method of monitoring vegetation volume. D) Biomass harvesting at the end of the study period in 2012.

Table 2.1: Summary of characteristics of the eight species chosen for this experiment.

Source: Vicky Bérubé

Species (short form)	**Family**	**Functional Group**	**Growth Form**	**Features**
Myrica gale (Mg)	Myricaceae	Shrub	Woody, 1 m high x 1 m wide, leaves decompose slowly	Ability to fix nitrogen
Trichophorum alpinum (Ta)	Cyperaceae	Sedge (Graminoid)	More or less dense tussocks; short rhizomes	Possibility to increase the absorption surface of the roots and release phosphatase
Trichophorum cespitosum (Tc)	Cyperaceae	Sedge (Graminoid)	Dense tussocks; no rhizomes	Identical to *T. alpinum*
Carex aquatilis (Ca)	Cyperaceae	Sedge (Graminoid)	Rhizome, up to 120 cm long	
Calamagrostis canadensis (Cc)	Poaceae	Grass (Graminoid)	Rhizome	N/A
Sphagnum warnstorfii (Sw)	Sphagnaceae	Bryophyte	Capitulated; pushed vertical	Grows on hummocks of minerotrophic peatlands

Species (short form)	Family	Functional Group	Growth Form	Features
Tomentypnum nitens (Tn)	Amblystegiaceae	Bryophyte	Tomentum present on the rod	Grows on hummocks of minerotrophic peatland, moderately rich
Campillium stellatum/ Scorpidium cossonii/Calliergon sp (Cs)	Amblystegiaceae	Bryophyte	N/A	Carpets of minerotrophic peatland, moderately rich

Table 2.2: Components of treatments that have been selected for this study. Each treatment is replicated in three blocks along a hydrological gradient. Treatments Mg, Ca, Tn, Mg.Tn., and Ca.Tn. were tested in both 2011 and 2012 growing seasons, and the rest were only measured in the 2012 growing season.

Source: Vicky Bérubé

Treatment short form	**Treatment components**
Ca	*C. aquatilis*
Cc	*C. canadensis*
Cs	*C. stellatum*
Mg	*M. gale*
Sw	*S. warnstorfii*
Ta	*T. alpinum*
Tc	*T. cespitosum*
Tn	*T. nitens*
Ca.Tn.	*C. aquatilis/T.nitens*
Mg.Ca.	*M. gale/C. canadensis*
Mg.Tn.	*M. gale/T. nitens*
Mg.Ca.Sw.	*M. gale/C. aquatilis/S. warnstorfii*
Mg.Tc.Ta.	*M. gale/T. cespitosum/T. alpinum*
Mg.Ca.Ta.Tc.Tn.Cs.	*M. gale/C. canadensis/T. alpinum/T. cespitosum/T. nitens/C. stellatum*

CHAPTER 3: RESULTS

3.1 Measured Data

In this section, I present the key observations of my measured data including patterns in seasonal weather, vegetation growth, and carbon (C) gas fluxes.

3.1.1 Weather Patterns

The year 2011 was wetter than 2012 with 339 mm of precipitation (Table 3.1) recorded at the on-site meteorological station during the measured growing season between May-August. This is just above the 1971-2000 average of 336 mm observed at the Rimouski weather station during these months. The average air temperature was 15.8 °C, fluctuating between -3.4 °C and 36.0 °C. The average soil surface temperature was 16.2 °C, ranging between -9.3 °C and 35.5 °C at the coldest and the warmest months, respectively. The standardized wetness scenarios (Table 3.2) for simulating 2011 seasonal fluxes were set based on conditions of that season with the water level (WL) at the dry scenario on average -18 cm (-33 to -1 cm), moderate, -12 cm (-30 to -3 cm), and wet, -1 cm (-27 to 4 cm).

The 2012 growing season was dry compared to the previous season. Due to instrumental malfunctions, I was unable to measure precipitation on site. However, data from the Rimouski weather station indicates 313 mm of rain were measured between May-August of that year (Environment Canada, 2013). Additionally, observations at the site proves that 2012 was a much drier year than 2011, as water levels were noticeably lower by an average of approximately 10 cm. The air temperature in 2012 averaged 20.9 °C and ranged between -0.8 °C and 47.2 °C according to the on-site weather station (Environment Canada data show an average of 16.5 °C, ranging from 0.4 °C to 35.5 °C). The soil surface temperature averaged 16.6 °C and ranged between 0°C and 36.2 °C. The standardized wetness scenarios used for modelling the 2012 season (Table 3.2), was determined based on

the hydrological conditions of that season. The dry scenario was on average of -27 cm (-52 to -12 cm), moderate, -18 cm (-43 to -2 cm), and wet, -8 cm (-21 to 1 cm).

3.1.2 Vegetation Growth Pattern

The two vascular species under study in 2011 were observed to differ in their maximum vegetation volume (VV) and growing pattern. *Myrical gale* (Mg) had a lower VV and shorter period of growth than *Carex aquatilis* (Ca) (Figure 3.1). The bryophyte *Tomenthypnum nitens* (Tn) had significantly lower VV than both vascular species, as expected. Both vascular species reached their maximum VV around the same time. The mixed collars of Ca.Tn. and Mg.Tn. reached their maximum growth later in the season and had longer growth period than their constituent monocultures. The maximum VV did not vary substantially between Mg.Tn. and Mg monoculture.

On average, the maximum VV was reached approximately a week earlier in 2012 compared to 2011. The three treatments that contained Ca had the largest VVs among treatments (Figure 3.2). The lowest VVs were in treatments with bryophytes, followed by treatments with short sedges and grass. All polycultures exceeded their component monocultures in maximum VV. The two treatments containing *Calamagrostis Canadensis* (Cc) reached their maximum VV earliest in the season, while most treatments with Ca and Mg reached their maximum VV later in the season.

A summary of the WL and biomass in each treatment and its replicates is presented in Appendix B.

3.1.3 Measured Methane Flux

In 2011, the measured daily methane (CH_4) flux in the natural fen adjacent to the study site ranged from -19.1 to 23.2 mg CH_4 m^{-2} d^{-1} with an average of 0.3 mg CH_4 m^{-}

^{2} d^{-1} (Appendix C). The average daily flux at hummocks was -1.1 mg CH_4 m^{-2} d^{-1} and at hollows was 1.7 mg CH_4 m^{-2} d^{-1}. In the traditional restoration site the measured daily flux ranged from -24.8 to 36.3 mg CH_4 m^{-2} d^{-1} with the average being -1.5 mg CH_4 m^{-2} d^{-1}. In the diversity-controlled portion of the restored site that is the focus of this study, the average daily CH_4 flux was 3.1 mg CH_4 m^{-2} d^{-1} (Appendix C). The measured daily flux ranged between -22.6 and 71.1 mg CH_4 m^{-2} d^{-1}. The biodiversity-controlled restoration site was on average a larger source of CH_4 to the atmosphere than traditionally restored or natural sites.

Among the biodiversity-controlled treatments, the wettest block (block 4), almost always had the highest CH_4 flux to the atmosphere, while the driest block (block 1) had the lowest CH_4 flux to the atmosphere. Highest CH_4 fluxes were measured in the two vascular monoculture treatments with lower fluxes in bryophyte and polyculture treatments.

In 2012, measured daily CH_4 flux in the natural fen was similar to the previous year, ranging from -21.8 to 23.9 mg CH_4 m^{-2} d^{-1} (Table 3.5). The average daily flux of the natural site was higher than the previous year at 2.9 mg CH_4 m^{-2} d^{-1} despite the drier seasonal conditions. Both hummocks and hollows exceeded the average daily flux of the previous season at 0.1 and 5.7 mg CH_4 m^{-2} d^{-1}, respectively. Similar higher average flux was observed in the traditionally restored site where the average daily measured flux was 0.39 mg CH_4 m^{-2} d^{-1} ranging from -44.6 to 34.2 mg CH_4 m^{-2} d^{-1}. The diversity-controlled treatments had measured flux that tended more towards the positive extreme in the range of -37.5 to 215.8 mg CH_4 m^{-2} d^{-1} with an average of 5.2 mg CH_4 m^{-2} d^{-1} (Table 3.6). Overall, despite the drier conditions, the average CH_4 flux in the 2012 growing season exceeded that of the previous season. The relative flux pattern between sites remained the same as the previous year: traditionally restored < natural < biodiversity controlled sites.

Among biodiversity-controlled treatments, block 4 had the highest CH_4 flux to the atmosphere, and block 1 or 3 had the lowest CH_4 flux, though in a few cases this was reversed. All treatments with Ca had uniformly positive CH_4 flux in all blocks. The highest CH_4 flux to the atmosphere was observed in Mg.Ta.Tc. polyculture.

3.1.4 Measured Photosynthesis and Respiration

Photosynthesis (GEP) and respiration (RESP) were measured as components of net carbon dioxide (CO_2) sequestration (Net Ecosystem Exchange, NEE). GEP is always measured as a negative value because it represents flux from the atmosphere to the peatland, and RESP is always measured as a positive value indicating flux from the peatland to the atmosphere. The NEE can be either positive or negative depending on the balance between GEP and RESP, where a negative value means that CO_2 was sequestered to the peatland and a positive value means that CO_2 was released to the atmosphere. When referring to the largest GEP or NEE value, I am referring to the lowest or most negative value where the greatest amount of CO_2 was sequestered, due to the sign convention of these fluxes. On the contrary, the largest RESP value refers to the highest or most positive value. All data are presented in Appendix D.

In the 2011, reference sites sequestered relatively little CO_2 at PAR≥1000 μmol m^{-2} s^{-1}. The NEE in *Sphagnum* transfer restoration sites averaged -1 g CO_2 m^{-2} d^{-1} at PAR≥1000 μmol m^{-2} s^{-1}. The natural site had an average NEE of -5 g CO_2 m^{-2} d^{-1} at PAR≥1000 μmol m^{-2} s^{-1} with hollows having the largest CO_2 sequestration (more negative NEE) among reference sites. The NEE in bare peat sites was equal to the RESP as GEP is zero in the absence of photosynthesizing plants. Hollows of the natural site had the largest photosynthesis (lowest GEP) and largest respiration (highest RESP) at -31 g CO_2 m^{-2} d^{-1} and 19 g CO_2 m^{-2} d^{-1}, respectively. The bare peat sites had the lowest RESP at 2 g CO_2 m^{-2} d^{-1}.

The biodiversity-controlled plots were measured to have noticeably larger CO_2 sequestration (lower NEE) than the reference sites (Appendix D). The largest CO_2

sequestration (lowest NEE) when PAR≥1000 μmol m^{-2} s^{-1} was measured in Ca.Tn. treatment with average NEE of -18 g CO_2 m^{-2} d^{-1}, while the lowest CO_2 sequestration (highest NEE) was measured in the Tn monoculture at 0 g CO_2 m^{-2} d^{-1}. The largest measured photosynthesis (lowest GEP) and the largest measured respiration (highest RESP) were both observed in Ca.Tn. treatment at an average of -44 and 27 g CO_2 m^{-2} d^{-1}. Meanwhile, the lowest measured photosynthesis (highest GEP) and lowest observed respiration (lowest RESP) were both observed in the Tn treatment at an average of -7 and 7 g CO_2 m^{-2} d^{-1} respectively.

In 2012, the highest CO_2 sequestration (lowest NEE) when PAR was above 1000 μmol m^{-2} s^{-1} among reference sites was observed in the hollows of the natural sites at an average of -9 g CO_2 m^{-2} d^{-1}, while hummocks were measured as having the lowest CO_2 sequestration (highest NEE) with an average of 8 g CO_2 m^{-2} d^{-1} (Appendix D). Average NEE of bare peat sites was positive, indicating a net source of CO_2 to the atmosphere at 4 g CO_2 m^{-2} d^{-1}. Hummocks had the largest photosynthesis (lowest GEP) averaging -27 while *Sphagnum* transfer restoration sites had the smallest photosynthesis (highest GEP) averaging -6 g CO_2 m^{-2} d^{-1}. Respiration was largest (highest RESP) in hummocks at an average of 26 g CO_2 m^{-2} d^{-1} and smallest (low RESP) in bare peat at 4 g CO_2 m^{-2} d^{-1}.

Among monocultures monitored in 2012, Ca had the largest average CO_2 sequestration (lowest NEE) when PAR was above 1000 μmol m^{-2} s^{-1} with an average of 28 g CO_2 m^{-2} d^{-1} and the bryophyte Cs had the smallest CO_2 sequestration (highest NEE) at an average NEE of -0.7 g CO_2 m^{-2} d^{-1}. Largest photosynthesis (most negative GEP) with average of -44.6 g CO_2 m^{-2} d^{-1} was measured in Ca treatment, while the Tn treatment had the smallest photosynthesis (highest GEP) averaging at -5.3 g CO_2 m^{-2} d^{-1}. Maximum respiration (high RESP) was measured in Ca treatment at an average of 17.3 g CO_2 m^{-2} d^{-1}. Three treatments, Sw, Cs, and Ta, had the smallest respiration (low RESP) at 4.7 g CO_2 m^{-2} d^{-1}.

All polyculture plots were net sinks of CO_2 (negative NEE) when PAR > 1000 µmol m^{-2} s^{-1}. The largest CO_2 sequestration (lowest NEE) was measured in Ca.Tn. treatment averaging -33 g CO_2 m^{-2} d^{-1}, while the smallest CO_2 sequestration (highest NEE) was observed in the treatment with six species. Photosynthesis was largest (lowest GEP) in Ca.Tn. treatment averaging -56 g CO_2 m^{-2} d^{-1} and smallest (highest GEP) in Mg.Ta.Tc. averaging -17 g CO_2 m^{-2} d^{-1}. Respiration showed the same pattern as photosynthesis with the largest respiration (highest RESP) measured in Ca.Tn. treatment averaging 22 g CO_2 m^{-2} d^{-1} and smallest respiration (lowest RESP) measured in Mg.Ta.Tc. averaging 9 g CO_2 m^{-2} d^{-1}.

3.2 Modelled Net Seasonal Carbon Flux

Parameter estimates, standard error, R-squared (R^2) value and mean squared residuals (MSR) for each of the CH_4, GEP, and RESP models for 2011 and 2012 are presented in Appendix E and Appendix F. The results of the three model simulations (CH_4, GEP, and RESP) for each treatment in 2011 and 2012 are reported in Tables 3.3 and 3.4. As stated in the methods section above, the results were standardized for three wetness scenarios: dry, moderate, and wet.

Methane accounts for a very small portion of the total C budget as evidenced in Tables 3.3 and 3.4; the net seasonal C flux is largely reflective of the difference between photosynthesis and respiration. Here, I highlight the noticeable patterns in net seasonal C flux.

In 2011, all three monocultures – Ca, Mg, and Tn – were net seasonal contributors of C to the atmosphere (positive C flux) under all wetness scenarios. The average net seasonal C flux of each monoculture treatment exceeded the average of both the bare peat and the polycultures in their C flux. The two polyculture treatments, Mg.Tn. and Ca.Tn., were a net sink of C under at least one wetness scenario. Both polycultures were smaller average contributors of C to the atmosphere than their monoculture components and bare peat.

In 2012, the number of treatments that were monitored for C flux was expanded to fourteen treatments, which included eight monocultures and six polycultures. Ca was the only monoculture treatment that acted as a net sink of C (negative C flux), and did so under all wetness scenarios. All other monocultures were net contributors of C to the atmosphere (positive C flux) under all wetness scenarios. All polycultures except Mg.Tn. were net C sinks (negative C flux) under at least one wetness scenario. When averaged for all wetness scenarios, only two polyculture treatments were a net C sink; both treatments included Ca as one of their component species. Mg.Tn. was a considerably larger C source than other polycultures. Bare peat was on average a larger C source to the atmosphere than any of the vegetated monoculture or polyculture treatments.

Figures 3.3-3.5 show the average net seasonal C flux of each treatment in 2011 and 2012. The error bars represent the standard error of the pseudo-replicates. Carbon flux was comparable between years. In both seasons, Mg and Tn monocultures were large C sources of comparable quantity to the atmosphere. While Ca monoculture was a large sink of C in 2012, it was on average a net source in the previous season. The same is true for the Ca.Tn. polyculture.

3.3 Biodiversity Effect

This section presents the results of the biodiversity tests on C dynamics.

3.3.1 Functional Groups Consistency and Redundancy

A mixed model ANOVA was conducted on net seasonal C flux as the dependent variable flux. Bryophyte functional group was set as a fixed independent variable having three categories; Cs, Sw, and Tn, and block was set as a random factor. No significant effect of either species type or block was found for bryophyte functional

group (Table 3.5). The interaction effect between species and block count not be tested due to lack of replicates.

The same test was repeated to compare the net seasonal C flux of four graminoid species; Ca, Cc, Ta, Tc, with block as a random factor. The effect of the interaction between species and block could not be calculated due to sample size, however, the test found a significant difference in net seasonal C flux between species of the graminoid functional group for the year 2012 (Table 3.6). Block was not a significant factor. Bonferroni multiple comparisons post-hoc test identified that Ca had significantly greater C sequestration than all other graminoid treatments ($p<0.05$), which were not significantly different from each other.

3.3.2 Species Richness Effect

Linear, quadratic, and exponential regressions between transformed net seasonal C flux and species richness in 2012 (Table 3.7) indicated that a quadratic fit explained more of the variance (R^2) in net seasonal C flux than the other two fits. However, R^2 values were overall low, meaning that the fits were generally poor in describing the richness effect, and were not significant in any of the cases. This is demonstrated in Figures 3.6 and 3.7.

Furthermore, mixed model ANOVA of net seasonal C flux with species number as a fixed factor and block as a random variable found no significant effect of species number, block, or the interaction between the two (Table 3.8). The model was overall not significant ($F=0.050$, $p=0.951$) and there was no need for further post-hoc testing.

3.3.3 Species/Functional Identity Effect

Multiple linear regression of net seasonal C flux against the biomass of each species was conducted in 2012. The biomass of Ca was found to be a significant predictor

($p<0.0005$). The regression was then repeated with only the significant predictor, Ca, and the regression was found to be significant ($F=89.28$, $p<0.0005$). The model had R^2 of 0.675, which indicates the biomass of Ca accounts for a large portion of the variance in net seasonal C flux. To test the importance of the presence of Ca, while accounting for the effect of block, mixed model ANOVA was constructed for the dependent variable net seasonal C flux with the presence of Ca as a fixed factor and block as a random factor (Table 3.9). The test found that the presence of Ca alone was significant, however, block and the interaction between the presence of Ca and block were not significant. On average, net seasonal C sequestration in the presence of Ca was -165.77 g C m^{-2} $season^{-1}$ for the year 2012, whereas in the absence of Ca it was 44.27 g C m^{-2} $season^{-1}$.

Multiple linear regression testing was then repeated with the biomass of functional groups (bryophyte, shrub, graminoid) as variables. The test found a significant effect of the biomass of graminoid functional group in 2012 ($p<0.0005$). The regression was then repeated with only the significant predictor, graminoid biomass, and the regression was found to be significant ($F=95.013$, $p<0.0005$). The R^2 value of 0.688 explained slightly more of the variance in net seasonal C flux than the regression of biomass of Ca alone. Mixed model ANOVA was used to test the effect of the graminoid functional group presence with block as a random factor in 2012 (Table 3.10). The test found that the presence of graminoids was a significant predictor of C sequestration, but neither block, nor the interaction between graminoids and block were significant. The average C sequestration with graminoids was -37.93 g C m^{-2} $season^{-1}$ and without graminoids was 62.55 g C m^{-2} $season^{-1}$.

3.3.4 Species Composition and Interaction Effect

To understand the overall effect of species interaction in polycultures, the *observed* net seasonal C flux was compared against the *expected* net seasonal C flux (Figure 3.7). In the first scenario, the expected net seasonal C flux was calculated based on

the biomass-weighted sum of monoculture components (Equation 2.9). The dotted line in Figure 3.7 indicates where the observed net seasonal C flux is equal to the expected sum of parts. Points above the line represent cases where polycultures sequestered more C than expected. As can be seen, most cases fall above the line. Summary of expected flux, observed flux, and overyielding can be found in Appendix G. Paired-samples T-test of observed versus expected (C $flux_{E1}$) net seasonal C flux for the year 2012 failed to find a significant difference between the two (t=-1.36, p=0.19).

Non-transgressive overyielding was calculated as the deviance of observed from expected net seasonal C flux (C $flux_{E1}$). Multiple linear regression of non-transgressive overyielding with the biomass of each species as predictors (i.e. species identity) found the biomass of every species except for Mg to be significant (Table 3.11). The model accounted for 84% of the variance in overyielding (F=5.884, p=0.008). *Tomenthypnum nitens* (Tn), *Sphagnum warnstorfii* (Sw), *Calamagrostis Canadensis* (Cc), and *Trichophorum cespitosum* (Tc) had negative coefficients, which indicate that increased biomass of these species were correlated with increased overyielding, where overyielding is measured as a negative value. *Carex aquatilis* (Ca), *Trichophorum alpinum* (Ta), and *Campillium stellatum* (Cs) had positive coefficients, which indicate increased biomass of these species decreased overyielding (i.e. increased underyielding).

Mixed model ANOVAs were then created to test the influence of species identity on non-transgressive overyielding, while accounting for the effect of block. The presence of each of the seven species and two functional groups that were significant in regression were individually tested as a fixed factor with block used as a random factor. A Bonferroni adjustment of 0.007 (i.e. 0.05/7) was used for species identity and 0.025 (i.e. 0.05/2) was used for functional group identity. The test did not find a significant effect of species identity on non-transgressive overyielding using the adjusted significance levels.

Despite this finding, graphical analysis of the average non-transgressive overyielding per polyculture treatment did reveal interesting patterns that could not be statistically demonstrated. Figure 3.8 depicts the average non-transgressive overyielding per polyculture treatment in 2012. A negative value indicates that polycultures sequestered more C than was expected (i.e. overyielding) and a positive value indicates that polycultures sequestered less C than was expected (i.e. underyielding). The two treatments that had the largest average C contribution to the atmosphere – Mg.Tn. and the treatment with six species (Figure 3.5) – showed the greatest average overyielding. All treatments that overyielding on average (i.e. sequestered more C than expected), had Mg as one of their components. The two treatments containing Ca that had the largest C sinks (Figure 3.5), sequestered on average less C than expected.

A comparison of *observed* net seasonal C flux against transgressive *expected* flux (C $flux_{E2}$, Equation 2.10), showed that about half the cases sequestered more C than was expected (Figure 3.9). Paired-samples T-test failed to find a significant difference between the expected and observed net seasonal C flux ($t=1.07$, $p=0.30$).

Visual assessment of average transgressive overyielding per polyculture treatment (Figure 3.10) showed a comparable pattern to that of non-transgressive overyielding (Figure 3.8). Polycultures containing Ca sequestered less C than expected on an average basis. Transgressive overyielding was observed for at least some plots of polyculture treatments where Mg was present.

3.3.5 Abiotic Factors

Nutrients

Pearson's correlation found significant relationships between the biomass of Ca (*C. aquatilis*) and PRS™ probe nutrient supply. Biomass of Ca was negatively

correlated with nitrate (r=-0.315, p=0.045) and positively correlated with phosphorus (r=0.550, p<0.0005).

Pearson's correlation also found that net seasonal C flux was significantly positively correlated with nitrate (r=0.334, p=0.033) and negatively correlated with phosphorus (r=-0.402, p=0.009). Net seasonal CH_4 flux was significantly correlated with nitrate (r=-0.457, p=0.003), calcium (r=-0.323, p=0.04), potassium (r=-0.46, p=0.002), iron (r=0.446, p=0.003), and sulphur (r=-0.471, p=0.002) supply rates.

Summary of PRS™ probe nutrient data can be found in Appendix H.

Soil Temperature

Pearson's correlation test found a significant negative correlation between the biomass of Ca and average seasonal temperature of the soil profile (r=-0.594, p<0.0005) in 2012. Biomass of Cs was significantly positively correlated with the temperature of the soil profile (r=0.345, p=0.025). Biomass of the graminoid functional group was negatively correlated with average seasonal temperature of the soil profile (r=-0.573, p<0.0005).

Water Level

Pearson's correlation test between average seasonal water level and the biomass of each species/functional group failed to find significant correlations. As well, no significant correlations were found between species/functional group richness and water level or soil volumetric water content.

Table 3.1: Precipitation (mm), soil surface temperature (T2,°C), and air temperature inside the chamber (Ta,°C) for the 2011 and 2012 growing seasons based on on-site weather station data (*Data derived from Rimouski Weather Station).

	Minimum	Maximum	Mean	Total
2011				
Precipitation (mm)	--	--	--	339
Ta °C	-3.4	36.0	15.8	
T2 °C	-9.3	35.5	16.2	
2012				
Precipitation (mm)	--	--	--	313*
Ta °C	-0.8	47.2	20.9	
Ta °C *	0.4	35.5	16.5	
T2 °C	0.0	36.2	16.6	

Table 3.2: Wetness scenarios for 2011 and 2012 seasons. Mean is given with minimum and maximum in brackets. Water level is measured in cm, where a negative value indicates distance below the surface of the peat.

	Dry (cm)	**Moderate (cm)**	**Wet (cm)**
2011 Wetness Scenarios	-18 (-33,1)	-12 (-30,-3)	-1 (-27,4)
2012 Wetness Scenarios	-27 (-52,-12)	-18 (-43,-2)	-8 (-21,1)

Table 3.3: Modelled seasonal photosynthesis (GEP), respiration (RESP), and methane (CH_4) flux of each treatment (g C m^{-2} $season^{-1}$) monitored in 2011, simulated for three wetness scenarios. Net seasonal carbon (C) flux is the sum of the three model simulations. [Ca= *Carex aquatilis*, Mg=*Myrica gale*, Tn=*Tomenthypnum nitens, P*= Bare Peat].

Treatment	Scenario	GEP (g C m^{-2} $season^{-1}$)	RESP (g C m^{-2} $season^{-1}$)	CH4 (g C m^{-2} $season^{-1}$)	Net Seasonal C (g C m^{-2} $season^{-1}$)
	Dry	-168.22	237.45	0.26	69.49
Ca	Moderate	-333.61	415.98	0.32	82.69
	Wet	-441.07	531.92	0.54	91.39
	Dry	-242.79	357.93	0.7	115.84
Mg	Moderate	-427.15	504.80	0.06	77.71
	Wet	-226.31	301.61	1.01	76.31
	Dry	-43.98	150.83	-0.03	106.83
Tn	Moderate	-88.32	182.70	-0.14	94.23
	Wet	-141.98	167.74	0.49	26.26
	Dry	-416.81	424.95	0.48	8.62
Ca.Tn.	Moderate	-321.47	253.32	0.2	-67.95
	Wet	-594.62	725.47	0.7	131.55
	Dry	-224.54	134.44	-0.29	-90.38
Mg.Tn.	Moderate	-316.66	259.71	-0.46	-57.41
	Wet	-408.44	546.42	0.22	138.20
	Dry	0.00	48.43	-0.06	48.37
P	Moderate	0.00	44.98	-0.01	44.97
	Wet	0.00	42.88	0.03	42.91

Table 3.4: Modelled seasonal photosynthesis (GEP), respiration (RESP), and methane (CH_4) flux for each treatment (g C m^{-2} $season^{-1}$) in 2012, simulated for three wetness scenarios. Net seasonal carbon (C) flux is the sum of the three model simulations. [Ca= *Carex aquatilis*, Cc=*Calamagrostis canadensis*, Cs=*Campillium stellatum*, Sw=*Sphagnum warnstorfii*, Ta=*Trichophorum alpinum*, Tc=*Trichophorum cespitosum*, Tn= *Tomenthypnum nitens,* Mg= *Myrica gale*].

Treatment	Block	GEP (g C m^{-2} $season^{-1}$)	RESP (g C m^{-2} $season^{-1}$)	CH4 (g C m^{-2} $season^{-1}$)	Net Seasonal C (g C m^{-2} $season^{-1}$)
	Dry	-598.03	438.06	0.92	-159.05
Ca	Moderate	-915.48	594.00	1.37	-320.11
	Wet	-882.09	601.82	1.52	-278.74
	Dry	-124.42	144.92	0.12	20.62
Cc	Moderate	-133.58	203.57	0.74	70.73
	Wet	-157.43	197.77	1.57	41.91
	Dry	-45.84	80.66	-0.37	34.46
Cs	Moderate	-49.07	73.44	-0.31	24.06
	Wet	-230.88	260.09	-0.29	28.93
	Dry	-365.53	461.85	-0.24	96.08
Mg	Moderate	-376.28	505.45	0.34	129.51
	Wet	-384.67	396.65	1.52	13.50
	Dry	-97.81	145.41	-0.53	47.07
Sw	Moderate	-57.50	136.24	-0.38	78.36
	Wet	-168.14	195.26	-0.19	26.94
	Dry	-135.68	227.04	-0.47	90.89
Ta	Moderate	-148.18	223.51	-0.44	74.89
	Wet	-224.24	251.03	-0.38	26.41
	Dry	-171.71	202.91	0.36	31.56
Tc	Moderate	-187.01	199.44	0.29	12.72
	Wet	-226.46	257.10	2.85	33.49

Treatment	Block	GEP (g C m^{-2} $season^{-1}$)	RESP (g C m^{-2} $season^{-1}$)	CH4 (g C m^{-2} $season^{-1}$)	Net Seasonal C (g C m^{-2} $season^{-1}$)
Tn	Dry	-66.75	143.35	-0.19	76.40
	Moderate	-100.99	194.44	-0.06	93.39
	Wet	-177.41	224.64	0.24	47.47
Ca.Tn.	Dry	-884.94	693.88	1.39	-189.66
	Moderate	-874.11	672.49	1.31	-200.31
	Wet	-960.44	750.00	1.32	-209.12
Mg.Cc.	Dry	-319.24	239.12	-0.51	-80.63
	Moderate	-317.57	274.01	-0.28	-43.84
	Wet	-277.99	426.34	-0.69	147.66
Mg.Tn.	Dry	-151.32	203.77	-0.10	52.36
	Moderate	-381.74	441.32	0.40	59.98
	Wet	-604.66	609.92	1.10	6.36
Mg.Ca.Sw.	Dry	-658.84	491.86	0.96	-166.01
	Moderate	-904.85	831.05	0.63	-73.17
	Wet	-731.18	834.56	0.89	104.26
Mg.Ta.Tc.	Dry	-326.71	321.55	-0.68	-5.85
	Moderate	-250.39	269.19	0.85	19.65
	Wet	-263.68	260.61	2.29	-0.78
Mg.Ta.Tc. Cc.Cs.Tn.	Dry	-175.26	251.47	-0.25	75.96
	Moderate	-349.29	384.44	0.15	35.3
	Wet	-412.27	328.47	0.83	-82.97
P	Dry	0	140.74	-0.1	140.64
	Moderate	0	109.85	-0.08	109.78
	Wet	0	60.69	-0.03	60.66

Table 3.5: Mixed model ANOVA of net seasonal carbon flux between three bryophyte monoculture treatments, in 2012, with block as a random factor. *Indicates significance.

Source		df	F	Sig.
Intercept	Hypothesis	1	32.22	0.03*
	Error	2		
Treatment	Hypothesis	2	5.43	0.072
	Error	4		
Block	Hypothesis	2	2.786	0.175
	Error	4.00		
Treatment * Block	Hypothesis	4.00	.	.
	Error	0.00		

Table 3.6: Mixed model ANOVA of net seasonal carbon flux between four graminoid monoculture treatments, in 2012, with block as a random factor. *Indicates significance.

Source		df	F	Sig.
Intercept	Hypothesis	1	5.30	0.148
	Error	2		
Treatment	Hypothesis	3	29.10	0.001*
	Error	6		
Block	Hypothesis	2	0.857	0.471
	Error	6		
Treatment * Block	Hypothesis	6	.	.
	Error	0		

Table 3.7: Linear, quadratic, and exponential regression parameters, R^2, and p value of net seasonal carbon flux by species/functional group richness, in 2012. Note that net seasonal carbon flux was transformed by addition of a constant to avoid negative flux values.

	R^2	F	df1	df2	Sig.	Constant	b1	b2
Species Richness - 2012								
Linear	0.019	0.845	1	43	0.363	342.137	-10.89	
Quadratic	0.096	2.233	2	42	0.12	404.408	-79.188	11.37
Exponential	0	0.015	1	43	0.904	263.003	0.013	

Table 3.8: Mixed model ANOVA results of net seasonal carbon flux by species richness level (Species #) with block as a random factor, in 2012. *Indicates significance.

Test	Source		df	F	Sig.
Species	Intercept	Hypothesis	1	4.499	0.168
Richness		Error	2		
	Species #	Hypothesis	4	2.707	0.108
		Error	8		
	Block	Hypothesis	2	0.085	0.918
		Error	26.27		
	Species# * Block	Hypothesis	8	0.411	0.905
		Error	30		

Table 3.9: Mixed model ANOVA results of net seasonal carbon flux with the presence of *Carex aquatilis* (Ca) as a fixed factor and block as a random factor, in 2012. *Indicates significance.

Source		df	F	Sig.
Intercept	Hypothesis	1	92.089	0.011
	Error	2		
Ca	Hypothesis	1	55.417	0.018*
	Error	2		
Block	Hypothesis	2	0.201	0.832
	Error	2		
Ca * Block	Hypothesis	2	1.093	0.345
	Error	39		

Table 3.10: Mixed model ANOVA results of net seasonal carbon flux with the presence of graminoids as a fixed factor and block as a random factor, in 2012. *Indicates significance.

Source		df	F	Sig.
Intercept	Hypothesis	1	7.249	0.115
	Error	2		
Graminoids	Hypothesis	1	18.909	0.049*
	Error	2		
Block	Hypothesis	2	0.157	0.865
	Error	2		
Graminoids * Block	Hypothesis	2	0.545	0.584
	Error	39		

Table 3.11: Multiple linear regression results for transgressive overyielding and biomass of species present in each plot as predictors, in 2012. *Indicates significance. [Ca= *Carex aquatilis*, Cc=*Calamagrostis canadensis*, Cs=*Campillium stellatum*, Sw=*Sphagnum warnstorfii*, Ta=*Trichophorum alpinum*, Tc=*Trichophorum cespitosum*, Tn= *Tomenthypnum nitens,* Mg= *Myrica gale*].

	Unstandardized Coefficients	**Std. Error**	**Standardized Coefficients**	**t**	**Sig**
Constant	41.136	61.79		0.666	0.522
Ca	0.777	0.333	0.48	2.331	0.045*
Mg	0.737	0.468	0.306	1.573	0.15
Tn	-2.826	0.965	-0.627	-2.93	0.017*
Cc	-20.555	6.256	-0.895	-3.286	0.009*
Tc	-115.715	34.919	-1.529	-3.314	0.009*
Ta	67.305	23.375	0.857	2.879	0.018*
Sw	-2.858	0.801	-0.677	-3.567	0.006*
Cs	71.937	22	1.202	3.27	0.01*

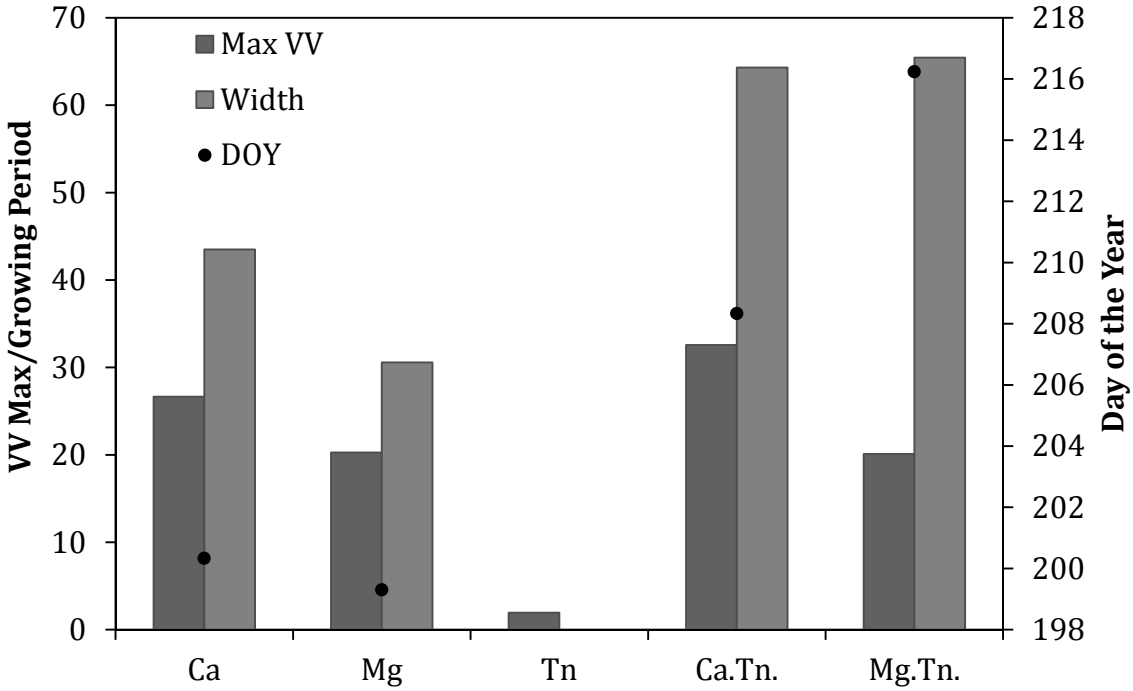

Figure 3.1: Vegetation growth pattern of treatments monitored in 2011. VV Max refers to the average maximum vegetation volume observed in the replicates of each treatment, DOY is the day of the year when VV Max was observed, and width refers to the spread of the vegetation growing period one standard deviation around the mean. [Ca= *Carex aquatilis*, Mg=*Myrica gale*, Tn=*Tomenthypnum nitens*].

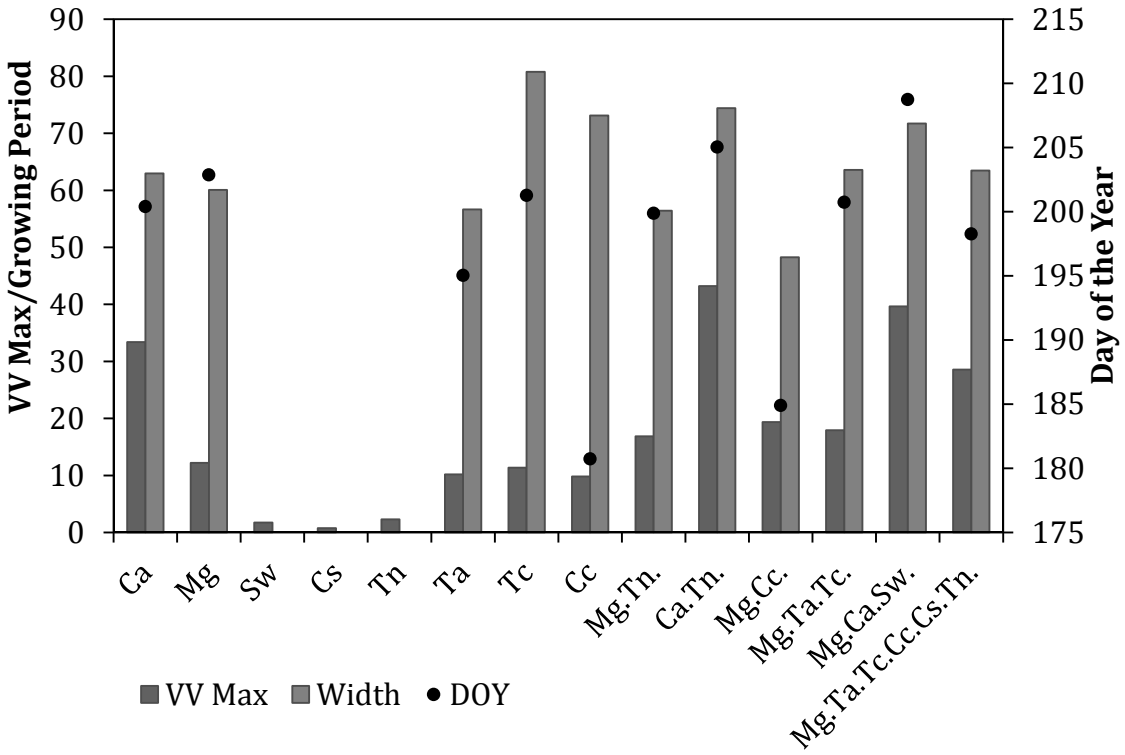

Figure 3.2: Vegetation growth pattern of treatments monitored in 2012. VV Max refers to the average maximum vegetation volume observed in the replicates of each treatment, DOY is the day when the maximum VV was observed, and width refers to the spread of the vegetation growing period one standard deviation around the mean. [Ca= *Carex aquatilis*, Cc=*Calamagrostis canadensis*, Cs=*Campillium stellatum*, Sw=*Sphagnum warnstorfii*, Ta=*Trichophorum alpinum*, Tc=*Trichophorum cespitosum*, Tn= *Tomenthypnum nitens,* Mg= *Myrica gale*].

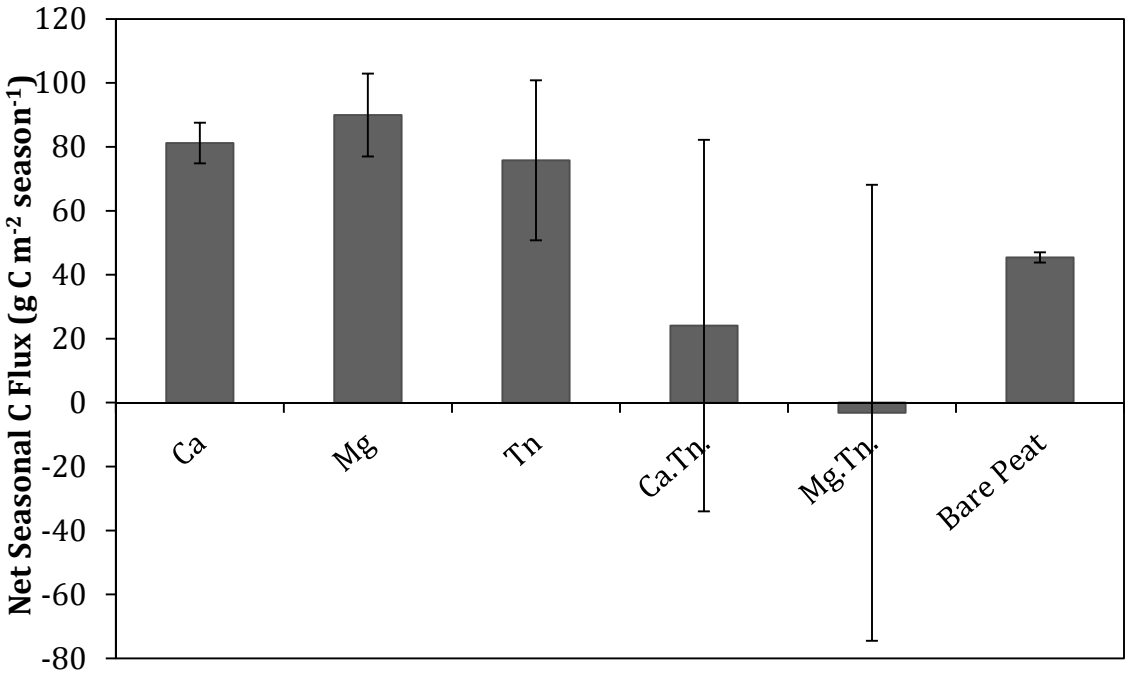

Figure 3.3: Average net seasonal carbon (C) flux (g C $m^{-2}season^{-1}$) of three wetness scenarios for five diversity-controlled treatment in 2011. Error bars represent standard error of the three replicates. Bare Peat is shown for reference. [Ca= *Carex aquatilis*, Mg=*Myrica gale*, Tn=*Tomenthypnum nitens*].

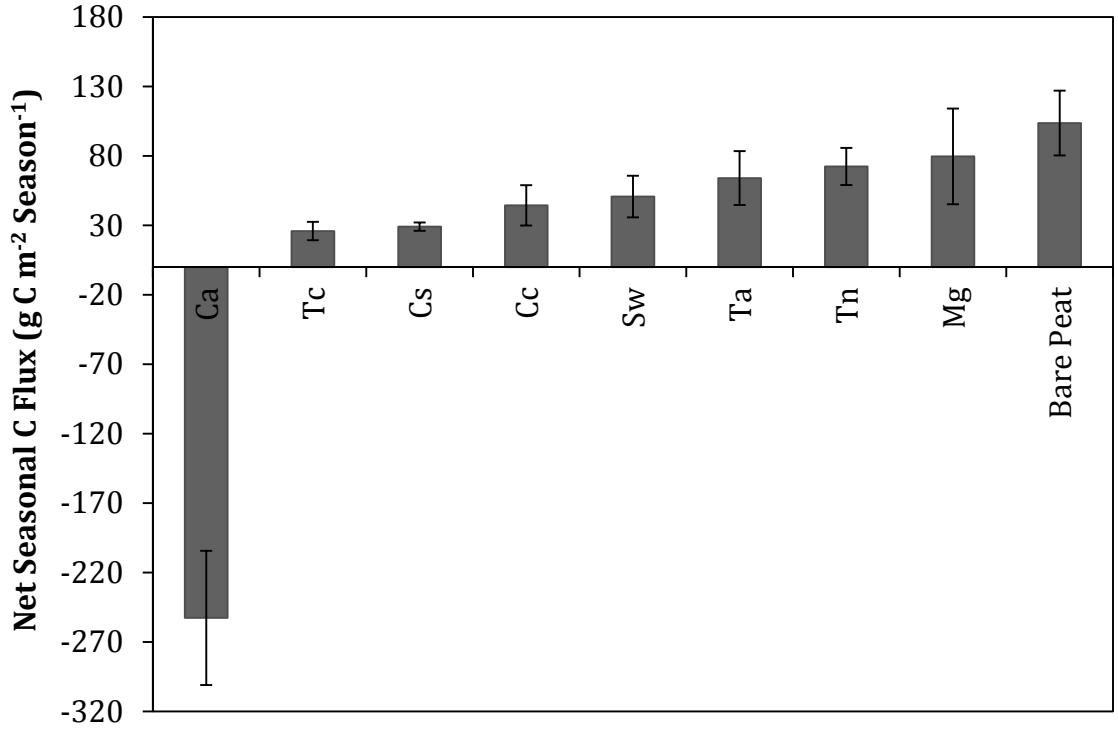

Figure 3.4: Average net seasonal carbon (C) flux (g C m^{-2} $season^{-1}$) of three wetness scenarios for monoculture treatments monitored in 2012. Error bars represent standard error of the three replicates. Bare peat is also shown for reference. [Ca= *Carex aquatilis*, Cc=*Calamagrostis canadensis*, Cs=*Campillium stellatum*, Sw=*Sphagnum warnstorfii*, Ta=*Trichophorum alpinum*, Tc=*Trichophorum cespitosum*, Tn= *Tomenthypnum nitens,* Mg= *Myrica gale*].

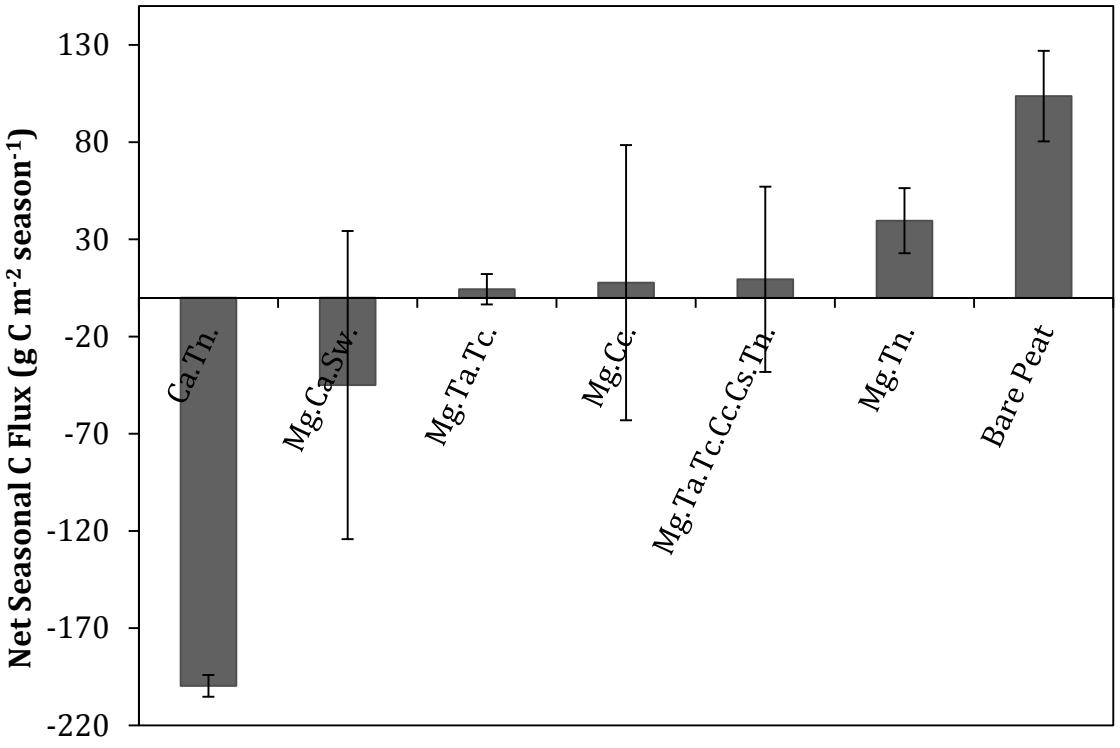

Figure 3.5: Average net seasonal carbon (C) flux (g C m^{-2} $season^{-1}$) of three wetness scenarios for polyculture treatments monitored in 2012. Error bars represent standard error of the three replicates and are large due to different carbon dynamics under varying hydrology. Bare peat is also shown for reference. [Ca= *Carex aquatilis*, Cc=*Calamagrostis canadensis*, Cs=*Campillium stellatum*, Sw=*Sphagnum warnstorfii*, Ta=*Trichophorum alpinum*, Tc=*Trichophorum cespitosum*, Tn= *Tomenthypnum nitens,* Mg= *Myrica gale*].

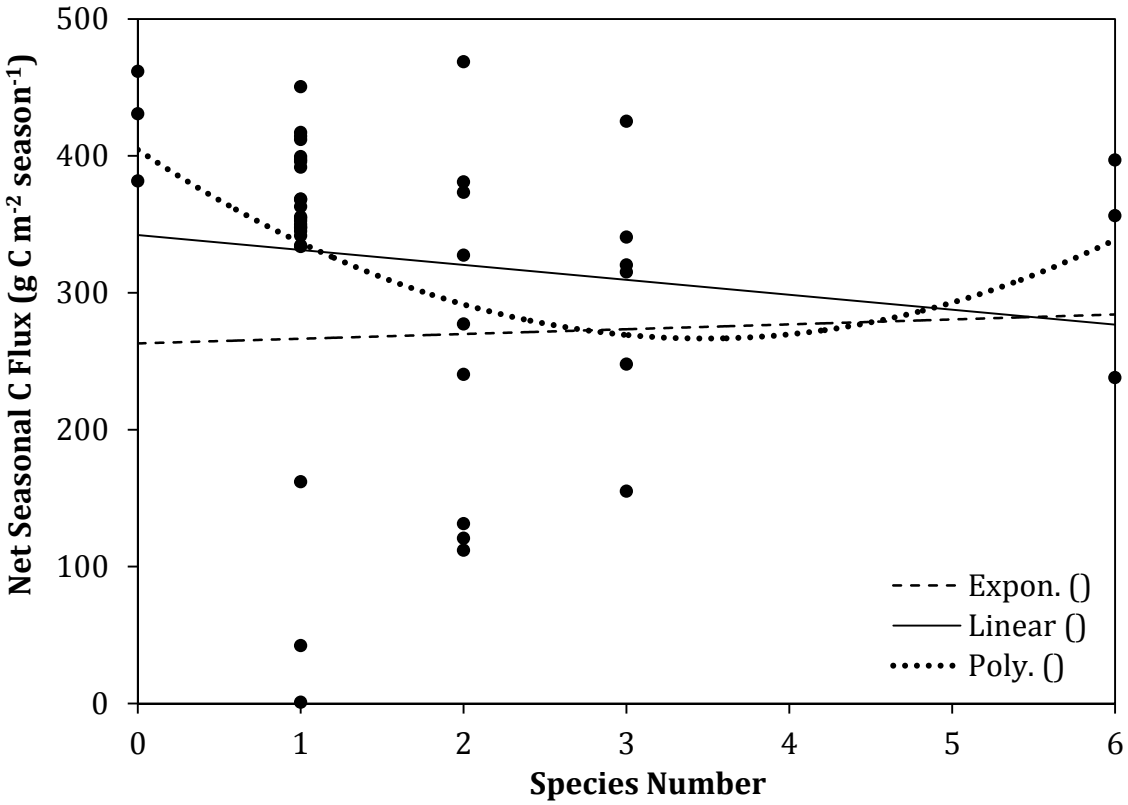

Figure 3.6: The relationship between species richness and net seasonal carbon (C) flux (g C m^{-2} $season^{-1}$) in 2012 expressed using linear, quadratic, and exponential fits. Equation parameters, R^2, and p value for each fit are summarized in Table 3.7. None of the fits were found to be significant.

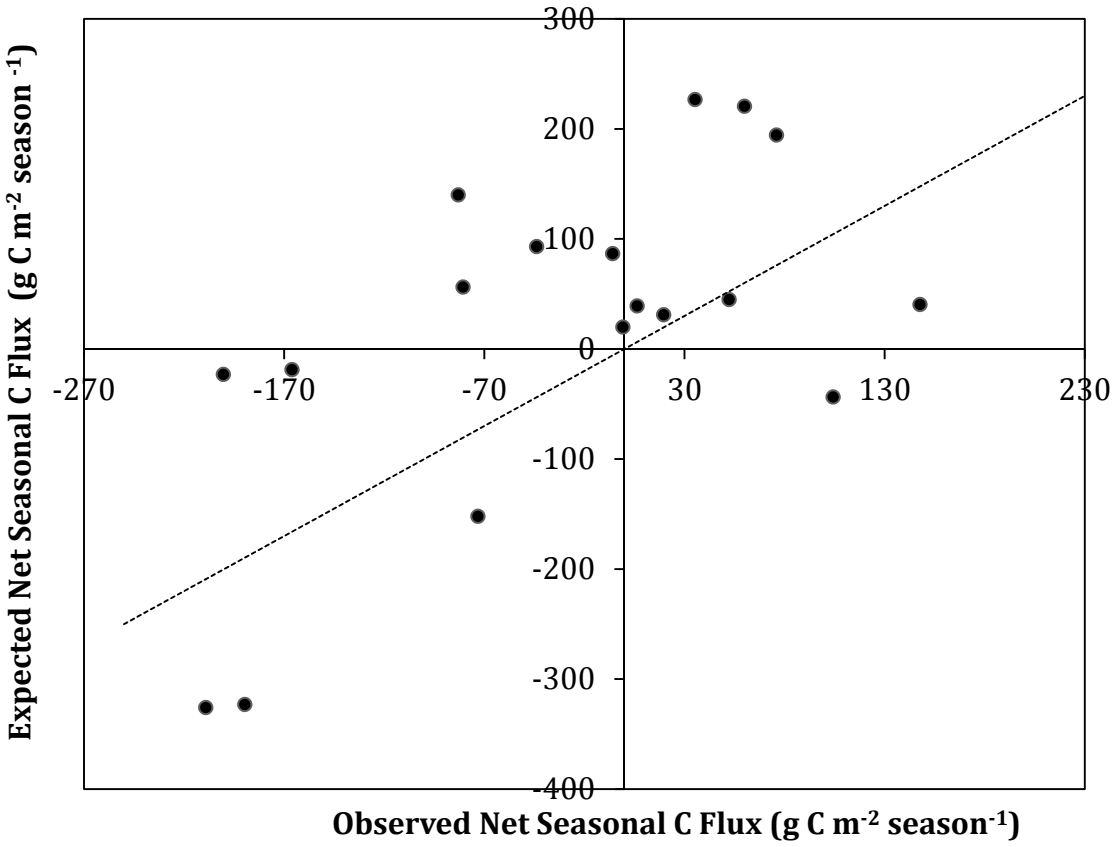

Figure 3.7: Comparison of the observed and expected net seasonal carbon (C) flux of polycultures (g C m^{-2} $season^{-1}$) in 2012, where expected flux is calculated as the sum of biomass proportioned C fluxes of monocultures that make up a polyculture (Equation 2.9).

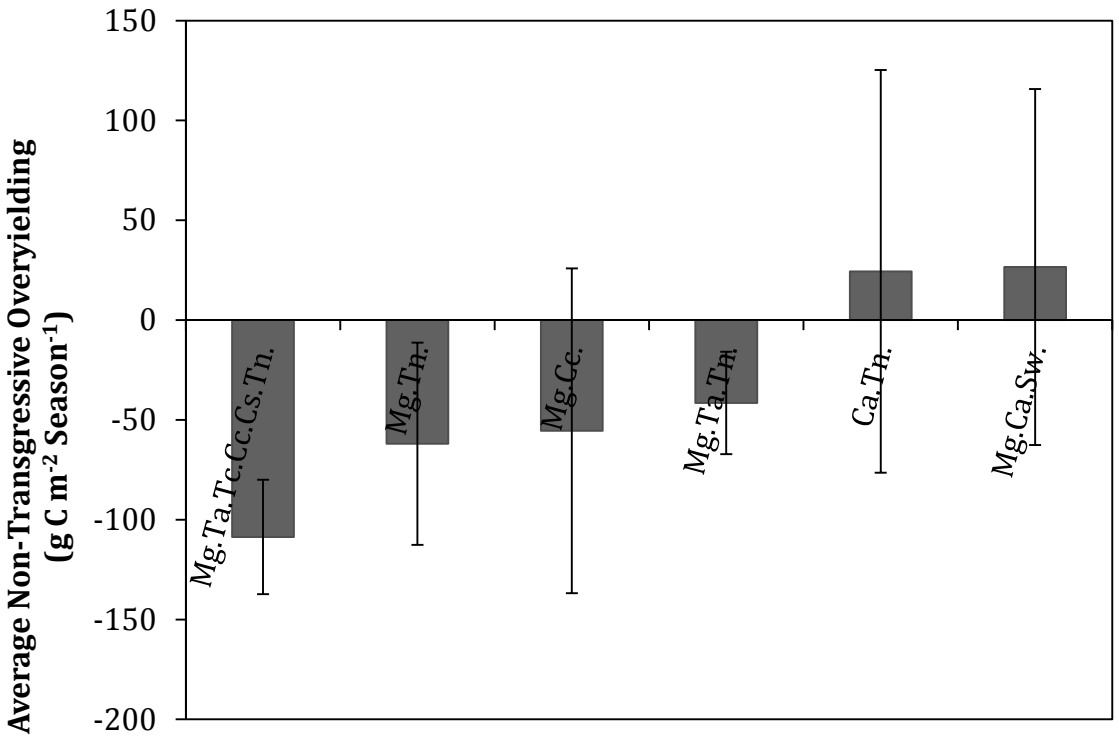

Figure 3.8: Average non-transgressive overyielding in polyculture treatments (g C m^{-2} $season^{-1}$) in 2012. Negative values indicate that the polycultures sequestered more carbon (C) than was expected (based on C $flux_{E1}$). [Ca= *Carex aquatilis*, Cc=*Calamagrostis canadensis*, Cs=*Campillium stellatum*, Sw=*Sphagnum warnstorfii*, Ta=*Trichophorum alpinum*, Tc=*Trichophorum cespitosum*, Tn= *Tomenthypnum nitens,* Mg= *Myrica gale*].

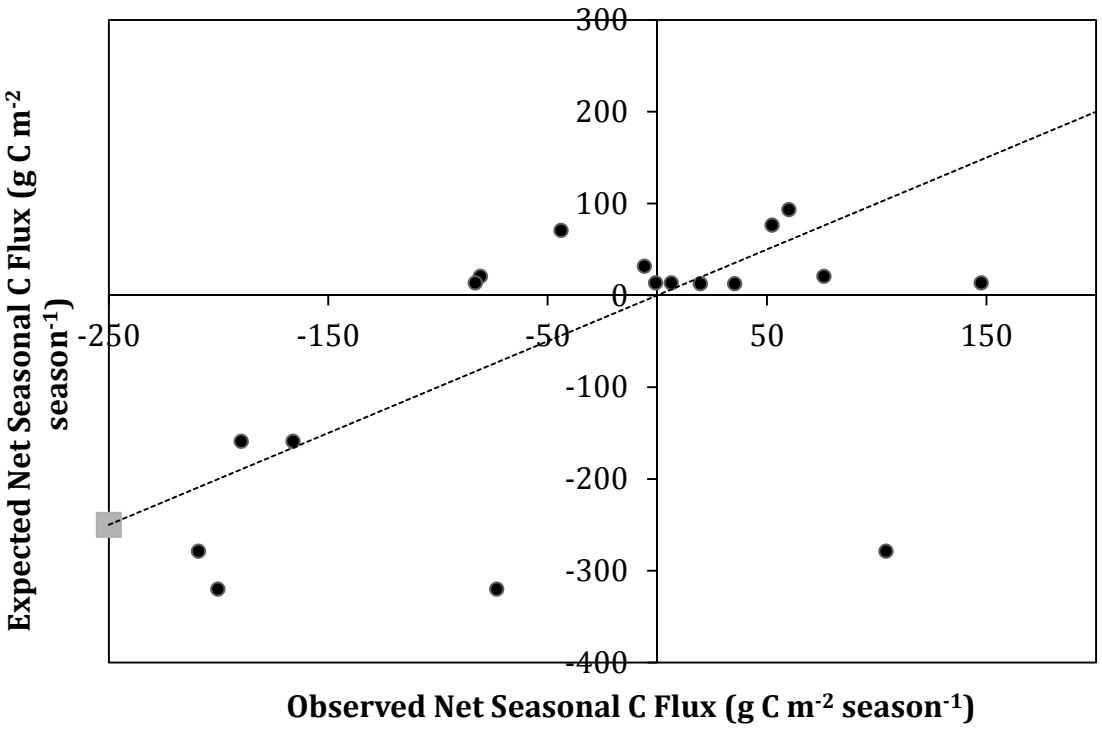

Figure 3.9: Comparison of the observed and expected net seasonal carbon (C) flux of polycultures (g C m^{-2} $season^{-1}$) in 2012, where expected C flux is equal to the largest C sequestering monoculture plot of a polyculture's component species.

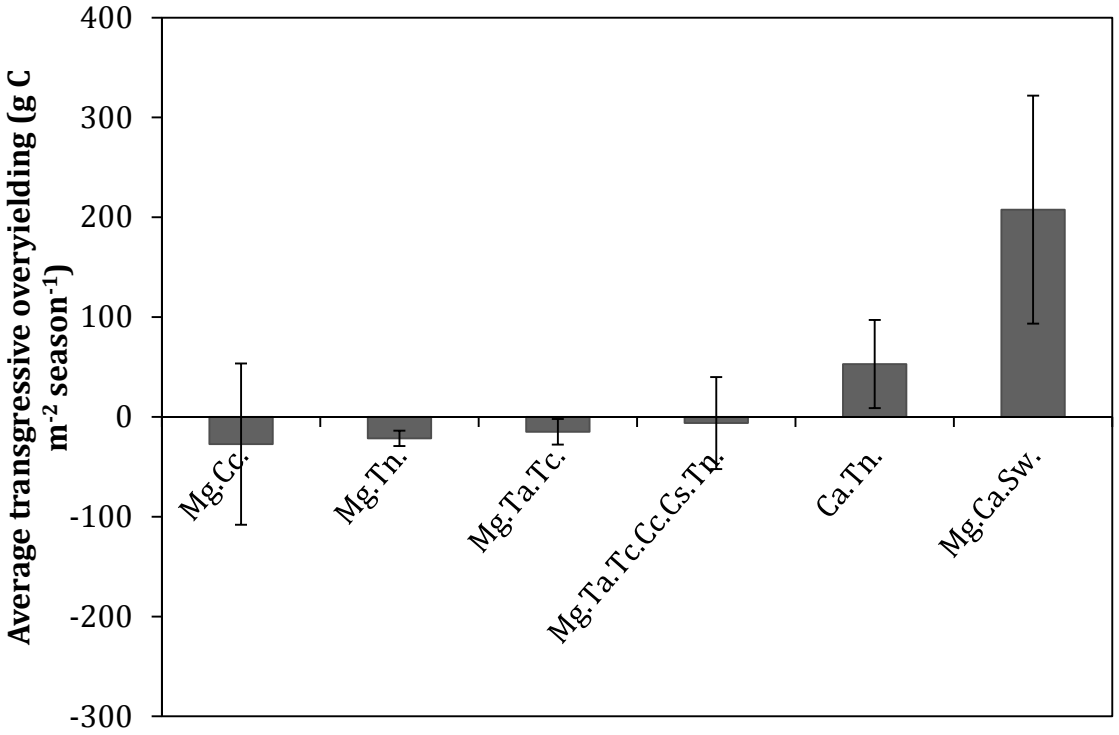

Figure 3.10: Average transgressive overyielding in polyculture treatments (g C m^{-2} $season^{-1}$) in 2012. Negative values indicate that the polycultures sequestered more C than was expected ($C\ flux_{E2}$). [Ca= *Carex aquatilis*, Cc=*Calamagrostis canadensis*, Cs=*Campillium stellatum*, Sw=*Sphagnum warnstorfii*, Ta=*Trichophorum alpinum*, Tc=*Trichophorum cespitosum*, Tn= *Tomenthypnum nitens,* Mg= *Myrica gale*].

CHAPTER 4: DISCUSSION

Testing the biodiversity effect in the last section revealed that the presence and increased biomass of the species *Carex aquatilis* (Ca) had a significantly positive influence on carbon (C) sequestration. Ca was the only graminoid species that had such effect on C sequestration, and was characteristically different from other species in the same functional group. None of the other species had a significant positive or negative relationsip with C sequestration; however, the presence and increased biomass of the graminoid functional group did have a positive impact on C sequestration. No significant effect of species richness on C sequestration was detected. Overall, restoration using species-rich plantings did not provide an overyielding advantage, as observed C sequestration was not significantly different from expected C sequestration. In addition, species richness and identity could not be linked to overyielding, although there was some qualitative and quantitative indication about the effect of species identity that will be discussed in this section.

This section will begin by discussing the main controls on C and methane (CH_4) fluxes. Although it was not a goal of this study to address the effect of plant diversity on CH_4 flux, CH_4 is an important Greenhouse Gas and will be qualitatively discussed in this section in terms of the controlling effect plant diversity. The biodiversity effect will be thoroughly examined in the context of C sequestration and implications for restoration will be discussed.

4.1 Controls on Methane Flux

The natural CH_4 flux at the Bic Saint-Fabien site was below the average CH_4 flux of 5-80 mg m^{-2} d^{-1} that is commonly observed in northern peatlands (Blodau, 2002). This low observed CH_4 flux may be due to the abundance of higher affinity electron acceptors such as sulphate, nitrate, or iron that allow other anaerobic microbes to outcompete methanogens (Watson and Nedwell, 1998). Soil nutrient analysis of the biodiversity experiment site at BSF found average PRS™ probe nutrient supply rate

of 33 μg/10 cm^2 Fe, 346 μg/10 cm^2 S, 32.3 μg/10 cm^2 Al, and 42.5 μg/10 cm^2 NO_3^- (Appendix H), where S and NO_3^- were respectively on average 3x and 10x higher than that found on an Alberta fen at Fort McMurray. The positive correlation between the concentration of Fe and CH_4 flux suggests that Fe is likely not the factor preventing methanogenesis. Although NO_3^- concentration is negatively correlated with CH_4 flux, this correlation may be related to the uptake of NO_3^- in treatments where Ca dominates, altering CH_4 flux as explained below. However, the negative correlation between peat S concentration and CH_4 flux, suggests that this may be one plausible explanation for low CH_4 production at BSF.

Average measured daily CH_4 flux in the *Sphagnum*-transfer restoration site for both 2011 and 2012 indicated the site has not yet become a source of CH_4 as naturally expected. The diversity-controlled restoration sites, however, had fluxes that were on average positive and larger than the average CH_4 flux observed in the natural site, suggesting that this method has been effective in restoring naturally positive CH_4 flux. The higher flux in diversity-controlled sites may be a result of the inclusion of numerous plots with high volume and density of graminoids that provide a considerable quantity of fresh labile litter, particularly Ca. For example, in both 2011 and 2012 the seasonal maximum vegetation volume (VV) in graminoid-dominated plots of the diversity-controlled site was approximately twice that of the natural site (i.e. ~21.2 vs. 10.1 in 2011 and 25.2 vs 14 .0 in 2012). This is in agreement with Couwenberg and Fritz's (2012) finding that the presence or absence of shunt species (e.g. *Carex*) is a strong indicator for CH_4 flux with increases in the aerial density of aerenchymatous leaves strongly correlated (R^2=0.91, $p<0.01$) with CH_4 release.

In 2012, despite the drier conditions of the season, average CH_4 flux in natural, *Sphagnum*-transfer, and diversity-controlled sites were all higher than 2011. The higher overall CH_4 flux in the 2012 growing season may be attributed to the higher soil and air temperature observed in this season compared to the previous growing

season (Figure 3.1). Air temperature was on average 0.7 °C higher, and soil temperature was on average 0.5 °C higher in 2012 compared to 2011, which may drive higher CH_4 production through increased methanogenesis (Crill *et al.*, 1988; Dise *et al.*, 1993; Frolking and Crill, 1994). However, some studies have found the effect of temperature on CH_4 flux to be inconsistent (Roulet *et al.*, 1992; Dijkstra *et al.*, 2012). Alternatively, the rise in CH_4 flux may be related to the replenishment of the active methanogenic population with time after hydrological and vegetation substrate restoration (Croft *et al.*, 2001).

Low CH_4 fluxes were observed in the bare peat collars for both seasons. The bare peat seasonal flux ranged -46.6 to 0.1 mg CH_4 m^{-2} $season^{-1}$ in 2011 and -136 to -34 mg CH_4 m^{-2} $season^{-1}$ in 2012, which is comparable to values reported by Waddington and Day (2007) in a nearby restored site (-0.3 ± 9.1 mg CH_4 m^{-2} d^{-1}). Almost all vegetated sites had positive CH_4 flux (except for bryophyte-only treatments), indicating the importance of vegetation establishment for restoring natural peatland CH_4 flux.

Among monocultures tested in 2011, the highest average CH_4 flux was observed in Ca and *Myrica gale* (Mg) treatments and the lowest average flux was seen in the *Tomenthypnum nitens* (Tn) treatment. Ca and Mg are both high biomass producing vascular plants, thus providing plenty of fresh labile substrate that enhances methanogenesis. Whiting and Chanton (1992) observed a positive linear correlation (R=0.93) between CH_4 emission and aboveground plant biomass across a range of wetlands, likely due to increased plant supply of labile C substrate for methanogenesis and increased plant-mediated ventilation of CH_4. Pearson's correlation test in this study found a positive correlation between CH_4 flux and the total living biomass in 2012 ($r=0.294$, $p=0.05$). In addition, graminoids such as Ca have deep roots that penetrate into the anoxic peat zone and enhance CH_4 production by root exudation (Lai, 2009). Some graminoids also have aerenchyma tissue that aids in diffusive transport of CH_4 from deep anoxic zones directly to the atmosphere, bypassing the oxidation zone above the water table and increasing

overall CH_4 emission (Whalen, 2005). In this study, Pearson's correlation found a strong positive correlation between the biomass of graminoids and CH_4 flux in 2012 ($r=0.509$, $p<0.0005$). Verville (1998) has reported finding that aerenchyma transport rather than enhanced methanogenesis is responsible for higher CH_4 emissions where graminoids dominate.

In contrast to graminoids, Tn produced relatively smaller quantities of biomass with recalcitrant litter, providing little labile substrate for CH_4 production (Graf and Rochefort, 2009). An incubation study of potential CH_4 production on BSF sites found no significant difference between the CH_4 production potential of near surface soil samples from Tn collars and deep peat soil samples from all other collars (Bird, 2013). This implies that the quality of relatively fresh Tn litter is no different than residual peat in the 40 cm deep horizon that is potentially thousands of years old. This provides a fair explanation for the negative mean CH_4 flux observed in almost all bryophyte plots.

In 2012, the relative CH_4 fluxes in Ca, Mg, Tn, Ca.Tn., and Mg.Tn. treatments were similar to the previous season, although CH_4 flux was generally higher in 2012. Several additional treatments were monitored in 2012. Both additional bryophyte monocultures – Sw and Cs – were an average sink of CH_4. Low biomass production and resistance of litter to decomposition are potential causes (Graf and Rochefort, 2009). *Trichophorum cespitosum* (Tc) and *Calamagrostis canadensis* (Cc) appear on the higher end of CH_4 flux, particularly in the wettest condition. This may be caused by moderate biomass production of these species, and the labile nature of these vascular graminoids (Graf and Rochefort, 2009). Additionally, Tc belongs to the graminoid functional group that can transport CH_4 through aerenchymatous tissue, bypassing oxidation in aerobic soil horizons. The short sedge *Trichophorum alpinum* (Ta), on the contrary, showed a negative flux. All the replicates of this species produced relatively small quantities of biomass, which is likely responsible for the low fluxes observed.

Schimel (1995) reported finding a strong correlation between the percent total biomass of Ca and CH_4 flux (R^2=0.68, p=0.014). They found that species composition was a stronger predictor of CH_4 flux than either water level (WL) or total aboveground plant biomass. Mahmood and Strack (2011) also found that CH_4 flux in vegetation communities naturally recolonized by Ca was an order of magnitude greater than natural hummocks, hollows, the sedge *Scirpus atrocinctus,* and the herbaceous species *Equisetum arvense*. In addition, the positive correlation between total living biomass and CH_4 flux in both years suggests that substrate quantity in addition to quality are key controls for CH_4 production.

Overall, CH_4 constitutes a small and negligible portion of the total C balance between peatlands and the atmosphere as evidenced by the model simulations for both 2011 and 2012 (Tables 3.3 and 3.4).

4.2 Controls on Carbon Sequestration

In the two growing seasons under study, there was considerable range in net seasonal C flux both between species and between years. In 2011, none of the monocultures had a negative net seasonal C flux under any of the wetness scenarios, meaning that there was no net C sequestration. However, both polycultures had a negative net seasonal C flux under at least one wetness scenario (Appendix D) and were on average more efficient at C sequestration than monocultures (Figure 3.3). This provided some preliminary evidence that polycultures are more efficient at C sequestration than monocultures.

In 2012, Ca was the only monoculture that had a negative net seasonal C flux (i.e. C sequestration). Pearson's correlation found a strong negative relationship between biomass of Ca and net seasonal C flux (r=-0.822, p<0.0005), indicating that the increased presence of Ca was important for C sequestration. This species was the most productive in terms of biomass among monocultures. The two polycultures containing Ca had the top productivity among polycultures. A strong correlation

was also found between total living biomass and net seasonal C flux (r=-0.454, p=0.001).

None of the other monocultures in this study were able to sequester C (i.e. negative net seasonal C flux) in either growing season under any of the wetness scenarios. This was a surprising finding that could be explained in several ways. One explanation may be that with only a few years having passed since the diversity-controlled treatments were planted, the new plantings may not have fully established and adapted to their environment. Several studies have reported that the productivity of planted species is temporally dynamic and often grows stronger through time (Cardinale *et al.*, 2004, 2007; Van Ruijven and Berendse, 2005). Different C dynamics may be observed in a few more years including the potential for C sequestration in the same treatments that had a positive net seasonal C flux in 2011 and 2012. Another reason may be the density of planting, which may not be conducive to the most efficient conditions for C sequestration. For example, visual examination of the density of Mg plantings appeared unfavourable, causing the plants to look weak and unhealthy in the middle of plots compared to those at the edges, which had greater room for extending roots, and looked much more voluminous and healthy. In addition, the presence and decomposition of straw mulch may have contributed to C release to the atmosphere, decreasing the overall observed C sequestration in each plot. Studies have found that the application of straw mulch can have significant effects on the C balance of a restored peatland in the short term, enhancing the emission of C from the system due to the decomposition of a labile C pool (Petrone *et al.*, 2001; Waddington *et al.*, 2003). Waddington *et al.* (2003) estimated that mulch decomposition can account for up to 30% of total respiration (RESP) and that approximately 75% of straw mulch will decompose in the first two years. Mulch was still present in many of the measurement plots and likely contributed to the measured RESP. Lastly, monocultures may not be efficient enough to sequester C on their own. It is important to note that peatlands can be both sources and sinks of C in any given year as temporal and spatial variability in C flux is large (Blodau, 2002).

Five out of six polyculture treatments in 2012 had a negative net seasonal C flux (i.e. C sequesteration) in at least one of the wetness scenarios (Table 3.4). Two treatments sequestered C when the three wetness scenarios were averaged; both of these included Ca as a component (Figure 3.5). Treatments with at least one other graminoid species as a component had a low positive average net seasonal C flux (i.e. small C source).

Overall, there is some indication that species number, identity, and biomass are important control factors for C sequestration.

4.3 Biodiversity Effect and Carbon Sequestration

4.3.1 Functional Group Consistency and Species Redundancy

No statistical difference was found in net seasonal C flux between the three bryophyte species (Cs, Tn, and Sw) in monoculture. It is, therefore, reasonable to believe that these three species act similar or equivalent to each other in terms of C sequestration ability, and this may be sufficient evidence to justify aggregating these species into a functional type for the purpose of representing C sequestration at plot scale. Furthermore, it could be said that bryophyte species have a functionally redundant role, where the loss of one bryophyte species could be functionally replaced by other similar species with minimal impact on ecosystem C exchange processes (Lawton and Brown, 1993). Species removal experiments have shown that redundant species are valuable in that they compensate for loss of similar species and thus provide a sort of insurance for persistence of community composition (Joner *et al.*, 2011). One implication of redundancy for restoration is that C sequestration can be more simply assessed at the plant functional level. However, it is important to acknowledge that even redundant species will differ to some degree and may not be redundant with respect to other important ecosystem functions (Rosenfeld, 2002).

On the contrary, the graminoid species Ca was found to sequester significantly more C than any of the other three species in the graminoid functional group in 2012 (Ca, Cc, Ta, and Tc). Ca was also the only monoculture treatment that had a negative net seasonal C flux (i.e. C was sequestered) for all wetness scenarios. Ca was evidently not functionally equivalent to the other graminoids and its absence could not be compensated for by the presence of other species in the same functional group. Aggregation of these four species would not allow for useful generalization about their functional capacity.

Restoration planners that aim to use ecosystem engineering to manipulate the C sequestration function of peatlands would benefit from encouraging the growth of Ca but may not find the same benefit with other species from the graminoid functional group. Ca is a highly prolific tall sedge species. This species has been successfully established in other peatland restoration studies (Vitt *et al.*, 2010; Mahmood, 2011). The importance of Ca for C sequestration will be further discussed in the species identity section.

The combined findings for both bryophytes and graminoids indicates that *a priori* method of classifying species into functional groups, while simple and in common use, can not always be useful for developing meaningful generalizations in C sequestration patterns and/or for planning and monitoring the state of restoration. As noted by Naeem and Wright (2003), some functional traits may only be expressed by one or a few species in a functional group, creating a significant challenge to classifying species into meaningful groups. Furthermore, it cannot be assumed by default that planting species of the same functional type is redundant, adding no extra benefits to restoration projects in terms of C dynamics. Some authors have questioned the utility of *a priori* functional classifications that oversimplify complex interactions (Polis and Strong 1996). I, therefore, reject the notion that generalization at the functional level is more appropriate for predicting C sequestration than at the species level.

4.3.2 Species Richness Effect

The results of linear and non-linear regression testing indicated that a unimodal fit accounted for more of the variance in net seasonal C flux using species richness as a predictor than a linear or exponential fit; however, none of the three regressions were statistically significant. The unimodal fit describes a relationship where C sequestration initially increased (net seasonal C flux decreased) with the addition of species until a threshold point, where the addition of more species caused a decrease in C sequestration (increase in net seasonal C flux). A review of 200 BEF studies by Waide *et al.* (1999) has shown that of the several types of relationships commonly used to describe the ecosystem function-species richness relationship, 30% were unimodal, 26% were positive linear, 12% were negative linear, and 32% were not significant (Waide *et al.*, 1999). My analyses revealed that none of the fits were statistically significant. I suggest that the higher R^2 value of the unimodal fit was masking the effect of species identity of the graminoid species Ca. Ca was found to be important for C sequestration and its presence at each species richness level resembled a unimodal form due to the study design/chosen treatments. The importance of Ca for C sequestration will be further discussed in the next section.

Mixed model ANOVA failed to find a significant difference between net seasonal C flux at different species richness levels with block as a covariate. Despite this lack of significance, I noted that the least efficient C sequestering polycultures released less C to the atmosphere (i.e. had smaller positive net seasonal C flux) than the least efficient monocultures, providing some evidence that the presence of multiple species is better than single species (Figure 3.4 and 3.5), despite the lack of statistical significance.

Numerous previous studies have examined the relationship between richness and ecosystem functions and have proposed that increasing species richness provides significant benefits to ecosystems (Tilman, 1996; van Ruijven and Berendse, 2005; Cardinale *et al.*, 2006; Cardinale *et al.*, 2007; Marquard *et al.*, 2009). Tilman *et al.*

(1996) provided unambiguous evidence from a field experiment that both plant productivity and resource utilization were significantly greater at higher plant species richness in developing grassland ecosystems. Tilman (1996) also found that higher species richness led to significantly greater temporal stability of aboveground plant production in a decade-long prairie experiment. These conclusions are inconsistent with the findings of this study. Although there is some suggestion that polycultures are smaller emitters of C than monocultures, my findings do not provide any conclusive statistical evidence that species richness is necessarily important or beneficial for restoring C sequestration function in peatlands. Few studies to date have found richness to be unrelated to ecosystem function (Naeem *et al.*, 1994, 1995; Wardle *et al.*, 1997; Tilman *et al.,* 1997).

Based on my findings in this study, there is no sufficient basis to suggest that plant species richness should be given value in peatland restoration guidelines from the perspective of enhanced C sequestration and climate change mitigation.

4.3.3 Species/Functional Identity Effect

Species and functional identity were found to have a statistically significant effect on peatland C sequestration. The presence and increased biomass of Ca was found to significantly increase C sequestration (i.e. lower net seasonal C flux), where average net seasonal C flux in the absence of Ca was 44.27 g C m^{-2} $season^{-1}$ and in its presence was -165.77 g C m^{-2} $season^{-1}$. Furthermore, the presence and increased biomass of graminoid functional group was a significant predictor of net seasonal C flux with average net seasonal C flux of -37.93 g C m^{-2} $season^{-1}$ in the presence of graminoids and 62.55 g C m^{-2} $season^{-1}$ in their absence. Despite this latter finding, there is reason to believe that the effect of graminoid identity is largely related to Ca. Ca was found to sequester significantly more C than other species in the graminoid functional group. The biomass of Ca accounted for 67.7% of the variance in net seasonal C flux, while the biomass of graminoids accounted for 68.8% of the variance, suggesting that the true effect is caused by species identity rather than

functional identity. No other species or functional group provided this C sequestration advantage. These findings provide evidence that Ca is a valuable species to recommend for inclusion in restoration of extracted peatlands for the purpose of enhancing the C sequestration potential and climate change mitigation at a regional scale.

This recommendation would be consistent with some reports that in minerotrophic fens "peat may consist predominantly of reed, cattail, and sedge remains" as opposed to ombrotrophic bogs where the peat may "consists primarily of the remains of *Sphagnum* mosses" (Gorham, 1991). Mahmood (2011) similarly found that spontaneously recolonizing vegetation communities with high C sequestration potential were dominated by *Carex aquatilis, Eriophorum vaginatum, Scirpus atrocinctus* and *Typha latifolia*. Several fen restoration projects in the past have focused on establishing vascular species for restoration of peat accumulation in disturbed peatlands (Roth, 1999; Wheeler and Shaw, 1999; Cooper and MacDonald, 2000; Lamers *et al.*, 2002). However, there is no agreement over which species or functional groups contribute most to C accumulation (Kubiw *et al.*, 1989; Nicholson and Vitt, 1990; Warner *et al.*, 1991; Hu and David, 1995; van Breemen, 1995; Vitt, 2000; Griffin, 1997; Chimner *et al.*, 2002).

One potential explanation for the high C sequestration ability of Ca may be related to the large quantity of roots and rhizomes produced by this species. Across plant species, root litter generally consists of lower quality recalcitrant material than shoots (Craine *et al*. 2005; Tjoelker *et al*. 2005). Ca spreads vegetatively and produces extensive belowground biomass consisting of a network of long, stout spreading rhizomes and short, tightly bunched clumping rhizomes (Shaver and Billings, 1975), as well as expansive meshes of fine roots. The roots of this plant may live for 1-4 years after the aboveground biomass has died. Shaver and Billings (1975) found that Ca had the highest root longetivity, the highest root weight per unit length, and the highest density among three tundra sedge species. This means that this species invests resources in producing belowground biomass that

preserves energy for other processes for a long time. This growth pattern may result in Ca species being conducive to increased C sequestration potential. Of note, is the ability of the dense rhizome network to contribute to substrate stabilization (Utah State University, 2014), which is an added side-benefit of establishing this species in a disturbed setting.

However, given that van der Valk *et al.* (1999) report that the seeds of Ca did not germinate to any appreciable extent in a restored wetland if they were more than six months old, this species would not be ideal for restoration through seeding. Young seeds from earlier in the same season kept at high soil moisture conditions were found to increase the success of seed recruitment. Rhizome-transfer from an intact site or planting of pre-grown seedlings may be alternatives worth exploring (Pfadenhauer and Grootjans, 1999). Rhizome reintroduction and seedling transplant have been found to be equally successful in establishing *Carex aquatilis* in restoration of an extracted peatland, with 50% survival rate for both methods after three summers (Cooper and MacDonald, 2000).

4.3.4 Species Composition and Interaction Effect

On average, polycultures sequestered more C than the biomass-proportioned sum of their parts (C $flux_{E1}$), but sequestered less C on average than the single most efficient monoculture component (C $flux_{E2}$). However, no statistically significant difference could be detected between the *observed* net seasonal C flux and either *expected* flux (C $flux_{E1}$, C $flux_{E2}$), indicating that overall, there was no significant effect of plant species interactions in polycultures. The overall interaction between species was not conducive to creating an advantageous environment for C sequestration. This result could be indicative of several scenarios: 1) any facilitation of resources between species is in balance with competition, overall; 2) resource partitioning is dominant; 3) there is no significant interaction between species. In addition, species richness and identity could not be linked with either transgressive or non-transgressive overyielding. This is contrary to the initial prediction that the

interaction between species in polycultures can create conditions suitable for increased C sequestration over monocultures. Therefore, the evidence doesn't provide grounds to suggest inclusion of species richness as a criterion for restoration planning and monitoring of peatland C sequestration function for the benefit of climate change mitigation.

Although species identity was not a statistically significant predictor of overyielding in any mixed model ANOVA, multiple linear regression found that the increased presence of two bryophytes (Tn and *Sphagnum warnstorfii* (Sw)) and two graminoids (Cc and Tc) significantly increased non-transgressive overyielding. Two graminoids (Ca and Ta) and one bryophyte (Cs) were linked to underyielding in multiple linear regressions. The relationship between Tn and Sw with overyielding suggests that the presence of these bryophytes influences companion species by either enhancing C uptake or reducing C loss, leading to overall greater C sequestration than expected. Studies have shown bryophytes to have properties that encourage C sequestration through inhibition of plant litter decay. Verhoeven and Toth (1995) have found that the addition of *Sphagnum* homogenates to plant litter inhibited decay of both *Sphagnum* and *Carex* litter, and suggested this was due to the presence of acid (Rudolph and Samland, 1985; Clymo, 1963) as well antibiotics (Swift *et al.*, 1979) in *Sphagnum* tissue, which reduced microbial breakdown of litter. Bryophytes also influence decay by reducing soil temperature and/or increasing soil moisture (Eckstein, 2000; Sveinbjornsson and Oechel, 1992; Van Cleve *et al.*, 1983), which can reduce the rate of respiration (Verhoeven and Toth, 1995). On the contrary, the association between the two graminoids, Ca and Ta with underyielding would be related to reduction in C uptake or enhancement of C loss, ultimately decreasing overall C sequestration of the community. A potential explanation could be enhanced litter decomposition of companion species caused by high rates of root exudation, high litter quality, and aerenchymatous oxidation of the root zone that are associated with graminoid species (Eviner and Chapin 2003; Cornelissen *et al*. 2007). Root exudation and high litter quality provide fresh labile litter to increase the activity of decomposers, while aerenchymatous transport of

oxygen from shoots to roots increases the rate of aerobic decomposition below the water table, leading to overall higher loss of C in polycultures that include graminoids.

Furthermore, visual analysis of the average transgressive and non-transgressive overyielding for each polyculture treatment seems to suggest a link between species identity and overyielding. All treatments that overyielded on an average basis included Mg as one of their components. In comparison, the two treatments containing Ca underyielded (sequestered less C than expected), which suggests that the presence of Ca may be linked to a negative interference that reduced overall C sequestration below the expected. This pattern was observed in both transgressive and non-transgressive overyielding. Findings of transgressive and non-transgressive overyielding are evidence of the dominance of facilitation effect, while underyielding is indication that negative interference such as competition is the dominant effect in some treatments. Transgressive overyielding is important because it is strong evidence for facilitation.

While further research into the effect of species identity on overyielding and its causative mechanisms would be necessary to clarify any links, a few preliminary suggestions can be made. A potential explanation for the average underyielding effect associated with Ca could be related to the negative correlation between Ca biomass and peat NO_3^- content. As the biomass of Ca increases, the concentration of NO_3^- in the peat surface decreases, suggesting that Ca has a competitive ability to take up NO_3^-. In a nutrient-limited system such as peatlands, this competitive advantage of Ca may interfere with the ability of other species to thrive and sequester C efficiently. The high NO_3^- uptake efficiency of graminoids in peatlands is also supported by Silvan *et al*. (2005).

All polycultures with average overyielding had the presence of Mg in common. There are several potential explanations why the presence of Mg may provide a C sequestration advantage. Mg is a known nitrogen (N)-fixer that has been estimated

to fix 4-5 times the amount of N in bulk precipitation (Schwintzer, 1979). This is an advantageous quality in N-poor peatland environments. N-fixing plants produce litter with high nutrient content, which can facilitate primary productivity of companion species and enhance C sequestration at a community level (Hooper *et al.*, 2005). Many BEF studies have found that the primary cause of overyielding is not the number of species, but the fertilization effect of N-fixers (Vitousek and Walker, 1989; Hooper, 1998; Fornara and Tilman, 2008; Loreau and Hector, 2001), which is in line with these findings. However, no significant effect of the presence or biomass of this species on N concentration was detected using nutrient data from the PRS™ probes, making it difficult to justify this claim. Mg may also influence C sequestration by increasing soil water availability through shading (Chapin, 2003; Farrick and Price, 2009); a stable moisture supply is important for enhancing photosynthesis and suppressing respiration in *Sphagnum* communities that are sensitive to desiccation (McNeil and Waddington, 2003). However, I was not able to detect any significant influence of Mg on soil moisture.

Kivimaki *et al.* (2008) also suggested that increased C sequestration observed in polyculture communities might be a result of facilitative interactions between bryophytes and vascular plants. *Sphagnum* mosses provide higher and more constant water level for vascular species, while vascular species provide a substrate-derived C source for *Sphagnum* through their respiration (Lamers *et al*, 1999; Smolders *et al.*, 2001). Resource partitioning was further suggested as a possible mechanism for positive biodiversity effect on C sequestration (Kivimaki *et al.*, 2008), where diverse communities benefit from the different timing of C sequestration efficiency among species to increase overall productivity. For example, *Eriophorum* and *Sphagnum* spp. were found to be more efficient than *Carex* spp. in spring and autumn, while *Carex* spp. was equally or more efficient during the mid-summer. Riutta *et al.* (2007) reported that peatland net ecosystem exchange (NEE) in species-rich communities was resilient to change with water level fluctuation, because sedges became dominant contributors to NEE in high water

scenarios and shrubs became dominant in dry scenarios. The study concluded that biodiversity was an effective buffer against environmental variability.

In summary, no significant overall difference between observed and expected net seasonal C flux was observed. Therefore, there is no reason to recommend inclusion of species richness as a criterion for restoration planning and monitoring in order to enhacing C sequestration function and climate change mitigation. Overyielding could not be definitively associated with richness or identity of species. However, qualitative reasoning and some statistical evidence suggest that bryophytes (Tn and Sw), shrub (Mg), and graminoids (Tc and Cc) were related to overyielding, while graminoids (Ca and Ta) as well as bryophyte (Cs) were linked to underyielding. Potential reasons for overyielding include decay inhibition and resource facilitation. Underyielding could be caused by decay enhancement and resource competition. If further research can conclusively connect the presence of particular species or functional groups to overyielding, restoration planning would benefit from inclusion of those species/functional groups on restoration sites

4.4 Study Limitations

The results of BEF studies such as this can be used to inform restoration guidline and management decisions, making it is integral to consider their limitations.

The number of replicates tested in this study restricted the statistical tests that could be run, and likely affected the results of those tests. For example, mixed model ANOVA used to test difference in C sequestration of species within the same functional group could not calculate the interaction effect between block and species, since there was only one of each treatment in each block. Since the experiment was designed by a collaborating student to seek answers to specific questions, it could not have been altered for my purposes. Collection of additional samples was not possible due to time, labour, and instrument restrictions related to C flux measurements. Similar studies in the future should consider alternative study

designs to overcome this problem and increase accuracy of results. One suggestion is to decrease the number of treatments in favour of more replicates. I also recommend future studies to manually design treatments with species composition based on previous knowledge rather than random combinations. Ca and Mg would be two species that could be specifically targeted for further research.

Furthermore, this study made use of pseudo-replicates (Hulbert, 1985) as opposed to true replicates. The pseudo-replicates in this study are not statistically independent because observations are spatially correlated. The study was conducted on a single experimental unit, which makes it difficult to estimate the true variability within treatments and make valid statistical inferences. While this design was sufficient for the scope of this study, it is recommended that future studies consider a study design where independent replicates are planted.

Another limitation of this study was the running length of the experiment. Preliminary testing for this study began two years after initial planting, and the main study was conducted three years after planting. The importance of the experimental length lies in the changing interaction between species over time. For example, Cardinale *et al.* (2007) found that as the running length of their experiment increased, so did the effect of biodiversity and the probability of overyielding. They suggested that this was due to an increase in complementarity between species over time. Rosenfeld (2002) criticised short-time BEF experiments because they fail to observe functional differences between species that are only expressed when the environment changes over larger space and time scales. Furthermore, Cardinale *et al.* (2004) suggested that as time goes on, competitive interactions become stronger, and dominant taxa overtake treatments. It was observed that by the intermediate stages of succession, 50% of the initially planted species were eliminated and only 25% remained by late succession. A number of previous research works have also shown that biodiversity effects as well as the underlying mechanisms may change over time (e.g. Tilman *et al.*, 2001; Hooper and Dukes, 2004; Spehn *et al.*, 2005; van Ruijven and Berendse, 2005; Fargione *et al.*,

2007; Weis *et al.*, 2007).

A longer running experiment would therefore have several benefits. It would allow the observer to detect changing functional behaviour of species under different environmental conditions. Species that outcompete others and those that are outcompeted could be strategically used in restoration projects to avoid lost time and money. Longer-term experiments would also allow for measurement of C sequestration without the distorting effect of decomposing straw mulch. For the purposes of this research, it was assumed that the same relative proportions in C sequestration would be maintained over time.

CHAPTER 5: CONCLUSIONS AND RECOMMENDATIONS

5.1 Summary

Plant species differ in their ability to influence ecosystem carbon (C) dynamics. Understanding the different ways in which plant diversity affects C sequestration is critical for predicting the consequences of environmental changes and shifts in vegetation composition, especially when the influence of C-based greenhouse gases on climate change are considered. An in-depth knowledge of plant diversity would provide a valuable tool for management and restoration of disturbed peatlands that have been extracted for horticultural purposes.

Much of the research on peatland restoration in North America has been conducted in ombrotrophic peatlands, although fens represent approximately 65% of the total peatlands across the boreal forests of North America (Vitt *et al.*, 2000). Given that undisturbed peatlands are long-term sinks for C, playing a role in mitigation of climate change, one goal of peatland restoration in North America is to return peatlands to C accumulating ecosystems (Rochefort *et al.*, 2003). Restoration strategies to date have neglected to address the changes in biodiversity on restored sites or to make effective use of controlled biodiversity as a means to achieve the goals of restoration.

My analyses of the effect of plant diversity on C sequestration failed to find significant evidence that species richness plays a positive role in C sequestration function of peatlands during the growing season. Although polycultures were on average smaller C emitters than monocultures, the difference in net seasonal C flux between the two was not statistically significant.

The presence and increased biomass of *Carex aquatilis* (Ca) was strongly correlated with increased C sequestration. None of the other species had any significant influence on C sequestration. All monocultures and polycultures that included Ca as

one of their constituent species sequestered C on an average basis. Presence and increased biomass of graminoid functional group was also significantly correlated with increased C sequestration, although this correlation is probably only a result of the influence of Ca and not any of the other graminoid species tested.

Analysis of variance in net seasonal C flux found that bryophyte species were comparable or redundant in C sequestration capacity; however, among graminoids, Ca differed significantly from species categorized in the same functional group by sequestering significantly more C than the other species.

Interactions between species in mixed plots did not lead to greater C sequestration than expected based on performance of monocultures. Overyielding could not be statistically associated with richness or identity of species. However, results of multiple linear regression testing found a link between overyielding and the biomass of *Tomenthypnum nitens* (Tn), *Sphagnum warnstorfii* (Sw), *Trichophorum cespitosum* (Tc), *Calamagrostis Canadensis* (Cc) which should be further investigated in future studies. The biomass of *Carex aquatilis* (Ca), *Trichophorum alpinum* (Ta), and *Campillium stellatum* (Cs) were linked to underyielding using multiple linear regression testing. Qualitative speculation suggested some link between average per treatment overyielding and each Ca and *Myrica gale* (Mg). Ca was associated with an underyielding effect when planted in combination with other species, possibly due to a competitive advantage in NO_3^- uptake that may restrict access of other species to this nutrient and therefore disadvantages companion species. Carbon sequestration of polycultures in the absence of Ca surpassed the expected C sequestration based on the performance of monocultures and displayed evidence of average transgressive and non-transgressive overyielding. All overyielding treatments included Mg as a component species. Mg is a known N-fixer and may be linked to complementarity in resource uptake.

5.2 Recommendations for Restoration

There is not significant ground to suggest that inclusion of increased species number in restored sites would benefit the goal of restoring the C sequestration function of peatlands. Restoration protocols for fen peatlands that aim to re-establish the C sequestration function would benefit from inclusion of high biomass producing graminoid species such as Ca that are efficient C accumulators. Rhizome transfer may be an effective way of transferring this species to the desired restoration site. However, it must be noted that graminoid species other than Ca may not provide the same C sequestration advantage. The inclusion of bryophyte species in combination with vascular species may also lead to additional C sequestration beyond the sum of the individual parts. Adopting these recommendations has an added advantage of contributing to climate change mitigation, on a small regional scale.

5.3 Future Biodiversity Research in Peatlands

Much work still remains to understand how biodiversity can be used as a tool to enhance the effect of restoration. Future BEF research should have a greater focus on a diversity of ecosystem functions including, but not limited to, C dynamics. I would recommend year-round monitoring of C dynamics and inclusion of Dissolved Organic Carbon (DOC) in future peatland BEF studies, in order to get a complete picture of the C balance. Future studies should also consider conducting longer-term experiments in order to get a better picture of temporal changes in C balance. Use of true replicates in place of pseudo-replicates would be essential to making definitive conclusions about the role of species richness and identity on C dynamics in restored peatlands. To delve deeper into the overall effect of biodiversity on C sequestration, a better understanding of the relationship between plant diversity and microbial function is also required, as heterotrophic respiration, methane production, and methane oxidation are facilitated by the work of microbes.

Peatland restoration projects may consider inclusion of Ca and Mg in mixed treatments to further test their effect on companion species.

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APPENDICES

APPENDIX A – PLANTING DETAILS

Figure A1 – Layout of biodiversity experimental plots. Field 6 contains block 1, field 7 contains block 3 in the northern part and a portion of block 4 in the southern part, and field 8 contains block 4. Distances are approximate and not to scale.

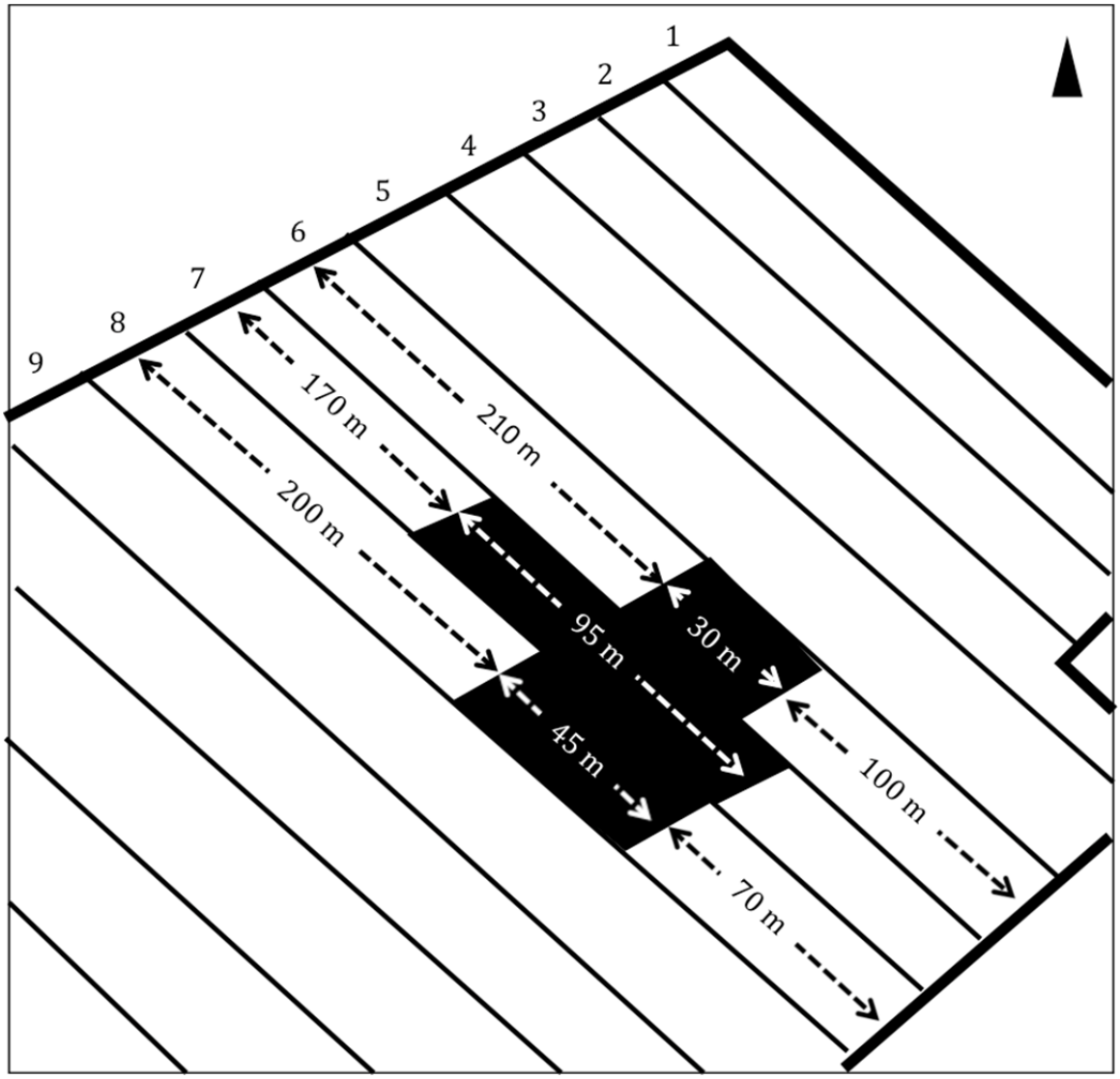

Figure A2 – Layout of Block 1 of 4, in field 6. [Ca= *Carex aquatilis*, Cc=*Calamagrostis canadensis*, Cs=*Campillium stellatum*, Sw=*Sphagnum warnstorfii*, Ta=*Trichophorum alpinum*, Tc=*Trichophorum cespitosum*, Tn= *Tomenthypnum nitens,* Mg= *Myrica gale*].

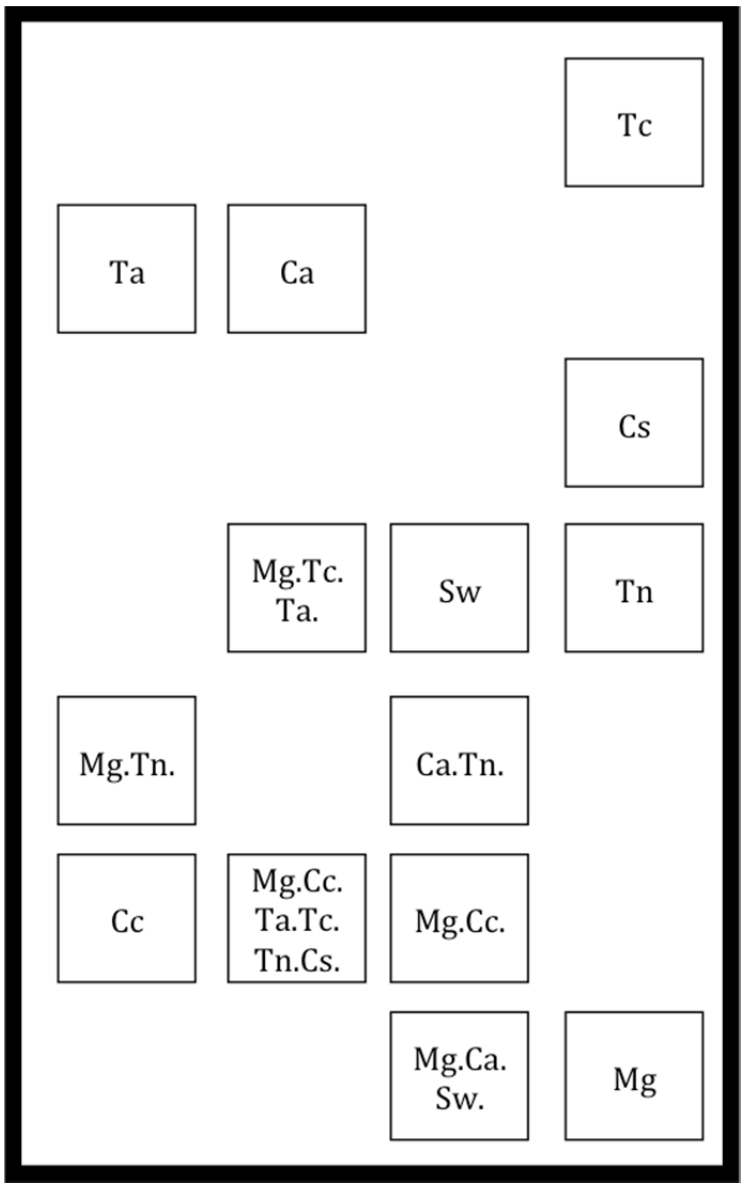

Figure A3 – Layout of Block 3 of 4, in field 7. [Ca= *Carex aquatilis*, Cc=*Calamagrostis canadensis*, Cs=*Campillium stellatum*, Sw=*Sphagnum warnstorfii*, Ta=*Trichophorum alpinum*, Tc=*Trichophorum cespitosum*, Tn= *Tomenthypnum nitens,* Mg= *Myrica gale*].

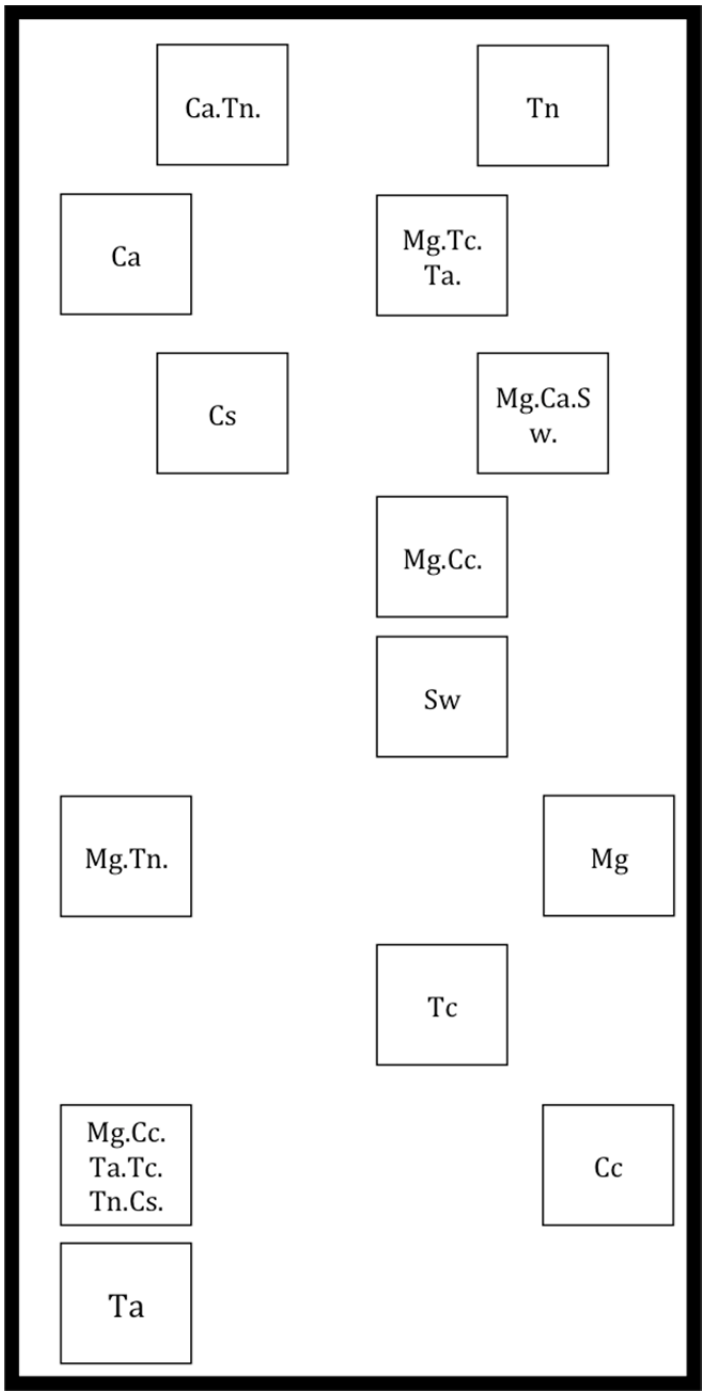

Figure A4 – Layout of Block 4 of 4, in fields 7 (right) and 8 (left). The dotted vertical line indicates the divide between fields 8 and 7. The upper portion of this block is located slightly further up from the remainder. [Ca= *Carex aquatilis*, Cc=*Calamagrostis canadensis*, Cs=*Campillium stellatum,* Mg= *Myrica gale*, Sw=*Sphagnum warnstorfii*, Ta=*Trichophorum alpinum*, Tc=*Trichophorum cespitosum*, Tn= *Tomenthypnum nitens*].

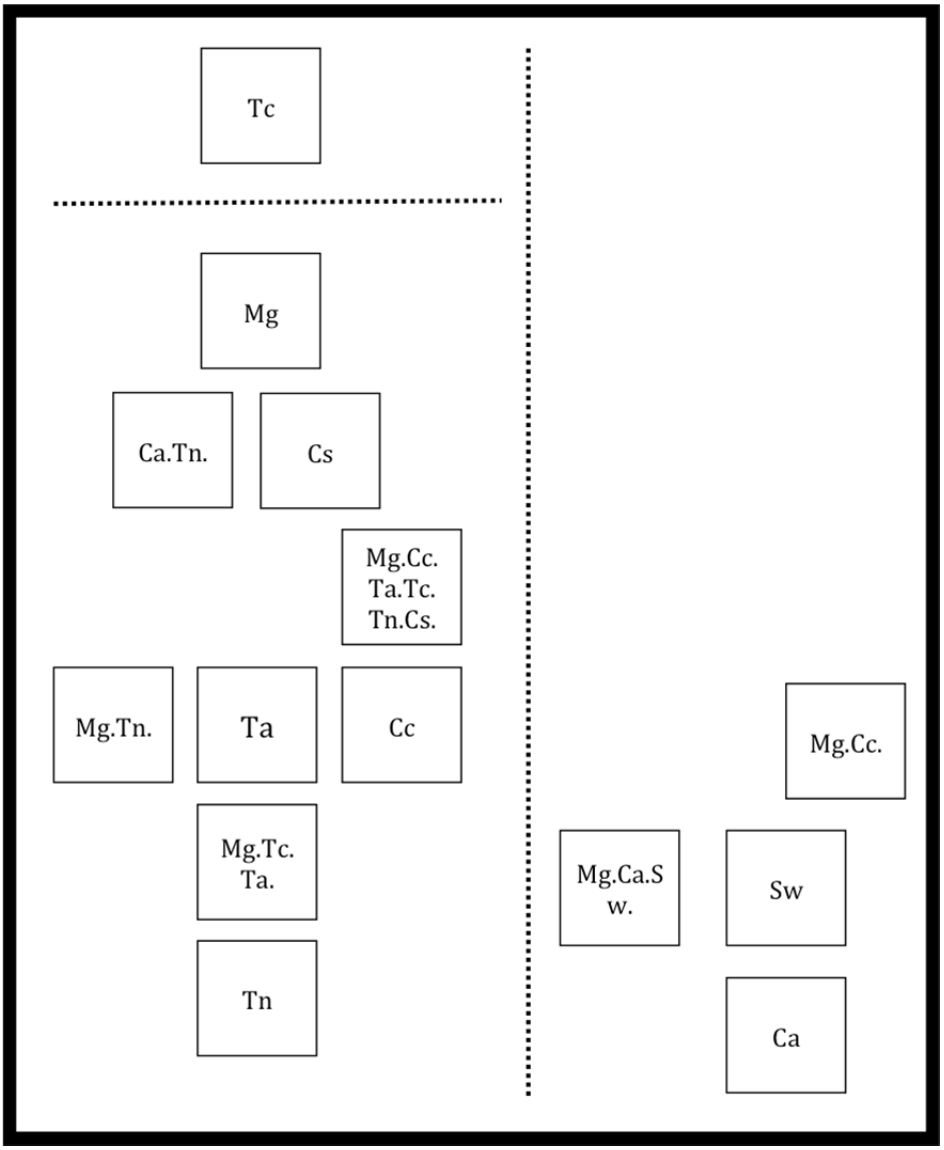

Table A1 – Number of plants per treatment plot of 3 m x 3 m. Mossses are quantified in units of m^2 collected/9 m^2 planted plot. [Ca= *Carex aquatilis*, Cc=*Calamagrostis canadensis*, Cs=*Campillium stellatum,* Mg= *Myrica gale*, Sw=*Sphagnum warnstorfii*, Ta=*Trichophorum alpinum*, Tc=*Trichophorum cespitosum*, Tn= *Tomenthypnum nitens*].

	Mg	**Ta**	**Tc**	**Ca**	**Cc**	**Tn**	**Cs**	**Sw**
Mg	121							
Ta		240						
Tc			240					
Ca				240				
Cc					240			
Sw						1.80		
Tn							1.80	
Cs								1.80
Ca.Tn.				240		1.80		
Mg.Tn.	121					1.80		
Mg.Cc.	60				120			
Mg.Ta.Tc.	40	80	80					
Mg.Ca.Sw.	60			120				1.80
Mg.Cc.Ta.Tn.Sw.Tn.Cs.	30	60	60		60	0.90	0.90	

APPENDIX B – BIOTIC AND ABIOTIC CONDITIONS

TABLE B1 – Mean water level (WL, cm) measured near each collar in the year 2011. [Ca= *Carex aquatilis*, Mg=*Myrica gale*, Tn=*Tomenthypnum nitens*].

Treatment	**Ca**			**Ca.Tn.**			**Mg**			**Mg.Tn.**			**Tn.**			**Bare Peat**			
Block	1	3	4	1	3	4	1	3	4	1	3	4	1	3	4	--	--	--	--
Mean WL (cm)	-15	-21	-3	-17	-17	-1	-12	-15	2	-22	-12	-1	-9	-20	-1	-6	-10	-21	-13

TABLE B2 – Mean water level (WL, cm) and vegetation biomass (g) for 60 cm x 60 cm monoculture collars for the year 2012 broken down by functional groups (shrub, graminoid, and bryophyte). [Ca= *Carex aquatilis*, Cc=*Calamagrostis canadensis*, Cs=*Campillium stellatum,* Mg= *Myrica gale*, Sw=*Sphagnum warnstorfii*, Ta=*Trichophorum alpinum*, Tc=*Trichophorum cespitosum*, Tn= *Tomenthypnum nitens*].

Treatment	**Ta**			**Tc**			**Cc**			**Sw**			**Cs**			**Ca**			**Mg**			**Tn**		
Block	1	3	4	1	3	4	1	3	4	1	3	4	1	3	4	1	3	4	1	3	4	1	3	4
Shrub (g)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	102	187	76	0	0	0
Graminoid (g)	9	6	16	16	5	21	31	9	15	0	0	0	0	0	0	73	148	175	0	0	0	0	0	0
Bryophyte (g)	0	0	0	0	3	19	0	0	4	102	27	252	21	17	118	0	0	3	0	0	0	31	54	82
Mean WL (cm)	-26	-21	-7	-23	-23	-1	-30	-28	-8	-24	-35	-14	-19	-27	-12	-23	-26	-13	-22	-21	0	-18	-25	-13

TABLE B3 – Mean water level (WL, cm) and vegetation biomass (g) for 60 x 60 cm polyculture collars in the year 2012 broken down by functional groups (shrub, graminoid, and bryophyte). [Ca= *Carex aquatilis*, Cc=*Calamagrostis canadensis*, Cs=*Campillium stellatum,* Mg= *Myrica gale*, Sw=*Sphagnum warnstorfii*, Ta=*Trichophorum alpinum*, Tc=*Trichophorum cespitosum*, Tn= *Tomenthypnum nitens*].

Treatment	**Ca.Tn.**			**Mg.Tn.**			**Mg.Cc.**			**Mg.Ta.Tc.**			**Mg.Ca.Tw.**			**Mg.Ta. Tc. C.c.Cs.Tn.**			**Bare Peat**			
Block	1	3	4	1	3	4	1	3	4	1	3	4	1	3	4	1	3	4	6	7	10	11
Shrub (g)	0	0	0	34	74	159	54	89	138	70	28	29	31	50	96	30	104	96	0	0	0	0
Graminoid (g)	165	133	213	0	0	0	9	9	7	4	3	10	45	133	41	6	8	18	0	0	0	0
Bryophyte (g)	19	112	20	16	76	70	0	0	0	0	2	1	94	38	20	78	27	100	0	0	0	0
Mean WL (cm)	-26	-22	-10	-32	-18	-6	-26	-30	-19	-31	-31	-6	-29	-28	-10	-21	-22	-7	-22	-18	-27	-27

APPENDIX C – MEASURED METHANE FLUX

TABLE C1 – Measured methane flux (CH_4, mg CH_4 m^{-2} d^{-1}) in bare peat, *Sphagnum* transfer restoration, and natural sites for the years 2011 and 2012. These can serve as a reference to compare against the flux pattern of biodiversity-controlled treatments.

Site	Type	Year	Mean CH_4 Flux (min, max) (mg $CH_4 m^{-2} d^{-1}$)
Bare Peat	Dry	2011	-0.6 (-5.8, 1.4)
		2012	-1.5 (-13.0, 11.7)
	Dry	2011	-6.1 (-75.0, 1.1)
		2012	-1.6 (-30.8, 6.5)
	Moderate	2011	3.4 (-0.4, 22.0)
		2012	-3.4 (-15.7, 1.0)
	Wet	2011	-0.4 (-4.9, 4.0)
		2012	4.3 (-1.8, 21.8)
Restored	Dry	2011	-3.3 (-18.0, 6.5)
		2012	-4.4 (-44.6, 34.2)
	Dry	2011	-0.9 (-23.0, 11.5)
		2012	-1.0 (-15.5, 12.9)
	Moderate	2011	-3.7 (-24.8, 6.3)
		2012	-5.5 (-30.4, 2.2)
	Moderate	2011	-0.2 (-3.6, 5.3)
		2012	4.3 (-1.1, 19.3)
	Wet	2011	4.0 (-7.4, 36.3)
		2012	4.0 (-5.9, 19.7)
	Wet	2011	-4.6 (-22.1, 11.0)
		2012	4.5 (-5.9, 24.1)

Site	Type	Year	Mean CH_4 Flux (min, max) ($mg\ CH_4 m^{-2} d^{-1}$)
Natural	Hummock	2011	-1.2 (-10.7, 14.3)
		2012	-1.6 (-9.1, 10.3)
	Hummock	2011	-2.8 (-11.0, 2.3)
		2012	2.3 (-2.7, 14.5)
	Hummock	2011	0.6 (-8.4, 12.3)
		2012	-0.5 (-21.8, 22.2)
	Hollow	2011	4.6 (-14.2, 23.2)
		2012	7.7 (-2.1, 23.9)
	Hollow	2011	1.6 (-19.1, 12.7)
		2012	5.8 (-1.4, 14.3)
	Hollow	2011	-1.1 (-15.6, 8)
		2012	3.6 (-4.4, 15.4)

TABLE C2 – Measured methane flux (CH_4, mg CH_4 m^{-2} d^{-1}) in diversity-controlled site for 2011 and 2012. [Ca= *Carex aquatilis*, Cc=*Calamagrostis canadensis*, Cs=*Campillium stellatum*, Sw=*Sphagnum warnstorfii*, Ta=*Trichophorum alpinum*, Tc=*Trichophorum cespitosum*, Tn= *Tomenthypnum nitens,* Mg= *Myrica gale*].

Treatment	**Block**	**Year**	**Mean CH_4 Flux (Min, Max) (mg CH_4 m^{-2} d^{-1})**
Ca	1	2011	-2.5 (-22.6, 5.0)
		2012	16.7 (-9.8, 36.6)
	3	2011	9.0 (-4.1, 23.6)
		2012	14 (-7.3, 36.5)
	4	2011	6.4 (-4.8, 19.3)
		2012	10.6 (-4.0, 24.8)
Cc	1	2011	-5.7 (-35.0, 16.8)
		2012	n.a.
	3	2011	2.0 (-6.6, 14.5)
		2012	n.a.
	4	2011	20.7 (-1.4, 38.0)
		2012	n.a.
Cs	1	2011	-3.3 (-11.6, 3.0)
		2012	n.a.
	3	2011	-2.9 (-10.3, 1.6)
		2012	n.a.
	4	2011	-4.6 (-10.7, 2.5)
		2012	n.a.
Mg	1	2011	4.2 (-8.6, 51.2)
		2012	-4.4 (-27.2, 22.9)
	3	2011	-0.2 (-8.5, 15.7)
		2012	4.4 (-17.7, 38.2)
	4	2011	22.9 (-15.3, 71.1)
		2012	43.2 (3.9, 215.8)

Treatment	Block	Year	Mean CH_4 Flux (Min, Max) ($mg\ CH_4\ m^{-2}\ d^{-1}$)
Sw	1	2011	-9.2 (-20.3, -1.1)
		2012	n.a.
	3	2011	-4.6 (-18.2, 1.2)
		2012	n.a.
	4	2011	-1.0 (-10.9, 6.7)
		2012	n.a.
Ta	1	2011	-3.9 (-13.6, 2.8)
		2012	n.a.
	3	2011	-2.5 (-6.2, 2.0)
		2012	n.a.
	4	2011	-1.3 (-4.9, 0.6)
		2012	n.a.
Tc	1	2011	4.2 (-3.4, 28.0)
		2012	n.a.
	3	2011	-1.9 (-11.3, 4.6)
		2012	n.a.
	4	2011	24.4 (-9.0, 98.4)
		2012	n.a.
Tn	1	2011	-2.5 (-6.9, 6.0)
		2012	0.7 (-7.9, 16.2)
	3	2011	-0.6 (-7.1, 6.3)
		2012	-3.0 (-34.5, 6.5)
	4	2011	11.2 (1.0, 21.6)
		2012	-4.0 (-10, 1.0)

Treatment	Block	Year	Mean CH_4 Flux (Min, Max) ($mg\ CH_4\ m^{-2}\ d^{-1}$)
Ca.Tn.	1	2011	1.7 (-15.7, 12.9)
		2012	14.6 (-1.9, 32.2)
	3	2011	7.1 (-8.5, 31.8)
		2012	13.4 (-0.2, 29.2)
	4	2011	9.7 (-9.8, 27.7)
		2012	13.4 (1.1, 29.2)
Mg.Cc.	1	2011	-3.5 (-17.1, 11.6)
		2012	n.a.
	3	2011	-5.7 (-24.5, 5.7)
		2012	n.a.
	4	2011	-6.3 (-15.3, 0.1)
		2012	n.a.
Mg.Tn.	1	2011	-3.4 (-9.4, 4.1)
		2012	1.2 (-37.5, 35.9)
	3	2011	-2.7 (-10.5, 6.2)
		2012	0.1 (-9.7, 21.2)
	4	2011	2.1 (-20.6, 17.1)
		2012	13.9 (-4.0, 64.2)
Mg.Ca.Sw.	1	2011	10.1 (1.0, 32.4)
		2012	n.a.
	3	2011	6.2 (-6.0, 20.3)
		2012	n.a.
	4	2011	6.5 (1.7, 12.5)
		2012	n.a.

Treatment	Block	Year	Mean CH_4 Flux (Min, Max) ($mg\ CH_4\ m^{-2}\ d^{-1}$)
Mg.Ta.Tc.	1	2011	-7.5 (-15.8, 2.3)
		2012	n.a.
	3	2011	0.8 (-1.0, 4.8)
		2012	n.a.
	4	2011	29.8 (-3.1, 93.3)
		2012	n.a.
Mg.Ta.Tc.Cc.Cs.Tn.	1	2011	-4.0 (-10.7, 1.3)
		2012	n.a.
	3	2011	-0.2 (-8.6, 7.0)
		2012	n.a.
	4	2011	9.1 (-3.5, 44.3)
		2012	n.a.

APPENDIX D – MEASURED CARBON DIOXIDE FLUX

TABLE D1 – Measured photosynthesis (GEP, where PAR≥1000 μmol m^{-2} s^{-1}), respiration (RESP), and net ecosystem exchange (NEE, where PAR≥1000 μmol m^{-2} s^{-1}) mean (minimum, maximum) in g CO_2 m^{-2} d^{-1} in bare peat, traditionally restored, and natural sites in 2011.

Site	Type	GEP (g CO_2 m^{-2} d^{-1})	RESP (g CO_2 m^{-2} d^{-1})	NEE (g CO_2 m^{-2} d^{-1})
Bare Peat	Dry	n.a.	1 (0,4)	1 (0,4)
	Dry	n.a.	3 (1,7)	3 (1,7)
	Moderate	n.a.	3 (1,5)	3 (1,5)
	Wet	n.a.	1 (0,2)	1 (0,2)
Restored	Dry	-9 (-18,0)	8 (3,15)	-1 (-7,4)
	Dry	-11 (-26,0)	9 (2,20)	-2 (-13,4)
	Moderate	-4 (-10,2)	5 (1,7)	1 (-5,5)
	Moderate	-4 (-11,7)	5 (1,10)	1 (-4,14)
	Wet	-11 (-20,-4)	10 (5,14)	-1 (-7,5)
	Wet	-12 (-23,-1)	8 (0,15)	-4 (-13,4)
Natural	Hummock	-15(-37,-4)	18 (7,42)	2 (-4,10)
	Hummock	-18 (-45,-3)	18 (7,37)	0 (-29,13)
	Hummock	-6 (-13,-1)	12 (2,21)	6 (1,16)
	Hollow	-30 (-69,-1)	17 (1,29)	-13 (-40,9)
	Hollow	-32 (-57,-2)	21 (2,34)	-11 (-35,7)
	Hollow	-31 (-65,0)	20 (1,33)	-11 (-47,6)

TABLE D2 – Measured photosynthesis (GEP, where PAR≥1000 μmol m^{-2} s^{-1}), respiration (RESP), and net ecosystem exchange (NEE, where PAR≥1000 μmol m^{-2} s^{-1}) mean (minimum, maximum) in g CO_2 m^{-2} d^{-1} in diversity-controlled site in 2011. [Ca= *Carex aquatilis*, Mg=*Myrica gale*, Tn=*Tomenthypnum nitens*].

Site	**Block**	**GEP (g CO_2 m^{-2} d^{-1})**	**RESP (g CO_2 m^{-2} d^{-1})**	**NEE (g CO_2 m^{-2} d^{-1})**
	1	-15 (-24,-7)	10 (8,14)	-5 (-14,3)
Ca	3	-31 (-53,-6)	21 (7,31)	-11 (-31,7)
	4	-53 (-79,-29)	32 (18,38)	-22 (-48,5)
	1	-30 (-52,1)	21 (0,30)	-9 (-27,4)
Mg	3	-42 (-78,1)	33 (6,46)	-9 (-35,9)
	4	-21 (-32,-1)	10 (1,21)	-11 (-20,-1)
	1	-6 (-10,-2)	6 (2,8)	0 (-4,4)
Tn	3	-4 (-6,-1)	6 (2,8)	2 (-1,4)
	4	-11 (-20,-6)	8 (1,16)	-3 (-8,7)
	1	-43 (-70,-13)	25 (12,36)	-18 (-40,3)
Ca.Tn.	3	-33 (-65,-4)	23 (7,31)	-10 (-42,10)
	4	-57(-110,-3)	33 (5,51)	-25 (-68,12)
	1	-15 (-26,0)	11 (5,15)	-5 (-11,5)
Mg.Tn.	3	-29 (-48,-1)	23 (6.35)	-6 (-24,4)
	4	-47 (-79,-9)	29 (7,50)	-18 (-41,2)

TABLE D3 – Measured photosynthesis (GEP, where PAR≥1000 μmol m^{-2} s^{-1}), respiration (RESP), and net ecosystem exchange (NEE, where PAR≥1000 μmol m^{-2} s^{-1}) mean (minimum, maximum) in g C m^{-2} $season^{-1}$ in bare peat, traditionally restored, and natural sites in 2012.

Site	**Type**	**GEP** ($g\ CO_2\ m^{-2}\ d^{-1}$)	**RESP** ($g\ CO_2\ m^{-2}\ d^{-1}$)	**NEE** ($g\ CO_2\ m^{-2}\ d^{-1}$)
Bare Peat	Dry	n.a.	3 (0,7)	3 (0,7)
	Dry	n.a.	6 (1,13)	6 (1,13)
	Moderate	n.a.	4 (-1,11)	4 (-1,11)
	Wet	n.a.	2 (0,6)	2 (0,6)
Restored	Dry	-6 (-13,-1)	7 (2,12)	0 (-3,2)
	Dry	-10 (-19,-1)	7 (2,14)	-3 (-7,1)
	Moderate	-3 (-6,0)	4 (0,9)	2 (-2,8)
	Moderate	-5 (-10,0)	4 (1,9)	-1 (-3,4)
	Wet	-12 (-18,-4)	7 (3,11)	-5 (-10,0)
	Wet	-18 (-31,-2)	12 (3,22)	-8 (-17,1)
Natural	Hummock	-11 (-18,-7)	22 (7,43)	4(-2,12)
	Hummock	-19 (-35,-7)	28 (7,44)	7(-5,26)
	Hummock	-15 (-24,-1)	28 (6,47)	13(3,24)
	Hollow	-27 (-49,-6)	15 (5,29)	-12(-26,1)
	Hollow	-29 (-41,-11)	16 (5,27)	-12(-19,-5)
	Hollow	-26 (-53,-3)	24 (6,42)	-4(-14,3)

TABLE D4 – Measured photosynthesis (GEP, where PAR≥1000 μmol m^{-2} s^{-1}), respiration (RESP), and net ecosystem exchange (NEE, where PAR≥1000 μmol m^{-2} s^{-1}) mean (minimum, maximum) in g C m^{-2} $season^{-1}$ in diversity-controlled monocultures in 2012. [Ca= *Carex aquatilis*, Cc=*Calamagrostis canadensis*, Cs=*Campillium stellatum,* Mg= *Myrica gale*, Sw=*Sphagnum warnstorfii*, Ta=*Trichophorum alpinum*, Tc=*Trichophorum cespitosum*, Tn= *Tomenthypnum nitens*].

Site	**Block**	**GEP** ($g\ CO_2\ m^{-2}\ d^{-1}$)	**RESP** ($g\ CO_2\ m^{-2}\ d^{-1}$)	**NEE** ($g\ CO_2\ m^{-2}\ d^{-1}$)
Ca	1	-36 (-62,-11)	15 (0,30)	-22 (-42,-1)
	3	-40 (-71,-1)	20 (2,35)	-24 (-51,1)
	4	-58 (-87,-39)	17 (6,29)	-38 (-67,-13)
Cc	1	-4 (-11,-1)	5 (2,14)	0 (-3,5)
	3	-6 (-8,-3)	5 (3,9)	0 (-4,4)
	4	-13 (-26,-1)	7 (2,13)	-6 (-16,1)
Cs	1	-4 (-6,-2)	3 (1,5)	-1 (-2,2)
	3	-2 (-5,0)	3 (1,5)	1 (-1,2)
	4	-15 (-22,-6)	8 (3,16)	-2 (-5,1)
Mg	1	-19 (-41,-3)	13 (4,19)	-6 (-23,5)
	3	-27 (-56,-1)	17 (2,26)	-9 (-38,6)
	4	-33 (-46,-13)	11 (1,23)	-3 (-27,-6)
Sw	1	-6 (-13,-2)	4 (1,8)	-2 (-5,3)
	3	-4 (-10,-1)	4 (2,8)	0 (-3,3)
	4	-11 (-16,-2)	6 (2,11)	-4 (-8,1)
Ta	1	-8 (-12,-3)	7 (2,12)	-1 (-5,6)
	3	-8 (-13,-5)	7 (3,11)	-1 (-4,2)
	4	-17 (-33,-4)	8 (2,14)	-8 (-21,0)
Tc	1	-17 (-25,-6)	9 (2,16)	-8 (-15,-1)
	3	-5 (-11,-1)	5 (1,9)	0 (-3,3)
	4	-19 (-42,-2)	7 (2,16)	-13 (-32,0)

Site	Block	GEP ($g\ CO_2\ m^{-2}\ d^{-1}$)	RESP ($g\ CO_2\ m^{-2}\ d^{-1}$)	NEE ($g\ CO_2\ m^{-2}\ d^{-1}$)
Tn	1	-6 (-9,-4)	5 (3,8)	-1 (-4,3)
	3	-3 (-6,0)	5 (1,12)	2 (-1,5)
	4	-7 (-13,-3)	5 (3,8)	-6 (-10,-2)

TABLE D5 – Measured photosynthesis (GEP, where PAR≥1000 μmol m^{-2} s^{-1}), respiration (RESP), and net ecosystem exchange (NEE, where PAR≥1000 μmol m^{-2} s^{-1}) mean (minimum, maximum) in g C m^{-2} $season^{-1}$ in diversity-controlled polycultures in 2012. [Ca= *Carex aquatilis*, Cc=*Calamagrostis canadensis*, Cs=*Campillium stellatum,* Mg= *Myrica gale*, Sw=*Sphagnum warnstorfii*, Ta=*Trichophorum alpinum*, Tc=*Trichophorum cespitosum*, Tn= *Tomenthypnum nitens*].

GEP	**Block**	**GEP** ($g\ CO_2\ m^{-2}\ d^{-1}$)	**RESP** ($g\ CO_2\ m^{-2}\ d^{-1}$)	**NEE** ($g\ CO_2\ m^{-2}\ d^{-1}$)
Ca.Tn.	1	-44 (-82,-11)	21 (-4,33)	-23 (-52,-3)
	3	-63 (-94,-18)	22 (6,36)	-40 (-73,0)
	4	-62 (-103,-38)	23 (8,35)	-36 (-79,-5)
Mg.Cc.	1	-10 (-24,0)	7 (3,10)	-4 (-17,4)
	3	-20 (-39,-4)	13 (0,27)	-6 (-18,2)
	4	-41 (-65,-1)	12 (-1,24)	-28 (-43,0)
Mg.Tn.	1	-15 (-34,-2)	9 (4,14)	-5 (-19,3)
	3	-22 (-44,-5)	14 (2,24)	-7 (-30,4)
	4	-30 (-61,-3)	17 (4,29)	-14 (-36,1)
Mg.Ca.Sw.	1	-33 (-58,-9)	16 (7,24)	-16 (-39,0)
	3	-59 (-157,-7)	28 (4,71)	-32 (-86,-1)
	4	-71 (-101,-36)	20 (2,40)	-47 (-66,-22)
Mg.Ta.Tc.	1	-18 (-34,-1)	9 (2,14)	-23 (-23,3)
	3	-11 (-20,0)	8 (2,13)	-11 (-11,3)
	4	-23 (-44,-5)	11 (1,17)	-28 (-28,-1)
Mg.Ta.Tc.Cc. Cs.Tn.	1	-13 (-26,-2)	10 (3,20)	-4 (-12,2)
	3	-12 (-32,-1)	9 (2,23)	-4 (-11,1)
	4	-29 (-64,-6)	16 (-1,28)	-16 (-45,2)

APPENDIX E – CARBON MODELS FOR THE YEAR 2011

$$GEP = \frac{GEPmax*PAR*VV}{k+PAR} * e^{\frac{-0.5*(Ta-Topt)^2}{Ttol}} * e^{\frac{-0.5*(WL-WLopt)^2}{WLtol}} + constant$$ Equation 2.2

$$GEP = \frac{GEPmax*PAR*(1-\exp(-a*VV))}{k+PAR} * e^{\frac{-0.5*(Ta-Topt)^2}{Ttol}} * e^{\frac{-0.5*(WL-WLopt)^2}{WLtol}} + constant$$ Equation 2.3

$$RESP = \frac{b1}{1+\exp(-b2*(Ta-b3))} + \frac{b4}{1+\exp(-b5*(WL-b6))} + b7*VV + constant$$ Equation 2.4

$$RESP = \frac{b1}{1+\exp(-b2*(Ta-b3))} + b7*VV + constant$$ Equation 2.5

$$RESP = \frac{b1}{1+\exp(-b2*(Ta-b3))} + \frac{b4}{1+\exp(-b5*(WL-b6))} + constant$$ Equation 2.6

$$CH4 = b1*T2 + b2*VV + b6*\mathrm{e}\left(\frac{-.5(WL-WLopt)}{WLtol}^2\right) + constant$$ Equation 2.7

$$CH4 = b1*T2 + b6*\mathrm{e}\left(\frac{-.5(WL-WLopt)}{WLtol}^2\right) + constant$$ Equation 2.8

TABLE E1 – Methane model parameters and standard error for the year 2011. [Ca= *Carex aquatilis*, Cc=*Calamagrostis canadensis*, Cs=*Campillium stellatum,* Mg=*Myrica gale*, Sw=*Sphagnum warnstorfii*, Ta=*Trichophorum alpinum*, Tc=*Trichophorum cespitosum*, Tn=*Tomenthypnum nitens*].

Parameter	**Ca**	**Mg**	**Tn**	**Ca.Tn.**	**Mg.Tn.**	**Bare Peat**
b1	-0.796 (0.414)	1.445 (1.042)	0.226 (0.243)	-0.084 (0.416)	-0.318 (0.245)	
b2	0.490 (0.171)	-0.311 (0.515)		0.448 (0.169)	0.323 (0.123)	0.026 (0.053)
b6	11.588 (7.109)	-19.598 (11.152)	-21.564 (28.632)	-13.962 (7.460)	-4.881 (3.346)	-18.230 (980.228)
constant	9.447 (6.652)	-4.190 (19.319)	13.898 (28.675)	-1.923 (7.269)	2.559 (4.650)	0.034 (2.108)
WL_{opt}	-22.675 (1.346)	-10.526 (2.862)	-13.217 (1.598)	-0.172 (0.290)	-11.596 (2.422)	-65.361 (986.468)
WL_{tol}	1.757 (1.439)	5.964 (4.832)	-10.599 (10.862)	-0.413 (0.285)	3.169 (2.647)	20.000 (231.075)
R^2	0.264	0.217	0.317	0.231	0.268	0.093
MSR	71.018	420.396	47.408	103.051	40.357	4.69

TABLE E2 – Photosynthesis (GEP) model parameters and standard error for the year 2011. [Ca= *Carex aquatilis*, Mg=*Myrica gale*, Tn=*Tomenthympum nitens*].

Parameter	**Ca**	**Mg**	**Tn**	**Ca.Tn.**	**Mg.Tn.**
GEPmax	-157.998 (44.496)	-88.366 (19.313)	-0.223 (0.031)	-163.854 (42.607)	-84.657 (12.844)
a	0.041 (0.013)	0.197 (0.047)		0.037 (0.014)	117.812 (97978759.506)
k	1482.797 (412.988)	978.116 (258.736)	695.836 (238.135)	1290.891 (344.014)	1125.444 (375.803)
T_{opt}	21.196 (6.451)	19.846 (13.059)	27.509 (3.369)	26.866 (1.471)	28.511 (0.616)
T_{tol}	20.000 (7.602)	20.000 (13.660)	20.000 (6.259)	12.911 (2.618)	7.346 (0.800)
b7					
WL_{opt}	-5.631 (4.075)	-14.243 (2.483)	-5.744 (1.485)	-8.757 (2.723)	-3.000 (2.255)
WL_{tol}	20.000 (5.380)	16.032 (2.755)	10.548 (1.601)	20.000 (4.459)	13.441 (2.065)
constant	-0.800 (1.147)	-0.577 (1.175)	-0.706 (0.355)	-0.630 (1.551)	-1.430 (1.490)
R^2	0.797	0.777	0.674	0.79	0.714
MSR	64.162	70.649	6.165	118.246	96.863

TABLE E3 – Respiration (RESP) model parameters and standard error for the year 2011. [Ca= *Carex aquatilis,* Mg= *Myrica gale*, Tn=*Tomenthypnum nitens*].

Parameter	**Ca**	**Mg**	**Tn**	**Ca.Tn.**	**Mg.Tn.**	**Bare Peat**
b1	9.699 (2.883)	12.121 (5.342)	3.459 (2.272)	30.000 (14.605)	23.527 (13.426)	9.991 (137.712)
b2	0.800 (0.686)	0.998 (1.209)	2.864 (8.067)	0.234 (0.168)	0.284 (0.254)	0.139 (0.412)
b3	25.812 (1.159)	27.852 (1.417)	30.412 (1.084)	25.513 (2.131)	25.114 (2.700)	40.000 (148.296)
b4			-2.618 (1.960)			-0.980 (7.268)
b5			26.351 (3901.97)			0.212 (1.405)
b6			-1.864 (5.280)			-25.280 (72.163)
b7	0.672 (0.084)	0.872 (0.184)	0.055 (0.039)	0.760 (0.073)	1.196 (0.131)	
constant	0.974 (2.638)	4.546 (3.993)	3.561 (1.742)	-10.379 (8.303)	-9.087 (8.845)	1.711 (6.949)
R^2	0.761	0.533	0.275	0.825	0.768	0.219
MSR	24.18	83.246	7.562	24.455	38.067	1.816

APPENDIX F – CARBON MODELS FOR THE YEAR 2012

$$GEP = \frac{GEPmax*PAR*VV}{k+PAR} * e^{\frac{-0.5*(Ta-Topt)^2}{Ttol}} * e^{\frac{-0.5*(WL-WLopt)^2}{WLtol}} + constant$$ Equation 2.2

$$GEP = \frac{GEPmax*PAR*(1-\exp(-a*VV))}{k+PAR} * e^{\frac{-0.5*(Ta-Topt)^2}{Ttol}} * e^{\frac{-0.5*(WL-WLopt)^2}{WLtol}} + constant$$ Equation 2.3

$$RESP = \frac{b1}{1+\exp(-b2*(Ta-b3))} + \frac{b4}{1+\exp(-b5*(WL-b6))} + b7*VV + constant$$ Equation 2.4

$$RESP = \frac{b1}{1+\exp(-b2*(Ta-b3))} + b7*VV + constant$$ Equation 2.5

$$RESP = \frac{b1}{1+\exp(-b2*(Ta-b3))} + \frac{b4}{1+\exp(-b5*(WL-b6))} + constant$$ Equation 2.6

$$CH4 = b1*T2 + b2*VV + b6*\mathrm{e}\left(\frac{-.5(WL-WLopt)}{WLtol}^2\right) + constant$$ Equation 2.7

$$CH4 = b1*T2 + b6*\mathrm{e}\left(\frac{-.5(WL-WLopt)}{WLtol}^2\right) + constant$$ Equation 2.8

TABLE F1 – Methane (CH_4) model parameters and standard error for monocultures in 2012. [Ca= *Carex aquatilis*, Cc=*Calamagrostis canadensis*, Cs=*Campillium stellatum,* Mg= *Myrica gale*, Sw=*Sphagnum warnstorfii*, Ta=*Trichophorum alpinum*, Tc=*Trichophorum cespitosum*, Tn= *Tomenthypnum nitens*].

Parameter	**Ca**	**Cc**	**Cs**	**Mg**	**Sw**	**Ta**	**Tc**	**Tn**
constant	-14.900	22.454	8.896	-16.304	-1.151	-20.996	-35.058	3.660
	(13.206)	(26.215)	(6.870)	(94.882)	(6.232)	(38.808)	(316.900)	(14.440)
b2	0.226	-1.063		0.247		-1.182	4.756	
	(0.098)	(0.603)		(2.184)		(0.532)	(1.950)	
b1	0.475	0.450	-0.293	3.021	-0.041	0.890	0.736	0.213
	(0.264)	(0.713)	(0.187)	(1.386)	(.370)	(.298)	(1.225)	(0.179)
b6	15.984	-30.000	-10.004	-117.097	-15.656	10.585	-28.912	-11.582
	(11.939)	(19.952)	(5.224)	(825.518)	(6.362)	(39.215)	(4288.136)	(13.580)
WL_{opt}	-15.962	-30.408	-20.050	-92.233	-39.986	-2.398	-118.393	-33.739
	(5.861)	(4.497)	(2.744)	(485.337)	(1.816)	(27.089)	(12394.837)	(9.628)
WL_{tol}	23.386	15.117	13.378	45.637	4.834	29.676	60.319	20.000
	(16.393)	(14.281)	(8.034)	(222.986)	(2.264)	(97.777)	(5149.406)	(26.537)
R^2	0.28	0.561	0.535	0.243	0.385	0.492	0.555	0.143
MSR	99.640	1316.249	61.954	12.953	412.414	45.738	194.191	13.822

TABLE F2 – Methane model parameters and standard error for polycultures in 2012. [Ca= *Carex aquatilis*, Cc=*Calamagrostis 160anadensis*, Cs=*Campillium stellatum,* Mg= *Myrica gale*, Sw=*Sphagnum warnstorfii*, Ta=*Trichophorum alpinum*, Tc=*Trichophorum cespitosum*, Tn= *Tomenthypnum nitens*].

	Ca.Tn.	**Mg.Tn.**	**Mg.Cc.**	**Mg.Ta.Tc.**	**Mg.Ca.Sw.**	**Mg.Ta.Tc.Cc. Cs.Tn.**	**Bare Peat**
Constant	15.501 (8.383)	-4.866 (8.294)	19.558 (9.049)	-2.325 (29.277)	-21.573 (105.238)	-16.434 (13.846)	0.246 (19.671)
b1	-0.545 (0.320)	0.220 (0.483)	-1.423 (0.595)	2.185 (0.956)	1.463 (0.840)	1.432 (0.587)	0.022 (0.218)
b2	0.344 (0.102)	0.621 (0.292)	-0.144 (0.296)	-1.088 (0.849)	-0.089 (0.131)	0.131 (0.211)	
b6	-5.211 (4.970)	-15.063 (8.496)	12.020 (6.792)	-30.000 (21.658)	7.800 (109.598)	-19.047 (10.374)	-2.048 (19.294)
WL_{opt}	-6.732 (12.910)	-35.369 (4.430)	-37.408 (1.613)	-39.691 (17.580)	-19.591 (21.211)	-34.110 (7.046)	-33.474 (44.571)
WL_{tol}	14.578 (21.775)	3.946 (4.046)	2.700 (2.286)	18.005 (25.320)	20.000 (192.506)	15.041 (12.330)	20.000 (166.217)
R^2	0.187	0.237	0.489	0.599	0.451	0.424	0.003
MSR	88.851	181.202	60.401	378.395	70.619	113.458	49.518

TABLE F3 – Photosynthesis (GEP) model parameters and standard error for monocultures in 2012. [Ca= *Carex aquatilis*, Cc=*Calamagrostis canadensis*, Cs=*Campillium stellatum,* Mg= *Myrica gale*, Sw=*Sphagnum warnstorfii*, Ta=*Trichophorum alpinum*, Tc=*Trichophorum cespitosum*, Tn= *Tomenthypnum nitens*].

Parameter	**Ca**	**Cc**	**Cs**	**Mg**	**Sw**	**Ta**	**Tc**	**Tn**
GEPmax	-189.162	-12.622	-0.300	-48.368	-0.138	-44.847	-28.834	-0.298
	(50.484)	(3.103)	(0.050)	(7.472)	(0.048)	(15.821)	(7.379)	(0.044)
a	0.049	4.284		244.379		0.111	30.000	
	(0.011)	(408.345)		(0.000)		(0.053)	(10e27)	
k	1355.530	479.464	1078.887	818.581	2508.699	1126.828	1029.866	578.559
	(426.510)	(324.138)	(326.033)	(299.079)	(1264.644)	(430.398)	(555.723)	(197.094)
T_{opt}	19.439	35.000	35.000	35.000	28.840	35.000	35.000	26.370
	(5.323)	(3.339)	(2.994)	(1.961)	(3.067)	(3.044)	(4.005)	(1.264)
T_{tol}	20.000	15.000	11.530	15.000	20.000	20.000	15.000	8.893
	(5.188)	(3.996)	(2.486)	(2.837)	(4.899)	(5.034)	(5.036)	(1.807)
WL_{opt}	-20.546	-3.000	-3.976	-16.791	-21.166	-4.864	-3.000	-7.978
	(1.431)	(18.002)	(1.890)	(3.205)	(2.451)	(5.177)	(8.559)	(0.356)
WL_{tol}	20.000	30.000	-9.974	30.000	-20.000	20.000	30.000	4.487
	(2.234)	(15.114)	(1.434)	(5.508)	(4.389)	(4.570)	(9.626)	(0.391)
constant	-5.092	-1.093	-1.097	-0.725	-1.161	-1.239	-0.800	-1.772
	(1.581)	(0.700)	(0.178)	(1.282)	(0.240)	(0.504)	(0.928)	(0.245)

Parameter	Ca	Cc	Cs	Mg	Sw	Ta	Tc	Tn
R^2	0.711	0.26	0.781	0.568	0.634	0.584	0.375	0.629
MSR	131.547	23.909	4.071	79.083	4.999	15.144	43.507	7.892

TABLE F4 – Photosynthesis (GEP) model parameters and standard error for polycultures in 2012. [Ca= *Carex aquatilis*, Cc=*Calamagrostis canadensis*, Cs=*Campillium stellatum,* Mg= *Myrica gale*, Sw=*Sphagnum warnstorfii*, Ta=*Trichophorum alpinum*, Tc=*Trichophorum cespitosum*, Tn= *Tomenthypnum nitens*].

Parameter	**Ca.Tn.**	**Mg.Tn.**	**Mg.Cc.**	**Mg.Ta.Tc.**	**Mg.Ca.Sw.**	**Mg.Ta.Tc.Cc.Cs. Tn.**
GEPmax	-229.515 (82.614)	-337.437 (276.098)	-34.572 (6.596)	-59.535 (14.669)	-700.000 (1038.851)	-52.901 (10.535)
a	0.030 (0.014)	0.013 (0.012)	255.635 (24e26)	0.087 (0.025)	0.006 (0.010)	0.081 (0.026)
k	1749.754 (631.812)	1070.743 (261.435)	469.966 (256.326)	606.606 (195.816)	1143.794 (369.869)	452.125 (196.235)
T_{opt}	31.549 (2.796)	30.025 (0.862)	29.340 (1.262)	35.000 (1.797)	35.000 (3.070)	35.000 (2.099)
T_{tol}	20.000 (4.914)	13.259 (1.194)	7.777 (1.873)	15.000 (2.448)	20.000 (3.749)	15.000 (2.867)
WL_{opt}	-18.630 (1.477)	-7.315 (5.655)	-23.040 (3.064)	-3.000 (9.233)	-25.859 (1.612)	-3.000 (6.200)
WL_{tol}	20.000 (2.265)	30.000 (7.667)	20.000 (4.929)	29.304 (6.905)	20.000 (2.350)	26.622 (5.516)
constant	-5.585 (2.036)	-1.686 (0.739)	-1.533 (1.494)	-.629 (0.796)	-2.923 (2.159)	0.054 (1.411)
R^2	0.680	0.809	0.388	0.622	0.668	0.489
MSR	217.086	39.377	122.942	35.982	254.320	106.593

TABLE F5 – Respiration (RESP) model parameters and standard error for monocultures in 2012. [Ca= *Carex aquatilis*, Cc=*Calamagrostis canadensis*, Cs=*Campillium stellatum,* Mg= *Myrica gale*, Sw=*Sphagnum warnstorfii*, Ta=*Trichophorum alpinum*, Tc=*Trichophorum cespitosum*, Tn= *Tomenthypnum nitens*].

Parameter	**Ca**	**Cc**	**Cs**	**Mg**	**Sw**	**Ta**	**Tc**	**Tn**
b1	14.581 (7.067)	9.564 (17.930)	4.702 (1.775)	8.035 (2.777)	4.604 (5.259)	4.020 (1.605)	8.083(8.758)	2.019 (1.040)
b2	0.217 (0.205)	0.100 (0.191)	6.027 (16.898)	0.609 (0.600)	0.174 (0.246)	0.321 (0.304)	0.166 (0.239)	18.333 (430371)
b3	21.580 (4.939)	20.839 (29.835)	18.580 (0.834)	24.652 (1.695)	16.718 (13.393)	24.833 (3.244)	20.938 (11.270)	23.659 (16740)
b4			-2.121 (2.222)		1.241 (0.898)			-3.066 (1.175)
b5			17.145 (1.09e9)			12.883 (3.13e19)		4.339 (955.370)
b6			4.339 (955.370)		12.883 (3.13e19)			17.145 (1.09e9)
b7	0.234 (0.074)	1.162 (0.245)	0.068 (0.022)	0.340 (0.138)	0.346 (0.182)	0.006 (0.004)	-0.147 (0.078)	0.055 (0.008)
constant			-1.566 (73.583)		-28.057 (5.24e18)			-3.976 (1.5e5)
R^2	0.488	0.631	0.331	0.424	0.272	0.25	0.248	0.633

Parameter	Ca	Cc	Cs	Mg	Sw	Ta	Tc	Tn
MSR	0.234 (0.074)	-0.147 (0.078)	0.055 (0.008)	1.162 (0.245)	0.006 (0.004)	0.340 (0.138)	0.346 (0.182)	0.068 (0.022)

TABLE F6 – Respiration (RESP) model parameters and standard error for polycultures in 2012. [Ca= *Carex aquatilis*, Cc=*Calamagrostis canadensis*, Cs=*Campillium stellatum,* Mg= *Myrica gale*, Sw=*Sphagnum warnstorfii*, Ta=*Trichophorum alpinum*, Tc=*Trichophorum cespitosum*, Tn= *Tomenthypnum nitens*].

Parameter	**Ca.Tn.**	**Mg.Tn.**	**Mg.Cc.**	**Mg.Ta.Tc.**	**Mg.Ca.Sw.**	**Mg.Ta.Tc.Cc. Cs.Tn.**	**Bare Peat**
b1	15.000 (13.751)	7.438 (2.767)	13.246 (4.605)	8.058 (3.990)	9.189 (4.222)	9.322 (3.194)	-1.598 (1.156)
b2	0.140 (0.183)	0.663 (0.729)	0.328 (0.243)	0.254 (0.218)	4.030 (18.770)	8.070 (26.566)	-19.856 (2.54e30)
b3	28.299 (9.445)	23.829 (1.951)	23.338 (2.482)	22.031 (4.130)	23.727 (0.618)	22.643 (0.327)	17.669 (2.2e29)
b4							4.464 (0.660)
b5							-1.218 (1.097)
b6							-24.112 (0.917)
b7	0.292 (0.121)	0.741 (0.093)	0.483 (0.118)	.0119 (0.069)	.770 (.145)	.157 (0.097)	
constant	4.132 (9.575)	-0.901 (2.672)	-3.936 (3.768)	1.787 (3.307)	-7.710 (4.867)	0.263 (3.367)	2.018 (0.433)
R^2	0.356	0.655	0.512	0.349	0.523	0.259	0.526

Parameter	Ca.Tn.	Mg.Tn.	Mg.Cc.	Mg.Ta.Tc.	Mg.Ca.Sw.	Mg.Ta.Tc.Cc. Cs.Tn.	Bare Peat
MSR	48.453	21.216	26.662	11.371	94.484	48.826	5.151

APPENDIX G – SUMMARY OF NET SEASONAL FLUXES AND OVERYIELDING

TABLE G1 – Seasonal photosynthesis (GEP), respiration (RESP), methane flux (CH4), net seasonal C flux (NET), Expected flux 1 and 2 (Exp 1, Exp2), non-transgressive overyielding (NTO) and transgressive overyielding (TO) are shown in g C m^{-2} $season^{-1}$ for 2011. [Ca= *Carex aquatilis*, Mg=*Myrica gale*, Tn=*Tomenthypnum nitens*].

Site	Scenario	GEP	RESP	CH4	NET	Exp 1	Exp 2	NTO	TO
Ca	dry	-168.2	237.5	0.26	69.5				
	med	-333.6	416.0	0.32	82.7				
	wet	-441.1	531.9	0.54	91.4				
Mg	dry	-242.8	357.9	0.70	115.8				
	med	-427.1	504.8	0.06	77.7				
	wet	-226.3	301.6	1.01	76.3				
Tn	dry	-44.0	150.8	-0.03	106.8				
	med	-88.3	182.7	-0.14	94.2				
	wet	-142.0	167.7	0.49	26.3				
Ca.Tn.	dry	-416.8	425.0	0.48	8.6	215.3	69.5	-206.6	-60.9
	med	-321.5	253.3	0.20	-68.0	271.7	82.7	-339.7	-150.6
	wet	-594.6	725.5	0.70	131.6	116.8	26.3	14.7	105.3
Mg.Tn.	dry	-224.5	134.4	-0.29	-90.4	94.2	106.8	-184.6	-197.2
	med	-316.7	259.7	-0.46	-57.4	168.6	77.7	-226.0	-135.1
	wet	-408.4	546.4	0.22	138.2	174.5	26.3	-36.3	111.9
Peat	dry	0.0	48.4	-0.06	48.4				
	med	0.0	45.0	-0.01	45.0				
	wet	0.0	42.9	0.03	42.9				

TABLE G2 – Seasonal photosynthesis (GEP), respiration (RESP), methane flux (CH4), net seasonal C flux (NET), Expected flux 1 and 2 (Exp 1, Exp2), non-transgressive overyielding (NTO), and transgressive overyielding (TO) are shown in g C m^{-2} $season^{-1}$ for 2012. [Ca= *Carex aquatilis*, Cc=*Calamagrostis canadensis*, Cs=*Campillium stellatum,* Mg= *Myrica gale*, Sw=*Sphagnum warnstorfii*, Ta=*Trichophorum alpinum*, Tc=*Trichophorum cespitosum*, Tn= *Tomenthypnum nitens*].

Site	Scenario	GEP	RESP	CH4	NET	Exp 1	Exp 2	NTO	TO
Ca	dry	-598.0	438.1	0.92	-159.1				
	med	-915.5	594.0	1.37	-320.1				
	wet	-882.1	601.8	1.52	-278.7				
Cc	dry	-124.4	144.9	0.12	20.6				
	med	-133.6	203.6	0.74	70.7				
	wet	-157.4	197.8	1.57	41.9				
Cs	dry	-45.8	80.7	-0.37	34.5				
	med	-49.1	73.4	-0.31	24.1				
	wet	-230.9	260.1	-0.29	28.9				
Mg	dry	-365.5	461.9	-0.24	96.1				
	med	-376.3	505.5	0.34	129.5				
	wet	-384.7	396.7	1.52	13.5				
Sw	dry	-97.8	145.4	-0.53	47.1				
	med	-57.5	136.2	-0.38	78.4				
	wet	-168.1	195.3	-0.19	26.9				
Ta	dry	-135.7	227.0	-0.47	90.9				
	med	-148.2	223.5	-0.44	74.9				
	wet	-224.2	251.0	-0.38	26.4				
Tc	dry	-171.7	202.9	0.36	31.6				
	med	-187.0	199.4	0.29	12.7				
	wet	-226.5	257.1	2.85	33.5				

Site	Scenario	GEP	RESP	CH4	NET	Exp 1	Exp 2	NTO	TO
Tn	dry	-66.8	143.4	-0.19	76.4				
	med	-101.0	194.4	-0.06	93.4				
	wet	-177.4	224.6	0.24	47.5				
Ca.Tn.	dry	-884.9	693.9	1.39	-189.7	-323.2	-159.1	133.5	-30.6
	med	-874.1	672.5	1.31	-200.3	-23.2	-320.1	-177.1	119.8
	wet	-960.4	750.0	1.32	-209.1	-325.9	-278.7	116.8	69.6
Mg.Tn.	dry	-151.3	203.8	-0.10	52.4	44.9	76.4	7.4	-24.0
	med	-381.7	441.3	0.40	60.0	220.5	93.4	-160.5	-33.4
	wet	-604.7	609.9	1.10	6.4	39.1	13.5	-32.7	-7.1
Mg.Cc.	dry	-319.2	239.1	-0.51	-80.6	56.2	20.6	-136.8	-101.3
	med	-317.6	274.0	-0.28	-43.8	93.0	70.7	-136.8	-114.6
	wet	-278.0	426.3	-0.69	147.7	40.4	13.5	107.3	134.2
Mg.Ca.	dry	-658.8	491.9	0.96	-166.0	-18.8	-159.1	-147.2	-7.0
Sw.	med	-904.9	831.1	0.63	-73.2	-152.2	-320.1	79.0	246.9
	wet	-731.2	834.6	0.89	104.3	-43.7	-278.7	148.0	383.0
Mg.Ta.Tc.	dry	-326.7	321.6	-0.68	-5.9	86.7	31.6	-92.5	-37.4
	med	-250.4	269.2	0.85	19.7	31.0	12.7	-11.4	6.9
	wet	-263.7	260.6	2.29	-0.8	19.9	13.5	-20.7	-14.3
Mg.Ta.Tc.	dry	-175.3	251.5	-0.25	76.0	135.1	20.6	-59.1	55.3
Cc.Cs.Tn.	med	-349.3	384.4	0.15	35.3	143.8	12.7	-108.5	22.6
	wet	-412.3	328.5	0.83	-83.0	75.4	13.5	-158.4	-96.5
Peat	dry	0.0	140.7	-0.10	140.6				
	med	0.0	109.9	-0.08	109.8				
	wet	0.0	60.7	-0.03	60.7				

APPENDIX H – PRS™ PROBE NUTRIENT CONTENT (2012)

TABLE H1 – Average nutrient supply rate (ug/10 cm^2/burial length) of four Plant Root Simulators (PRS™) per plot in 2012. [Ca= *Carex aquatilis*, Cc=*Calamagrostis canadensis*, Cs=*Campillium stellatum*, Mg= *Myrica gale,* Sw=*Sphagnum warnstorfii*, Ta=*Trichophorum alpinum*, Tc=*Trichophorum cespitosum*, Tn= *Tomenthypnum nitens,* n.m.= Not measured].

Site	Block	Total N	NO3-N	NH4-N	Ca	Mg	K	P	Fe	Mn	Cu	Zn	B	S	Pb	Al	Cd
Ca	1	5.78	3.26	2.52	2965.26	347.99	14.21	0.04	9.86	4.53	0.21	0.71	0.82	568.61	0.02	22.48	0.11
	3	6.94	2.50	4.44	2400.96	379.74	20.90	0.28	12.91	1.56	0.08	0.02	1.43	254.03	0.00	43.48	0.06
	4	8.96	2.23	6.73	2260.25	429.54	20.09	0.10	36.27	4.43	0.12	0.22	1.82	319.39	0.00	27.83	0.16
Cc	1	33.44	30.08	3.36	2728.73	317.36	18.00	0.00	9.59	3.70	0.10	0.58	2.08	365.68	0.00	37.36	0.07
	3	100.21	94.26	5.96	2686.64	337.12	27.56	0.00	16.39	3.21	0.07	0.44	1.98	489.65	0.00	40.84	0.02
	4	10.52	6.09	4.43	2477.01	456.70	16.50	0.00	118.97	5.94	0.14	0.38	1.98	107.74	0.00	24.47	0.09
Cs	1	53.29	50.65	2.64	2927.30	411.53	23.79	0.00	8.65	7.07	0.12	0.34	2.24	465.25	0.00	23.44	0.06
	3	86.91	82.44	4.47	2680.64	315.53	22.88	0.02	11.97	3.63	0.16	0.43	1.64	536.61	0.05	38.21	0.08
	4	14.02	7.65	6.37	2692.49	367.08	15.21	0.00	80.90	8.14	0.17	1.18	1.71	405.56	0.00	20.84	0.12
	1	49.04	45.08	3.96	2811.76	364.02	22.91	0.00	23.01	9.68	0.08	0.51	1.34	201.86	0.08	20.94	0.08
Mg	3	n.m.	n.m.	n.m.	n.m.	n.m.	n.m.	n.m.	n.m.	n.m.	n.m.	n.m.	n.m.	n.m.	n.m.	n.m.	n.m.
	4	17.04	5.80	11.2	2544.29	480.62	18.37	0.02	68.61	11.1	0.12	0.24	2.53	45.99	0.00	21.26	0.12

Site	Block	Total N	NO3-N	NH4-N	Ca	Mg	K	P	Fe	Mn	Cu	Zn	B	S	Pb	Al	Cd
Sw	1	65.06	61.96	3.11	2771.92	344.10	19.70	0.00	4.36	5.73	0.09	0.46	1.56	632.96	0.00	22.86	0.14
	3	110.16	104.57	5.59	2379.71	334.43	41.29	0.09	12.39	1.87	0.07	0.47	1.85	271.03	0.00	46.97	0.06
	4	12.08	7.25	4.83	2508.89	393.09	15.83	0.00	51.97	6.78	0.19	0.66	2.35	660.89	0.00	29.22	0.09
Ta	1	76.99	73.00	3.99	2606.75	290.16	26.70	0.00	9.59	3.27	0.14	0.81	1.73	631.53	0.00	27.87	0.07
	3	97.03	90.27	6.76	2588.93	347.76	28.14	0.09	11.48	3.38	0.18	2.08	0.89	649.65	0.00	22.33	0.11
	4	9.87	1.60	8.27	2403.48	467.69	20.20	0.00	64.17	4.79	0.12	0.63	2.34	66.19	0.00	32.13	0.10
Tc	1	10.11	7.20	2.91	2822.56	360.08	10.13	0.06	14.08	3.53	0.06	0.57	1.94	609.64	0.00	24.28	0.08
	3	51.14	48.07	3.07	2692.79	345.63	16.82	0.00	14.30	3.64	0.18	0.43	1.37	614.21	0.03	28.09	0.04
	4	5.93	2.57	3.37	2407.00	336.65	14.96	0.00	47.92	2.62	0.03	1.57	1.37	99.80	0.01	21.10	0.26
Tn	1	93.99	91.88	2.11	2802.69	383.49	13.65	0.53	5.28	3.99	0.07	0.24	1.27	529.84	0.00	21.67	0.04
	3	46.34	43.88	2.46	2327.41	330.25	36.57	0.00	13.90	2.76	0.07	0.06	0.88	258.47	0.00	51.42	0.08
	4	10.47	2.27	8.20	2558.45	500.08	24.08	0.20	85.52	5.40	0.71	0.23	3.42	39.61	0.00	36.73	0.11
Ca.Tn.	1	11.58	5.36	6.22	2986.47	346.26	18.50	0.54	6.32	7.08	0.18	0.24	3.25	365.13	0.00	38.40	0.03
	3	21.17	15.37	5.81	2465.95	385.83	16.59	1.06	30.55	2.57	0.10	0.04	0.81	340.74	0.01	26.09	0.04
	4	9.49	3.68	5.81	2528.93	450.74	18.17	0.49	60.20	4.37	0.18	0.34	1.65	117.69	0.00	23.67	0.10
Mg.Tn.	1	195.12	191.75	3.38	2762.51	324.65	20.46	0.00	9.69	6.20	0.21	0.64	1.38	467.68	0.00	27.76	0.11
	3	40.39	35.91	4.48	2591.47	349.65	23.30	0.00	24.98	2.91	0.15	0.32	1.39	509.54	0.00	31.24	0.12
	4	8.46	3.20	5.26	2444.08	429.61	20.80	0.87	47.53	3.15	0.17	0.31	1.20	36.29	0.00	20.52	0.08

Site	Block	Total N	NO3-N	NH4-N	Ca	Mg	K	P	Fe	Mn	Cu	Zn	B	S	Pb	Al	Cd
Mg.Cc.	1	57.37	52.61	4.77	2541.17	297.45	21.00	0.00	6.25	6.13	0.04	0.83	3.15	469.46	0.00	37.71	0.22
	3	54.39	49.60	4.79	2656.07	414.77	26.05	0.08	33.61	5.00	0.05	0.40	1.20	184.38	0.00	31.96	0.06
	4	64.17	58.80	5.37	2762.24	466.92	40.74	0.22	17.82	2.59	0.22	0.44	2.11	138.01	0.00	55.47	0.09
Mg.Ca.Sw.	1	32.41	25.13	7.28	2583.25	312.30	47.29	0.12	3.37	2.48	0.01	1.35	1.83	322.89	0.00	41.88	0.14
	3	66.29	61.75	4.54	2404.01	375.16	23.98	0.02	8.64	1.80	0.10	0.07	2.54	306.27	0.00	66.47	0.05
	4	8.51	3.02	5.50	2472.80	455.37	14.36	0.20	96.18	6.13	0.08	2.03	1.62	45.14	0.00	22.07	0.07
Mg.Ta.Tc.	1	100.99	96.08	4.91	2760.86	294.92	18.23	0.00	7.20	5.66	0.14	1.38	0.76	319.91	0.00	32.48	0.08
	3	33.78	27.45	6.34	2572.59	402.17	20.18	0.78	18.08	1.89	0.01	0.45	1.34	317.52	0.00	36.49	0.06
	4	10.48	5.02	5.46	2516.99	429.37	21.89	0.00	80.15	5.39	0.07	2.28	2.17	141.45	0.00	25.77	0.08
Mg.Ta.Tc.	1	17.49	11.16	6.33	2682.36	329.86	16.29	0.01	6.91	5.87	0.13	0.65	2.71	463.59	0.00	42.67	0.08
Cc.Cs.Tn.	3	69.58	65.82	3.76	2735.74	366.66	21.46	0.00	28.79	2.95	0.17	1.37	1.86	546.13	0.00	32.33	0.10
	4	8.88	3.33	5.56	2274.82	347.04	20.74	0.12	58.72	4.51	0.10	21.7	1.12	97.05	0.04	17.99	0.04