7-20-2016 12:00 AM

Ecosystem Level Effects of Climate Change on Northern Peatlands

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Graduate Program in Biology
A thesis submitted in partial fulfillment of the requirements for the degree in Doctor of Philosophy

Recommended Citation
Dieleman, Catherine M., "Ecosystem Level Effects of Climate Change on Northern Peatlands" (2016). *Electronic Thesis and Dissertation Repository*. 4030.
https://ir.lib.uwo.ca/etd/4030

Abstract

Northern peatlands are the world's most efficient terrestrial ecosystems at storing carbon. The effects of global climate change are expected to be intensified in high latitude regions of the northern hemisphere, where peatlands are a dominant landscape feature. Accordingly, there is concern that climate change will change peatlands from carbon sinks into carbon sources. In order to better understand the impacts of climate change on peatland ecosystems, the research presented in this dissertation focuses on several mesocosm experiments conducted to develop a better understanding of the interactive effects of three key climate change stressors (increased atmospheric CO_2, increased temperature, decreased water table elevation) on northern peatland vegetation structure and carbon cycling functions. Experimental findings include observations that temperatures between 4 and 8°C above ambient conditions triggered a plant community restructuring event, supporting the expansion of graminoids at the expense of *Sphagnum* mosses. This change in plant community was associated with an increase in dissolved organic carbon (DOC) concentration and lability, characteristics that indicate enhanced carbon release and a threat to northern peatland carbon stores. These findings were extended through further analysis to determine that differences in plant community structure were mechanistically linked to changes in carbon cycling functions through the introduction of microbial priming-like effects. Specifically, rooting growth forms increased belowground DOC lability, stimulating microbial activity and increasing respired CO_2 rates — likely through the introduction of simple root exudates. These findings were then placed into the broader context of northern peatland climate change research using stable state theory as a framework to clarify the key factors that threaten peatland stability, point towards disturbance thresholds, and provide insights on the short- and long-term impacts of state shifts on northern peatland carbon uptake and storage.

Keywords

Aboveground-belowground linkages, carbon cycling, dissolved organic carbon, ecosystem stability, EEMs, graminoids, plant growth form, *Sphagnum* moss, $SUVA_{254}$.

Co-Authorship Statement

For all co-authored work presented in this dissertation, the author order convention is first name is lead author, following authors in order of contribution, with last author as anchor/senior author.

A version of Chapter 2 was published in *Global Change Biology*[1] with Dr. Brain A. Branfireun (BB), Dr. James W. McLaughlin (JM), and Dr. Zoë Lindo (ZL). The original experimental design, field site selection, field sampling and laboratory experimental maintenance and sampling were by ZL and BB with input from JM, who facilitated the sampling from a long-term field site maintained by the Ontario Ministry of Natural Resources and Forestry. At the outset of my doctorial degree I was granted oversight of this experiment, and assumed responsibility for the maintenance of the experiment, plant species identification, porewater sampling collection, data analysis, and initial manuscript development. ZL and BB made significant contributions to data interpretation, presentation, and manuscript writing.

A version of Chapter 3 is published in *Biogeochemistry*[2] with ZL, JM, Aaron E. Craig, and BB. These data are from the same experiment as described above. Litterbag-derived decomposition that is included in this chapter were generated and provided by ZL, who was significantly assisted by Asma Asemaninejad. A.E. Craig contributed to initial sample collection as part of an undergraduate thesis project, which formed the initial conceptual basis of this chapter and contributed data that preceded my involvement in the experiment. I was responsible for protocol development, monthly sample collection and analysis, data analysis and interpretation, and preparation of the manuscript with input on data interpretation and manuscript preparation from BB and ZL.

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[1] Dieleman, CM, Branfireun, BA, McLaughlin, JW, Lindo, Z. 2015. Climate change drives a shift in peatland ecosystem plant community: Implications for ecosystem function and stability. *Global Change Biology* 21: 388-395.

[2] Dieleman, CM, Lindo, Z, McLaughlin, JW, Craig, AE, Branfireun, BA. 2016. Climate change effects on peatland decomposition and porewater dissolved organic carbon biogeochemistry. *Biogeochemistry*1-12.

A version of Chapter 4 has been submitted to the *Plant and Soil*[3] with BB and ZL. I conceived the experimental hypotheses and design, conducted field sampling, maintained the experiment, collected and analyzed physical samples, conducted data analysis and wrote the manuscript with editorial input from BB and ZL.

A version of Chapter 5 is being prepared for submission with BB and ZL as co-authors. BB and ZL developed the general concept as the basis of peatland experiments described above. I pursued the development of the idea into a unifying framework for this dissertation, and executed the research associated with the development of the more broad review of available information on peatland stable states. Specifically, I led the meta-style analysis within which my own research is contextualized and wrote the manuscript with editorial input from BB and ZL.

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[3] Dieleman, CM, Branfireun, BA, Lindo, Z. Under Review. Northern peatland carbon dynamics driven by plant growth form — evidence of graminoid priming effects. *Plant and Soil*.

Acknowledgments

First of all I would like to sincerely thank my two supervisors Dr. Brian Branfireun and Dr. Zoë Lindo, who have guided me throughout the Ph.D. process with remarkably patience and drive. I have ever been encouraged to dream bigger, to seize every opportunity, and to face seemingly daunting challenges without fear or hesitation. Working alongside them one really does start to believe anything is possible with hard work and a creative mind. I know both Brian and Zoë have worked tirelessly to hone in me a unique skill set that will be priceless in all of my future endeavors, and for that I am forever grateful.

Of course this Ph.D. wouldn't be what it is today without the unconditional support of both the Branfireun and Lindo lab members, current and alumni. The friendship and academic discourse you have all provided at one time or another has just been plain wonderful. I suspect, if closely examined, this document has the 'fingerprints' of each and every one of you, where advice, support, or feedback was provided along the way. This is particularly true for the numerous volunteers that aided in this research project over the years, especially C. Chemali, N. Erampamoorthy, R. Doyle, J. Warner, Z. Moore, C. Carvalhal, N. Chattergoon, and L. Albano. A special thank-you is also due to A. Craig, whose tireless efforts in the Boreal Peat Project and general support of my research made so much possible. I don't want to know how many beers I owe you.

A special thank-you must also be given to my family, both immediate and extended. You have all been so wonderfully excited about my progress and so openly proud when my studies have become published articles. My parents, Rick and Darlene Dieleman, as well as my siblings, Carolynne Jewett (*et al.*), Colleen Wolski (*et al.*), and Daniel Dieleman are due particular recognition for their deep and endless support of my endeavors. You bring new meaning to 'standing on the shoulders of giants' as you are all larger than life in so many ways and an important part of my Ph.D. experience.

To Michael Brookfield, I couldn't have hoped for a better life partner on this journey. In so many tangible ways this accomplishment is as much yours as it is mine. There simply are no words to express how grateful I am you were by my side every step of the way on this adventure.

Table of Contents

List of Tables

List of Figures

List of Appendices

Abbreviations

ANOVA	Analysis of Variance
ANOSIM	Analysis of similarities
AWCD	Average Well Colour Development
BIX	Freshness Index
CH_4	Methane
CO_2	Carbon Dioxide
DOC	Dissolved Organic Carbon
EEMs	Excitation-Emission Matrices
FI	Fluorescence Index
HIX_{EM}	Humification Index
MANOVA	Multivariate Analysis of Variance
PCA	Principle Component Analysis
SOM	Soil Organic Material
$SUVA_{254}$	Specific Ultraviolet Absorbance at Wavelength 254 nm

Chapter 1

1 General Introduction

1.1 Global Climate Change

The International Panel on Climate Change (IPCC), as well as numerous research teams around the globe, has repeatedly reviewed and synthesized thousands of lines of empirical data and sophisticated models at a range of scales to conclude that there is not only clear evidence of rapid climate change, but also that there is clear evidence anthropogenic activities are responsible for altering global climate. The most recent publication by the IPCC (2013) reaffirms that an overall warming of global atmospheric temperatures by 0.3 – 4.8° C above 1986 – 2005 conditions is anticipated by the end of the century. These trends are still being driven dominantly by humanity's ever increasing contributions of CO_2 to the atmosphere via fossil fuel combustion, where atmospheric CO_2 concentrations have increased by 40% above preindustrial levels (IPCC, 2013; Stern and Kaufmann, 2014). These atmospheric CO_2 concentrations have a linear relationship with average global atmospheric temperatures (Allen *et al*., 2009; Gillett *et al*., 2013), with anthropogenic CO_2 emissions alone account for approximately 73% of the current positive change in energy flux measured in 2011 relative to 1750, corresponding with a current global atmospheric warming of 0.85°C from 1880 to 2012 (IPCC, 2013). These changes in CO_2 and temperatures are also predicted to drive altered precipitation patterns. Changes in precipitation are expected to vary regionally; some areas, such as northern temperate regions will experience an increase in annual precipitation, while other areas such as the subtropics are anticipated to experience significant declines (IPCC, 2013; Liu *et al*., 2013). The combined effects of these climate change factors (temperature, atmospheric CO_2, and precipitation) are expected to alter ecosystems around the globe, impacting many important ecosystem structures and functions (Grimm *et al*., 2013). Consequently, determining the individual and interactive effects of these climate change factors on fundamental ecosystem processes has become a research priority for many.

Global climate change is not occurring homogeneously around the Earth. Instead, climate change conditions are already being observed at high latitudes, and are predicted to be intensified in that region (IPCC, 2013; Xia *et al*., 2014). For example, high latitude regions are expected to be warmed by up to 11°C above historical norms by 2100, approximately 7°C more than the anticipated average global warming for that same time (IPCC, 2013). Research by Holland and Bitz (2003) describes this intensified warming in high latitude regions as 'polar amplification'. Specifically, warming in these regions prompts sea-ice loss, decreasing the regional albedo and creating a warming feedback (Holland and Bitz, 2003). Recent empirical data indicates that this intensified warming is already occurring in high latitude systems. For example, polar regions have warmed by 1.18°C in the past 30 years, while the global average warming during this time frame is approximately 0.26°C (IPCC, 2013; Wang and Dillion, 2014). High latitude systems are also expected to have a disproportionate increase in precipitation under future climate conditions, particularly during the winter (IPCC, 2013). However, increased precipitation may not result in an increase in available moisture in ecosystems. Instead, warming conditions are expected to significantly increase evapotranspiration rates in northern regions, potentially causing a significant and persistent water table drawdown in some ecosystems (Roulet *et al*., 1992). Combined, these intensified climate change conditions may cause some high latitude ecosystems to become warmer and drier at a faster rate than many other ecosystems around the globe. Consequently, understanding the cascading effects of climate change on ecosystem structure and function in high latitude ecosystems is a particularly important research priority.

1.2 Northern Peatlands

Of the ecosystems found at high latitudes a particular research focus has been given to northern peatland ecosystems. Northern peatlands are defined as wetlands that accrue or store partially decomposed organic matter known as peat to a depth of at least 40 cm (Warner and Rubec, 1997; Rydin and Jeglum, 2013). The build-up of this organic material makes northern peatlands crucial repositories of terrestrial carbon, as they constitute 3% of the Earth's terrestrial surface but store approximately 30% of the Earth's terrestrial carbon (Gorham, 1991). Unlike tropical peatlands, northern peatlands have low primary productivity, limiting carbon uptake. Instead, the inhibitory effect of the prevailing climate on microbial decomposition processes facilitates carbon accumulation (Laiho, 2006; Wu and Roulet, 2014). The naturally cool, acidic, and saturated soil conditions of northern peatlands are energetically unfavourable reaction conditions for decomposition (Davidson and Janssens, 2006; Laiho, 2006). Accordingly, there is concern that the intensified climatic warming and drying conditions that are anticipated for higher latitude regions will remove these environmental constraints on the decomposition process in northern peatlands, potentially increasing carbon release through decomposition.

Northern peatland vegetation also strongly influences carbon cycling processes. In general, peatlands are dominated by vegetation that produces highly recalcitrant litter that is difficult to decompose, contributing to the aforementioned slow decomposition rates that characterize this ecosystem (Dorrepaal *et al*., 2005). However, different plant species have contrasting effects on carbon cycling processes. To address this researchers have found grouping vegetation by plant growth form particularly effective (Dorrepaal, 2007). These groupings can be done more broadly (vascular, non-vascular) or more narrowly (trees, dwarf shrubs, graminoids, forbs, mosses) (Dorrepaal, 2007; Walker *et al*., 2015). The narrow plant growth form grouping has recently been found to be a particularly effective predictor of decomposition rates, due to the contrasting traits that characterize these growth forms (Ward *et al*., 2015; Walker *et al*., 2016). For example, graminoids are known to produce highly biodegradable litters that enhance decomposition (Dorrepaal *et al*., 2005), while dwarf-shrubs and *Sphagnum* mosses can produce inhibitory compounds that slow decomposition rates (Fenner and Freeman, 2011; Bragazza *et al*., 2013). That said, mechanistic relationships between plant growth form and northern peatland carbon dynamics remain poorly understood, but are considered a current research priority for this ecosystem (Dunn *et al*., 2016).

As peatland vegetation can strongly influence carbon dynamics, changes in plant community structure have also been an area of active research. A suite of studies has demonstrated that northern peatland plant communities are sensitive to climate change stressors, including increased atmospheric CO_2, increased temperatures, and water table drawdown (Weltzin *et al*., 2003; Strack *et al*., 2006; Breeuwer *et al*.,2009; Bragazza *et al*., 2013; Churchill *et al*., 2014; Siegenthaler *et al*., 2014; Gerdol and Brancaleoni, 2015). Mounting evidence indicates the warmer and drier climate change conditions anticipated for northern peatlands will give vascular vegetation a competitive advantage over non-vascular species, such as *Sphagnum* mosses (Weltzin *et al*., 2000; Fenner *et al*., 2007; Bragazza *et al*., 2013). However, key climate change stressors (increased atmospheric CO_2 concentration, increased temperature, water table drawdown) are expected to arise in tandem (IPCC, 2013), with potential interactive effects on peatland plant communities that cannot be anticipated by studying such stressors in isolation. To date, no research has considered the interactive effects of the three main climate change stressors on peatlands plant individual species or plant community structure — a critical knowledge gap to anticipating how important peatland structures will be affected by climate change.

1.3 Northern Peatland Carbon Dynamics

Carbon cycling in northern peatlands, like in any ecosystem, is an emergent ecosystem level process that is produced by numerous small-scale reactions and facilitated by plant and soil interactions (Figure 1.1). Carbon cycling is predominately governed by two core processes: carbon uptake through photosynthesis, and carbon release through microbial decomposition and respiration (Ahlström *et al*., 2015). Aboveground plant material undertakes photosynthesis, incorporating atmospheric CO_2 into both its above- and belowground biomass. This carbon is then transferred to the belowground environment through multiple processes including the deposition and subsequent breakdown of plant litter, the release of plant root exudates, and direct physical leaching from both living and senesced plant biomass (Kalbitz *et al*., 2000; Kögel-Knabner, 2002). Complete mineralization of these plant inputs by the microbial community releases carbon compounds back to the atmosphere as CO_2, completing carbon cycling through both aboveground and belowground components of the peatland ecosystem.

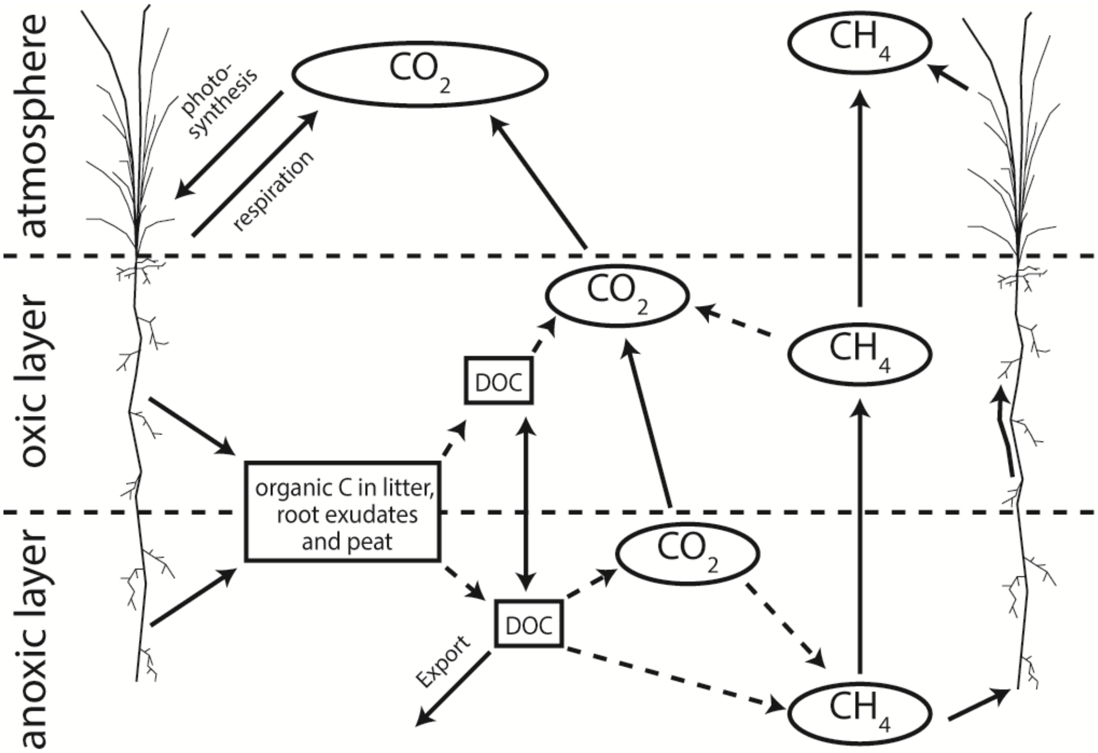

Figure 1.1 Carbon flow patterns through the atmosphere as well as the oxic and anoxic peat layers of northern peatlands. Dashed arrows represent microbially mediated biotic transfers, while solid arrows represent all other biotic and abiotic transfers. The encircled symbols represent the gas phase of carbon cycling, while the boxed symbols represent all other phases. Image adapted from Rydin and Jeglum (2013) and Holden (2005).

Carbon cycling in peatlands is strongly influenced by the waterlogged belowground conditions that characterize this particular ecosystem, rendering methane (CH_4) and dissolved organic carbon (DOC) important components of the peatland carbon cycle in addition to CO_2 (Holden, 2005). For example, the anoxic, highly-reduced conditions that can arise in waterlogged peats are ideal for the production and release of CH_4 (Moore and Dalva, 1993). Consequently, CH_4 alone accounts for 5 – 10% of the carbon cycling in northern peatlands (Koehler *et al*., 2011). Waterlogged, organic-rich peats also support the production of DOC, a carbon pool functionally defined as any suspended organic carbon compound less than 0.45 nm in size (Blodau, 2002; Leenheer and Croué, 2003; Roulet and Moore, 2006). In peatland ecosystems DOC can comprise a notable portion of carbon export, constituting more than 20% (Roulet *et al*., 2007). Carbon dioxide efflux comprises the majority of the remaining northern peatland carbon budget, accounting for approximately 70% (Koehler *et al*., 2011).

1.3.1 Environmental Controls and Climate Change

Carbon cycling processes in peatlands are well established to be strongly regulated by local environmental conditions, particularly temperature and water table position (Limpens *et al*., 2008). Accordingly, climate change induced alterations in these environmental conditions are likely to impact carbon cycling processes; however, the interactive effects of the main climate change variables (increased atmospheric CO_2 concentration, increased temperature, water table drawdown) remains unclear. It is understood that rising temperature conditions can enhance carbon cycling rates by stimulating both microbial and plant metabolic activity in northern peatlands (Davidson and Janssens, 2006; Weltzin *et al*., 2000). For example, under warming conditions peatland porewater DOC concentrations consistently increase as a product of increased microbial extracellular enzyme production and activity (Kane *et al*., 2014), as well as increased belowground plant biomass production and root exudate release (Fenner *et al*., 2007). These same warming conditions also consistently contribute to increased peatland CO_2 and CH_4 release (Moore and Dalva, 1993; Blodau, 2002). In the cases of CO_2 and CH_4, rising temperatures directly stimulates the microbial communities that break down carbon compounds, and consequently enhance the release of CO_2 and CH_4 as metabolic by-products (Yavitt *et al*., 1997).

Like temperature, water table position is also a well-accepted control on carbon cycling processes in northern peatlands (Moore and Dalva, 1993; Blodau *et al*., 2004). Water table strongly influences the availability of energetically favourable electron acceptors used in decomposition processes, such as oxygen (Blodau *et al*., 2004; Limpens *et al*., 2008). Under saturated conditions peat can quickly become anoxic, leading to highly reduced belowground conditions and, consequently, slower decomposition rates. These slower decomposition rates are generally associated with decreased DOC peatland porewater concentrations and slowed CO_2 release (Blodau *et al*., 2004). Some authors suggest that, in addition to providing energetically favourable electron acceptors, more aerobic conditions can increase decomposition rates by promoting the degradation of microbial metabolic inhibitors, such as fatty acids and phenolic compounds (Fenner and Freeman, 2011; Hribljan *et al*., 2013). Other authors contend that aerobic conditions cause a shift in peatland vegetation structure, promoting more vascular species and increasing root exudate and litter production, ultimately increasing DOC production (Strack *et al*., 2008).

Unlike DOC and CO_2, CH_4 release strongly increases under saturated conditions (Moore and Dalva, 1993). Anaerobic peats support the metabolic pathways that produce CH_4 and simultaneously suppresses the activity of microbes that breakdown CH_4 as an energy source, increasing CH_4 release from peatlands (Jakobson *et al*., 1981; Bridgham *et al*., 2013). That said, saturated, anaerobic peats tend to slow overall carbon cycling processes by slowing the production of CO_2 and DOC (Blodau *et al*., 2004; Strack *et al*., 2008), pools that constitute approximately 90% of the carbon exported from northern peatlands (Roulet *et al*., 2007).

1.3.2 The Importance of Dissolved Organic Carbon

Unlike CO_2 and CH_4, the DOC pool contains a complex mixture of different carbon compounds, all of which contribute to and influence peatland carbon cycling. These compounds can range from large, complex, aromatic-ring structures to small, simple, aliphatic chains (Kalbitz *et al.*, 2000; Leenheer and Croué, 2003). Measuring DOC concentrations of porewater in peatlands has been done with relative ease in numerous peatland studies for decades, with values generally ranging from 20 – 60 mg/L (Urban *et al.*, 1989; Waddington and Roulet, 1997; Blodau, 2002; Kane *et al*., 2014). Consideration of DOC characteristics, however, is a relatively new and challenging field of study, but essential to discerning drivers of DOC dynamics in northern peatlands. As identifying all compounds that comprise the DOC pool is still considered unfeasible, bulk characteristics (aromaticity, humification, 'freshness', molecular weight, polarity, functional groups) are commonly used to summarize this complex pool (Olefeldt and Roulet, 2012; Kalbitz *et al*., 2000). Generally peatland DOC is reported as highly aromatic (Tfaily *et al*., 2013), humified carbon (Olefeldt *et al*., 2014), comprised of high molecular weight compounds (Strack *et al*., 2011; Kiikkilä *et al*., 2014), although evidence of low molecular weight, protein-like carbon compounds is also commonly found (Wickland *et al*., 2007). By measuring these bulk DOC characteristics, other important features of the DOC pool can be inferred. For example, by determining whether the dominant DOC source is decomposing plant tissues, decomposing peat, microbial products, or a combination there of can help develop a mechanistic understanding of the factors that enhance DOC production (McKnight *et al*., 2001). We can also infer if the DOC pool is predominantly comprised of labile, biodegradable compounds or recalcitrant, stable compounds to understand rates of DOC breakdown (Kalbitz *et al*., 2003). Thus, by considering DOC characteristics in association with DOC concentration we can develop a full understanding of the factors that govern DOC dynamics, and ultimately peatland carbon cycling.

Dissolved organic carbon characteristics are important because they influence ecosystem structure and function within peatlands, as well as receiving downstream aquatic environments, such as streams and lakes. While DOC characteristics can alter numerous important ecosystem properties including pH (Erlandsson *et al*., 2010), light attenuation (Karlsson *et al*., 2009), and heavy metal transport (Evans *et al*., 2005; French *et al*., 2014), one of its greatest impacts is on microbial communities. Dissolved organic carbon serves as a key energy source for microbes, and in turn influences important microbial community properties like biomass, composition, and enzyme production (Fenchel *et al*., 1998; Allison *et al*., 2010; Blagodatsky *et al*., 2010). That said, relationships between DOC characteristics and microbial communities are, as of yet, relatively poorly understood in the organic soils that characterize peatlands. For example, research in mineral soils has demonstrated that labile, biodegradable DOC inputs, such as root exudates, can stimulate or ‘prime’ the microbial community to decompose the stable organic fraction of the soil matrix and enhance CO_2 release (Kuzyakov et al., 2001); however, few studies have considered this DOC-microbial relationship in northern peatlands, despite the implications for carbon storage.

1.4 Northern Peatland Stable State Shifts

Like carbon cycling, the overall state of any ecosystem is inherently an emergent ecosystem level characteristic, produced by the fundamental structures and functions that define that ecosystem. Naturally, a central concern of climate change impacts on northern peatlands is a fundamental change in the ecosystem structures and functions that characterize this ecosystem, such as the plant community composition and carbon cycling dynamics. Such a change in any ecosystem’s core properties can be described, by definition, as an ecosystem state shift (Beisner, 2003; DeAngelis, 2012). These ecosystem state shifts can be easily conceptualized using the ‘ball-in-cup’ analogy commonly used in this field of study (see Beisner, 2003). When a ball is placed inside a cup, the ball can be disturbed, causing it to roll within the cup. Once the disturbance is removed the ball rolls downhill and returns to the cup’s center. Only with a consistent or intense disturbance will the ball actually exit the cup. In the context of ecosystem stable states the cup represents a potential ecosystem stable state for a given ecosystem, while the ball represents the current state of that ecosystem. (Figure 1.2) (Beisner, 2003). A given ecosystem can be moved both within and among ecosystem states by disturbances, such as climate change (Beisner, 2003). If these disturbances are sufficient the ecosystem will exit the cup by crossing what is termed a critical threshold. A critical threshold is defined as a unit of disturbance eliciting a relatively disproportionate effect on ecosystem structure and function (Andersen *et al*., 2009; Brook *et al*., 2013). Once the critical threshold is crossed a new positive feedback loop forms, promoting the establishment of new core ecosystem structures and functions (Andersen *et al*., 2009).

Building evidence in the literature demonstrates northern peatlands most likely have multiple stable ecosystem states (Eppinga *et al*., 2004; Granath et al., 2010; Scheffer *et al*., 2012); implying rapid transition between these states may be possible under climate change disturbances. However, research applying stable state theory to northern peatlands is highly limited, rendering many important variables needed to predict and prevent state shifts undefined.

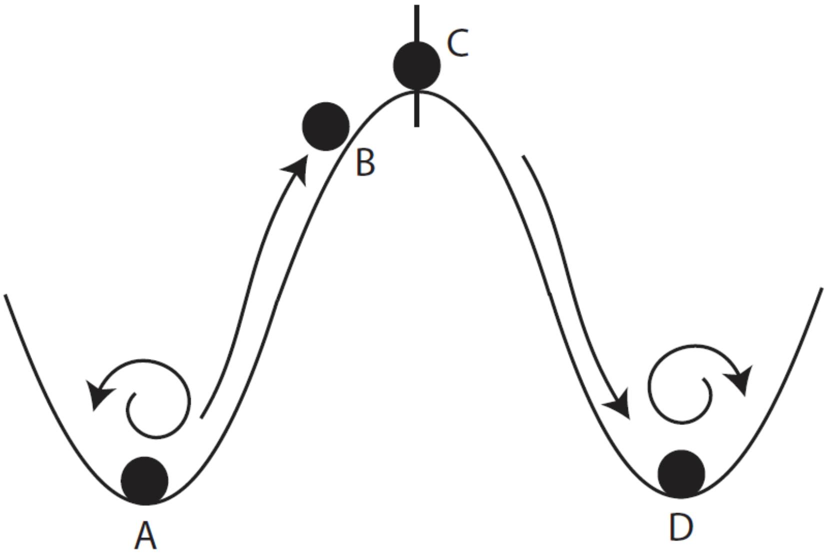

Figure 1.2 A graphical depiction of multiple ecosystem stable states using the ball-in-cup analogy. The ball represents the current state of the ecosystem, while the two cups represent two different stable states. Position A depicts an ecosystem in one state, wherein its structure and core functions are stabilized by a positive feedback loop. In position B a forcing factor causes the ecosystem to approach a critical threshold as depicted in position C. In position D the ecosystem has entered a new state, wherein its core structure and ecosystem functions are stabilized by a new and unique positive feedback loop.

1.5 Rational and Objectives

Northern peatlands are unique ecosystems, providing critical carbon storage functions. In order to anticipate the long- and short-term stability of this ecosystem and its core functions, it is critical to consider how multiple interacting climate change factors will alter the structures and functions that define this ecosystem, especially plant community structures and carbon cycling functions. Accordingly, the main focus of this thesis was to understand the interactive effects of climate change stressors on northern peatland plant community structure, ecosystem function and stability and to determine the mechanisms propagating these changes. The specific research objectives in the chapters of this thesis were to:

1) Determine the interactive effects of climate change stressors on aboveground peatland plant community structure and ecosystem stability (Chapter 2)

2) Ascertain the interactive effects of climate change stressors on belowground peatland carbon dynamics (Chapter 3)

3) Identify plant growth form-specific effects on belowground peatland carbon dynamics (Chapter 4)

4) Outline peatland potential alternative stable states, key disturbance factors, and the long- and short-term consequences for carbon dynamics (Chapter 5)

In my second chapter I determined how aboveground northern plant communities in a nutrient-poor fen peatland can respond to multiple interacting climate change stressors. This work focuses specifically on evidence of climate change induced plant community restructuring, ecosystem stability loss, and ecosystem critical thresholds under future environmental conditions that bracket IPCC (2013) predictions for the next century. Specifically I monitored the quarter annual changes in plant species' abundances/percent cover as a direct measure of plant community change, as well as belowground pH as a measure of ecosystem stability.

In my third chapter I build on the work of the previous chapter to discern the interactive effects of multiple climate change stressors on belowground carbon dynamics in a northern poor fen peatland. In doing so I consider the importance of direct (temperature, water table, atmospheric CO_2) and indirect (plant community shifts) effects of climate change stressors on carbon dynamics by quantifying monthly changes in DOC quantity and quality and reporting quarter annual changes in decay rates.

In my fourth chapter I determined the governing role of common plant growth forms (*Sphagnum* mosses, graminoids) on belowground carbon dynamics in a northern fen mesocosm environment. The results of my second and third chapters indicated changes in aboveground plant community structure may drive changes in belowground carbon dynamics. Here, I conducted a separate experiment to elucidate mechanistically how common peatland plant growth forms can influence belowground carbon cycling processes. In doing so I quantified DOC quantity and quality, microbial metabolic activity, decomposition rates as well as respired CO_2 flux to document the cascading changes common peatland plant growth forms can create in the belowground environment.

In my fifth and final data chapter I place my empirical research in the broader context of peatland stable state literature by conducting a meta-style analysis of research to date. Specifically, I reviewed relevant peatland literature to identify the main drivers of peatland stable state shifts, the positive feedback loops associated with each driver that promotes the state shift, as well as the current understanding of driver specific critical thresholds in northern peatlands. In doing so I was able to develop a conceptual model of potential peatland stable states and the allogenic factors that shift peatland ecosystems between these states. To understand the long- and short-term consequences of these ecosystem state shifts for northern peatlands, I also compared year round, continuous CO_2 flux studies conducted at a variety of different ecosystems representing potential end point stable states for northern peatlands.

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Chapter 2

2 Climate change drives a shift in peatland ecosystem plant community: Implications for ecosystem function and stability[4]

2.1 Introduction

Boreal peatlands provide globally important ecosystem functions such as the regulation and maintenance of the hydrological cycle, and carbon storage (Limpens *et al*., 2008). In particular, the long-term accumulation of slowly decomposing plant material (peat) allows these ecosystems to store approximately 30% of the Earth's terrestrial soil carbon while only comprising approximately 3% of the Earth's land area (Gorham, 1991; Clymo *et al*., 1998). The main mechanism of peat accumulation is slow decomposition rates regulated by saturated, anaerobic soils, and cool climate conditions associated with the relatively northern latitudes where peatlands are dominantly found (Yavitt *et al*., 1997). In northern peatlands, *Sphagnum* mosses are fundamental to this carbon sequestration and are key to the stability and resilience of this system (Turetsky *et al*., 2012). *Sphagnum* spp. comprises up to 90% of peat (Kuhry, 1997; Turetsky, 2003; Hájek *et al*., 2011) because the recalcitrant and antibacterial nature of *Sphagnum* inhibits decomposition (Painter, 1991; Kroken *et al*., 1996), particularly when compared to the relatively decomposable tissues of vascular plants (Hobbie, 1996). This accumulation of peat changes the local hydrology and porewater biogeochemistry, making environmental conditions generally more advantageous for *Sphagnum*; as a result, *Sphagnum* is often considered an ecosystem engineer (van Breemen, 1995). The importance of the *Sphagnum* dominated peatland vegetation community is consistently highlighted in the literature as a key component of many ecosystem functions, including carbon storage (Weltzin *et al*., 2000; Limpens *et al*., 2008; Bragazza *et al*., 2013; Kuiper *et al*., 2013). Thus, changes in peatland plant community composition, especially ones that reduce

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[4] Published as: Dieleman, CM, Branfireun, BA, McLaughlin, JW, Lindo, Z. 2015. Climate change drives a shift in peatland ecosystem plant community: Implications for ecosystem function and stability. *Global Change Biology* 21: 388-395.

Sphagnum dominance in favour of vascular vegetation, particularly graminoids, are anticipated to have significant effects on carbon storage.

Anthropogenic-driven climate change (*i.e.* post-industrial elevated temperature and atmospheric CO_2 concentrations) has the potential to significantly change northern ecosystems, particularly peatlands (IPCC, 2007). Fenner *et al.* (2007) proposed that increased temperature and atmospheric CO_2 concentrations will increase vascular plant growth leading to a decrease in *Sphagnum* spp. cover while stimulating belowground microbial activity through increased labile carbon in vascular plant root exudates, and a release from the inhibitory polyphenol compounds exuded by the *Sphagnum* spp. (Fenner and Freeman, 2011, Bragazza *et al.*, 2013). The increased abundance of vascular plants and microbial activity is subsequently expected to alter soil nutrient content and pH conditions to further reinforce this increase in vascular plants. Further consequences of this change are increased decomposition rates, increased CO_2 release, and changes to dissolved organic carbon (DOC) quality. Forecasted elevated temperatures at northern latitudes are also anticipated to increase evapotranspiration rates, lowering the water table relative to the ground surface (Rouse *et al*., 1997). This lower water table would further favour vascular plants and potentially challenge *Sphagnum* spp., which rely on capillarity for moisture supply, further reinforcing changes in biogeochemical processes (Bragazza and Iacumin, 2009; Eppinga *et al*., 2009; Fenner and Freeman, 2011; Jassey *et al*., 2013).

Peatlands are not a singular type of ecosystem, but range from more groundwater-connected, minerotrophic and graminoid-dominated rich fens, to purely precipitation-fed, ombrotrophic and moss-dominated bogs. The intermediate stage(s) between a rich fen and a bog is generally described as a poor fen (Kuhry *et al*., 1993). A poor fen, often considered a successional precursor to a more ombrotrophic bog, will become increasingly dominated by *Sphagnum* mosses over time, which in turn will develop the peat profile and move toward hydrologic isolation (van Breemen, 1995; Klinger, 1996). During the poor fen stage, the presence of *Sphagnum* mosses and the physico-chemical conditions that they promote will tend to lower species diversity relative to more mineral-rich peatlands (Vitt *et al.*, 1995). Weltzin *et al.* (2000) demonstrated that changing climate conditions, in particular elevated temperature, could competitively advantage dominant rich fen species and revert a poor fen to a rich fen-like state with high graminoid abundance. From a carbon perspective, this reversion of a poor fen to a rich fen squanders the carbon accumulating potential of the system as rich fens do not accumulate carbon at the same rate as a bog (Thormann *et al.*, 1999). As such, understanding how poor fens will respond to climate change pressures is central to anticipating changes in carbon sequestration in peatlands as a whole.

Turetsky *et al.* (2012) identified temperature, water table position, and atmospheric CO_2 concentrations as important interactive climate change stressors that can alter the resilience and stability of peatlands. Losses in the key individual species (*e.g. Sphagnum* mosses) can lead to further shifts in vegetation communities and the weakening of key ecosystem functions such as carbon accumulation. As such, it is important to understand both individual species responses and the community-level properties in order to identify mechanisms that may govern key feedbacks, and be indicators of (impending) state shift (Weltzin *et al*., 2000). These shifts are foreshadowed by increased variance in ecosystem parameters (Carpenter and Brock, 2006), and demonstrated non-linear responses in abundance or growth of constituent species (Guttal and Jayaprakash, 2008). For instance, de Mazancourt *et al.* (2013) suggested that reductions in plant species richness, concomitant with changes to overall community level biomass are warning signs of ecosystem instability. In peatlands, the direction and magnitude of responses of vascular plant species and *Sphagnum* mosses to environmental changes are the indicators of a shift in plant community composition and ecosystem functions (Dise, 2009). There are no studies, to the best of my knowledge, that have fully addressed the interactive effects of the main climate change factors (changes in temperature, CO_2 and water table position) that affect peatland vegetation communities identified by Turetsky *et al.* (2012), despite the potentially dramatic alteration of functions identified by this important paper that would accompany a transition from a moss-dominated to a vascular-plant dominated ecosystem.

The overall objective of the work presented here was to experimentally quantify the impacts of elevated temperature and CO_2, and changes in water table position on a poor fen peatland plant community. Specifically, I seek to determine if climate change factors produce a shift in plant community composition, with an increase in abundance of graminoids and a decrease in abundance of *Sphagnum* spp., accompanied by indicators of instability that would suggest a trajectory toward a shift in stable state.

2.2 Methods

2.2.1 Study Site

Intact vegetated peat monoliths were taken from a 4.5 ha, poor fen near White River, Ontario, Canada (48°21’N, 85°21’W) that is part of a long-term experimental site (White River Experimental Watershed Study) maintained by the Ontario Ministry of Natural Resources - Ontario Forest Research Institute (see Webster and McLaughlin, 2010 for detailed description). The 26-year annual average precipitation and temperature is 980 mm and 2.1°C respectively (Webster and McLaughlin, 2010). The poor fen is dominated by a typical assemblage of vegetation including *Sphagnum* mosses, ericaceous shrubs, and conifers. The shrub community generally consists of *Chamaedaphne calyculata* (L.) Moench (leatherleaf), *Rhododendron groenlandicum* (Oeder) Kron & Judd (Labrador tea), and *Andromeda polifolia* L (bog rosemary). The dominant trees are *Picea mariana* (Mill.) B.S.P. (black spruce) and *Larix laricina* (Du Roi) K. Koch (tamarack).

2.2.2 Experimental Design

In August 2012, 100 intact cylindrical peat monoliths (30 cm diameter × 35 cm deep) were collected from the study peatland. The sampling locations were selected such that each mesocosm would include a representative species assemblage, including mosses, vascular groundcovers, small ericaceous shrubs (with at least one *C. calyculata* as it is the dominant shrub in these systems) and graminoids. All efforts were made to sample from uniform lawns dominated by *Sphagnum magellanicum* Brid.; other *Sphagnum* species that occurred in the system (<20%) include *S. angustifolium*, *S. fallax*, *S. cuspidatum,* and *S. fuscum*. Graminoids at the time of sampling were not an obvious feature of the plant community but included *Carex magellanica* Lam. (boreal bog sedge) and *Carex disperma* Dewey (softleaf sedge).

The peat monoliths were carefully cut using a 40 cm narrow-blade saw, lifted and placed into individual 5 gallon pails (30.5 cm diameter, 18.93 L). After returning the mesocosms to the University of Western Ontario's Biotron Institute for Experimental Climate Change, a tapered hole was drilled 2 cm from the bottom of each mesocosm, and a 25 cm length of perforated, 16 mm diameter PVC pipe was inserted into the bottom peat to serve as a bottom drain. A ½ inch threaded ABS barbed fitting was screwed into the sidewall, coupling with the drain. A 30 cm length of clear vinyl tubing was then connected to this fitting to control water level in the mesocosm (discussed below) and for water sampling. These mesocosms were then all placed in a staging greenhouse under ambient growing conditions for 10 weeks to stabilize under the new environmental conditions.

In December 2012, 12 randomly selected mesocosms were destructively sampled for initial above- and belowground biomass, peat chemistry, and biodiversity studies that are not reported here. Four additional mesocosms were set aside due to visually apparent disturbance that was considered unrepresentative. The remaining 84 mesocosms were numbered and randomly divided among six environmentally controlled greenhouses (6.1 m × 3.4 m × 4.7 m = 97.5 m^2) under a full factorial experimental design (3 × temperature, 2 × CO_2, and 2 × water table treatments, × 7 replicates) (see Appendix A, Figure A.1, Figure A.2). The six experimental greenhouses are south facing, and located on the roof of the five-story Biotron building, flanked on either side by staging greenhouses to ensure even temperature and solar radiation regimes in the experimental systems. Relative humidity, temperature, and atmospheric CO_2 concentrations were automatically controlled and monitored using a computerized environmental control system (ARGUS Control Systems Ltd., White Rock, BC, Canada). Across all treatments over the entire experiment, relative humidity was set to a minimum of 60%, and all treatments received ambient solar radiation, with uniform midday shading to control daytime temperature fluctuations from solar gain. Is important to note this experimental design utilized a mesocosm approach under laboratory conditions, and consequently has various inherent caveats and limitations to interpretation that are outlined in full in Chapter 6, Section 6.3.

TEMPERATURE*:* The experimental greenhouses were run with two temperature programs, depending on time of year. From May 1 to October 31 (growing season) temperature in the ambient greenhouse pair were programmed to temperature set points equal to the 5-year running mean daily maximum and minimum temperatures in London, Ontario (and the corresponding timing of those averages) with a constant ramp between set point temperatures. The +4°C and +8°C greenhouses were programmed in an identical fashion, but with the respective offsets. As the experimental greenhouses used had limited cooling capacity the growing season ambient temperatures were defined using London, Ontario average growing season temperatures. Consequently, the growing season ambient temperature treatment in our study was approximately 5°C above the poor fen study site where study material was collected (see Appendix A Figure A.3). As the infrastructure in the experimental greenhouses cannot be reliably operated at <10°C, the experimental greenhouse temperatures were set at a constant temperatures between November 1 to April 30. The ambient greenhouse pair was set to 11.5°C, which is the mean growing season temperature for the experimental poor fen from which the samples were taken. The +4°C and +8°C greenhouse pairs were programmed in an identical fashion, but with the respective offsets.

CARBON DIOXIDE: In one of each of the temperature treatments, the CO_2 concentrations in experimental greenhouse air reflected the ambient exterior air in the vicinity of the building (mean = 427.8 ppm, S.D. 3.55) and were not adjusted in any way experimentally. In the second of each of the temperature treatments, the greenhouse CO_2 concentrations were set at 750 ppm. This additional CO_2 was supplied by a compressed CO_2 source, and the elevated CO_2 condition was maintained dynamically by the environmental control system. The CO_2 regulating system was calibrated weekly against a known gas standard.

WATER TABLE: In each of the experimental greenhouses, seven replicate mesocosms were randomly selected for a higher water table treatment (~5 cm from the peat surface) with the remaining seven subjected to a lower water table treatment (~25 cm from the peat surface). The two water table treatments were held constant at their respective levels throughout the experiment to isolate the main effects that could be confounded by interactions among temperature, plant community changes and evapotranspiration. Water levels were set in each of the mesocosms by fixing the end of the clear vinyl drain tube at the appropriate level on the outside of the mesocosm. This allowed for visual inspection of the water table position in the mesocosm, and prevented over-wetting beyond the target water table level as excess water would simply drain until the level in the mesocosm was level with the overflow tube. Water was added to all of the mesocosms evenly over the course of the experiment. To mimic the total water and nutrient delivery in rainfall and to not artificially disadvantage *Sphagnum* through ionic or pH effects, 700 ml of Rudolph's Solution (diluted by a factor of 4 and adjusted to pH 5.8; see Faubert and Rochefort, 2002) was added evenly over the vegetation twice weekly. On alternate days, small additions of reverse osmosis water were made at the edge of the mesocosms if the water level in the sight tube was below the target.

2.2.3 Vegetation and pH

Vegetation surveys were performed initially at the end of the recovery period (December 2012), and every 4 months for 1 year to capture one full growing season (peak = April 2013 – August 2013). Plant species were identified and enumerated in all of the mesocosms every four months. Plant identification was based on Newmaster *et al.* (1997) and Legasy (1995). For *Sphagnum* spp. and *Carex disperma* Dewey (softleaf sedge) that could not be counted individually because of density or size, percent cover was recorded using an adapted Braun-Blanquet scale as recommended by Rochefort *et al.* (2013). Water was sampled monthly from the drain tubes in each mesocosm, and pH was measured almost immediately after sampling using a calibrated standard pH glass electrode.

2.2.4 Data Analysis

A three-way, repeated measures analysis of variance (RM-ANOVA) with a Tukey *post hoc* test was used to test for changes in absolute and percent change in plant species abundance and for species richness under the different experimental conditions (Statistica 7, StatSoft. Inc., 2004). As increased variance in ecosystem parameters and nonlinear responses in plant species abundance are considered precursors to shifts in ecosystem stability, the variance of species abundance and pH measures were calculated from within-treatment replicates. At the community level, I quantified total variability (or dissimilarity) for main experimental effects using SIMPER analysis in Primer 5 (Primer-E Ltd., 2001). This test calculates a community compositional similarity coefficient within and between mesocosm treatments based on species abundance data using the methods described by Bray and Curtis (1957). Plant community compositional data (11 dominant plant species) were analyzed using principle components analysis (PCA) in Statistica 7.0. Case scores for the first two principal components were analyzed with an ANOVA for the main effects of temperature, CO_2 concentration, and water table level, and by regression for pH to determine species-specific response to different variables. Factor coordinates based on species correlations were used to interpret the PCA. Product-moment correlations were performed on plant abundance at each time point. Analysis of similarities (ANOSIM) was performed on total plant community composition among treatments.

2.3 Results

A total of 16 plant species were observed across all mesocosms and sampling times (see Appendix A, Table A.1). There was no initial difference in richness (Dec. 2012 average = 7.3 ± 0.1 (S.E.) species) across mesocosms in all treatments, however it increased over the summer season (Aug. 2013 average = 7.8 ± 0.2 species; $F_{3,216} = 6.02$, $P < 0.001$). No significant relationship was found among species richness and any of the main climate change factors (temperature: $F_{2,72} = 2.64$, $P = 0.079$; water table position: $F_{1,72} = 1.27$, $P = 0.264$; CO_2: $F_{1,72} = 2.14$, $P = 0.148$), or their interactions.

There was no difference in *Sphagnum* spp. cover between the ambient and +4°C treatments; however, it decreased significantly at +8°C (temperature: $F_{2,72} = 5.49$, $P = 0.006$), which intensified over time (temperature × time: $F_{4,144} = 2.63$, $P = 0.037$) (Figure 2.1a). *Carex disperma* increased in cover over time in all treatments, however the +8°C treatment showed a much greater increase in cover over time (temperature: $F_{2,72} = 5.49$, $P = 0.006$; temperature × time: $F_{6,216} = 3.35$, $P = 0.004$) (Figure 2.1b). Although mesocosms were allocated to the experimental treatments using a fully randomized scheme, the mesocosms in the +4°C and +8°C treatments had, on average, a higher initial abundance of the large graminoid *Carex magellanica* than ambient. Despite this, a significant pattern over time is clear. *Carex magellanica* abundance was unchanged under ambient temperatures, but increased significantly by 8 months under both +4°C and +8°C (temperature: $F_{2,72} = 8.64$, $P < 0.001$; temperature × time: $F_{6,216} = 6.38$, $P < 0.001$) (Figure 2.2a). Interactive effects of the experimental treatments on the dominant plant species were only observed for *C. magellanica*; this species significantly increased under elevated temperature (+8°C) and elevated CO_2 conditions ($F_{6,216} = 2.76$, $P = 0.013$) during the first 8 months of the experiment (T_0 – T_8 change in abundance $F_{2,72} = 5.28$, $P = 0.007$) resulting in 15 times greater abundance than under ambient temperature and CO_2 (Figure 2.2b). *Sphagnum* was significantly negatively correlated with the abundance of *C. disperma* at all sampling times (T_4: $R = 0.753$, $P < 0.001$; T_8: $R = 0.753$, $P < 0.001$; T_{12}: $R = 0.600$, $P < 0.001$), but had no relationship with *C. magellanica* abundance.

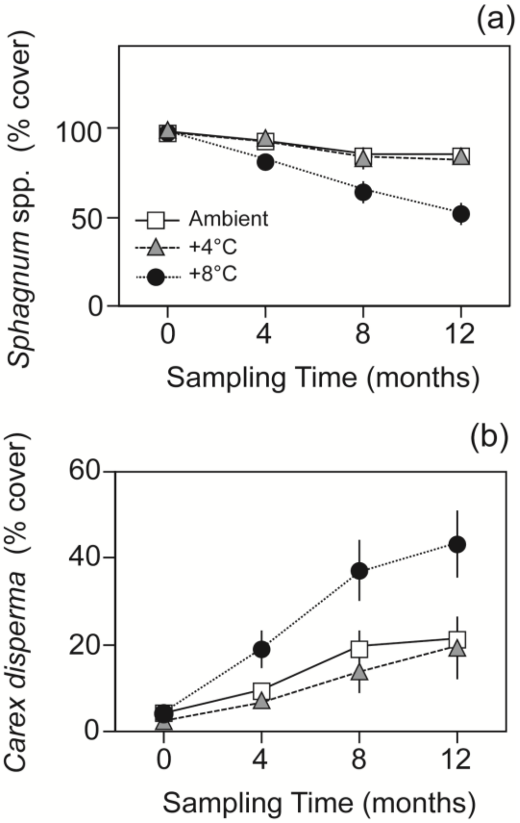

Figure 2.1 Changes in peatland vegetation (a) *Sphagnum* spp. and (b) *Carex disperma* percent cover (mean ± SE) under elevated temperature conditions from December 2012 (T_0) to December 2013 (T_{12}) in experimental mesocosms.

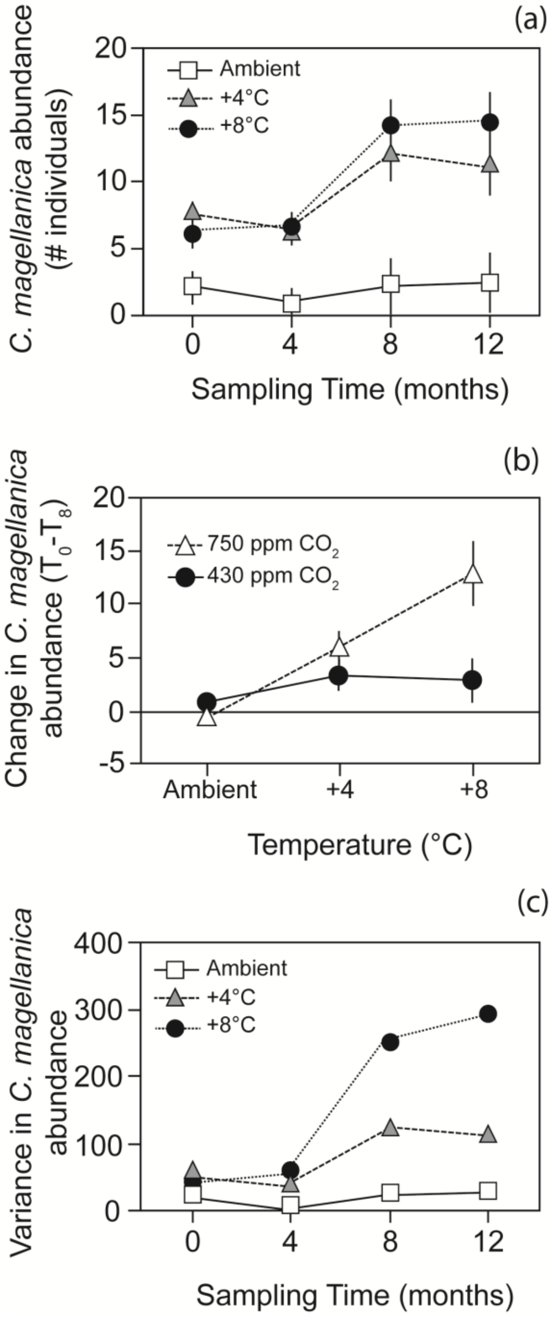

Figure 2.2 (a) *Carex magellanica* abundance (mean ± SE) under elevated temperature conditions from December 2012 (T_0) to December 2013 (T_{12}) in experimental mesocosms, (b) change in *C. magellanica* abundance over the first 8 months (T_0–T_8) under elevated temperature and CO_2 conditions, and (c) variance in *C. magellanica* abundance under elevated temperature in experimental mesocosms over the duration of the experiment.

Water table position and CO_2 concentration also showed main and interactive effects but only for the less abundant species. The ericaceous shrub *Kalmia polifolia* Wangenh (bog laurel) significantly increased in abundance under lower water table conditions ($F_{3,216}$ = 8.50, $P < 0.001$). *Rhododendron groenlandicum* increased in abundance under ambient (temperature and CO_2) and lower water table conditions ($F_{6,216}$ = 3.78, $P = 0.001$). Elevated CO_2 conditions decreased *Vaccinium myrtilloides* Michx (blueberry) ($F_{6,216}$ = 2.81, $P = 0.012$) abundance at 8 months, but only under ambient temperature. *Chamaedaphne calyculata* increased by one or two individuals under elevated temperature by the end of the experiment ($F_{6,216}$ = 4.50, $P < 0.001$).

The first two PCA components explained 31% of the variance (16.6% and 14.7%, respectively). Case scores of PC 1 were significantly related to pH ($R^2 = 0.242$, $P < 0.001$), whereas PC 2 was significantly related to temperature ($F_{2,79}$ = 4.04, $P = 0.021$) (Figure 2.3). Species driving PC 1 were *Sphagnum* spp. (0.64), *C. magellanica* (0.64) associated with acidic conditions, and *C. disperma* (0.66) associated with higher pH conditions. For PC 2, *A. polifolia* (0.65), *V. myrtilloides* (0.46), and *Lycopodiella inundata* (L.) Holub (northern bog club moss) (0.44) were associated with ambient temperatures, while *Vaccinium oxycoccos* L. (bog cranberry) (-0.52) was associated with elevated (+8°C) temperatures. ANOSIM revealed significant differences in community composition between water table positions (Global $R = 0.027$, $P = 0.042$) and temperature (Global $R = 0.091$, $P = 0.010$) whereby communities under ambient temperature were significantly different from +4 and +8°C (pairwise comparisons P = 0.030, 0.020, respectively).

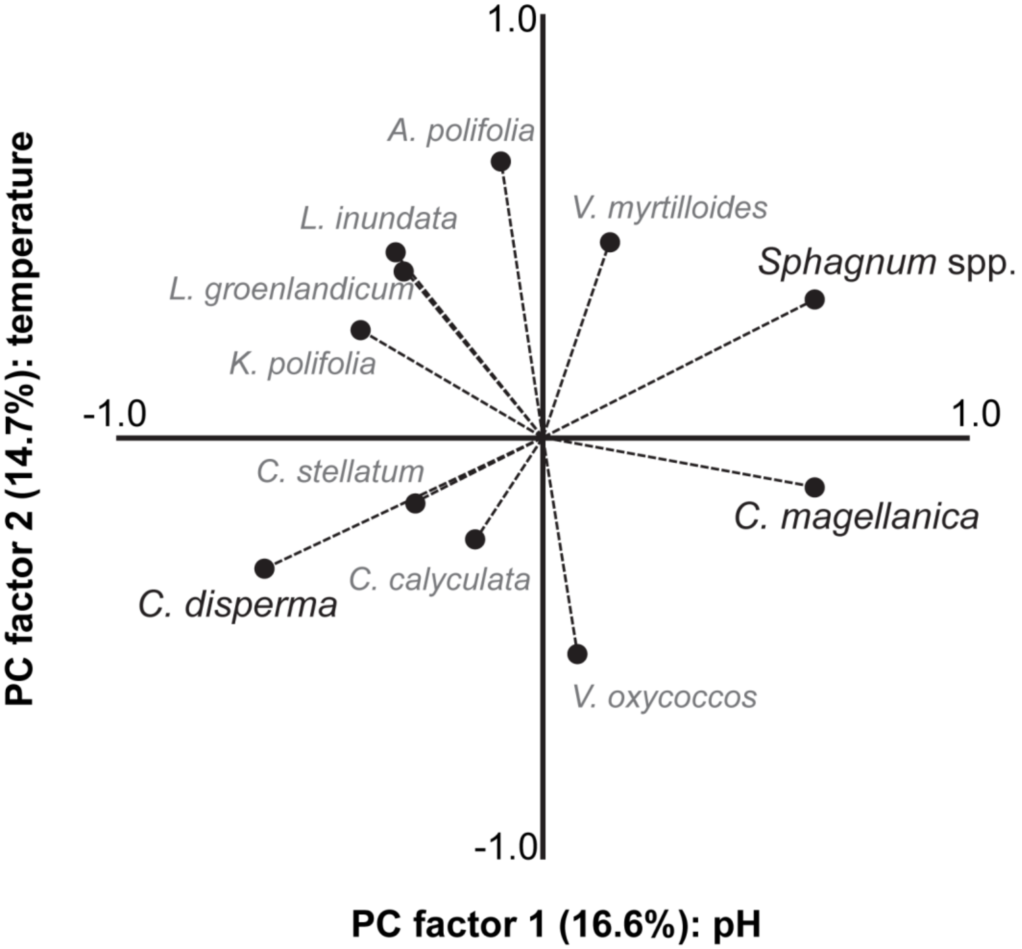

Figure 2.3 Plot of the first and second principal components (PC) with percent explained variation for poor fen plant community based on abundance of 11 species collected from experimental mesocosms under elevated temperature, elevated CO_2, and water table manipulation. Positive PC 1 axis loading is associated with low pH conditions; positive axis loadings for PC 2 are ambient temperature conditions, while negative axis 2 loadings are associated with +8°C conditions.

2.3.1 System Variance

Variance in *C. magellanica* abundance increased after 8 months in elevated temperature treatments (Figure 2.2c). The SIMPER test corroborated greater total community variability (dissimilarity) within +8°C elevated temperature mesocosms (ambient = 38%, +4°C = 35%, +8°C = 46% dissimilar). As expected for poor fen peat, the pH of all of the experimental mesocosms at all times was acidic (4.2 – 4.6), however; pH was higher under ambient temperatures than other treatments ($F_{2,69} = 25.74$, $P < 0.001$). Over time, there was an increase in variance in pH across the experimental system, increasing from 0.03 early in the experiment to 0.24 at the end of 12 months.

2.4 Discussion

Boreal peatlands depend on the presence of *Sphagnum* spp. for carbon accumulation and ecosystem-level hydrological and biogeochemical stability. Particularly at the poor fen stage of peatland development, *Sphagnum* promotes a positive feedback that inhibits decomposition and reinforces the likely successional trajectory toward a stable, ombrotrophic bog. Temperature, moisture, and CO_2 concentrations have been identified as direct controls on *Sphagnum* productivity (Turetsky *et al.*, 2012). Here I demonstrate that elevated temperature is the main driver of *Sphagnum* decline; I posit that this is due to the loss of competitive advantage over vascular plant species (graminoids). While drought and elevated atmospheric CO_2 conditions have been shown to affect the structure and productivity of peatlands plant communities (Heijmans *et al.*, 2002; Stack and Waddington, 2007), temperature effects are often identified as the dominant driver of change (Weltzin *et al*., 2000; Breeuwer *et al.*, 2008; Heijmans *et al*., 2013). I found that temperature increases of +4°C or higher, particularly when combined with elevated atmospheric CO_2 concentrations, stimulated *C. magellanica*. For the shorter, denser *C. disperma,* elevated temperatures between +4°C and +8°C were the tipping point, and the expansion of this species is believed to be the driver of *Sphagnum* decline in my experiment due to competitive shading effects.

In peatlands, a shift toward a more shrub-dominated system driven by warmer and drier conditions has been well-explored in the literature (Weltzin *et al*., 2000; Oechel *et al*., 2000; Breeuwer *et al*., 2009; Molau, 2010; Bragazza *et al*., 2013). I measured only minor changes in the shrub species abundances; however I would not expect to have observed significant changes in these slower growing/propagating plants over the course of one experimental growing season. Other studies have considered changes in peatland vegetation abundance (Breeuwer *et al*., 2010), percent cover (Ballantyne *et al*., 2013) and biomass (Weltzin *et al*., 2000) in response to environmental change, but few consider measures of species richness. Generally, changes in plant species richness would be expected to occur over longer timescales (Menéndez *et al*., 2006; Suttle *et al*., 2007). The experimental design here is short-term and precludes dispersal and colonisation events that would influence natural patterns of species richness.

Experimental climate conditions created three trajectories of the peatland plant community: ambient conditions maintained *Sphagnum* dominance, but elevated temperature pushed the system towards the expansion of two different graminoid communities; one of which co-occurred with *Sphagnum*, while the other displaced it. Primarily through porewater acidification and the promotion of anoxia under waterlogged conditions, *Sphagnum* spp. maintain a competitive advantage over rooted species under nominal conditions (Malmer *et al*., 1994, 2003; van Breeman, 1995). Intermediate temperature increases combined with elevated CO_2 conditions benefitted the sparser, taller *C. magellanica* with little effect on the underlying *Sphagnum*. The *C. magellanica* trajectory was associated with more acidic conditions in the elevated temperature and CO_2 treatment, indicating that the favourable temperature and CO_2 conditions for the vascular *C. magellanica* outweighed the inhibitory effects of acidic pH. Under the +8˚C temperature, the densely growing *C. disperma* displaced *Sphagnum*, and was accompanied by a slight shift toward less acidic porewaters, suggesting a stronger trajectory toward a more intermediate fen-like state. Most surprising, this was observed within a single growing season, indicating a latent seed-bank and/or rapid rhizomal expansion under favourable environmental conditions. Fenner *et al*. (2007) is one of the few other studies that has quantified the interactive and synergistic effects of elevated temperature and CO_2 in simplified peatland plant communities, and found that the percent cover of *Carex* increased most under this interactive treatment. I confirm these findings here in a natural plant community assemblage, and importantly demonstrate that the species of *Carex* that becomes dominant is very important in determining whether *Sphagnum* cover can be maintained. The ecosystem-level implications of a shift away from a *Sphagnum*-dominated to a *Carex*-dominated peatland are significant. Significant increases in *Carex* abundance are expected to substantially increase belowground biomass as well as the nutrient and carbon contributions made to the soil matrix from the rhizosphere (Hobbie, 1996; Fenner *et al*., 2007; Bragazza *et al*., 2013; Jassey *et al*., 2013). This increase in nutrient and labile carbon quantity in both the litter and root exudates to the soil matrix will further promote vascular plants, promote microbial growth and activity, and potentially lead to a degradation of the carbon stock (van Breeman, 1995; Berendse *et al*., 2001; Larmola *et al*., 2013).

Competition for light and moisture are the main variables that can tip the competitive advantage from mosses to vascular plants, but these dynamics are expected to play-out over decades (Turetsky *et al.*, 2012). While water table was manipulated in this experiment, bi-weekly top watering and fertilization precluded moisture from being a limiting factor for *Sphagnum* maintenance and growth. Rather, my main effect variables of elevated temperature and CO_2 enrichment gave vascular plants a competitive advantage, rather than disadvantaging *Sphagnum*. Under forecasted climate change conditions, I would expect these competitive factors to be at play simultaneously, further increasing ecosystem instability and movement toward a stable-state shift. Increased variance in porewater pH, graminoid abundance, and overall plant community composition measured here further suggested incipient ecosystem instability and possible state transition.

It is important that my observed shift in plant community structure is interpreted with some caution. Due to infrastructure constraints the ambient temperature treatment employed throughout the growing season followed London, Ontario norms, approximately 5°C above the sample source site’s growing season norms. Thus, my experimental temperature treatments (ambient, +4°C above ambient, +8°C above ambient) could be described as +5°C above source site, +9°C above source site, and +

13°C above source site respectively. This interpretation indicates northern peatlands found at high latitudes may have a high resilience to future climate change conditions, with only the most extreme anticipated climate scenarios likely to generate warming sufficient to prompt a state transition (IPCC, 2007). That said many *Sphagnum* moss dominated peatlands similar in structure to the White River source peatland have ambient growing season temperatures comparable to London, Ontario. I posit that this subset of northern peatlands is likely to undergo plant community restructuring events that more closely reflect the trends presented here.

2.4.1 Significance

Identifying and understanding critical thresholds in ecosystems is an important knowledge in ecological sciences (Moritz and Agudo, 2013; Sutherland *et al*., 2013). Despite the obvious interest in identifying these thresholds, the challenges and lack of experimental control in field studies obfuscate changes in key variables (Moritz and Agudo, 2013). Under highly controlled environmental conditions such as those described here, I was able to identify the key climate change drivers of plant community composition in a poor fen peatland, and importantly identify threshold temperature changes that led to shifts away from *Sphagnum* toward graminoid dominance. The very rapid shift in *Sphagnum* and graminoid abundance observed in this study suggest that ecosystem shifts in peatlands may occur much more quickly than previously thought once temperature thresholds are exceeded, particularly in transitional peatland types like poor fens.

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Chapter 3

3 Climate change effects on peatland decomposition and porewater dissolved organic carbon biogeochemistry[5]

3.1 Introduction

For peatlands in northern regions, a cool, wet climate, acidic, nutrient-poor soils, low ecosystem productivity, and low decomposition rates support high carbon storage (Yavitt *et al.*, 1997; Rydin and Jeglum, 2013). In fact, northern peatlands are the most efficient terrestrial ecosystem at storing carbon per unit area in the world (Parish *et al*., 2008), currently accounting for approximately 30% of the Earth's terrestrial carbon (Gorham, 1991). Changes to the carbon balance of northern peatlands is likely under global climate change, where elevated temperature and changes to the water balance drive enhanced decomposition, increasing carbon loss as CO_2, CH_4 and dissolved organic carbon (DOC) (Roulet *et al.*, 1992; Rouse *et al*., 1997) — potentially driving these systems toward net carbon sources, rather than sinks. Although considerable effort has gone into understanding the processes controlling the exchange of CO_2 and CH_4 between peatlands and the atmosphere, slightly less effort has been committed to exploring the role of porewater DOC production and export in the carbon balance of peatlands, particularly in the context of future climates. Loss of DOC, while dependent on porewater DOC concentration and hydrologic conditions (e.g. water runoff), may comprise up to 20% of a peatland carbon balance (Koehler *et al*., 2011). As both decomposition processes releasing DOC into porewater and changes in hydrologic conditions within peatlands are expected to change under future climate scenarios, understanding how global change factors affects DOC production will be a critical part of understanding peatland carbon budgets.

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[5] Published As: Dieleman, CM, Lindo, Z, McLaughlin, JW, Craig, AE, Branfireun, BA. 2016. Climate change effects on peatland decomposition and porewater dissolved organic carbon biogeochemistry. *Biogeochemistry* 1-12.

Dissolved organic carbon compounds in peatlands are derived primarily from the decomposition of peat and plant tissue, but also through contributions from plant root exudates and microbial activity, such as extracellular enzymes (Kalbitz *et al*., 2000). The production of DOC through all these processes is dependent on environmental variables such as temperature and water table (Moore and Dalva, 2001; Clark *et al*., 2009). Elevated temperature, in particular, has been shown to be an important driver of increased porewater DOC concentrations, through increased aboveground litter production and leaching, as well as increased microbial extracellular enzymes production and activity belowground (Fenner *et al*., 2007; Kane *et al*., 2014). Warming, as well as increased atmospheric $CO_{2,}$ also enhances the production of root exudates and increases belowground plant root biomass, contributing to increased porewater DOC concentrations (Fenner *et al*., 2007). Peatland water table position is another important control on DOC production (Worrall *et al*., 2006; Clark *et al*., 2009) where lower water tables and more aerobic conditions in surface peats are linked to increased DOC production (Worrall *et al*., 2006) through enhanced decomposition processes. Increased aerobic conditions can also promote vegetation growth, resulting in increased litter and root exudates that add to the DOC pool (Strack *et al*., 2008).

The chemical composition of carbon compounds in peatland DOC ranges from simple, aliphatic carbon chains to complex, aromatic ring structures (Kalbitz *et al*., 2003),with simple compounds often derived from microbial material, litter leachate or root exudates, while complex compounds are predominately produced via decomposition processes. The relative proportion of these ‘labile’ versus ‘recalcitrant’ DOC compounds (sometimes referred to high and low DOC quality, respectively) is a critical component of the net carbon balance of northern peatland ecosystems under climate change. For instance, the quality of DOC determines whether DOC acts as a terminal electron acceptor for biogeochemical reactions, as a substrate for fermentative processes such as methanogenesis, or as a source of energy to both *in situ* and *ex situ* microbial metabolism (Marschner and Kalbitz, 2003; Tfaily *et al*., 2013). Functionally, quality defines the role DOC has in biogeochemical cycles, affecting decomposition process pathways and rates, and determining the available basal energy in an ecosystem — but characterisation of DOC quality has proven to be challenging.

DOC quality has been explored using techniques such as column-based fractionation or gas chromatography-mass spectrometry (GC-MS) that elucidate the source of DOC (e.g. plant or microbial) and the stage of decomposition. Generally, these techniques have shown that peatland DOC is dominated by high molecular weight carbon compounds (Strack *et al*., 2011; Kiikkilä *et al*., 2014) rich in lignin, phenols, and polysaccharides (Kracht and Gleixner, 2000; Biester *et al*., 2014; Treat *et al*., 2014). However, these methods are limited by challenging preparation, instrumentation, and interpretation of results. An alternative is specific UV absorbance (SUVA) and fluorescence spectroscopy. Specific UV absorbance at 254 nm ($SUVA_{254}$) is a proxy for DOC aromaticity and has proven to be a widely adopted and straightforward measure (Weishaar *et al*., 2003). Fluorescence spectroscopy, conversely, uses excitation-emission spectra to make sophisticated but indirect measures of DOC quality (Cory and McKnight, 2005). Ratios of specific excitation-emission values and other matrix derivatives have been compellingly linked to the source of DOC, freshness of the compounds, and degree of humification (Fellman *et al*., 2010); information that can indicate significant changes in carbon quality in peatland ecosystems.

When applied to peatland systems studies have linked a decrease in $SUVA_{254}$ values with inputs of more labile, lower molecular weight DOC from root exudates or microbial sources under elevated temperatures due to increasing photosynthesis, metabolic rates, and/or microbial turnover (Kane *et al*., 2014; Lou *et al*., 2014). More aerobic peat conditions, conversely, are associated with higher $SUVA_{254}$ indicating an increase in the aromatic fraction of DOC (Höll *et al*., 2009; Kiikkilä *et al*., 2014). In the case of emission-excitation matrices (EEMs) and their derivatives, peatland DOC has consistently and perhaps unsurprisingly been described as having a highly humified and recalcitrant character of terrestrial origin (Wickland *et al*., 2007; Olefeldt *et al*., 2014). However, to the best of my knowledge, only a limited number of studies have applied either of these techniques to specific investigations of climate change factors on peatland DOC quality (but see Kane *et al*., 2014 and Lou *et al*., 2014), and fewer still have considered the interacting effects of such factors.

Here I determine the independent and interactive effects of temperature, atmospheric CO_2 concentrations, and water table position on peat decomposition rates as well as DOC quantity and quality using intact, vegetated peat mesocosms and a replicated, factorial experimental design. As my treatment mesocosms transition from a *Sphagnum* moss to a graminoid dominated community during my study (see Dieleman *et al*., 2015) increased vegetative inputs from litter and root exudates were possible. Accordingly, I wanted to determine if interacting climate change factors affecting intact mesocosms enhance decomposition rates to increase DOC concentrations and recalcitrance, or alternatively if these conditions increase labile DOC production. Based on the current literature I predicted that rising temperatures, elevated atmospheric CO_2, and lowered water table conditions would interact to synergistically increase DOC production. I also anticipated that the strong influence of lowered water table conditions and rising temperatures on decomposition rates would render DOC more recalcitrant than that produced under ambient conditions. With such information, we can better define the trajectory of peatland DOC concentrations as well as the changes in its composition that may affect its biogeochemical properties and ultimately peatland ecosystem stability.

3.2 Methods

3.2.1 Mesocosms and Experiment Treatments

Intact, vegetated cylindrical peat monoliths (30 cm diameter × 35 cm depth) were collected in August 2012 from a *Sphagnum*-dominated nutrient-poor fen near White River, Ontario, Canada (48°21’N, 85°21’W) to create the 84 peatland mesocosms used in this experiment. Dieleman *et al*. (2015) describe the specifics of the source site, the experimental design, and the vegetative community, including the observed shift in plant composition. Briefly, the mesocosms (19 litres, 30 cm diameter, 35 cm tall) were fitted with a 2 cm ABS barbed fitting port attached to a 16 mm diameter, 25 cm long perforated PVC pipe drain to collect DOC samples and monitor water table levels. In the University of Western Ontario’s Biotron Environmental Climate Change Research Centre, seven replicates of each low (25 cm below the peat surface) and high (5 cm below the peat surface) water table treatment mesocosms were randomly placed in six environmentally controlled, state-of-the-art greenhouses at three temperature (ambient, ambient +4°C, ambient +8°C) and two atmospheric CO_2 conditions (430 ppm, 750 ppm). The greenhouses were divided into two replicates of the temperature treatment, one set paired with ambient atmospheric CO_2 conditions and the second paired with elevated atmospheric CO_2 conditions. The specific temperature and CO_2 treatments were selected to bracket IPCC (2013) predictions for higher latitude northern ecosystems in the next 50 to 100 years, while the water table treatments reflect the predictions of Roulet *et al*. (1992) for northern peatlands.

Temperature, atmospheric CO_2 concentrations, and relative humidity were regulated using an automated environmental control system (ARGUS Control Systems Ltd., White Rock, BC, Canada), while water table conditions were manually maintained. Relative humidity was regulated to no less than 60%. The temperature conditions were maintained under two regimes corresponding to the growing and dormant seasons. During the growing season (May 1 – October 31), ambient temperatures matched the hourly five-year average daily temperatures for the region. During the dormant period (November 1 – April 31) the experimental greenhouse temperatures were limited to temperatures >10°C due to logistics pertaining to the infrastructure, so ambient temperatures were maintained at the average growing season temperature for the region, approximately 11.5 °C, while the other experimental treatments were maintained at the same +4°C and +8°C offsets. The two different water table treatments were held constant to avoid any confounding influence of temperature and/or changes in aboveground vegetation via simulated rain events biweekly at the individual mesocosm surface, and supplemental water additions below the moss layer as needed. The individual mesocosms were randomly relocated within their individual greenhouse on a monthly basis, and transferred to a different greenhouse with replicate conditions every six months to address both microclimate and greenhouse effects (Hurlbert, 1984).

3.2.2 Decomposition

Decomposition rates were quantified via mass loss of *Sphagnum* litter collected from destructively sampled mesocosms prior to the experiment. Three replicate decomposition bags (10 cm × 7 cm with 1 mm mesh) were inserted 10 cm below the peat surface in four of the seven mesocosms under each experimental combination (48 treatments; 144

litterbags in total) at the beginning of the experiment in December 2012. Each litterbag contained ~30 g wet weight homogenized peat (~3 g dry weight); initial absolute dry weights were determined for every litterbag. One litterbag from each mesocosm was retrieved every four months (4, 8, 12 months) over the course of the experiment. Collected bags were oven-dried for 72 hours at 60°C, reweighed and mass loss (%) calculated relative to the initial dry mass.

3.2.3 Dissolved Organic Carbon Sampling and Analysis

Porewater samples were collected monthly from the ports at the bottom of the mesocosms for all 84 mesocosms (7 replicate mesocosms for each treatment) from December 2012 to December 2013. These monthly samples were assessed for changes in carbon quantity, measured as DOC in mg L^{-1}, and carbon quality, measured as specific ultraviolet absorbance at a wavelength of 254 nm ($SUVA_{254}$) in L mg C^{-1} m^{-1}. To further quantify changes in carbon quality additional samples for excitation-emission matrix (EEMs) fluorescence spectroscopy analysis were collected at the experiment end in December 2013. All porewater samples were collected using pre-cleaned tubing and a peristaltic pump to collect 200 mL samples that were stored (maximum of 48 hours) in 500 mL Nalgene^{TM} bottles in the dark at 4°C. All samples were then filtered using ashed glass filters (pore size 0.5 μm) and split into 50 mL HDPE bottles for DOC samples, and 20 mL glass vials for $SUVA_{254}$ samples as well as for EEMs samples when applicable. All samples were promptly stored in the dark at 4°C until processed.

Dissolved organic carbon concentration was determined using an iTOC Aurora 1030 (OI Analytical, College Station, TX, USA) via the persulfate wet oxidation method. The measurement of $SUVA_{254}$ used methods modified from Weishaar *et al*. (2003). Absorbance was measured at $\lambda = 254$ nm using 200 μL sample aliquots in UV transparent 96-well plates read on a Spectramax® M2 spectrophotometer in cm^{-1}. Absorbance values were then converted to m^{-1} and divided by the DOC concentration of the sample to determine the $SUVA_{254}$ value. All absorbance values were corrected for potential Fe interference from low Fe concentrations associated with added simulated rainwater. Fe absorbance at $\lambda = 254$ nm were calculated based on Weishaar *et al*. (2003) published extinction coefficient of 0.08 and maximum Fe concentrations (0.114 – 1.058 mg/L) in December 2013. Therefore, the $SUVA_{254}$ may be considered conservative as in some cases they may be overcorrected for Fe interference.

Fluorescence excitation-emission matrices for DOC samples from December 2013 were used to calculate informative optical indices that are indicative of changes in carbon quality; here I focus on three common indices: the fluorescence index (FI), the humification index (HIX_{EM}) and the 'freshness' index (BIX) (Fellman *et al.*, 2010). Fluorescence excitation and emission was measured on a Horiba Aqualog® spectrofluorometer with a xenon lamp in the Watershed Hydrology Group Laboratory at McMaster University. The excitation wavelengths ranged from 240 to 600 nm with 10 nm increments and the emission wavelengths ranged from 210 to 620 nm with 3.27 nm increments, all with an integration time of 0.5 s. All samples were diluted 1:4 with ultra-pure deionised water to minimize the attenuation of light by the sample itself (inner filtering effects). To address changes in lamp intensity due to natural decay all samples were normalized using the area under the water Raman peak at an excitation of 350 nm (Lawaetz and Stedmon, 2009). The produced EEMs were then used to calculate the aforementioned optical indices using R Software (R Core Team, 2012) and the most recent mathematical methods outlined in Fellman *et al*. (2010).

3.2.4 Statistical Analyses

Three-way repeated measures ANOVA (RM-ANOVA) with Tukey *post-hoc* tests where necessary were used to quantify the changes in decomposition rates, porewater DOC concentration, and porewater $SUVA_{254}$ values under treatment conditions (Statistica 7, StatSoft. Inc. 2004). A multivariate ANOVA (MANOVA) was utilized to test for experimental effects on the florescence index, the humification index, and the freshness index (Statistica 7, StatSoft. Inc. 2004) at the end of the experiment. A Pearson correlation test was also conducted to determine the relationship between endpoint $SUVA_{254}$ values and FI, HIX_{EM}, and BIX.

3.3 Results

3.3.1 Decomposition

Sphagnum litter decomposition (expressed as percent mass loss relative to initial mass) was apparent across all experimental treatments over time (Figure 3.1). The main driver of decomposition was water table, with significantly greater mass loss under the lowered water table treatment across all conditions (water table: $F_{1,36} = 118.68$, $P < 0.001$). The rate of mass loss (i.e. the time × water table interaction) was also greater under a lowered water table ($F_{2,72} = 19.55$, $P < 0.001$), but no other interactive effects were noted. Under both water table treatments, mass loss was positively and significantly related to temperature (temperature: $F_{2,36} = 25.56$, $P < 0.001$) with mass loss approaching 40% in some replicates under +8˚C and lowered water table conditions. Under both water table treatments the difference between +8˚C and the other temperature treatments was greater than that between ambient and +4˚C (Figure 3.1). There was also a significant, but weaker relationship between percent mass loss and atmospheric CO_2 treatments, with greater decomposition under ambient atmospheric CO_2 conditions ($F_{1,36} = 4.77$, $P = 0.036$) (ambient $CO_2 = 17.6 \pm 1.19\%$, elevated $CO_2 = 15.6 \pm 1.06\%$).

3.3.2 Dissolved Organic Carbon Concentration

Despite placing the mesocosms in a four month acclimation period under ambient conditions from the time of field sampling to the initiation of the experiment (August 2012 – December 2012), a steady decline in DOC concentrations (starting at quite elevated concentrations >80 mg/L) from December 2012 through February 2013 followed by a stabilization suggests that the initial 3 months of water chemistry data were more strongly influenced by the field sampling and disturbance than experimental treatments. However, overall, total DOC concentrations were positively and significantly higher under the +8°C treatment (temperature: $F_{2,61} = 39.60$, $P < 0.001$) and continued to rise over time (temperature × time: $F_{22,671} = 4.58$, $P < 0.001$), while mean concentrations under ambient and the +4°C temperature treatments were not significantly different over the course of the experiment (Figure 3.2). The pattern of DOC concentrations over time differed between the two water table treatments at +8°C (water table × time: $F_{22,671} =$

2.89, $P < 0.001$). Under low water table conditions DOC concentrations show an increase over May-July, falling in August-September then gently rising again toward the end of the experiment. The pattern under high water tables was quite different with a steady increase over the experiment, reaching the highest concentrations of any of the experimental treatments (discounting the recovery period) in December (Figure 3.2). DOC concentrations were also significantly influenced by the interactive effects of elevated atmospheric CO_2 and increased temperature conditions over time (CO_2 × temperature × time: $F_{22,671} = 2.12$, $P = 0.002$), where DOC values continually increased throughout the experiment under the +8°C/elevated atmospheric CO_2 conditions (Table 3.1). The DOC concentration under the ambient atmospheric CO_2 treatment, conversely, remained relatively static from April-Oct, only rising slightly near the experiment's end and only under the +8°C treatment.

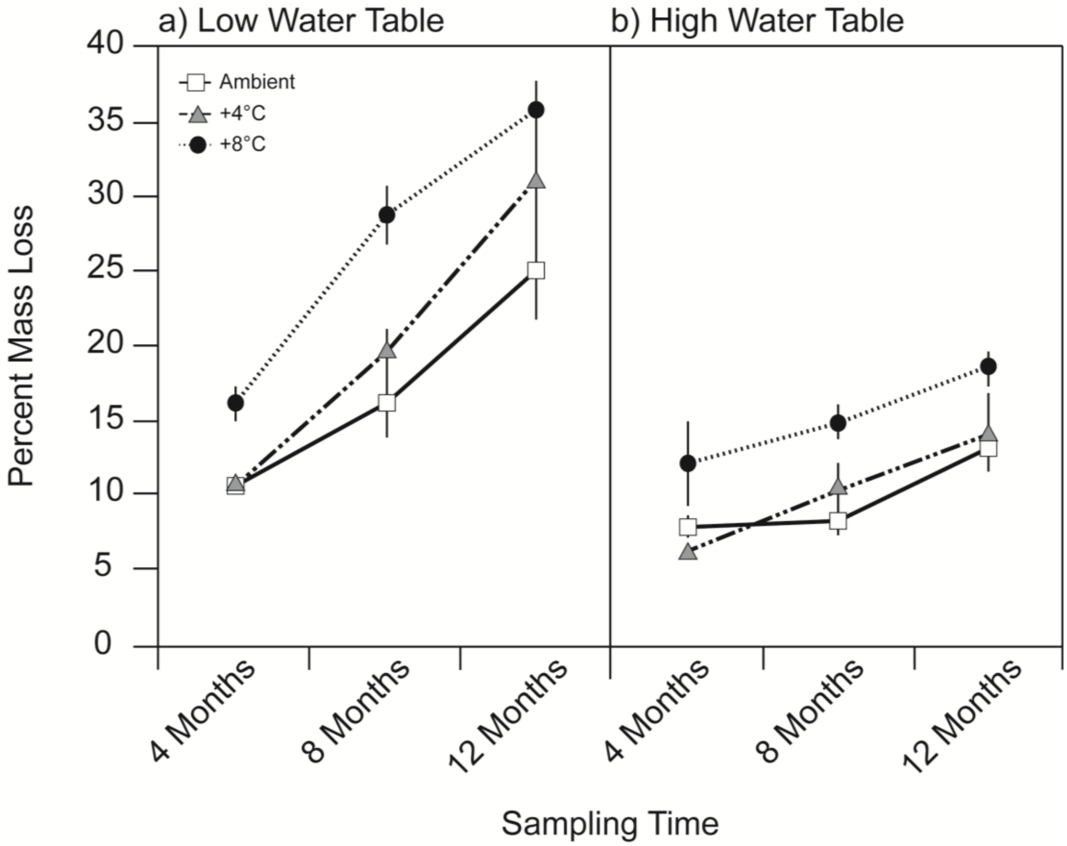

Figure 3.1 The percent mass loss of homogenized *Sphagnum* litter (mean ± SE) indicating the decomposition rates of experimental mesocosms under temperature and water table treatments from December 2012 to December 2013. Low water table conditions (a) indicate the water table was approximately 25 cm below the peat surface, while high water table conditions (b) dictate that the water table was approximately 5 cm from the peat surface.

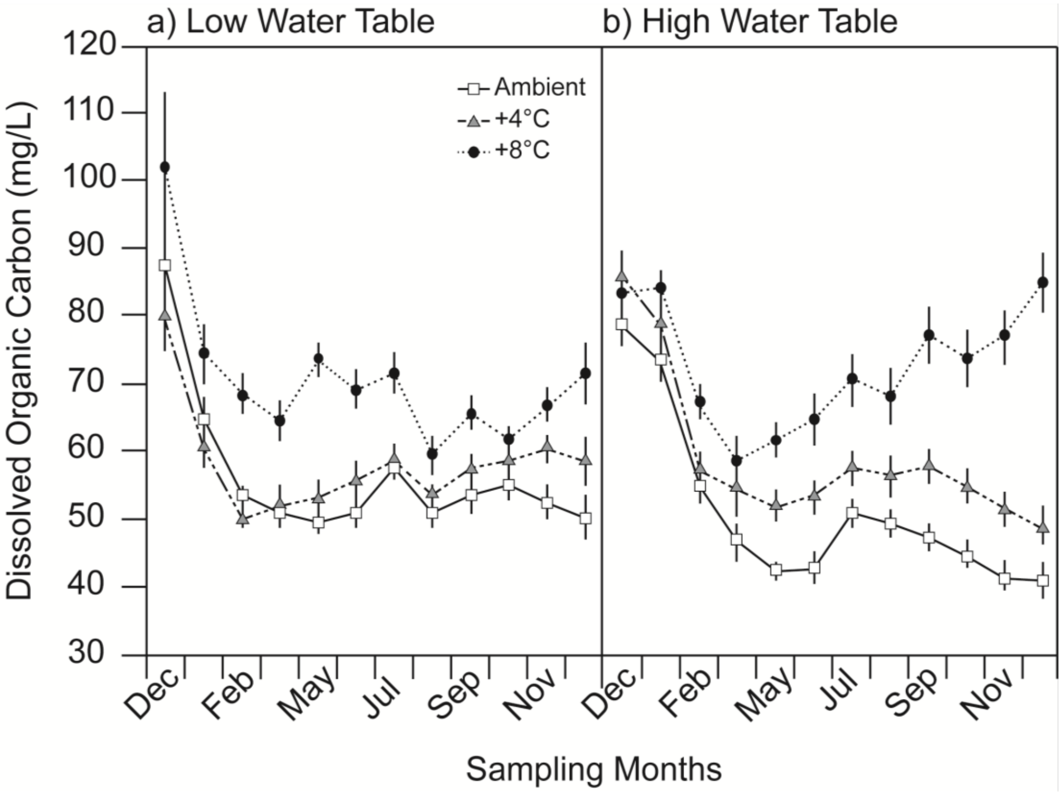

Figure 3.2 The interactive effects of temperature and low water table (a) and high water table (b) conditions on dissolved organic carbon concentrations (mean ± SE) in northern peatland mesocosms over one year. Elevated values were recorded for the first four months due to mesocosm collection disturbance; however, a full recovery is apparent by April 2013.

3.3.3 Specific UV Absorbance

Discounting the first three sampling times as artefacts of the acclimation period, the low water table conditions across all experimental treatments had consistently higher $SUVA_{254}$ values than under high water tables (water table: $F_{1,57} = 80.79$, $P < 0.001$) indicating greater DOC aromaticity. Under both water table treatments there was an early summer peak in $SUVA_{254}$ in May under ambient and the +4°C temperature treatments that were not observed under +8°C. After this point in time, the two water table treatments behaved quite differently, with $SUVA_{254}$ values being relatively stable under low water tables, while steadily declining under high water tables through to the end of the experiment (water table × time: $F_{11,627} = 7.79$, $P < 0.001$) (Figure 3.3). The lowest values for $SUVA_{254}$ were recorded for the +8°C treatment under high water tables. Indeed, overall $SUVA_{254}$ was significantly lower under the higher temperature treatments (temperature: $F_{2,57} = 10.42$, $P < 0.001$) with the *post-hoc* test indicating $SUVA_{254}$ values from the +8°C treatment were significantly lower than $SUVA_{254}$ values from both ambient and +4°C treatments — a trend that intensified over time (temperature × time: $F_{22,627} = 2.18$, $P = 0.002$). $SUVA_{254}$ values also significantly decreased under elevated atmospheric CO_2 conditions ($SUVA_{254} = 4.124 \pm 0.036$ L mg C^{-1} m^{-1}) compared to ambient CO_2 conditions ($SUVA_{254} = 4.253 \pm 0.037$ L mg C^{-1} m^{-1}) (CO_2: $F_{1,57} = 6.22$, $P = 0.016$), with the greatest decreases occurring steadily under the +8°C treatment from April-December (CO_2 × time: $F_{22,627} = 1.86$, $P = 0.010$) (Table 3.1). Finally, I found that endpoint $SUVA_{254}$ values were significantly correlated with both the FI ($R = -0.61$, $P < 0.001$) and the HIX_{EM} ($R = 0.56$, $P < 0.001$).

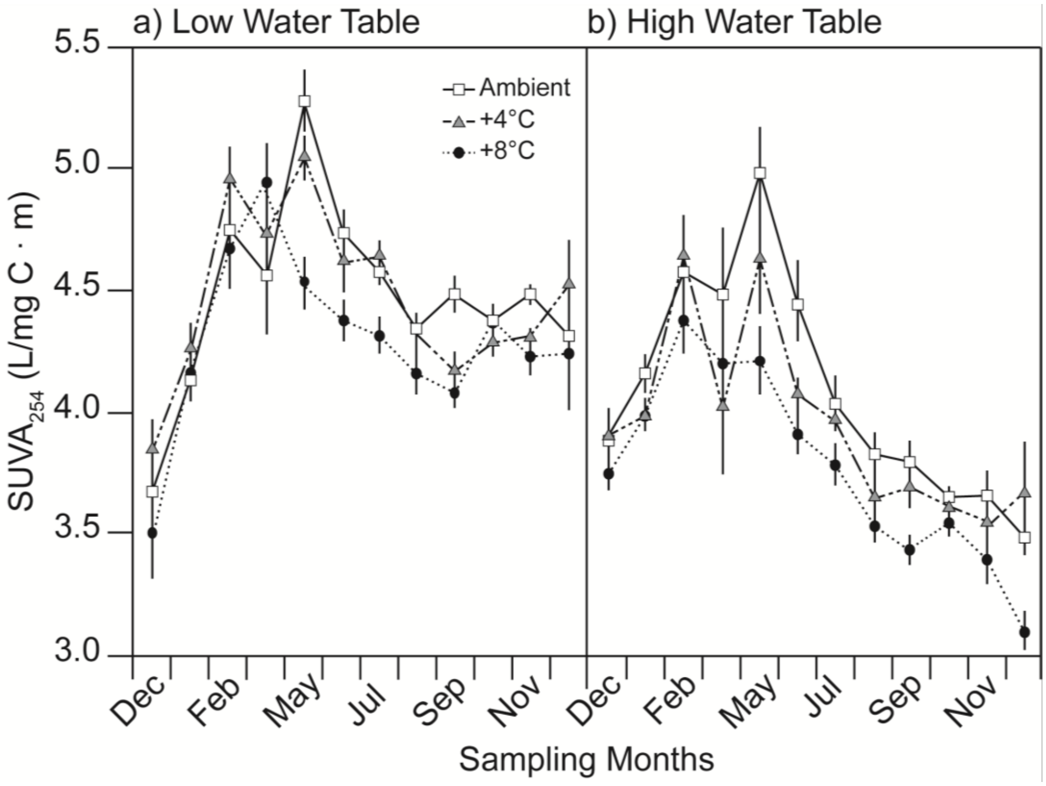

Figure 3.3 The trends in mesocosm porewater carbon quality as measured by specific ultraviolet absorbance at the wavelength 254 nm ($SUVA_{254}$) over one year in response to elevated temperature conditions in conjunction with low water table (a) and high water table treatments (b) (means ± SE).

Table 3.1 The mean observations and standard error of dissolved organic carbon (DOC, mg/L) and specific ultraviolet absorbance at 254 nm ($SUVA_{254}$, L mg C^{-1} m^{-1}) under two atmospheric CO_2 concentrations (430 ppm, 750 ppm) and three temperature treatments (ambient, +4°C above ambient, +8°C above ambient).

Measure	Ambient Atmospheric CO_2			Elevated Atmospheric CO_2		
	Ambient	+ 4°C	+ 8°C	Ambient	+ 4°C	+ 8°C
DOC	53.8 ± 2.6	60.2 ± 2.7	72.6 ± 2.6	53.8 ± 3.6	57.4 ± 2.8	72.7 ± 2.0
$SUVA_{254}$	4.4 ± 0.1	4.3 ± 0.1	4.1 ± 0.1	4.2 ± 0.1	4.1 ± 0.1	3.9 ± 0.1

3.3.4 EEMs Fluorescence Indices

Carbon quality, as inferred from EEMs fluorescence measurements, was influenced by both water table and temperature treatments (Table 3.2). Specifically, both the fluorescence index and the humification index were dominantly determined by the water table (FI: $F_{1,81} = 184.10$, $P < 0.001$; $\mathrm{HIX_{EM}}$: $F_{1,81} = 188.90$, $P < 0.001$), where the lowered water table treatment decreased FI values (more aromatic carbon, terrestrially sourced) while raising $\mathrm{HIX_{EM}}$ values (more humified carbon). Conversely, raising temperature conditions prompted slightly higher FI (less aromatic carbon, microbially sourced) and $\mathrm{HIX_{EM}}$ values (more humified carbon) under +4°C and +8°C treatment conditions when compared to ambient temperature conditions (FI: $F_{2,81} = 10.30$, $P < 0.001$; $\mathrm{HIX_{EM}}$: $F_{2,81} = 7.40$, $P = 0.001$). Unlike the other indices, the temperature, water table, and atmospheric CO_2 treatments had no clear effects on the BIX freshness index.

Table 3.2 The mean observations and standard error of fluorescence indices indicative of carbon quality under water table (low = 25 cm below the peat surface, high = 5 cm below the peat surface) and temperature (ambient, +4°C above ambient, +8°C above ambient) treatments. Lower values (1.2) of the Fluorescence Index (FI) indicate the dissolved carbon is more aromatic, composed of large molecules (e.g. fulvic acids), while higher values (1.8) suggest the dissolved carbon is similar to bacterial biochemicals. For the Humification Index (HIX_{EM}) higher values (1) indicate the carbon is more degraded, composed of highly condensed molecules. Higher values of the Freshness Index (BIX), conversely, suggest the carbon contains a larger fraction of simple proteins recently produced, generally by a microbial source. All indices are unitless.

Index	Low Water Table			High Water Table		
	Ambient	+4°C	+8°C	Ambient	+4°C	+8°C
FI	1.295 ± 0.010	1.334 ± 0.010	1.329 ± 0.010	1.403 ± 0.010	1.442 ± 0.010	1.450 ± 0.010
HIX_{EM}	0.926 ± 0.005	0.9445 ± 0.005	0.938 ± 0.005	0.869 ± 0.005	0.887 ± 0.005	0.884 ± 0.005
BIX	0.389 ± 0.003	0.403 ± 0.003	0.398 ± 0.003	0.401 ± 0.003	0.398 ± 0.003	0.390 ± 0.003

3.4 Discussion

Northern peatlands are a globally relevant carbon sink (Gorham, 1991), that will be affected by climate change factors such as elevated temperature, increased atmospheric CO_2 concentrations, and lowered water table positions (Bragazza *et al*., 2013). Of particular concern are changes in peatland decomposition rates and vegetation inputs, as the recalcitrant character of peatland vegetation paired with the unusually slow rate of decomposition in this ecosystem results in its notable carbon accumulation (Ward *et al*., 2015). In my experimental system I found that warming conditions increased both decomposition rates and DOC production resulting in increased porewater DOC concentrations, but the associated quality of that DOC was dependent on other factors, such as water table position and atmospheric CO_2 concentration.

A growing number of studies have demonstrated that higher temperatures and lower water table position in northern peatlands increases DOC production and export (Höll *et al*., 2009; Hribljan *et al*., 2014). In fact, authors from across Europe and North America are reporting increasing DOC concentrations in systems downstream of peatlands in association with ongoing atmospheric warming as a product of warming-enhanced decomposition (Freeman *et al*., 2001; Evans *et al*., 2005; Kane *et al*., 2014). While my study is in line with these other observed impacts of warming on DOC production, I found that warming conditions synergistically interacted with *higher* water tables as well as elevated atmospheric CO_2 to further increase DOC concentrations in peatland porewaters. As decomposition rates were reduced under these conditions, I suggest that warmer, wetter, and higher atmospheric CO_2 conditions stimulate vegetative inputs of DOC, explaining my observed patterns. Specifically, graminoid biomass and abundance (both aboveground and belowground) have been shown to significantly increase under the aforementioned climate change conditions (Weltzin *et al*., 2000), a trend that was observed in other results reported from this experiment (Dieleman *et al*., 2015, 2016). This increased presence of graminoid biomass can enhance the availability of labile carbon through litter inputs and root exudates (Hobbie, 1996; Fenner *et al*., 2007). In my study this is further supported through a pattern of increased DOC production during the growing season (May – October), mirroring vegetative productivity trends. This does not imply that decomposition processes are not contributing to DOC concentrations under wetter and elevated CO_2 conditions, but that other sources, such as graminoids, are enhancing DOC production rates.

Plant inputs, particularly root exudates, are generally a complex mixture of carbohydrates, amino acids, and simple organic acids that tend to be labile, aliphatic compounds (Jones *et al*., 2009). The products of advanced decomposition, conversely, include condensed lignins and humic acids — all highly recalcitrant carbon compounds (Berg and McClaugherty, 2014). The optical indices I employed to monitor changes in carbon quality indicated both the labile and recalcitrant signals increased under warming conditions, providing evidence that the DOC in my study was in fact coming from two sources. The $SUVA_{254}$ data were highly suggestive of a strong vegetative influence, as the least aromatic values throughout the study were consistently observed under the same wetter and CO_2 enriched conditions that are established to support enhanced graminoid productivity (Weltzin *et al*., 2000; Fenner *et al*., 2007). These plant inputs may have stimulated microbial growth or directly prompted the slight increase in FI values I observed under warming by supplying microbial-like, labile carbon compounds. Unlike $SUVA_{254}$ and FI, the HIX_{EM} values indicated an increase in recalcitrant-humified carbon production with warming, reflecting my *Sphagnum* litter decomposition trends. These findings pair well with other recent warming studies such as Kane *et al*. (2014) who also report simultaneous increases in carbon recalcitrance and lability with warming. That said, when interpreting results like ours it is important to note that measures of carbon quality, such as EEMs, can only reveal a subset of carbon molecules that are responsive to the technique. Consequently, relatively less responsive carbon molecules, like some recalcitrant tannins compounds, may constitute a larger portion of the carbon pool than revealed. Nonetheless, my results suggest that warming conditions significantly alter carbon quality; however, the prevailing characteristics of peatland DOC are determined by indirect, temperature-driven changes in both the aboveground plant productivity and belowground microbial activity.

Unlike my warming treatments, the lowered water table treatment consistently resulted in a signature of increased carbon recalcitrance. Various studies, including my own, have demonstrated that decomposition is intensified under the more aerobic conditions lowered water table treatments produce (Bergman *et al*., 1999; Šantrůčková *et al*., 2004). These conditions increase the availability of effective electron acceptors, such as O_2, increasing decomposition reaction rates, which causes the rapid break down of simple carbons, ultimately leaving mostly recalcitrant compounds in solution (Höll *et al*., 2009). However, as previously mentioned, high water table treatments enhances graminoid productivity and biomass in peatlands, in general (Weltzin *et al*., 2000), and in my specific experiment (Dieleman *et al*., 2016); biomass that is a source of labile carbon (Hobbie, 1996; Cornelissen *et al*., 2007). Such inputs could increase the lability of the high water table treatment, rendering the low water table more recalcitrant by comparison. My $SUVA_{254}$ data are suggestive of just that, as its values progressively decline under the high water table conditions that enhance graminoid biomass production, while the low water table values remain relatively constant throughout most of the growing period. That said it is important to note that I did not allow for natural variation in my water table treatments, a factor that could influence how water table conditions drive carbon quality. Yet my reported trends are in accordance with a study where water tables treatments did naturally vary. Specifically, Hribljan *et al*. (2014) observed a decrease in peatland carbon aromaticity under more saturated conditions due to increased labile carbon production by algae. Taken together I suggest that while future water table drawdown events are likely to enhance the recalcitrant carbon signal in northern peatlands via decomposition, it is increased vegetation inputs that can strongly alter DOC quality.

3.4.1 Significance

I experimentally demonstrated that future climate change conditions may strongly influence dissolved carbon quantity and quality in northern peatlands. Specifically, these environmental conditions interact to enhance decomposition rates and vegetative inputs to increase DOC production and predominately increase lability. For naturally occurring low-turnover ecosystems, like peatlands, this increased organic matter cycling can cause the ecosystem to become ‘leaky’, exporting nutrients and energy to surrounding ecosystems (Wardle *et al*., 2004). My findings indicate that warmer conditions in particular can accelerate material cycling, ultimately observed as increased DOC concentrations and lability in peatland porewaters. The consequences of these ecosystem changes are significant. If such DOC rich porewaters are exported, they could significantly alter the environmental conditions and ecosystem structure of receiving downstream aquatic ecosystems (Karlsson *et al.*, 2009; Erlandsson *et al.*, 2010). The enhanced decomposition rates could slow or reverse peat accumulation, compromising the stability of the peatland. Finally, more rapidly cycling peatlands are likely to have a diminished capacity to store carbon, and a greater potential to become a globally significant carbon source.

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Chapter 4

4 Northern peatland carbon dynamics driven by plant growth form — evidence of graminoid priming effects

4.1 Introduction

Plant communities have a central role in ecosystem carbon dynamics, driving carbon uptake via photosynthesis processes and indirectly regulating carbon release through decomposition processes (Dorrepaal, 2007). Different plant species vary greatly in their capacity to take up or release carbon, with implications for ecosystem level carbon cycling. To address this researchers have organized species into plant functional groups, grouping together species with similar effects on ecosystem processes (Lavorel and Garnier, 2002). Building evidence has demonstrated the success of this approach, with the plant growth form grouping acting as a particularly effective predictor of carbon dynamics — especially for decomposition processes (Armstrong *et al*., 2012; Robroek *et al*., 2016; Walker *et al*., 2016). In fact, plant growth form is such a strong determinant of carbon dynamics that it can have a greater influence on decomposition rates than even warming conditions (Ward *et al*., 2015), a well-established control on decomposition (Davidson and Janssens, 2006). Yet, despite the clear predictive capacity of plant growth form on carbon release, we have a very limited mechanistic understanding of how different plant growth forms influence belowground carbon processes (Ward *et al*., 2015; Dunn *et al*., 2016; Robroek *et al*., 2016).

It is understood that plant growth form determines the quantity and quality of primary, carbon-rich material introduced into the belowground environment (Hobbie, 1996; Dorrepaal *et al*., 2005) — factors that in turn drive microbial decomposition rates (Blagodatsky *et al*., 2010). The quantity and quality of plant contributions to the dissolved organic carbon (DOC) pool are especially salient to decomposition because DOC comprises a key energy source for microbial communities (Allison *et al*., 2010; Blagodatsky *et al*., 2010). Simple, high-quality root inputs can be particularly important because labile DOC compounds can significantly enhance decomposition of the soil organic matter by stimulating or ‘priming’ the microbial community (Bengtson *et al*., 2012). However, the specific effect of different plant growth forms on overall belowground DOC quantity and quality remains unclear, even though this information is key to developing a mechanistic understanding of how plant growth forms influence belowground carbon dynamics.

Plant and soil linkages that dictate ecosystem-level carbon dynamics are particularly pertinent for peatland ecosystems, as peatlands store approximately 30% of the Earth's terrestrial carbon (Gorham, 1991). These vast stores of carbon in northern peatlands have accumulated due to the remarkably slow decomposition rates that characterise this ecosystem (Rydin and Jeglum, 2013). Plant growth forms, such as *Sphagnum* moss, can strongly contribute to these slow decomposition rates by producing highly recalcitrant litter (Straková *et al*., 2010). Conversely, other peatland plant growth forms, such as graminoids, may actually stimulate decomposition rates by producing comparatively readily-degradable litter (Bombonato *et al*., 2010; Straková *et al*., 2010). Graminoids may also stimulate decomposition rates by introducing simple carbon compounds into the belowground system as root exudates, providing energy that stimulates microbial activity, priming microbial communities for enhanced decomposition (Kuzyakov *et al*., 2000); however, very few studies have considered such priming effects in peatland systems (but see Fan *et al*., 2013).

Peatland plant growth forms have the potential to strongly alter belowground carbon dynamics via differing carbon inputs (Dunn *et al*., 2016; Walker *et al*., 2016). Among the few studies that have considered peatland plant growth form and belowground DOC relationships, the findings have been largely incongruent. For example, even broad DOC concentration trends are wide ranging in the literature, where both non-significant and significant effects of plant form are reported (Armstrong *et al*., 2012; Dunn *et al*., 2016; Robroek *et al*., 2016). These contrasting findings in the literature appear to reflect the various limitations of the experimental approaches employed, such as single time point measurements, the absence of living plants, and natural variability in local environmental conditions. My experiment builds on this knowledge base by studying belowground carbon dynamics in replicated, intact mesocosms populated exclusively by *Sphagnum* mosses, graminoids, or bare peat maintained under standardized environmental conditions for nine months. In addition, my study presents one of the first applications of Biolog Ecoplates® as a measure of microbial activity in peatland environments. In doing so, my main objective was to determine if different plant growth forms influence belowground DOC quantity and quality to stimulate microbial activity and carbon release. As graminoids produce root exudates and relatively high quality litters I anticipated this growth form would increase both belowground DOC quantity and quality, resulting in increased microbial activity, decomposition rates, and ultimately carbon release — providing novel evidence of priming effects in peatland systems.

4.2 Methods

4.2.1 Study Site

Intact, vegetated monoliths were collected from a 5.3 ha, graminoid-dominated fen located near the city of White River, Ontario, Canada (48°21'N, 85°21'W). The research area is part of the White River Experimental Watersheds Study maintained by the Ontario Ministry of Natural Resources and Climate Change - Ontario Forest Research Institute; a long-term program that has previously established the plant community structure, hydrology, and carbon dynamics for this field site (McLaughlin and Webster, 2010; Webster and McLaughlin, 2010). The 31-year annual average precipitation and temperature is 970 mm and 2.2°C respectively, with a growing season ranging from 70 – 100 days (McLaughlin and Webster, 2010; Webster *et al*., 2013). In January and July the mean temperature values are -14.2°C and 14.7°C respectively, although temperatures were rarely above 0°C during the winter and 30°C in summer periods (McLaughlin and Webster, 2010). The precipitation at this site dominantly falls as rain, although 40% occurs as snowfall (McLaughlin and Webster, 2010). Previous vegetation surveys of the site have documented that approximately 80% of the fen is vegetated by graminoid species, primarily *Carex lasiocarpa* Ehrh. and *Carex stricta* Lam. The shrub and bryophyte species include sweet gale (*Myrica gale* L.), bog rosemary (*Andromeda polifolia* (L.)) leatherleaf (*Chamaedaphne calyculata* (L.) Moench), with *Sphagnum angustifolium* (Warnst.) C.E.O. Jensen and *Sphagnum capillifolium* (Ehrh.) Hedw. as dominate bryophytes.

4.2.2 Experimental Design

In August 2014, 18 intact peat monoliths (10 cm diameter × 20 cm deep) were collected from the study site; six monoliths of exclusively bare soil, *Sphagnum* moss cover, or graminoid cover (3 treatments × 6 replicates = 18 mesocosms). The monoliths were extracted from regions of relatively homogenous cover, reflecting treatment conditions. Monoliths were collected by cutting a 10 cm diameter ring using a 40 cm narrow blade saw and then carefully inserting a PVC pipe into the ground (10 cm diameter × 25 cm deep) to extract the intact peat core within the PVC pipe. The collected monolith was then capped at the base and transported to the University of Western Ontario's Biotron Institute for Experimental Climate Change. Once at the institute a tapered hole was drilled 1 cm from the base of each mesocosm and fitted with ½ inch threaded ABS barbed fitting to form a drain. A 30 cm length of clear vinyl tube was attached to the fitting for water sample collection as discussed below. All mesocosms were then placed in a greenhouse under the ambient growing conditions (described below) for 16 weeks to stabilize after the initial collection disturbance.

The greenhouse used throughout this experiment was an environmentally controlled system, regulating environmental humidity, atmospheric CO_2, and temperature conditions through fully automated processes (ARGUS Control Systems Ltd., White Rock, BC, Canada). Specifically, the relative humidity conditions were not less than 60%, while the atmospheric CO_2 concentrations matched outdoor ambient conditions, averaging 426 ppm. The temperature conditions purposefully followed two regimes, reflecting pre-growing and growing seasons. During the pre-growing season (November 1 – April 31) temperature conditions were held at the average growing season temperature for the source site at 11.5°C, allowing us to quantify and control for differences in belowground chemistry when plant inputs were minimal. Throughout the growing season (May 1 – October 31) temperatures were programmed to the five year running average local daily maximum and minimum with a maximum annual summer temperatures of 35°C on 8 Jul 2016. This temperature program allowed us to discern how belowground chemistry changed when plant inputs were at their highest during the growing season. Unlike the other environmental variables water table height was maintained manually, held at 2 cm below the peat surface via biweekly top and bottom water additions using dilute Rudolph's solution (Faubert and Rochefort, 2002). The mesocosms were also randomly relocated within the greenhouse on a monthly basis to address any microclimate effects.

4.2.3 Dissolved Organic Carbon Sampling and Analysis

Porewater samples were collected on a monthly basis from the vinyl tubes at the base of the mesocosms from February 2015 – October 2015 to determine the dissolved organic carbon content measured as DOC in mg L^{-1}, and carbon quality measured as the specific ultraviolet absorbance at a wavelength of 254 nm ($SUVA_{254}$) in L mg C^{-1} m^{-1}. Carbon quality was also determined using excitation-emission matrix fluorescence spectroscopy analysis and summarized using three common indices, the fluorescence index (FI), the humification index (HIX_{EM}), and the freshness index (BIX). Porewater (200 mL) was collected in clean, pre-rinsed 500 mL Nalgene® bottles, filtered using ashed glass filters (pore size 0.5 µm) and the filtrate was then divided into 30 mL HDPE bottles for DOC and $SUVA_{254}$ analysis, and 20 mL acid-washed, glass bottles for excitation-emission matrix fluorescence spectroscopy analysis. All samples were stored in the dark at 4°C until analyzed.

The DOC content of the porewater samples was determined using the persulfate wet oxidation method using an iTOC Aurora 1030 (OI Analytical, College Station, TX, USA). The $SUVA_{254}$ character was quantified using methods outlined by Weishaar *et al.* (2003). Specifically, the ultraviolet absorbance at $\lambda = 254$ nm for each sample was determined using a quartz cuvette with a 1 cm path length in conjunction with a Spectramax® M2 spectrophotometer (Molecular Devices Corp., Sunnyvale, CA, USA). Absorbance values were then converted to m^{-1} and divided by the DOC concentration of the sample to determine the $SUVA_{254}$ value. The excitation-emission matrices were used to calculate common indicators of carbon quality as summarized by Fellman *et al.* (2010), specifically FI, HIX_{EM}, and BIX. The fluorescence excitation and emission was determined using a Horiba Aqualog® spectrofluorometer with a xenon lamp in the Watershed Hydrology Group Laboratory at McMaster University, Ontario, Canada. The excitation wavelengths ranged from 240 to 600 nm with 10 nm increments and the emission wavelengths ranged from 210 to 620 nm with 3.27 nm increments, with an integration time of 0.5 s. Samples were diluted 1:1 with ultra pure deionised water to diminish any attenuation of the light by the sample itself (inner filtering effects). All samples were normalized using the area under the water Raman peak at an excitation of 350 nm to address natural changes in lamp intensity due to decay (Lawaetz and Stedmon 2009). The produced excitation and emission matrices were then used to calculate the aforementioned carbon quality indices using R software (R Core Team, 2012) in combination with the most recent index equations described by Fellman *et al*. (2010).

4.2.4 Respired Carbon Dioxide

Respired carbon dioxide was determined on a monthly basis from February 2015 – October 2015 following the methodology established by Carroll and Crill (1997). The dark static chamber measurements were completed using a Licor-8100A infrared gas analyzer (LI-COR, Lincoln, NE, USA) in combination with a custom chamber head. The chamber head was 2.3 L in volume, with a foam seal, and was constructed of opaque PVC to stop photosynthesis during readings. No internal fans were placed in the chamber head as initial trials demonstrated the sampling unit could adequately mix the gas within the relatively small chamber head. The LI-8100A unit was programmed to record the air CO_2 concentration every 0.5 seconds, averaging these values every 4 seconds over a 2.5 minute collection period. The final CO_2 flux values were corrected for the chamber volume, soil temperature (top 5 cm), air moisture content, initial CO_2 concentration, and initial pressure as measured by the LI-8100A unit. The final CO_2 flux values are presented as µmol of CO_2 per m^2 per second (µmol CO_2 $m^{-2}s^{-1}$).

4.2.5 Microbial Community Level Physiological Profiling

All mesocosms were destructively sampled after nine months to collect peat substrate for microbial community level physiological profiling. Aboveground vegetation was clipped at the surface before the monoliths were carefully extracted from their containers, and the coarse root biomass (diameter > 0.2 cm) was removed by hand. The peat substrate for each mesocosm was then homogenized by hand, placed in a plastic bag, and stored in the dark at 4°C until further processing for microbial community profiling.

Differences in the microbial community metabolic profiles of peat substrate were determined using Biolog Ecoplates® (Biolog Inc., Hayward, CA, USA) for nine of the eighteen mesocosms (3/6 replicates). Ecoplates are 96 well microplates that contain a triplicate set of 31 different carbon substrates as well as three water control wells. The carbon substrates vary in quality including ten carbohydrates, nine carboxylic/acetic acids, four polymers, six amino acids, and two amine/amide compounds (see Table 3 in Frąc *et al*., 2012). The metabolism of a particular carbon substrate by a microbial community is indicated by a colour change caused by the redox-indicator tetrazolium. To determine the microbial metabolic profile, peat samples were processed using the methods established by Garland (1996). Specifically, 10 g fresh weight peat was suspended in 100 mL of sterile ultra pure water using sterile techniques, and shaken for 10 min on a wrist shaker at maximum speed. The sample then settled for 10 min before being serially diluted to 10^{-3}. A plate was then inoculated with the resultant suspension by adding 150 µl of it to each well. Three replicate sets of carbon substrates within a plate were averaged for each mesocosm examined. The well absorbance at 590 nm was determined using a Spectramax® M2 spectrophotometer (Molecular Devices Corp., Sunnyvale, CA, USA) at the time of inoculation, and every 24 hours for 7 days while being incubated at 22°C.

The raw absorbance data were corrected by subtracting both the control values and the absorbance values recorded at the time of inoculation. All resultant negative values were converted to zero as suggested by Garland (1997). For each time point the carbon substrate utilization richness of the microbial community was determined as an indicator of metabolic diversity by deriving the number of wells with metabolic activity (absorbance at 590 > 0.25). The average well colour development (AWCD) was also determined as an indicator of overall metabolic activity using following equation:

$$\mathrm{AWCD} = \Sigma\,(C - R)/31 \qquad (1)$$

where C is the raw absorbance value at 590 nm for each well containing carbon substrate, and R is the raw absorbance value of the control well (Garland and Mills, 1991).

4.2.6 Decomposition

Decomposition rates were measured using cellulose strips (Bragazza *et al*., 2013). Whatman® #2 cellulose filters were oven dried at 60°C for 24 hours before being weighted and placed into individual mesh decomposition bags (7 cm × 4 cm with 1 mm mesh). Duplicate decomposition bags were placed just below the peat surface in each mesocosms for the duration of the growing season (18 mesocosms, 36 decomposition bags). The cellulose strips were retrieved at the end of October 2015, gently cleaned of debris, oven dried at 60°C for 24 hours, and weighted. Percent mass loss was then calculated relative to the initial dry weight of the cellulose strips.

4.2.7 Statistics

A one-way repeated measures ANOVA (RM-ANOVA) with a Tukey *post-hoc* test was used to consider the effects of plant growth form on DOC, $SUVA_{254}$, the fluorescence index, the humification index, the freshness index, respired CO_2, carbon substrate utilization richness, and AWCD over time (Statistica 7, StatSoft. Inc. 2004). *A priori* contrasts were used to separate the sampling time points into pre-growing and growing seasons for the respired CO_2 flux data as the transition between pre-growing and growing seasons (May) elected high variability in respiration. A subsequent RM-ANOVA was conducted without the disturbed month of May for the respired CO_2 flux data, considering the effects of plant growth form (see results). A one-way ANOVA with a Tukey *post-hoc* test was used to examine differences in decomposition rates by treatment.

4.3 Results

4.3.1 Dissolved Organic Carbon Quantity and Quality

The concentration of DOC varied significantly throughout the experiment, with the lowest values reported for all mesocosms during the pre-growing season and at the end of the growing season ($F_{8,120} = 37.31$, $P < 0.001$) (Figure 4.1a). Throughout the pre-growing season the different treatment types had relatively similar DOC concentrations ranging from 17 – 40 mg L^{-1} across all treatments. During the growing season, however, DOC concentrations significantly increased and were significantly different among treatments (time × treatment: $F_{16,120} = 1.88$, $P = 0.029$) (Figure 4.1a). Specifically, the graminoid treatment produced consistently lower DOC porewater concentrations than either the *Sphagnum* moss or the control treatments during the growing season. The concentrations of DOC under the *Sphagnum* moss and control treatments were relatively similar throughout the entire experiment. At the end of the growing season all treatments began to converge, tending towards pre-growing season DOC concentrations.

The indicators of carbon quality (*i.e*. $SUVA_{254}$, EEMs fluorescence measurements) had contrasting responses to the treatment conditions. The $SUVA_{254}$ measurements, like DOC, differed significantly among treatments over time ($F_{16,120} = 4.02$, $P < 0.001$), but had the highest values during the pre-growing season across all treatments, indicative of higher molecular aromaticity (Figure 4.1b). All $SUVA_{254}$ values decreased in parallel during the early growing season, but diverged and increased again after July 2015. In the latter half of the growing season the $SUVA_{254}$ values increased across treatments in the following order: graminoid < *Sphagnum* moss < control peat. The EEMs fluorescence measurements, conversely, did not show any clear seasonal trends, but instead were relatively consistent throughout the experiment (see Appendix A, Figure A.4). Unlike the humification and freshness indices, the fluorescence index did indicate that *Sphagnum* moss communities produce significantly and consistently higher FI values (more microbial-like carbon) throughout the experiment ($F_{2,14} = 17.66$, $P < 0.001$).

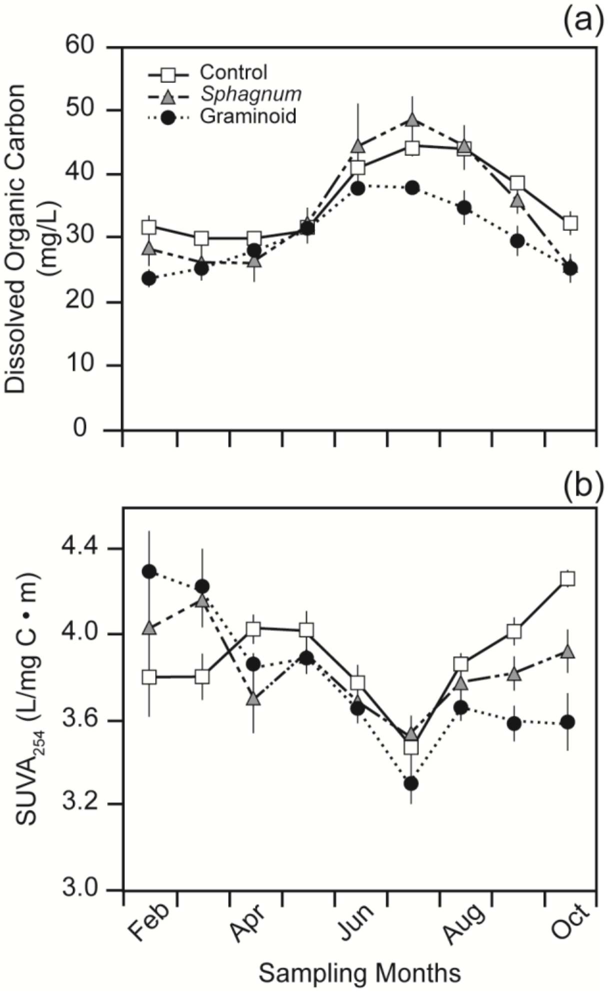

Figure 4.1 The influence of plant growth form over time on (a) dissolved organic carbon concentration and (b) carbon quality measured as specific ultraviolet absorbance at the wavelength 254 nm ($SUVA_{254}$) in peatland mesocosm porewater (mean ± SE). Two temperature regimes were implemented with the pre-growing season occurring from February 2015 to April 2015, and the growing season occurring May 2015 to October 2015.

4.3.2 Respired Carbon Dioxide

Respired carbon dioxide levels responded strongly to the transition from the pre-growing to the growing temperature schemes, resulting in a spike in respired carbon dioxide flux values in May 2015. During this month some individual measures were 139% greater than average carbon flux values for the experiment. This disturbance response masked much of the treatment response over time, as substantiated by the *a priori* contrast test, which demonstrated that pre-growing season respiration was significantly lower than the growing season when May was excluded from the contrasts ($F_{3,43} = 4.53$, $P = 0.008$). Prior to the change to variable temperature regimes, respired carbon dioxide rates were highly uniform across treatments; but from July until the end of the growing season, the graminoid community produced significantly higher values than either the *Sphagnum* moss or control treatments ($F_{14,105} = 2.74$, $P = 0.002$) (Figure 4.2).

4.3.3 Microbial Community Level Physiological Profiling and Decomposition Rates

The AWCD, carbon substrate utilization richness, and decomposition rates all indicated that the microbial community characteristics significantly differed among treatments (Figure 4.3). The AWCD demonstrated that after 72 hours of incubation the graminoid and *Sphagnum* moss communities had significantly higher microbial activity compared to the control treatment (incubation time × treatment: $F_{12,36} = 3.24$, $P = 0.003$), with the greatest microbial activity occurring under the graminoid treatment. The carbon substrate utilization richness indicated that after 72 hours of incubation the graminoid treatment had a microbial community that utilized a greater number of carbon substrates then either the *Sphagnum* moss or control treatments (incubation time × treatment: $F_{12,36} = 2.07$, $P = 0.045$). The microbial decomposition rates also significantly differed between plant growth form treatments. The cellulose strip percent mass loss approached 100% for both the control (93 ± 4%) and the *Sphagnum* moss communities (95 ± 2%), while the graminoid communities had significantly lower rates of loss of 80 ± 6% ($F_{2,15} = 3.74$, $P = 0.048$).

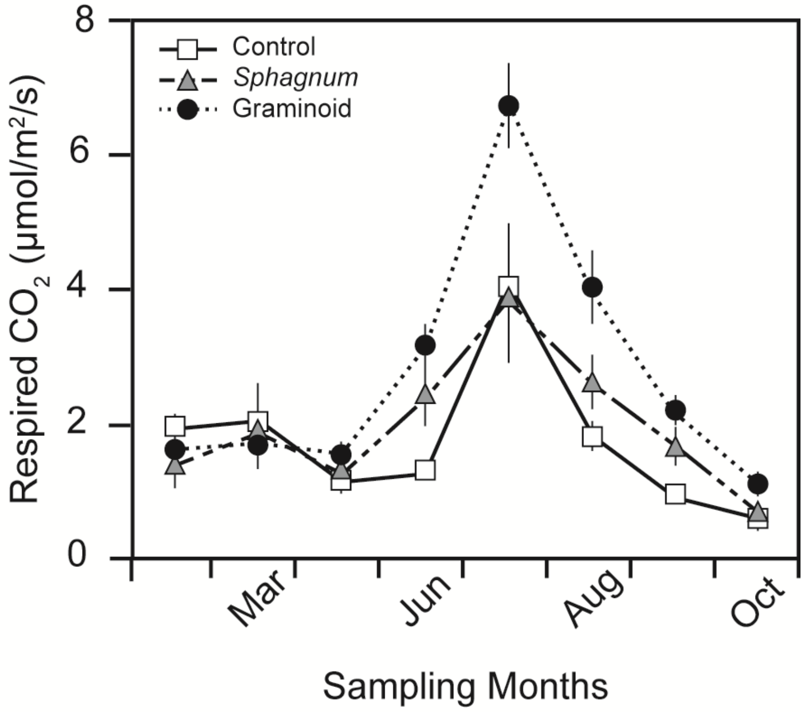

Figure 4.2 The effect of different plant growth forms on respired CO_2 rates reported monthly for the duration of the experiment (mean ± SE).

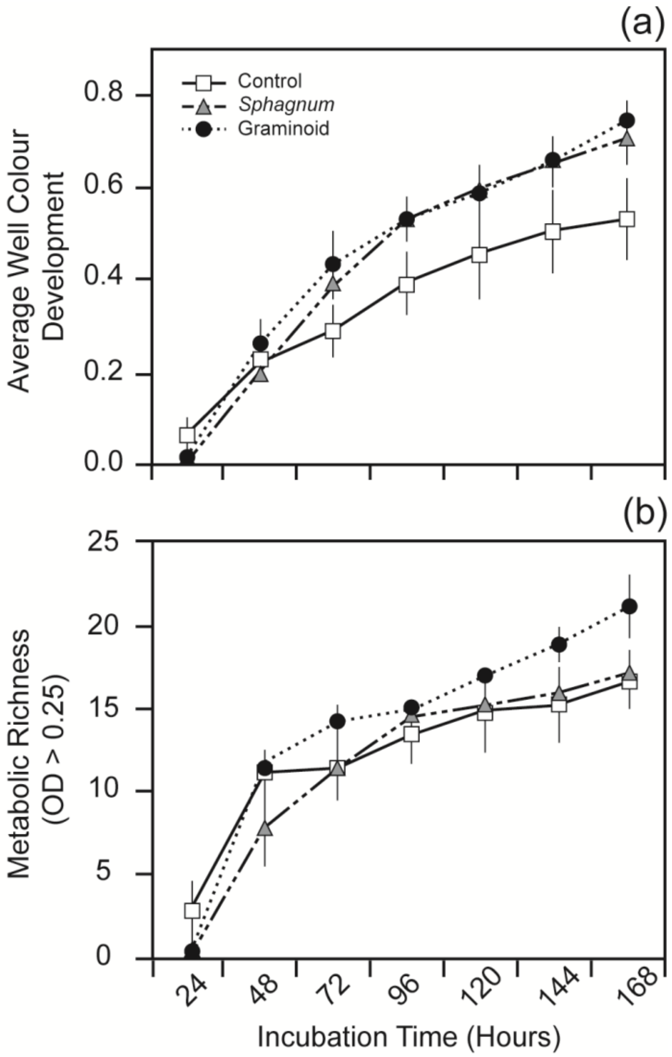

Figure 4.3 Measures of microbial activity and microbial metabolic diversity as indicated by (a) average well colour development and (b) carbon substrate utilization richness (mean ± SE). Both average well colour development and carbon substrate utilization richness were determined from peat samples collected at the end of the experiment and incubated in Biolog Ecoplates® for seven days.

4.4 Discussion

Northern peatlands store globally significant quantities of terrestrial carbon (Gorham, 1991), carbon that if released into the atmosphere could intensify climate change conditions. As northern peatlands predominately occur at high latitude locations where ongoing climate change impacts are anticipated to be severe (IPCC, 2013, Seddon *et al*., 2016), many studies have predicted that peatland plant communities will undergo restructuring events, increasing the prevalence of vascular growth forms like graminoids at the expense of *Sphagnum* moss (Weltzin *et al*., 2000; Wiedermann *et al*., 2007; Dieleman *et al*., 2015). Consequently, understanding the influence different plant growth forms have on important ecosystem functions, like carbon storage, has become an important research prerogative for many (Armstrong *et al*., 2015; Ward *et al*., 2015; Dunn *et al*., 2016; Robroek *et al*., 2016). In my experimental system I found that plant growth form does significantly affect belowground carbon dynamics. Specifically, graminoids were associated with increased DOC lability, microbial activity, metabolic diversity and increased carbon release as respired CO_2 in a manner suggestive of microbial priming effects.

Priming effects have been well established in mineral soils, where the addition of organic or mineral substances prompts changes in soil organic material (SOM) turnover rates, as indicated by increased respired CO_2 release produced via elevated microbial metabolism, microbial biomass production, and microbial exoenzyme release (Blagodatskaya and Kuzyakov, 2008). My experiment indicates that during the growing period graminoids increase respired CO_2 release, due to cascading belowground changes. I suggest this respired CO_2 is a product of graminoid DOC inputs to the belowground component, most likely in the form of senescing fine root biomass and root exudates (Crow and Wieder, 2005). The complete mineralization of these simple carbon compounds keeps belowground DOC porewater concentrations relatively low in comparison to other treatment conditions, while enhancing respired CO_2 release. These findings contrast with studies by Armstrong *et al*. (2012) and Dunn *et al*. (2016) who also considered the effect of plant growth from on belowground C processes. Both studies report that graminoids increased belowground DOC concentrations in comparison to *Sphagnum* moss treatments; although, Dunn *et al*. (2016) did observe the same significant increase in respired CO_2 with graminoids. Presumably, graminoid belowground carbon inputs exceeded microbial mineralization rates in those studies, keeping DOC concentrations high while still enhancing SOM turnover and respired CO_2 release. Regardless, it is clear that graminoids can alter belowground DOC production and CO_2 release in a way that strongly resembles priming effects.

Priming effects in mineral soils often occur in response to the introduction of simple organic carbon compounds into the belowground environment (Kuzyakov *et al*., 2000; Zhu *et al*., 2014). The significantly lower $SUVA_{254}$ values found under the graminoid treatments, provide further evidence this plant growth form was introducing labile carbon compounds into the belowground environment during the growing season, again most likely as root inputs (Crow and Wieder, 2005). However, the clear effect of different plant growth forms on $SUVA_{254}$ values did not become apparent until July 2015, after which the bare peat, *Sphagnum* moss, and graminoid treatments diverged. These trends fit well with established soil microbial biomass seasonal trends, where the microbial community rapidly builds biomass using carbon resources from April until June, only to have notable decline or stabilization in biomass for the remainder of the growing season (see Buckeridge *et al*., 2013). These seasonal trends in $SUVA_{254}$ values may also be due to natural variation in root exudate quality, as a number of environmental variables that vary with season influence root exudate composition (Badri and Vivanco, 2009). Regardless, the $SUVA_{254}$ trends paired well with the microbial activity and functional diversity measured via the Biolog Ecoplates®. Specifically, measures of microbial activity and metabolic diversity were greatest under the vegetated treatments, with the highest values consistently observed under the graminoid treatments; however, these trends were strongest for metabolic diversity values. These finding suggest that the microbial community under the graminoid treatment was more active than control treatments, with a more complex community structure able to decompose a wider range of carbon compounds. Research by Fisk *et al*. (2003) supports my work, also demonstrating that microbial activity significantly differs under contrasting peatland plant communities; although these authors found that shrub/*Sphagnum* moss communities maximized microbial activity. Taken together my results suggest the labile carbon inputs from graminoids can stimulate microbial activity and community metabolic complexity to enhance respired CO_2 release in organic peatland soils.

One of the simplest measures of long-term SOM turnover rates is decomposition bags. Due to the duration of my experiment and the potential confounding effects of introduced plant litter I installed cellulose strips to measure decomposition rates, as done by Bragazza *et al*. (2013). Cellulose, however, represents a relatively labile fraction of the carbon pool available for decomposition within a peatland (Brown *et al*., 1988). Accordingly, under the bare peat and *Sphagnum* moss treatments, where labile plant inputs were significantly lower, the cellulose was rapidly decomposed. Under the graminoid treatments, however, I posit that the abundance of plant sourced labile carbon protected the cellulose strip from enhanced decomposition. Labile carbon inputs trigger belowground priming effects by providing a stable energy supply needed to produce exoenzymes capable of decomposing complex compounds (Fontaine *et al*., 2007). Thus, the apparent protection of the labile cellulose carbon does not imply a slowed decomposition of the recalcitrant carbon pool. Indeed, an abundance of labile DOC compounds in combination with a metabolically more diverse microbially community are ideal conditions for priming effects (Fontaine *et al*., 2007).

While my study presents clear evidence for priming effects in peatland ecosystems, it is not possible to confidently discern if these priming effects are what the literature terms ‘real’ or ‘apparent’ (Blagodatskaya and Kuzyakov, 2008). Real priming effects occur when the microbial community is stimulated to breakdown SOM, releasing the soil carbon as CO_2. Apparent priming effects also increase CO_2 release but are due to intensified microbial metabolism and biomass turnover, leaving SOM decomposition rates unaltered (Blagodatsky *et al*., 2010). That said, the increase in metabolic diversity I report is indicative of an increased capacity to decompose a wide range of carbon compounds, as would be expected with real priming effects (Fontaine *et al*., 2007). Apparent priming effects are also generally considered highly transient, lasting less than 14 days (Blagodatsky *et al*., 2010; Blagodatskaya *et al*., 2011). Real priming effects, conversely, can be sustained for several months (Blagodatsky *et al*., 2010). In fitting with real priming effects the graminoid increased CO_2 response was maintained for the duration of the growing season, decreasing but not rejoining *Sphagnum* moss and control treatments by October. Real priming effects also corroborate emerging research on peatland plant growth forms which demonstrates graminoids enhance ancient SOM release (Walker *et al*., 2016), where my research suggests labile carbon from the graminoids primes microbes to decompose ancient SOM — in turn providing a mechanistic explanation for the findings of Walker *et al*. (2016).

Throughout my study I used EEMs values in addition to $SUVA_{254}$ to monitor changes in DOC quality. Unlike $SUVA_{254}$ these indices were generally not sensitive to plant induced changes in DOC lability. Only the Fluorescence Index (FI) reported a difference in DOC quality with treatment, however, the consistently more microbial-sourced carbon found under the *Sphagnum* moss communities did not increase during the growing season when *Sphagnum* moss growth was maximized and temperatures were highest. Instead it remained a constant trend for the duration of the experiment, indicating this DOC characteristic was not a direct product of the plant community *per se.* Nor is it likely these FI trends reflected increased microbial production under *Sphagnum* moss. In that scenario FI values would be expected to vary seasonally, reflecting the strong relationship between temperature and microbial production (Davidson and Janssens, 2006). Moreover, the Ecoplate® metabolic diversity and activity measures do not indicate the *Sphagnum* moss microbial community was significantly more productive than both the graminoid and control treatments. Instead, the FI values appear to reflect a stable and unique characteristic of the peat below the *Sphagnum* moss community influencing porewater DOC, and not a microbial source as suggested by the index. While this DOC characteristic had no obvious experimental effect in my study, peatland DOC characteristics using EEMs indices originally designed for use in river or lake ecosystems should be interpreted with caution (Olefeldt and Roulet, 2012).

4.4.1 Significance

The carbon stores of northern peatlands have been the focus of a remarkable research effort, resulting in the discovery of numerous carbon cycling controls (Limpens *et al*., 2008). Recent research efforts have demonstrated the importance of plant growth forms in governing carbon processing in peatlands (Ward *et al*., 2015, Walker *et al*., 2016), although our mechanistic understanding of these findings has remained limited (Dunn *et al*., 2016). As future climate change conditions are anticipated to restructure peatland plant communities (Wiedermann *et al*., 2007; Dieleman *et al*., 2015) this knowledge gap has become important to anticipating the stability of peatland carbon stores in the future (Armstrong *et al*., 2015). My work demonstrates that graminoids significantly alter belowground processes by introducing labile DOC, which in turn increases microbial activity and metabolic diversity to increase respired CO_2 release. These findings are indicative of microbial priming effects demonstrated in mineral soils, suggesting that organic soils populated with graminoid species can also support this effect. Accordingly, climate change driven shifts in peatland plant communities, from *Sphagnum* moss to graminoid dominated systems, are likely to prime belowground environments and potentially enhance the release of recalcitrant carbon stores.

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Chapter 5

5 The push, the point, the plunge: defining the mechanisms behind shifts in peatland stable states

5.1 Introduction

Northern peatlands contain globally significant quantities of carbon that if released could intensify climate change impacts. However, northern peatland ecosystems will be directly impacted by predicted changes in global climate and greater anthropogenic activity in increasingly remote locations. Higher average temperatures and changes in precipitation frequency and duration are predicted to be most amplified in northern latitudes where peatlands are abundant (IPCC, 2013), while concomitant natural resource development and increased human activity will also have direct impacts on the landscape (Kadlec and Bevis, 2009). Whether or not these factors, independently or in combination, will drive gradual transitions or rapid shifts in biological communities and ecosystem-level processes in the future, and over what time frame, remains unclear. Dise (2009) and Turetsky *et al*. (2012) suggest that peatland systems are generally robust or resilient to perturbation, but may have points at which the system is irreversibly changed. This phenomenon is more generally articulated within the framework of complex adaptive systems (Levin, 1998) and alternative stable state theory (Beisner *et al*., 2003).

The argument for peatlands as complex adaptive systems (Dise, 2009) is based on the strong positive autogenic feedback mechanisms associated with the influence that peatland vegetation, such as *Sphagnum* spp., have on their natural environment (Klinger, 1996). However, many allogenic forcing factors, such as climate, land use change, and their combined effects, increase the possibility of rapid change for peatland ecosystems (Dise, 2009; Scheffer *et al*., 2012b). Recent work by Dieleman *et al*. (2015) demonstrates that changes in climate (elevated temperature, elevated atmospheric CO_2 concentration, decreased water table position) on peatland systems can result in a fairly rapid shift in the plant community, from a *Sphagnum*-dominated to a graminoid-dominated system — fitting with work by Kéfi *et al*. (2016) that suggests alternative stable states often manifest as a switch from one dominant functional group to another.

The main driver of this shift was temperature increases between +4 and +8°C, switching the competitive advantage to vascular plants over *Sphagnum* spp. The response to increased temperature conditions was non-linear, and the observed effects synergistically enhanced by the presence of elevated atmospheric CO_2 (Dieleman *et al*., 2015). Such sudden aboveground community-level changes have been linked to changes in carbon export via both enhanced decomposition as well as contributions via root exudates (Bragazza *et al*., 2013; Dieleman *et al*., 2016). These ecosystem-level changes are thought to reinforce favourable conditions for the continued dominance of the vascular plant community, with further cascading effects to the belowground components of the system.

Unfortunately, the critical community and ecosystem-level environmental thresholds (e.g. critical temperature thresholds or changes in moisture), the underlying mechanisms of these thresholds, and what the consequences will be following critical thresholds, are not yet well quantified (Scheffer *et al*., 2015). Here I use the framework of alternative stable state theory to describe the three phases of peatland shift under different allogenic stressors. The premise is based on the 'ball-in-cup' analogy, where the ball represents the peatland system and the cup is the theoretical stable state (Beisner *et al*., 2003; Scheffer and Carpenter, 2003). Movement of the ball within and between two stable states requires a 'push', which is the allogenic forcing factor (Beisner *et al*., 2003; Andersen *et al*., 2009) (e.g. increase in temperature, reduction in rainfall, land use change). To be fully pushed into an alternative stable state a critical threshold or a tipping 'point' is reached (Scheffer *et al*., 2015). The tipping point is defined as the point where a relatively minor change in key factors causes a disproportionately large response in defining ecosystem characteristics and thus ecosystem state (Brook *et al*., 2013). Once the tipping point is surpassed, the ball 'plunges' into a new state, which is then reinforced through other positive feedback mechanisms (DeAngelis, 2012).

In this review I identify: 1) the key drivers and mechanisms that disturb peatland systems and 'push' them towards a tipping point, 2) the tipping 'points' for peatlands, where known, and 3) the potential alternative ecosystem states peatlands may 'plunge' into and the consequences for peatland carbon dynamics. In doing so, I hope to identify the important knowledge gaps, while facilitating land use planning policy, sustainable industrial development, and efficient remediation efforts in peatland-dominated regions.

5.2 'The Push'– Identifying the Drivers of Change

There are three main allogenic drivers of change to peatland ecosystems that can occur independently, co-occur, or can act as a primer for more change. These are changes in water table position, changes in nutrient supply/availability (including atmospheric CO_2), and changes in temperature (both average, and range). In northern peatlands, all of these factors act in a similar direction; they alter the balance of competitive dominance between peat-forming *Sphagnum* spp. and vascular plant species, specifically graminoids, shrubs, and trees (Eppinga *et al*., 2009). The presence and establishment of *Sphagnum* spp. is self-reinforcing in the development of a peatland by perpetuating the high-water table, low nutrient conditions, and low belowground temperatures that support low rates of decomposition and peat accumulation (van Breemen, 1995). For example, during drought conditions *Sphagnum* spp. in association with *Sphagnum* peat can maintain surface moisture by transporting water upwards via capillary action (Waddington *et al*., 2014) until the water table drops 40 – 50 cm below the surface. At that point *Sphagnum spp*. desiccate, taking on a lighter colouration that increases local albedo and decreases local evapotranspiration rates (Nungesser, 2003). Persistently lowered water table conditions, however, favours the growth of vascular species while limiting *Sphagnum* spp. productivity (Eppinga *et al*., 2009). Once dominant, vascular vegetation can continue to destabilize peat accumulation and compromise *Sphagnum* spp. by lowering the water table through increasing evapotranspiration and precipitation interception rates (Dubé and Plamondon, 1995; Waddington *et al*., 2014); in turn creating a larger aerated zone belowground and reducing water stress on rooting plants, particularly trees and shrubs (Sarkkola *et al*., 2013).

Nutrients are limiting in northern peatland bog systems in part due the high interception of atmospherically-deposited nutrients by *Sphagnum* spp., followed by the slow decomposition of recalcitrant *Sphagnum* peat (Turetsky, 2003). Long-term nutrient addition experiments in peatlands have shown an increase in the abundance and biomass of vascular vegetation (Laine *et al*., 1995; Bubier *et al*., 2007; Juutinen *et al*., 2010), resulting in the rapid transition to treed (Laine *et al*., 1995), herbaceous (Gunnarsson *et al*., 2008; Juutinen *et al*., 2010; Bragazza *et al*., 2013), or graminoid-dominated (Tomassen *et al*., 2003; Wu and Blodau, 2013) community states. Under high nutrient loading, particularly nitrogen loading, *Sphagnum* spp. productivity is inhibited and nutrient rich amino acids are released by the moss into the peat matrix to reduce internal loading (Gunnarsson and Rydin, 2000; Limpens and Berendse, 2003; Limpens *et al*., 2011). This response further increases the available nutrients in the belowground peat matrix, fertilizing rooting species (Wu and Blodau, 2013). Once vascular vegetation is prevalent it can maintain these enriched nutrient conditions by stimulating nutrient turnover rates and importing more nutrient laden water from surrounding systems via their rooting systems (Hobbie, 1996; Rietkerk *et al*., 2004).

Elevated atmospheric CO_2 will also fertilize vascular plant growth by increasing photosynthesis rates (Kimball *et al*., 1993). Some work has suggested that this environmental advantage can allow graminoid species to outcompete *Sphagnum* spp., prompting *Sphagnum* spp. decline (Fenner *et al*., 2007b). However, a number of other studies have also reported conflicting effects of elevated CO_2 treatments ranging from stimulatory, inhibitory, to null-effects on *Sphagnum* and graminoid species alike (Berendse *et al*., 2001; Hoosbeek *et al*., 2001; Heijmans *et al*., 2002; Milla *et al*., 2006; Toet *et al*., 2006; Siegenthaler *et al*., 2014), suggesting that the effects of elevated CO_2 on peatland plant communities is species/community dependant.

Sphagnum spp. and peatland vascular vegetation have differing optimum temperatures for maximum productivity, where *Sphagnum* spp. photosynthetic processes are the most efficient at temperatures below 15°C and vascular vegetation are optimized at temperatures above 15°C (Hobbie *et al*., 1999). As poor thermal conductors, *Sphagnum* spp. are thought to competitively suppress vascular plant species by keeping belowground conditions cool (van Breemen, 1995; Blok *et al*., 2011). Accordingly, under anticipated future warming conditions there is strong evidence that an increased presence of vascular plants will be seen (Fenner *et al*., 2007a; Bragazza *et al*., 2013; Heijmans *et al*., 2013). In the majority of studies a significant increase in shrub abundance and biomass has been observed, however, increases in graminoid (Weltzin *et* *al*., 2000; Wiedermann *et al*., 2007; Dieleman *et al*., 2015) and tree (Heijmans *et al*., 2013) presence are also noted at the expense of *Sphagnum* spp. cover. Once dominant, the lower albedo of vascular plants can enhance the warming of peatlands, further encouraging vascular plant success (Sturm *et al*., 2005).

These allogenic impacts on peatland stability (lower water table, increased nutrient availability, increased temperature) tend to interact to promote vascular vegetation biomass and abundance as well as *Sphagnum* spp. decline (Wiedermann *et al*., 2007; Heijmans *et al*., 2013). Generally studies have considered the interaction between temperature and another driver (water table elevation, nutrient availability, atmospheric CO_2 concentrations) reporting synergistic and not just additive effects (Fenner *et al*., 2007a; Dieleman *et al*., 2015). For example, as previously noted, elevated atmospheric CO_2 conditions can have variable effects on peatland plant communities, but combined with elevated temperature conditions this driver strongly enhances vascular plant growth at the expense of *Sphagnum* spp. (Fenner *et al*., 2007a), resulting in interactive effects that could not be predicted by studying these factors in isolation.

5.3 'The Point'– The Known and Important Unknown Tipping Points

Critical thresholds, or 'tipping points', arise when a relatively small disturbance causes a system to shift from one state into a contrasting one (Scheffer *et al*., 2015). These shifts in stable state generally manifest as a rapid transition from one dominant functional group to another due to the formation of a self-reinforcing positive feedback loop (Kéfi *et al*., 2016), like those described throughout 'The Push'. In order to predict the conditions that precipitate changes in stable states, it is necessary to identify critical thresholds in systems (Scheffer *et al*., 2012a). Generally, the peatland literature only identifies coarse ranges of disturbances that result in dramatic changes in ecosystem structure. For instance, the time scale of a perturbation necessary for a change in the aboveground plant community in peatlands is generally reported to be between 1 and ~50 years (see Table 5.1). Such community changes are intrinsically linked to the intensity as well as the duration of the perturbation in question. For example, Laine *et al.*, (1995), Straková *et al*. (2012) and Talbot *et al*. (2014) all demonstrated that after approximately 40 years of sustained lowering of water table position, ranging from 15 to 170 cm below local ambient conditions, a peatland can shift into a forest state. Weltzin *et al*. (2003), Breeuwer *et al*. (2009), and Potvin *et al*. (2015) all show that in mesocosm studies moss-dominated peat systems transition towards a shrub-dominated state when the water table elevation is dropped by only 5 – 10 cm for less than 5 years. These studies indicate that as a driver, water table position may have multiple tipping points that can result in a number of different plant communities depending on the intensity and duration of the perturbation.

Table 5.1 A summary of key potential peatland state shifts by allogenic forcing factor and the associated potential tipping points based off of the current literature.

Driver	**Potential Regime Shift**			**Tipping Point Range**	**Literature**
Water Table	*Sphagnum* Moss Bog	→	Treed Bog/ Forest	15 – 170 cm (-) 40 years	Laine *et al*., 1995 Straková *et al*., 2010 Talbot *et al*., 2014
	Sphagnum Moss Bog	→	Shrub Bog/ Shrubland	5 – 10 cm (-) 5 years	Weltzin *et al*., 2000 Breeuwer *et al*., 2009 Bragazza *et al*., 2013 Potvin *et al*., 2015
	Brown Moss Fen	→	Shrub Fen	30 cm (-) 50 years	Pedrotti *et al*., 2014
	Graminoid Fen	→	Treed Fen/ Forest	50 – 70 cm (-) 30 – 50 years	Minkkinen *et al*., 1999 Laiho *et al*., 2003
	Swamp	→	Graminoid Fen	-	Hájková *et al*., 2012
Nutrients	*Sphagnum* Moss Bog	→	Treed Bog/ Forest	0.72 g N m^{-2} yr^{-1} 40 years	Gunnarsson *et al*., 2002
	Sphagnum Moss Bog	→	Shrub Bog/ Shrubland	1.5 – 3.2 g N m^{-2} yr^{-1} 6.0 – 6.4 g P m^{-2} yr^{-1} 5.0 g K m^{-2} yr^{-1}	Breeuwer *et al*., 2010 Juutinen *et al*., 2010 Chong *et al*., 2012

				4 – 9 years	
	Sphagnum Moss Bog	→	Graminoid Bog/ Fen	0.9 – 6.4 g N m^{-2} yr^{-1} 2 – 80 years	Gunnarsson and Flodin, 2007 Heijmans *et al*., 2002 Wu and Blodau, 2015
	Shrub Bog	→	Graminoid Bog/ Fen	4.7 g N m^{-2} yr^{-1} 5 years	Sheppard *et al*., 2011
	Sphagnum Moss Fen	→	Shrub Fen	3.0 g N m^{-2} yr^{-1} 8 years	Wiedermann *et al*., 2007
	Graminoid Fen	→	*Typha* spp. Marsh	7 P mg L^{-1} 3.5 N mg L^{-1} 30 years	Kaldec and Bevis, 2009
Temperature	*Sphagnum* Moss Bog	→	Treed Bog/ Forest	+1°C 50 years	Heijmans *et al*., 2013
	Sphagnum Moss Bog	→	Shrub Bog/ Shrubland	+1.3°C 2 years	Jassey *et al*., 2013 Bragazza *et al*., 2013
	Sphagnum Moss Bog	→	Graminoid Bog/ Fen	+3°C 3 years	Fenner *et al*., 2007a
	Sphagnum Moss Fen	→	Shrub Fen	+6°C 1 year	Brancaleoni and Gerdol, 2014
	Sphagnum Moss Fen	→	Graminoid Fen	+4 – +8°C 1 year	Dieleman *et al*., 2015

Increased nutrient loading can also cause significant changes in peatland plant communities as the vegetation, particularly *Sphagnum* spp., are highly adapted to the nutrient-poor conditions common in most peatlands (Rydin and Jeglum, 2006). A review by Vitt *et al*. (2003) established that nitrogen loading above 1.5 g N $m^{-2}year^{-1}$ decreases *Sphagnum* spp. productivity. Subsequent research conducted in more complex peatland communities supports the findings of Vitt *et al*. (2003) (Wiedermann *et al*., 2007; Juutinen *et al*., 2010; Sheppard *et al*., 2011; Bragazza *et al*., 2013; Larmola *et al*., 2012), demonstrating that 3 – 9 years of simulated nutrient deposition at approximately 3 g N $m^{-2}year^{-1}$ can cause significant *Sphagnum* spp. die off in northern peatlands. Paired with this *Sphagnum* spp. loss, is significant shrub or graminoid expansion along the same timescale. For example, Tomassen *et al*. (2003) reported a 300% increase in graminoid biomass when the community was exposed to 4 g N $m^{-2}year^{-1}$ for 3 years. More intensive disturbance studies, such as Kadlec and Bevis (2009), show that a fen can rapidly shift into a *Typha* spp. dominated marsh after 30 years of nutrient-rich (total phosphorus = 3.5 mg L^{-1}, dissolved inorganic nitrogen = 7 mg L^{-1}) wastewater addition into the system. These studies suggest that changes in the vegetation community in a nutrient impacted peatland can be observed in as little as 3 years, and stabilized after 30 years of constant disturbance. The different natural biogeochemical, hydrological and topographical conditions innate to a fen versus a bog will likely cause these systems to have unique tipping points under the same nutrient addition conditions; however, the complexities of these tipping points remain unexplored.

Elevated CO_2 conditions can also provide a competitive advantage for vascular plants over *Sphagnum* spp. (Fenner *et al*., 2007b; Dieleman *et al*., 2015), although it is unclear whether increased atmospheric CO_2 alone can instigate a significant change in peatland vegetation structure and ecosystem state. The research that has explored elevated CO_2 conditions as an independent variable has predominately found only marginal effects on the plant community structure. Interestingly, these studies have predominately used the same treatment conditions, wherein ambient conditions are approximately 360 ppm and elevated conditions are approximately 560 ppm (Berendse *et al*., 2001; Heijmans *et al*., 2002; Milla *et al*., 2006; Toet *et al*., 2006; Siegenthaler *et al*., 2014). Thus, it is unknown if predicted atmospheric CO_2 conditions of 600 – 1000 ppm by 2100 (IPCC, 2013) will have a yet unrecognized independent role in peatland vegetation assembly. Certainly, it has been observed that elevated atmospheric CO_2 conditions do consistently result in peatland plant community changes when combined with elevated temperature (Fenner *et al*., 2007a; Dieleman *et al*., 2015).

Unlike atmospheric CO_2, higher temperatures clearly encourage vascular plant expansion independently, where warming by as little as 1°C has been modeled to cause moss-dominated peatlands to transition into forest ecosystems (Heijmans *et al*., 2013). Short-term studies substantiate this finding, showing that changes in the vegetation structure can start to appear in as little as 3 years and under 1°C warming (Weltzin *et al*., 2000; Fenner *et al*., 2007a; Jassey *et al*., 2013; Munir *et al*., 2014). Dieleman *et al*., (2015) demonstrated elevated temperature (>4°C above ambient) can significantly increase graminoid abundance in a mesocosm study in a single growing season, although the loss of *Sphagnum* spp. was only seen at temperatures +8°C above ambient conditions. However, not all studies report a significant community restructuring under warming conditions. For example, Keuper *et al*. (2011) found no change in vegetation structure after 8 years of manipulated temperature conditions, albeit their warming treatments generally averaged below the 1°C that Heijmans *et al*. (2013) suggested as a threshold value. More long-term studies examining the effects of active warming above 1°C on the peatland plant community structure would be an asset in further defining northern peatland tipping points.

5.3.1 Important Unknown Interactions and Tipping Points

Understanding how drivers interact is arguably the most important step to predicting tipping points that will be applicable in real world scenarios. Ecosystems tend to move past tipping points due to multiple concurrent disturbances (Scheffer and Carpenter, 2003). Many peatland studies have considered the effects of multiple drivers simultaneously, typically elevated temperature conditions and a single other driver (increased atmospheric CO_2 concentration, lower water table elevation, increased nutrient conditions) (Weltzin *et al*., 2000; Wiedermann *et al*., 2007; Dieleman *et al*., 2015).

These interactions often have displayed synergistic effects on peatland vegetation structure and ecosystem function, further emphasizing the importance of interactive effects for anticipating tipping points in peatlands. For example, Munir *et al*. (2014) report an 88% and 141% increase in hummock vascular vegetation biomass under simulated warming (+0.8°C) and drought treatments (74 cm below control water table height) respectively, but found these two treatments interacted synergistically when combined to increase vegetation biomass by 355%. While a growing number of studies have documented the interactive effects of the climate change (e.g. increased temperature, elevated atmospheric CO_2 concentration, decreased water table position) and land use stressors (e.g. nutrient addition) the associated tipping points for these interactions still remain almost completely unknown. This is of particular concern as these specific variables are all likely to be intensified in the next 30 – 100 years due to anthropogenic activities (Millennium Ecosystem Assessment, 2005).

One approach to help identify exact tipping points is to employ regression style experimental designs with multiple treatment points along continuous variables. The majority of previous experiments have used a factorial design, which is a well-established and accepted experimental approach; however, the statistical power of the full-factorial design is dependent on the number of replicates the researchers employ, limiting the number of treatment conditions that can be feasibly considered (Cottingham *et al*., 2005). Regression analyses, conversely, are not limited by such conditions as statistical power increases as the number of variable states increases (Cottingham *et al*., 2005). With this, regression type experimental designs could provide more information on the shape and type of relationship between two variables — information that is critical for identifying unknown tipping points.

5.4 ‘The Plunge’– Peatland Stable State Shifts and CO_2 Flux

The allogenic drivers identified in my study are expected to prompt a number of possible regime shifts in peatland ecosystems based on current knowledge (see Figure 5.1). Considerable evidence has been produced demonstrating a shift from a *Sphagnum*-dominated bog state to a tree or shrub-dominated state. For instance, Laine *et al*. (1995), Heijmans *et al*. (2013), and Talbot *et al.* (2014) all provide convincing evidence that ombrotrophic *Sphagnum* bogs can rapidly transition into a stable forest ecosystem (Table 5.1). Similarly, studies by Gunnarsson and Flodin (2007), Heijmans *et al*. (2002) as well as Wu and Blodau (2015) suggest *Sphagnum*-dominated bogs can become dominated by graminoids, particularly when nutrient loading and temperature conditions increase. Remarkably less work has considered vegetation shifts in fen systems, despite the evidence that these systems also undergo rapid and significant changes, like the transition of a graminoid fen into a stable, non-peat forming *Typha* marsh documented by Kadlec and Bevis (2009). Accordingly, the regime shifts I present here summarize the current evidence available in peatland literature; however, notable knowledge gaps still remain.

Regime shifts, like those outlined above, are perhaps most concerning as they alter core ecosystem processes (Andersen *et al*., 2009). As peatlands store globally significant quantities of carbon, the long- and short-term consequences of such shifts are highly pertinent. I estimated the potential long-term effects by comparing different ecosystem CO_2 uptake and release rates in the literature. Specifically, I surveyed relevant studies and summarized a subset of year-round, ecosystem-level eddy covariance carbon flux values reported for various peatland types, as well as boreal forest and northern marsh systems (Figure 5.2). I found that in all cases the ecosystems considered were either approximately CO_2 neutral or CO_2 sinks. In fact, peatland bogs and mature boreal forest systems were on average weaker CO_2 sinks than peatland fen, northern marsh, or young boreal forest systems (Figure 5.2). This suggests that in the long-term even major transitions, such as a bog to a forest, will still result in some degree of continued CO_2 uptake. Current literature indicates that the short-term effects, however, will most likely enhance carbon release in excess of carbon uptake (Gerdol *et al*., 2008; Juutinen *et al*., 2010; Munir *et al*., 2015). A number of factors surrounding short-term effects remain unclear. For example, based off of current literature it is difficult to disentangle the direct stimulatory role of state drivers (i.e. water table, nutrients, temperature) on carbon dynamics versus the direct effects of peatland state transitions. The potential duration and intensity of short-term transitional effects also remain unknown. For example, if these short-term effects are relatively prolonged and/or intense, peatland carbon stores maybe significantly reduced by even minor ecosystem state transitions.

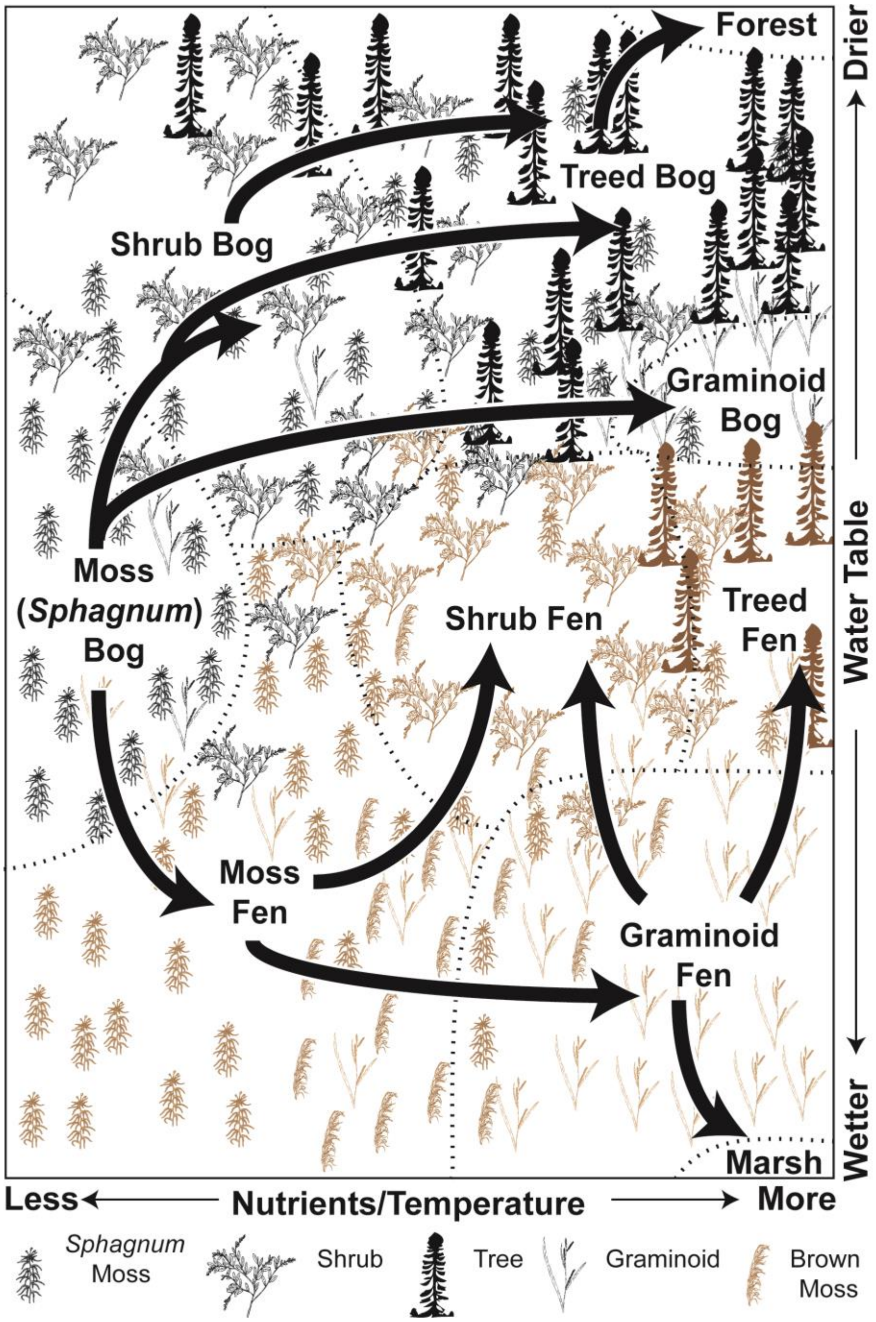

Figure 5.1 A summary of potential peatland stable state shifts as prompted by the allogenic factors, nutrients (including atmospheric CO_2 concentration), temperature, and water table conditions. The arrows indicate the direction of a system state shift while the position of the peatland system indicates increases or decreases in different allogenic factors. Marsh and forest systems are included on the figure's edge as potential states that arise under particularly long-term or intense disturbances. The vegetation indicates

the dominant functional plant groups associated with different systems while also illustrating how these groups occur in a continuum across conditions. The colouration of the vegetation indicates if the vegetation is generally bog plants (dark colour) or fen plants (light colour).

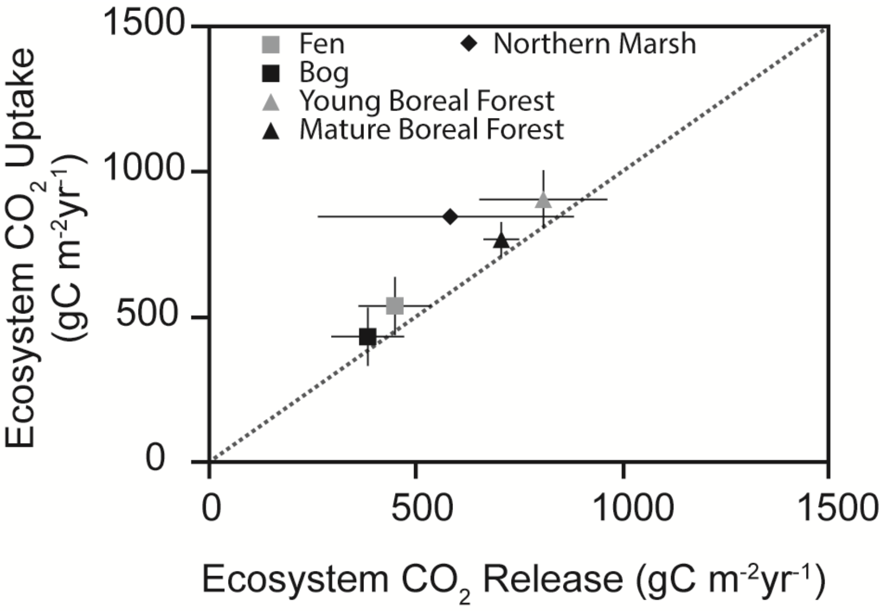

Figure 5.2 A summary of annual, ecosystem level CO_2 uptake and release values averaged for northern peatland, boreal forest and northern marsh systems. The dotted line indicates equal CO_2 uptake and release rates in an ecosystem. Accordingly, values above the 1:1 relationship indicate an overall CO_2 uptake for a system, while values below the line would indicate overall CO_2 release. Carbon dioxide flux sources: Aurela *et al*. (2004), Syed *et al*. (2006), Aurela *et al*. (2007), Lund *et al*. (2007), Luyssaert *et al*. (2007), Bonneville *et al*. (2008), Sulman *et al*. (2009), Lund *et al*. (2010), Wu *et al*. (2012), Humphreys *et al*. (2014), McVeigh *et al*. (2014), Peichl *et al*. (2014), Chu *et al*. (2015), Helfter *et al*. (2015).

5.5 Conclusions

Climate and land use change events are anticipated to cause significant environmental changes in the high latitude regions where northern peatlands commonly occur (IPCC 2013). Such notable environmental changes are likely to have rapid and long lasting effects on peatland ecosystems. Using the stable state framework I identified the key drivers and the associated feedbacks that will push peatland ecosystems towards a regime shift, while providing discussion on our current understanding of peatland tipping points that will plunge peatlands into a new state. I found that these drivers generally give a strong competitive advantage to vascular plants over *Sphagnum* spp., prompting peatlands to shift towards more vegetated states, such as a forest or shrubland systems. Such notable changes in ecosystem structure and state will alter core ecosystem functions, such as carbon sequestration and storage. The relatively short-term transitional effects prompted by an ecosystem state shift will likely be the greatest threat to the stability of peatland carbon stocks, depending on the intensity and duration of the transition. Taken together my work provides the foundation for anticipating these changes in peatland ecosystems, while identifying key knowledge gaps that, if addressed and applied, could significantly enhance land management practices and policies.

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Chapter 6

6 General Discussion

Over the past 30 years there has been a growing recognition that anthropogenic induced climate change may elicit notable change in ecosystems around the world (Seddon *et al*., 2016). A particular research focus has been applied to high latitude ecosystems, like northern peatlands, as climate change impacts are predicted to be particularly intensified in that region (IPCC, 2013). As a result of this effort it has become clear that peatland structures and functions are sensitive to many climate change stressors, including increased atmospheric CO_2 concentration (Fenner *et al*., 2007), increased temperatures (Weltzin *et al*., 2000), and water table drawdown (Strack *et al*., 2008). Consequently there is concern these climate change stressors may transition peatlands from established carbon sinks into notable carbon sources (Gorham, 1991; Limpens *et al*., 2008), and in turn augment climate change impacts around the world. Of greatest concern are the potential interactive effects of all three key climate change stressors and their cascading impacts (Turetsky *et al*., 2012), as they remain largely unknown in northern peatlands. Accordingly, my doctorial research was designed to advance our understanding on the interactive effects of climate change stressors on peatland structure and function while identifying mechanisms that propagate their effects at the local and ecosystem scales.

6.1 Influence of Climate Change on Northern Peatland Ecosystem Structure and Function

6.1.1 Structure

Ecosystem structure is a core system property that influences an array of important ecosystem functions (Grimm *et al*., 2013). As in most ecosystems, northern peatland plant community composition forms a central structure influencing a variety of ecosystem processes, including carbon dynamics (Walker *et al*., 2016). Research over the past decade has determined northern peatland plant community structure is sensitive to a variety of climate change stressors (Weltzin *et al*., 2000), which may interact to intensify plant community change (Fenner *et al*., 2007). Research by Turetsky *et al*.

(2012), specifically predicted that increased atmospheric CO_2 concentration, increased temperature, and decreased water table position would, over hundreds of years, interactively suppress *Sphagnum* moss prevalence to decrease peatland carbon storage and threaten peatland stability. The second chapter of my thesis empirically tests these predictions by considering the interactive effects of these three key climate change stressors on northern peatlands. In doing so I demonstrate rising temperatures, indeed trigger plant community restructuring events in northern peatlands. However, these structural changes were apparent within a single growing season, suggesting plant communities may restructure much faster than previously thought (Turetsky *et al*., 2012). This study is also one of the few to empirically quantify northern peatland stability loss under climate change conditions, demonstrating that temperatures between 4°C – 8°C above ambient conditions represent a previously unknown critical disturbance threshold for northern peatlands. This study is also one of the first to demonstrate that the same critical disturbance threshold in a northern peatland system can elicit contrasting plant community structures (graminoid dominance, graminoid-*Sphagnum* moss co-dominance), depending on the pre-existing system characteristics. Cumulatively, this research chapter indicates northern peatlands are likely to undergo plant community restructuring events under future climate change conditions, but resulting community structures may vary and be difficult to anticipate.

6.1.2 Function

Northern peatlands, like any ecosystem, perform a range of critical ecosystem functions, including hydrological and biogeochemical cycling (Moreno-Mateos *et al*., 2012). Of these there has been a particular research focus on carbon dynamics due to its role in global climate regulation (Limpens *et al*., 2008). My third chapter contributes to this field of study by considering the interactive effects of the three main climate change stressors on key aspects of northern peatland carbon dynamics, including decomposition rates and dissolved organic carbon (DOC) concentration and characteristics. In doing so I found clear signals that climate change stressors directly and indirectly alter carbon cycling in northern peatlands. Specifically, I found that warmer and drier conditions directly increased decomposition rates of the peat matrix, most likely increasing the complete mineralization of simple DOC compounds, which renders the remaining DOC more humified and recalcitrant in nature. These findings correspond well with established decomposition drivers (Davidson and Janssens, 2006) and past peatland decomposition studies considering raised temperatures and water table drawdown (Hilasvuori *et al*., 2013; Ise *et al*., 2008). That said I also found that increased atmospheric CO_2, increased temperature, and high water table position increased both DOC concentration and lability, most likely as an indirect effect of stimulating graminoid productivity. These indirect effects were arguably stronger drivers of peatland DOC dynamics as they clearly influenced both DOC concentration and characteristics, unlike the direct effects of climate change stressors. These findings also support the work of Ward *et al*. (2015) who conclude plant community characteristics can be a stronger driver of carbon cycling processes than local environmental conditions. Taken together this data chapter illustrates that when interactive effects are considered, indirect drivers can become central to understanding ecosystem level changes in functions like carbon cycling.

6.1.3 Local Mechanisms

Changes in core ecosystems structures are expected to intrinsically alter many core ecosystem functions; however, the mechanisms that link these changes are often unknown or poorly constrained. Northern peatlands are no exception to this knowledge gap. Accordingly my fourth chapter builds on the findings reported in the data chapters preceding it, to discern how common plant growth forms that comprise different peatland community structures mechanistically influence northern peatland carbon dynamics. In doing so I found that the graminoid growth form significantly increases belowground dissolved carbon lability, stimulating microbial activity and metabolic diversity to increase respired CO_2 release; a mechanism that strongly resembles the microbial priming effects commonly reported in mineral soils (Kuzyakov *et al*., 2000). That said, research considering priming effects in boreal systems, no less northern peatlands, has long been highly limited (Fan *et al*., 2013; Linkosalmi *et al*., 2015). Of the remarkably few studies that have considered priming effects in peatlands, researchers have reported no, or limited evidence of this phenomenon (Basiliko *et al*., 2012; Linkosalmi *et al*., 2015). These studies, however, did not consider graminoid or *Sphagnum* growth forms, nor did they employ intact monoliths as a study medium — rendering the structure of the plant community and the supporting peats incomparable. The addition of my research to the literature implies that microbial priming-like effects can mechanistically link changes in northern peatland structure and function for select plant communities, although additional research is needed to determine the nuances of this relationship.

6.2 Influence of Climate Change on Northern Peatland Stable States

Fundamental changes in ecosystem structure and function constitute, by definition, an ecosystem state shift. This renders stable state theory an ideal framework to consider the mechanisms that propagate changes in structure and function at the ecosystem scale. By applying stable state theory to northern peatlands in my fifth chapter I was able to identify key drivers of peatland state shifts, describe the positive feedbacks that facilitate these shifts, outline associated disturbance thresholds for these shifts, and discern the short- and long-term effects for carbon storage. In doing so, I identify changes in temperature, water table position, and nutrient supply (including atmospheric CO_2) as key drivers of peatland vegetation structure. These factors alter the competitive relationship between *Sphagnum* moss and vascular species, allowing different growth forms to proliferate under different conditions (Eppinga *et al*., 2009). The phenomena is similar to one observed in boreal forest systems, where the severity and/or frequency of fire disturbances influences the competitive relationship between black spruce and broadleaf species — and thus the resultant vegetation structure (Johnstone *et al*., 2010). That said studies that identify key disturbance factors for ecosystems, particularly in the context of stable state theory, are rare. Yet, only by doing so is it possible to identify ecosystem vulnerabilities, and target conservation efforts to minimize ecosystem loss. For example, it is clear from my fifth chapter that all three main climate change stressors threaten peatland stability, emphasizing the need for preventative efforts.

6.3 Caveats and Limitations of the Experimental Designs

As much of my research was conducted using a mesocosm approach under controlled laboratory conditions there are important caveats and limitations to the interpretation of my work. While the trends presented throughout all of my data chapters remain sound, it is important that these trends are considered in the appropriate context. For example, the mesocosms used in Chapter 2 and Chapter 3 were 30 cm in diameter, precluding the inclusion of mature trees — trees that directly alter carbon cycling and plant community structure. Mature black spruce (*Picea mariana*) trees are particularly common in northern peatlands, at times comprising up to 70% of the fine-root biomass that strongly influences organic carbon introduction into soils (Kalyn and Van Rees, 2006; Noguchi *et al*., 2016). Consequently, climate change driven alterations in mature black spruce fine root biomass could strongly influence peatland carbon dynamics, potentially eclipsing the trends I reported. Mature trees could also influence the plant community structure that forms under future climate conditions, potentially competitively suppressing the graminoid expansion I observed. Thus, without mature trees in my study, the trends I report have a limited applicability to *forested* northern peatlands.

The mesocosm approach I applied also limited the soil space available to the plants in my study, a notable limitation when considering plant community dynamics. In my first experiment (Chapter 2, Chapter 3) destructive sampling revealed roots became space limited by the experiment’s end, forming a mat approximately 5 – 10 cm thick at the base of many of the mesocosms. This high concentration of roots most likely intensified the root exudate signal as the experiment progressed, potentially over emphasizing the importance of this carbon pool under future climate change conditions. Space limitation may have also caused many species to occur in unusually high densities, intensifying intra-species interactions. For instance, space limitation may have intensified competition between *Sphagnum* moss and graminoid species contributing to the rapid shift in plant community structure I observed in Chapter 2.

Conducting my research under stable laboratory conditions allowed for the control and standardization of many environmental factors central to my research questions. However, laboratory infrastructure constraints can limit accurate simulations of field conditions, thereby introducing experimental artifacts. In both of my experiments

(Chapter 2, Chapter 3, Chapter 4) an accurate simulation of winter climate conditions was not possible as the environmentally controlled greenhouses used could not maintain temperatures below 10°C. Instead ambient temperature conditions were held at 11.5°C during the dormant season (Nov-Apr), coinciding with the averaging growing season temperature of the source peatland. While these temperature conditions reduced plant productivity (also due to changes in photoperiod), typical winter senesce of aboveground biomass did not occur — most likely causing shifts in plant community structure and carbon dynamics to arise unrealistically fast. That said we were also limited in providing an accurate simulation of the source peatland photoperiod, as the greenhouses used were dependent on the natural photoperiod of London, Ontario. This change in light availability (e.g. an increased 40 minutes on Dec 21) may have unintended effects on plant phenology, with potential cascading effects on plant productivity and belowground carbon release. Infrastructure limitations also imposed isothermal mesocosm soil profiles, contrasting with the depth dependent decline in temperature found under natural conditions (see Nichols, 1998). Under future climate change conditions we can expect surface air to warm, contributing to warmed surface soils (IPCC, 2013); however, it is highly unlikely that the top 35 cm of soil will warm uniformly to match surface air temperatures. Accordingly, the isothermal soils in my experiment may over emphasize future changes in ecosystem structure and function, as they may provide an unrealistic competitive advantage to graminoids over *Sphagnum* mosses (Eppinga *et al.*, 2009), and intensify microbial metabolic activity (Davidson and Janssens, 2006).

As suggested above and discussed in Chapter 2, a main caveat of these experiments are the temperature treatments. Infrastructure limitations required a modified growing season temperature program, as the environmentally controlled greenhouses used had a limited cooling capacity. To address this constraint I defined my ‘ambient’ treatment as the recent (last 5 years) growing season temperatures of London, Ontario. This rendered the growing season ambient temperature treatment approximately 5°C above the 30 year historical average for the sample source peatland. Thus, my experimental temperature treatments (ambient, +4°C above ambient, +8°C above ambient) could be interpreted as +5°C above source site, +9°C above source site, and + 13°C above source site respectively. Using this interpretation northern peatlands found at high latitudes could be described as highly resilient to future climate change conditions, with only very extreme warming conditions likely to induce changes in ecosystem structure and function (IPCC, 2013). That said many *Sphagnum* moss dominated peatlands can be found at latitudes similar to London, Ontario. Accordingly, I would anticipate that the trends I have presented throughout my experimental chapters (Chapter 2, Chapter 3, Chapter 4) to best represent future changes in this specific subset of northern peatlands.

Lastly, the hydrology of my mesocosms also did not equate to natural field conditions. Of particular note is the lack of lateral water flow in the peat matrix of my mesocosms. While water was added below the moss surface to simulate flushing dissolved compounds by lateral flow, it is unlikely this was accurately simulated. Lateral water flow can also be an important nutrient source for peatland vegetation (Damman, 1986), a nutrient source that was limited in my studies. Thus, natural lateral flows could generate distinctly different carbon dynamics and plant community responses then observed in my study. The rainwater used in my experiment was also simulated, using dilute Rudolph’s solution (see Faubert and Rudolph, 2002). The Rudolph’s solution used was originally designed to provide the nutrients needed to maximize *Sphagnum* moss growth, and then subsequently diluted to better represent the field conditions observed by Faubert and Rudolph (2002). Thus, the nutrients found in my dilute Rudolph’s solution likely do not reflect the rainwater found at the source peatland. As such it is possible the nutrients I added via my rainwater simulation created a fertilization effect. Depending on the extent of this fertilization I may have competitively disadvantaged *Sphagnum* mosses (Eppinga *et al*., 2009; Limpens *et al*., 2011), a disadvantage that could have been amplified under warmer climate conditions.

6.4 General Conclusions and Future Efforts

Taken together as a whole my doctorial research provides insights into the interactive and cascading effects of climate change stressors on a subset of northern peatlands. Specifically, this body of work collectively indicates climate change conditions can restructure northern peatland vegetation, prompting microbial priming-like effects that modify belowground carbon chemistry and potentially threaten the persistence of established peatland carbon stores. The changes in peatland structure and function presented here, combined with examples from the literature, provide strong evidence climate change can rapidly induce stable state shifts in some northern peatlands. Over the long-term these state shifts will result in continued CO_2 accrual, albeit with perhaps lost capacity. Over the short-term, however, the destabilized transitory phase between states is likely to pose the greatest threat to peatland carbon stores, as ecosystem structures, functions, and supporting mechanisms respond to the new conditions.

While my research presents new insights in a number of fields, including climate change biology, ecosystem ecology, and biogeochemistry, future research is needed to build on the findings presented herein. For example, mesocosm studies are intended to replicate natural systems while controlling confounding factors and treatment conditions; however, they also have accepted limitations that render them imperfect representations as discussed above (Stewart *et al*., 2013). My findings using this approach indicate more resource intensive climate change simulations in the field are now not only warranted, but an important research gap for climate change research in northern peatlands. Such research could incorporate the influence of naturally varying environmental conditions, such as water table, evapotranspiration, wet deposition, and solar irradiation, which were beyond the scope of my research. Field studies can also support long-term experiments, which may reveal important plant community and carbon dynamics changes driven by slower growing peatland vegetation, such as shrubs and trees.

My research also emphasizes the importance of continued efforts examining northern peatland carbon dynamics, and the mechanisms that govern them. Beyond the scope of my research was the relationship between carbon and other biogeochemical cycles known to influence carbon movement, such as nitrogen (Wu and Blodau, 2013). Work furthering the links between these biogeochemical cycles, and discovering changes that arise under climate change conditions will provide a deeper mechanic understanding of northern peatland carbon storage and stability. Associated with this biogeochemistry work should also be research on microbial priming effects in northern peatlands. This phenomenon is remarkably understudied (Linkosalmi *et al*., 2015), with the potential to be the driving mechanism of carbon release under future climate change conditions. Of particular interest is the proposed role of root structures and root exudates as a trigger for microbial priming effects and as a driver of peatland carbon dynamics.

An additional area with high potential for research is stable state theory itself, particularly in the context of northern peatlands. My research identifies that, to date, the critical thresholds associated with peatland state shifts are poorly defined if coarsely outlined at all. Research identifying thresholds for a variety of peatland structures is a necessity to determine a safe operating space for humanity (*sensu* Rockström *et al*., 2009) if peatlands and their ecosystem functions are to be maintained. Continued research considering the short-term effects of northern peatland state shifts is also critical to assess the vulnerability of established carbon stores. Only by determining the expected longevity and intensity of the short-term, transitory phase can adequate predications be made regarding northern peatlands' potential contributions to global atmospheric CO_2 concentrations and global climate change impacts.

6.5 Concluding Remarks

Northern peatlands represent a globally significant carbon store with the potential to augment climate change impacts around the world. In addressing this issue research has now started to consider how a variety of climate change stressors can interact to elicit yet unforeseen changes in ecosystem structure and function. Applications of stable state theory provides excellent promise as a framework to consider these interacting climate change stressors, and determine their ecosystem level effects in northern peatlands. By doing so in a concerted research effort we can ultimately determine if northern peatlands' end role will be as a continued carbon sink or transitory carbon source in the coming century.

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Appendices

Appendix A: Chapter 2 and Chapter 4 Supplementary Material

Table 1.A Chapter 2 supplementary material: A summary of the plant species observed throughout the 12 month mesocosm study. The average frequency describes the average number of mesocosms (n= 84 total) which contained the associated species throughout the experiment. The average abundance/percent cover describes the average number of individual or cover which was observed across all mesocosms for a species. The presence of *Vaccinium oxycoccos* L., *Carex disperma* Dewey, *Sphagnum* spp., *Gaultheria hispidula* (L.) Muhl. ex Bigelow, and *Campylium stellatum var. stellatum* (Hedw.) were all recorded in terms of percent cover. All remaining species were monitored by changes in abundance.

Scientific Name	**Common name**	**Average Frequency**	**Average Abundance/Percent Cover**
**Chamaedaphne calycalata* (L.) Moench	Leatherleaf	83	8
**Rhododendron groenlandicum* (Oeder) Kron & Judd	Bog Labrador Tea	49	2
**Lycopodiella inundata* (L.) Holub	Northern Bog Club Moss	47	3
**Kalmia polifolia* Wangenh	Bog Laurel	76	7
**Andromeda polifolia* (L.)	Bog Rosemary	54	3
**Vaccinium myrtilloides* Michx.	Velvetleaf Blueberry	20	1
**Vaccinium oxycoccos* L.	Cranberry	79	8
**Carex disperma* Dewey	Softleaf Sedge	69	16
**Sphagnum* spp.	Peat Moss	82	86
**Carex magellanica* Lam.	Poor Sedge	45	7
**Campylium stellatum* var. *stellatum* (Hedw.)	Star Campylium Moss	9	2
Picea mariana (Mill.) B.S.P.	Black Spruce	4	0

Drosera rotundifolia L.	Round-Leaved Sundew	8	0
Abies balsamea (L.) Mill.	Balsam Fir	1	0
Gaultheria hispidula (L.) Muhl. ex Bigelow	Creeping Snow Berry	1	0
Maianthemum trifolium (L.) Sloboda	Three-leaf Solomon’s Seal	2	0

*Designates species that were included in the principal component analysis

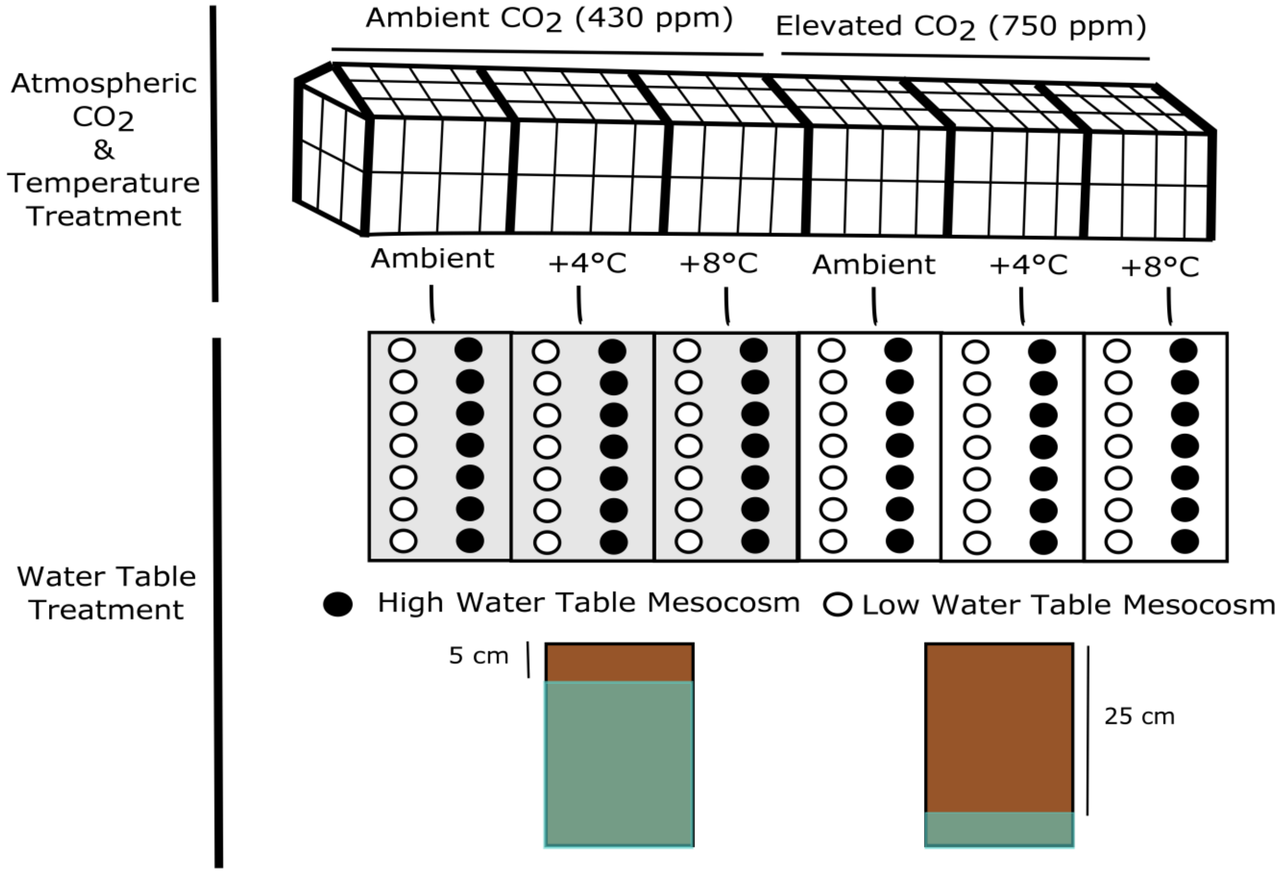

Figure A.1 Chapter 2 supplementary material: A schematic of the full factorial experimental design employed in six fully environmentally controlled greenhouses at the Biotron Center for Experimental Climate Change in London, Ontario. Two atmospheric CO_2 treatments were maintained in the greenhouses, with three greenhouses under ambient CO_2 (430 ppm) and three under elevated CO_2 (750 ppm). Under each atmospheric CO_2 treatment three temperature treatments were employed, namely ambient, +4°C above ambient, and + 8°C above ambient. Within each greenhouse two water table treatments were maintained, a high water table (5 cm below the mesocosm peat surface) and a low water table (25 cm below the mesocosm peat surface). Each water table treatment had seven replicates for a total of 84 experimental mesocosms.

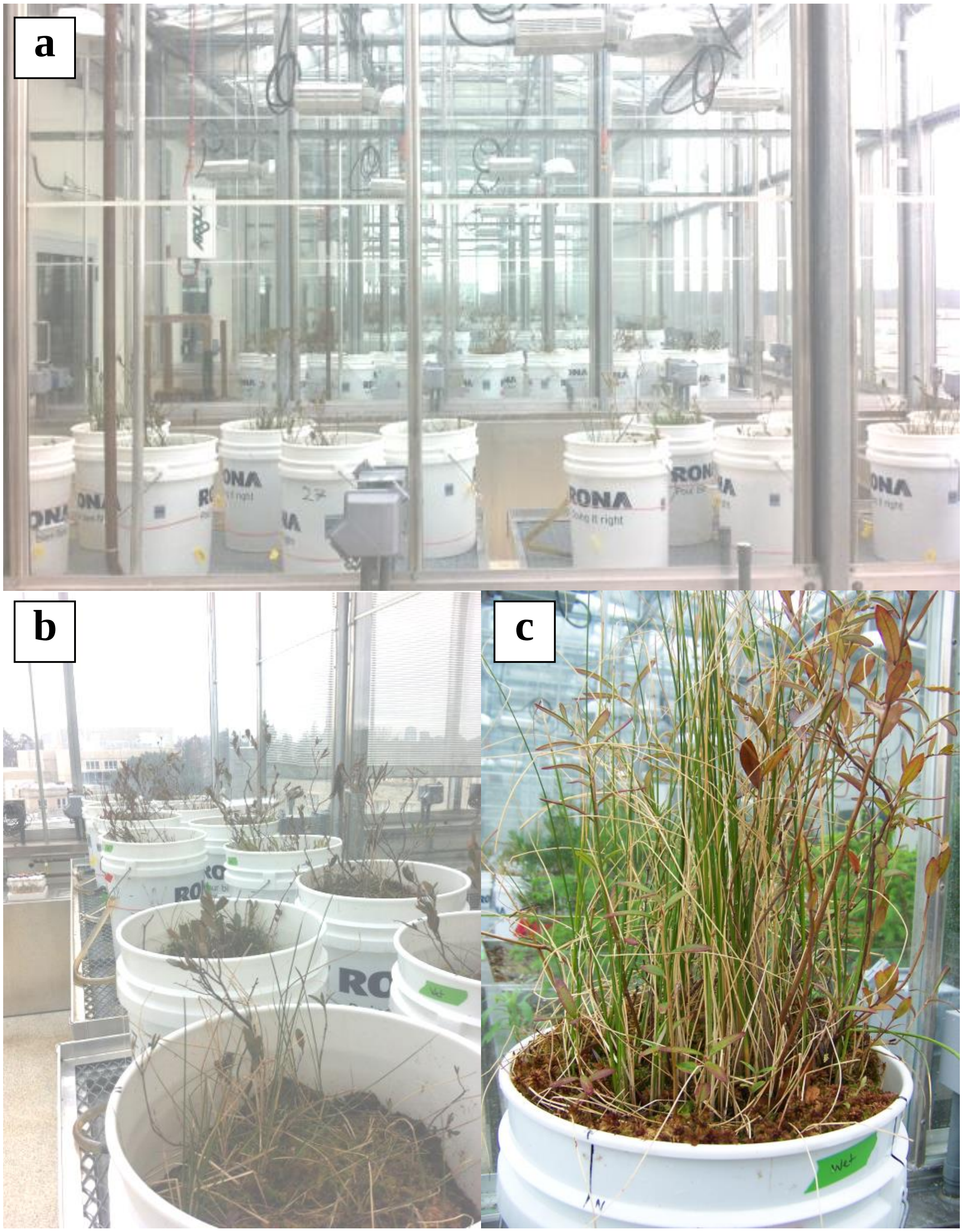

Figure A.2 Chapter 2 supplementary material: Images of the experimental setup at the Biotron Center for Experimental Climate Change in London, Ontario where (a) depicts all experimental mesocosms distributed evenly throughout six fully environmental controlled greenhouses, (b) mesocosms distributed within a single greenhouse at the experiment's initiation, and (c) a single mesocosm under the elevated CO_2 (750 ppm) and +8°C above ambient temperature treatment at the experiment's end.

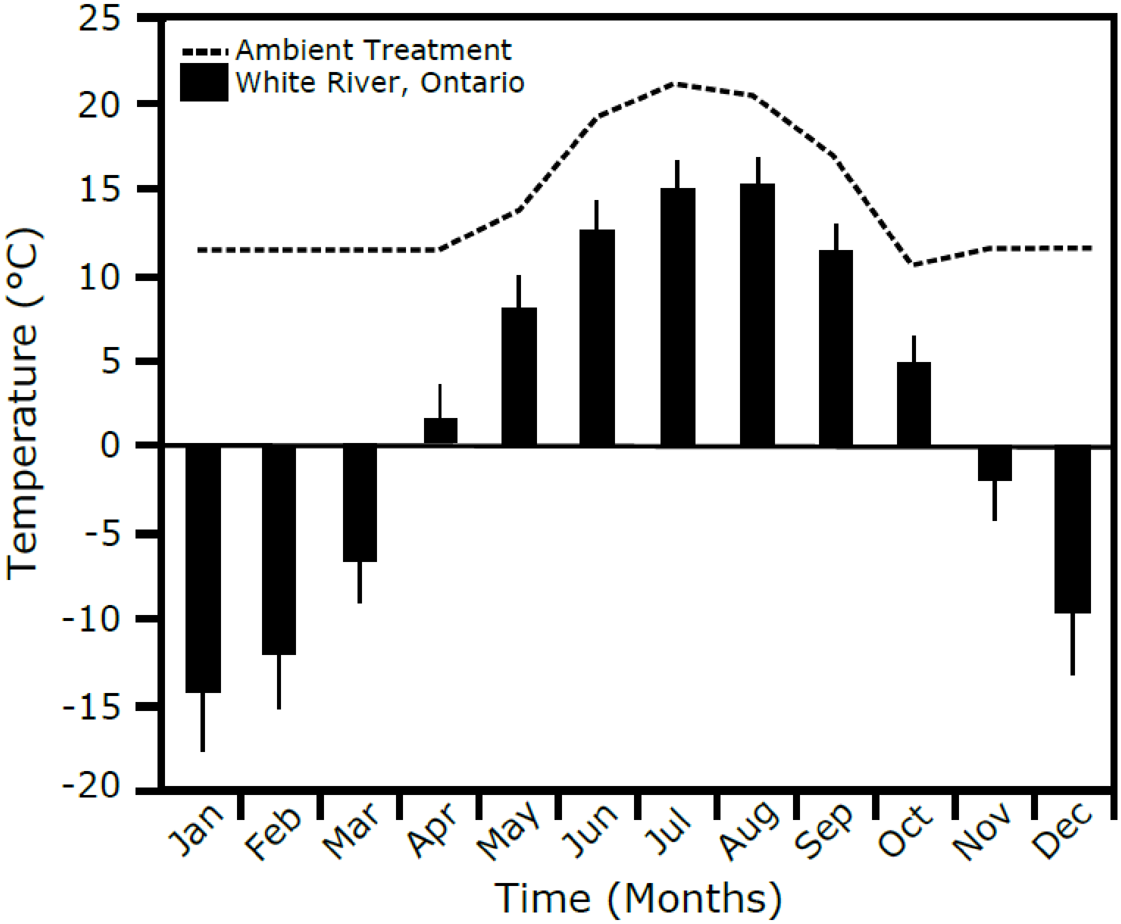

Figure A.3 Chapter 2 supplementary material: A comparison of the experimental ambient temperature treatment and the 30 year historical average temperatures in White River, Ontario where study material was collected. Throughout the growing season (May – Oct) the ambient treatment temperatures were approximately 5°C above White River, Ontario historical norms. Due to infrastructure constraints ambient temperatures during the dormant season were held constant at 11.5°C, reflecting the averaging growing season temperature of White River, Ontario.

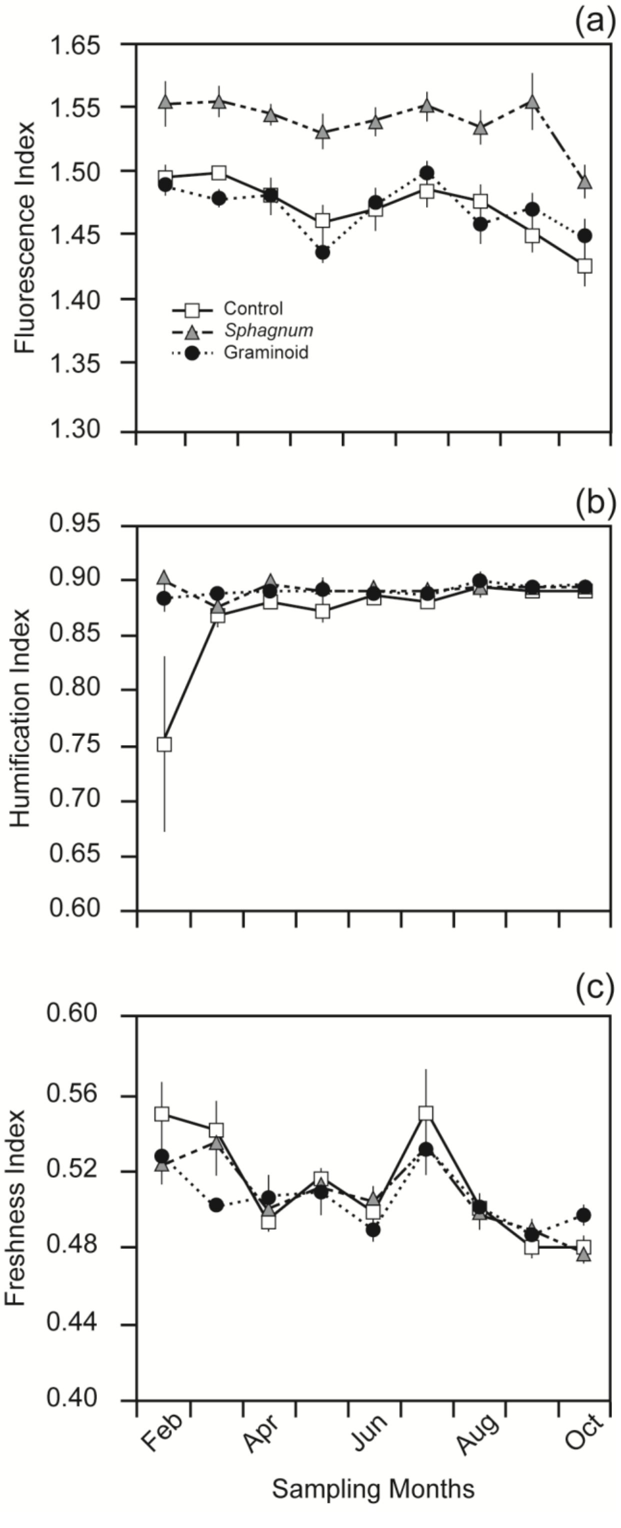

Figure A.4 Chapter 4 supplementary material: Excitation-emission matrix (EEMS) measures of mesocosm porewater dissolved carbon quality summarized by the fluorescence index, the humification index, and the freshness index as defined by Fellman *et al*. (2010).

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Curriculum Vitae

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Education

Ph.D. Biology (Environment and Sustainability) University of Western Ontario	**Sept 2012 - Present**
M.Sc. Conservation Biology McMaster University	**May 2010 - April 2012**
B.Sc. (Honours) Biology, GIS minor McMaster University	**Sept 2006 - April 2010**

Awards and Honours

2016 - Environment and Sustainability Travel Award- academic distinction and thesis ingenuity
2016 - Biology Graduate Travel Award- excellence in research
2015 - Biology Graduate Research Forum Best Three Minute Thesis Presentation
2015 - Dr. Irene Uchida Fellowship in Life Sciences- academic distinction and scientific success
2015 - Environment and Sustainability Travel Award- academic distinction and thesis ingenuity
2015 - Environment and Sustainability Award of Excellence- notable extracurricular involvement
2014 - David E. Laudenbach Scholarship- research excellence and extracurricular involvement
2014 - Canadian Society for Ecology and Evolution Presentation Honourable Mention- exemplar communication skills and research excellence
2014 - Ontario Graduate Scholarship- academic distinction and thesis ingenuity
2014 - Northern Science Training Program Grant- thesis ingenuity
2014 - Environment and Sustainability Award of Excellence- notable extracurricular involvement
2013 - Biology Graduate Research Forum Best Oral Presentation- communication excellence
2013 - Society of Graduate Students Travel Grant- academic distinction
2013 - Canadian Water Resources Association Graduate Scholarship- academic and thesis excellence
2013 - Environment and Sustainability Award of Excellence- academic distinction and leadership
2013 - Northern Science Training Program Grant- thesis ingenuity
2011 - A.D. Latornell Conservation Symposium Grant
2011 - Ontario Graduate Scholarship- academic distinction and thesis ingenuity
2011 - Philip H. Jones Award - Central Canadian Symposium on Water Quality Research Best Student Presentation

2010 - McMaster Graduate Entrance Scholarship- academic distinction
2010 - Graduation with Distinction - cumulative average above 80%
2010 - Canadian Sportsmanship Scholarship- leadership in conservation and academic achievement
2010 - McMaster University Biology Undergraduate Symposium Best Ecology Presentation
2010 - Dean's Honour List - average above 78% in last 10 completed classes
2009 - Dean's Honour List - average above 78% in last 10 completed classes
2008 - Dean's Honour List - average above 78% in last 10 completed classes
2006 - McMaster Entrance Award Scholarship - graduation average of 88%
2006 - Queen Elizabeth Aiming for the Top Scholarship - academic distinction and leadership

Publications

Dieleman, C.M., Branfireun, B.A., McLaughlin, J.W., & Lindo, Z. (2015) Climate change drives a shift in peatland ecosystem plant communities: Implications for ecosystem function and stability. Global Change Biology. 21, 388-395. DOI: 10.1111/gcb.12643

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Dieleman, C.M., Branfireun, B.A., Lindo, Z. (Under Review) Peatland plant growth form effects on dissolved organic carbon characteristics and carbon release — evidence of graminoid priming effect. Plant and Soil.

Conference Presentations

Dieleman, C.M., Branfireun, B.A., McLaughlin J.W. & Lindo Z. (2016, Aug) Ecosystem level changes associated with *Sphagnum* decline under future climate change conditions in northern peatlands. Ecological Society of America, Fort Lauderdale, USA

Dieleman, C.M., Branfireun, B.A., & Lindo Z. (2016, July) What happens above matters below: Linking plants and soils in northern peatlands. Canadian Society of Ecology and Evolution Conference, St. John's, Canada

Dieleman, C.M., Branfireun, B.A., McLaughlin, J.W., & Lindo, Z. (2016, Feb) Enhanced carbon release under future climate conditions in a peatland mesocosm experiment: The role of phenolic compounds. Student Canadian Geophysical Union Conference, Waterloo, Canada

Dieleman, C.M., Lindo, Z., McLaughlin, J.W., & Branfireun, B.A. (2015, Mar) Warmer and drier northern peats are not subjected to runaway decomposition under future climate change conditions. Mer Bleue Peatland Workshop, Montreal, Canada

Dieleman, C.M., Lindo, Z., McLaughlin, J.W., & Branfireun, B.A. (2015, Feb) Warmer and drier northern peats are not subjected to runaway decomposition under future climate change conditions. Science for a Changing North Conference IV, Sudbury, Canada

Dieleman, C.M., Lindo, Z., McLaughlin, J.W., Craig, A., & Branfireun, B. (2015, Feb) Accelerated decomposition under experimental climate change drives shifts in both the quantity and quality of peatland dissolved organic matter. Student Canadian Geophysical Union Conference, Waterloo, Canada

Dieleman, C.M., Branfireun, B.A., McLaughlin J.W., & Lindo Z. (2014, May) Climate change drives a shift in peatland ecosystem plant communities: Implications for ecosystem function and stability. Canadian Society of Ecology and Evolution Joint Conference, Montreal, Canada

Dieleman, C.M., Branfireun, B.A., McLaughlin J.W., & Lindo Z. (2014, Feb) Climate change drives a shift in peatland ecosystem plant communities: Implications for ecosystem function and stability. Mer Bleue Peatland Workshop, Montreal, Canada

Dieleman, C.M. & Chow-Fraser, P. (2013, Oct) Periphyton growth as an indicator of agricultural impacts in low-order streams in the Beaver Valley watershed, Ontario, Canada. Biology Graduate Research Forum, London, Canada.

Dieleman, C.M. (2013, Jul) On the vague and metaphorical definitions of "good ecosystem functioning". International Society for the History, Philosophy and Social Sciences for Biology Meeting, Montpellier, France.

Dieleman, C.M. & Branfireun, B. (2013, Apr) The impact of climate change on the biogeochemistry of peatland pore water in the Hudson Bay Lowlands. NSERC Canadian Network for Aquatic Ecosystem Services Meeting, Sudbury, Canada.

Dieleman, C.M. & Chow-Fraser, P. (2013, Mar). Don't backwash: the continuously monitored effects of livestock practices on a first-order stream. Western Research Forum, London, Canada.

Dieleman, C.M. & Chow-Fraser, P. (2011, Nov). Effect of agricultural practice, landform features and storm events on the water quality of first-order streams in the Beaver Valley watershed. A.D. Latornell Conservation Symposium, Alliston, Canada

Dieleman, C.M. & Chow-Fraser, P. (2011, Feb). Effect of agricultural practice, landform features and storm events on the water quality of first-order streams in the Beaver Valley watershed. 46th Central Canadian Symposium on Water Quality Research, Burlington, Canada

Dieleman, C.M. & Chow-Fraser, P. (2010, Apr) The effects of agricultural practice and storm events on water quality of first order streams in the Beaver Valley, Ontario, Canada. McMaster University Biology Undergraduate Symposium, Hamilton, Canada

Dieleman, C.M. & Chow-Fraser, P. (2010, Mar). The effects of agricultural practice and storm events on water quality of first order streams in the Beaver Valley, Ontario, Canada. Ontario Biology Day, Toronto, Canada

Professional Experience

Research Assistant **Jan 2013 - May 2013**

University of Western Ontario, London, ON

Collaborated weekly with Rotman Institute of Philosophy and Western University biology professors to help produce a high quality paper on ecosystem function

Research Assistant **Apr 2009 - Sep 2009**

McMaster University, Hamilton, ON

Deployed a Van Dorn, Seki Disk, YSI 6600 and ISCO 6720 auto sampler to collected discrete and continuous water samples
Independently performed complex lab procedures including sample analysis and instrument calibration
Identified wetland fish and aquatic flora to species throughout Georgian Bay, Ontario

Research Assistant **Apr 2008 - Sept 2008**

McMaster University, Hamilton, ON

Monitored *Larus smithsonianus* egg to fledgling abundances in water fowl colonies
Maintained nesting diversion devices to lower *Phalacrocorax carbo* populations
Assisted in the mark, recapture and DNA collection of *Phalacrocorax carbo* study specimens
Utilized non-invasive techniques to collect *Phalacrocorax carbo* dietary samples

Personal Experience

Biology Graduate Education Representative **Sep 2013 – Sep 2014**

University of Western Ontario Biology Graduate Society

Fairly and responsibly ranking graduate major scholarship applications to identify candidates to compete at the university level

Assessing and advising on admission packages presented by potential new graduate biology students

Earth Day Conference Organizer and Co-Chair **Sep 2012 - Present**

University of Western Ontario Earth Day Conference

Creatively planning and executing a two day conference attracting graduate students across Canada and local community members

Professionally assisting the committee to obtain >$5,000 in funding

Responsibly contacting and organizing conference keynote speakers

Biology Representative **Sep 2012 – Aug 2015**

University of Western Ontario Society of Graduate Students

Informing graduate representatives of graduate biology student issues

Performing democratic duties at each monthly meeting to handle the day-to-day issues of the graduate society

Sustainability Committee Member **Sep 2012 - Apr 2014**

University of Western Ontario Sustainability Committee

Consistently performing environmental waste audits of graduate student organizations

Ecology Representative

McMaster Graduate Biology Society **May 2010 - May 2011**

Represented ecology students in graduate student issues