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Carbon Cycling in Northern Fen Peatlands – Implications for Climate-Driven Changes of Ecosystem Carbon Fluxes

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Abstract

Northern peatlands are important long-term carbon (C) sinks with one-third of northern hemisphere soil organic carbon being stored there. Cool and wet environments at higher latitudes promote C accumulation in northern peatlands by limiting the C loss from decomposition. Northern latitudes are anticipated to experience disproportionately faster climate warming in the future, putting the vast C stores in northern peatlands at risk. There is a concern that northern peatlands are becoming net C sources and further accelerate climate warming. Using both laboratory and field experiments, this doctoral research aimed to explore the potential response of C cycling in northern peatlands to future climate change with the altered vegetation community, increased temperature and elevated atmospheric carbon dioxide (CO_2).

Sedge-dominated peatlands are expected to become increasingly prevalent relative to *Sphagnum*-dominated peatlands under future climate change. By comparing C fluxes between a sedge-dominated intermediate fen and a *Sphagnum*-dominated poor fen, this doctoral study showed that northern peatlands would become a smaller CO_2 sink by at least 16% but a larger methane (CH_4) source by at least 15% if the ecosystem is shifted from *Sphagnum* to sedge-dominated. Additionally, with this vegetation shift, northern peatlands will exhibit a more biodegradable dissolved organic carbon pool; the constituent would have lower molecular weight and aromaticity.

The vegetation composition together with CO_2 and CH_4 fluxes remained stable in the *Sphagnum*-dominated poor fen under *in situ* passive warming. In the sedge-dominated intermediate fen, however, the net CH_4 emission decreased by 11% under a moderate increase in temperature, owing to the greater CH_4 oxidation with increased plant productivity. The elevated atmospheric CO_2, together with more pronounced warming, concurrently increased aboveground plant productivity and belowground microbial decomposition, leaving the C sink function maintained in the sedge-dominated intermediate fen. Collectively, both warming and elevated CO_2 could extend the growing season, which could potentially increase the CO_2 uptake in northern peatlands.

Taken together, climate change can, both directly and indirectly, affect C fluxes in northern peatlands via altered vegetation community, vegetation biomass C allocation and the length of growing season. Vegetation-induced changes in C fluxes of northern peatlands should therefore be incorporated into atmosphere-ecosystem models to increase our ability in predicting the future climate.

Keywords

Carbon cycling, carbon dioxide, dissolved organic carbon, elevated atmospheric CO_2, fen-peatland, methane, sedge, *Sphagnum*, warming

Co-Authorship Statement

I understand that this dissertation will be made electronically available to the public. I hereby declare that Jing Tian (JT) is the sole author of this doctoral dissertation except for chapters described below:

Chapter 2 to 4 are prepared in the format of manuscripts to be submitted for publication in scientific journals. For the first manuscript (Chapter 2), Dr. Brian Branfireun (BB) and Dr. Zoë Lindo (ZL) designed the experiment and collected peat monoliths in the field with help from Dr. James McLaughlin (JM). I (JT) collected gas and water samples, analyzed samples, interpreted results and wrote the manuscript as the lead author, with contributions from BB and ZL.

The second and third manuscripts (Chapter 3 & 4) were based on a field experiment that was designed and deployed by BB and ZL with contribution from JM. For Chapter 3, the field sampling method was developed by Dr. Richard Petrone and JT. JT collected the samples, analyzed the data, interpreted the results and wrote the manuscript as the lead author. BB and ZL contributed to results interpretation and manuscript editing.

For Chapter 4, the field sampling method was developed by JT, BB and ZL. JT collected the samples, analyzed the samples and data, interpreted the results and wrote the manuscript as the lead author. BB and ZL contributed to results interpretation and manuscript editing.

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Abbreviations

ANCOVA	Analysis of Covariance
ANOVA	Analysis of Variance
BIX	Freshness Index
C	Carbon
C:N ratio	Carbon: nitrogen ratio
CH_4	Methane
CO_2	Carbon Dioxide
DOC	Dissolved Organic Carbon
EEMs	Excitation-Emission Matrices
ER	Ecosystem Respiration
FI	Fluorescence Index
GEP	Gross Ecosystem Productivity
HIX	Humification Index
IPCC	Intergovernmental Panel on Climate Change
MANOVA	Multivariate Analysis of Variance
NEE	Net Ecosystem Exchange
PCA	Principal Component Analysis
RM-ANOVA	Repeated Measures Analysis of Variance

$SUVA_{254}$	Specific Ultraviolet Absorbance at Wavelength 254 nm

Chapter 1

1 General Introduction

1.1 Global Carbon Cycle

Carbon (C) is an essential element of life on the Earth, and the C cycle is a vital part of biogeochemistry. Globally, there are four major C reservoirs on the Earth: the atmosphere, oceans, terrestrial ecosystems and fossil fuels. The oceans contain the most substantial amount of C on the Earth (Houghton, 2003). However, only about 1.7% of this C storage is within the surface ocean that interacts with the atmosphere (Folkowski *et al.*, 2000). Also, the photosynthesis rates in the oceans are relatively slow in relative to terrestrial ecosystems owing to the nutrient limitation in the sea water (Bashkin & Priputina, 2008), thus, a majority of C (~97.4%) in the oceans is inorganic C, which exists mostly in non-living organism (Houghton, 2003).

Even though C is only made up ~ 0.03% of the atmosphere, the atmosphere C pool connects with all three other C reservoirs, and there are large C exchanges (e.g., carbon dioxide, CO_2) between the atmosphere and other C reservoirs. For example, the annual CO_2 exchange between the atmosphere and the land is about 56 Pg (1 Pg = 1×10^{12} g) C via plant photosynthesis and plant respiration (Field *et al.*, 1998). Likewise, the chemical equilibrium among dissolved CO_2, carbonate and bicarbonate is of great importance in determining the atmospheric CO_2 concentration (Bashkin & Priputina, 2008). There is about 90 Pg C being released from surface ocean to the atmosphere each year via the diffusion of CO_2 (Houghton, 2003).

Organic matters stored in the fossil forms, including oil, coal and natural gas, represent a long-term C cycle whose accumulation rate is about 1000 times slower than C cycling within terrestrial ecosystems (Houghton, 2003). Prior to the industrial revolution, C stored in fossil fuels were relatively stable and were not cycled between different reservoirs; however, since the industrial revolution, the combustion of fossil fuel has contributed significantly to increased CO_2 emissions to the atmosphere (Janzen, 2004), and is primarily responsible for increasing CO_2 concentration in the atmosphere.

According to the recent Intergovernmental Panel on Climate Change (IPCC) Synthesis Report, the atmospheric CO_2 concentration has increased by 40% since pre-industrial times, and it is estimated to continue to rise to ~500 ppm by the end of this century (IPCC, 2014).

Terrestrial ecosystems play an essential role in the global carbon cycle, and it was reported that there were approximately 500 and 1200 Pg C stored in living vegetation and soil organic matter, respectively (Folkowski, 2000). Owing to small stocks and large fluxes, terrestrial C can be more sensitive to changes in the climate system in comparison to the oceans (Houghton, 2003). Meanwhile, the global temperature is projected to increase by ~ 4 to 11°C by 2100, with the most pronounced increase at high latitudes (IPCC, 2014), where there are large areas of terrestrial ecosystems such as Boreal forest, Boreal peatland and Arctic tundra. As estimated by the latest IPCC Special Report, the rate of climate warming could be higher on terrestrial ecosystems than oceans (IPCC, 2018). Hence, there are more substantial uncertainties regarding C storage and fluxes in terrestrial ecosystems as well as their feedbacks to future climate conditions.

1.2 Peatland Ecosystems

Peatlands, a type of wetland, are characterized by the accumulation of a thick layer of organic soil (peat) due to primary production exceeding organic matter decomposition (Joosten & Clarke, 2002). In Canada, the minimum depth of peat accumulation required to classify a wetland as a peatland is 40 cm (Warner & Rubec, 1997). Globally, peatlands exist in over 170 countries, most of which are located in the northern hemisphere, especially in Russia and Canada (Charman, 2002). Although only occupying ~ 3% of the global land surface, about 30% of global soil carbon (C) is stored in northern peatlands (Gorham, 1991). The main reason for the extensive peatland area in the northern region is its cool and wet climate, which significantly reduces C loss via decomposition (Clymo, 1984). Consequently, the peatland ecosystem is a valuable model for studying terrestrial-atmospheric C feedback, especially in the context of global change when the cool and wet climate is changed.

Peatlands are primarily classified into bogs and fens based on their vegetation, hydrology, trophic status, geomorphology, or a combination of those factors (Rydin & Jeglum, 2013; Sjörs, 1959). Bogs are ombrotrophic ecosystems – they receive water and nutrients solely from precipitation, due to increasing hydrologic decoupling from the surrounding environment with the accumulation of peat (Rydin & Jeglum, 2013). The dominant vegetation community in bogs is the *Sphagnum* moss, and *Sphagnum*-dominated bogs are acidic (pH ranged from 4.0 to 4.8) and nutrient-poor ecosystems (Gorham & Janssens, 1992; Warner & Rubec, 1997).

Minerotrophic fens by definition receive water, nutrients and minerals from multiple sources, including precipitation, mineral-rich groundwater and surface runoff (Rydin & Jeglum, 2013). Fens also have a relatively wide range for pH, ranging from 5.16 to as high as 7.40 (Gorham & Pearsall, 1956). There are also often higher concentrations of cations, such as Ca^{2+} and Mg^{2+} in fens than bogs (Rydin & Jeglum, 2013; Vitt *et al.*, 1995). Fens are often dominated by vascular plants, especially sedges. Fens can be classified into poor, intermediate, and rich fens, which represents a continuum of increasing pH, base cation concentrations, and average water table elevation (Rydin & Jeglum, 2013; Webster & McLaughlin, 2010). Poor fens are more similar to bogs, and are also *Sphagnum*-dominated, acid and nutrient poor ecosystems, whereas rich fens are sedge-dominated, alkaline, and nutrient-rich ecosystems (Rydin & Jeglum, 2013; Webster & McLaughlin, 2010).

Peatland ecosystems provide a variety of crucial ecosystem services, including the regulation of water quality and nutrient supply to downstream ecosystems (Kimmel & Mander, 2010). Peatlands are also long-term atmospheric CO_2 sinks and natural CH_4 sources and play an essential role in global C cycling (Smith *et al.*, 2004). Peatland C cycling tends to respond differently to climate change among peatland types, making understanding of potential responses of different types of peatland to future climate changes highly important (Sulman *et al.*, 2010; Wu & Roulet, 2014). For example, Wu & Roulet (2014) quantitatively predicted that bogs might remain net C sinks in 2100 since the increase in plant productivity would offset the increase in ecosystem respiration. By contrast, fens are likely to switch to net C sources due to a larger increase in ecosystem respiration than plant productivity under warming and drying (Wu & Roulet, 2014). Many previous peatland studies have focused on *Sphagnum*-dominated peatlands such as bogs and poor fens while sedge-dominated peatlands, including intermediate and rich fens, have received much less attention (Limpens *et al.*, 2008). More in-depth studies of C cycling in less-studied peatland types is necessary in order to better understand the magnitude and direction of peatland-climate change feedbacks (Wu & Roulet, 2014).

1.3 Carbon Cycling in Peatlands

Peatland net ecosystem exchange (NEE) is the difference between CO_2 uptake via plant photosynthesis during the growing season (as measured by gross ecosystem productivity (GEP)) and CO_2 loss via ecosystem respiration (ER). The net CO_2 uptake of peatlands in North America is ~ 29 Tg C yr^{-1} (Bridgham *et al.*, 2006); however, NEE is variable over time and among peatland types, ranging from a net CO_2 sink of ~64 g C m^{-2} yr^{-1} to a net source of 145 g C m^{-2} yr^{-1} (Carroll & Crill, 1997; Griffis *et al.*, 2000; Hanis *et al.*, 2015; Moore *et al.*, 2002; Waddington & Roulet, 2000; Yurova *et al.*, 2007). Peatland GEP is primarily controlled by vegetation type, total plant biomass and some abiotic factors such as temperature and photosynthetically active radiation (Bubier *et al.*, 1998). Typically, vascular plants such as shrubs and sedges have substantially higher productivity than *Sphagnum* mosses (Ward *et al.*, 2013). At the ecosystem level, however, leaf area and the growing season length are more important variables in controlling the seasonal CO_2 uptake with higher leaf area and longer growing season supporting larger CO_2 sink capacities into peatlands (Lund *et al.*, 2010). Even though sedges generally have higher productivity than mosses, mosses have longer growing seasons than sedges due to an earlier start of photosynthesis in the spring (Moore *et al.*, 2006; Ward *et al.*, 2013). Thus, the plant productivity can be higher in the *Sphagnum*-dominated peatlands than vascular plant-dominated peatlands before the start of the peak growing season such as in the spring.

A significant proportion of C being assimilated by plant growth returns back to the atmosphere as CO_2 by ER, which include both autotrophic (plants) and heterotrophic (microbial) respiration (Glenn *et al.*, 2006; Griffis *et al.*, 2000; Riutta *et al.*, 2007; Sulman *et al.*, 2010; Waddington & Roulet, 2000). On average, heterotrophic respiration accounts for 50 to 78% of ER in peatlands (Frolking *et al.*, 2002; Trumbore *et al.*, 1999). Ecosystem respiration positively correlates with soil temperature (e.g., 5 cm below the surface), and it is a strong control on CO_2 emission at the ecosystem level (Bubier *et al.*, 1998; Lafleur *et al.*, 2005). The water table is another critical control of ecosystem respiration. A lower water table with a deeper aerobic zone could substantially enhance the rates of CO_2 emission from peatlands as aerobic respiration is significantly faster than the anaerobic respiration (Moore & Dalva, 1993; Munir *et al.*, 2014). Juszczak *et al.* (2013) suggested that increased temperature and decreased water table could interactively increase the ecosystem respiration by 5 to 18% in a temperature peatland.

The relative biodegradability of soil C is also a strong control on microbial decomposition rates. Sedge litter is easier to decompose than more decay-resistant *Sphagnum* mosses (Moore *et al.*, 2007), which leads to higher CO_2 emissions from sedge-dominated than *Sphagnum*-dominated peatlands (Glenn *et al.*, 2006). Additionally, the rhizosphere activity of vascular plants, including root respiration and the decomposition of root exudates, significantly contribute 35 to 57% of the total peatland ecosystem respiration (Crow & Wieder, 2005). Hence, the presence of vascular plants, in particular sedges, tends to reduce the carbon sink capacity of peatlands at the ecosystem level (Kivimäki *et al.*, 2008).

Under anaerobic conditions, methane (CH_4) can be produced by the degradation of organic matter by methanogens (a group of Archaea) via methanogenesis (Lai, 2009; Segers, 1998). Fermentation-derived acetate and hydrogen are two main methanogenic substrates that support two different methanogenic pathways in peatlands (acetoclastic and hydrogenotrophic, respectively) (Segers, 1998). Meanwhile, CH_4 can also be oxidized to CO_2 by methanotrophs under both aerobic and anaerobic conditions. Thus, CH_4 emission from peatlands is controlled by the net balance between CH_4 production and oxidation. Globally, the wetland is the most significant natural CH_4 source to the atmosphere, emitting up to ~200 Tg yr^{-1} (Cao *et al.*, 1998). However, CH_4 emissions from peatlands also have high temporal and spatial variability owing to the complex controls on CH_4 production, consumption and transport from peatlands. Temperature and water table depth are two primary controls on CH_4 emissions from peatlands (Dunfield *et al.*, 1993; Yvon-Durocher *et al.*, 2014). Increased temperature can increase net CH_4 emissions from peatlands with increased CH_4 production (Dunfield *et al.*, 1993), whereas lower water table can decrease net CH_4 emissions from peatlands via enhanced CH_4 oxidation (Blodau *et al.*, 2004).

The vegetation type is frequently considered as an important control on CH_4 emissions, particularly in fens, which are dominated by vascular plants (Turetsky *et al.*, 2014). Vascular plants, especially sedges, play an important role in controlling the net CH_4 emissions through three mechanisms (Joabsson *et al.*, 1999). First, the labile C from plant photosynthesis and root exudation can provide C substrate that can be readily utilized by methanogens for CH_4 production (Chanton *et al.*, 1995; Öquist & Svensson, 2002; Ström *et al.*, 2003; Whiting & Chanton, 1993). Second, the aerenchyma tissues of sedges can increase the net CH_4 emissions by providing an efficient conduit for CH_4 transport from the subsurface to the atmosphere (Joabsson *et al.*, 1999; Öquist & Svensson, 2002). Lastly, the presence of vascular plants can also lead to a reduced CH_4 emission from peatlands, which is because the well-developed aerenchyma tissues in vascular plants (especially sedges) could largely enhance the transport of oxygen to plant roots and, therefore, increases the chance of CH_4 oxidation within the vascular plants rhizosphere (Luan & Wu, 2014; Öquist & Svensson, 2002; Strack *et al.*, 2006). Typically, the presence of vascular plants is correlated with higher CH_4 emissions, but those three processes might respond differently to increasing temperatures, making the net effect highly uncertain under climate change.

1.4 Peatland Carbon Cycling and Climate Change

1.4.1 Increased Temperature Effects

Temperature is a critical control on aboveground and belowground biological and chemical processes in peatlands. Higher temperature increases both aboveground plant productivity (C input) and belowground decomposition rates (C output), resulting in larger uncertainties on long-term C accumulations in northern peatlands. Previous studies have found a range of responses of peatland net C balances to increased temperatures, from an increase (Day *et al.*, 2008; Munir *et al.*, 2015), neutral (Chivers *et al.*, 2009) to decrease (Voigt *et al.*, 2017).

Aboveground plant productivity and rates of C uptake into peatlands will increase under increased temperatures in the absence of other limiting factors. For example, the warming condition was found to increase the total aboveground biomass or leaf area, especially for vascular plants such as shrubs, in tundra ecosystems (Sistla *et al.*, 2013; Voigt *et al.*, 2017; Walker *et al.*, 2006). Similarly, warming increased plant CO_2 assimilation by 23% to 34% in a vascular plant-dominated tundra (Day *et al.*, 2008) and by ~16% in an Alaskan rich fen that was dominated by both mosses and sedges (Chivers *et al.*, 2009). The increase of aboveground plant productivity under warming can be explained by the alleviated temperature constraints for plant growth (Weltzin *et al.*, 2003) as well as the alleviated nutrient limitation (e.g., increased N availability) due to increased microbial decomposition under warmer conditions (Li *et al.*, 2017; Natali *et al.*, 2012).

Microbial metabolism is temperature-dependent, and increases in temperature can significantly increase decomposition rates and subsequent C loss from northern peatlands in both gaseous (i.e., CO_2 and CH_4) and dissolved forms (i.e., dissolved organic carbon (DOC)) (Davidson & Janssens, 2006; Dunfield *et al.*, 1993; Flanagan & Syed, 2011; Pastor *et al.*, 2003; van Winden *et al.*, 2012; Wilson *et al.*, 2016). Pore water DOC concentrations in peatlands have been shown to increase considerably under warmer conditions, owing to the direct effect of increased temperature on enzyme activity and subsequent DOC production through decomposition (Dieleman *et al.*, 2016; Fenner *et al.*, 2005). With temperature increased by only 1°C, 65% more DOC was exported from a British peatland, which has the potential to alter water quality in surrounding rivers, streams and ultimately in the oceans (Freeman *et al.*, 2001a). Due to higher plant productivity, DOC leaching from fresh plant materials and the production of the fresh litter, which partially contribute to DOC production, would also occur at a faster rate under the increased temperature (Moore & Dalva, 2001; Ritson *et al.*, 2014; Voigt *et al.*, 2017). Some studies have attributed this increased DOC in peatland pore waters and runoffs to increased phenol oxidase concentrations under warming-associated drier conditions, which was responsible for enhancing the decomposition of what would otherwise be more recalcitrant soil organic matter (Freeman *et al.*, 2001b, 2004b). In contrast, other studies have found that DOC concentrations decreased with passive warming through open top chambers due to DOC consumption by microbes outpacing any increase in DOC production (Delarue *et al.*, 2014).

There is a good agreement in the literature that rising temperatures will lead to higher CO_2 emissions from northern peatlands via increased ER (Davidson & Janssens, 2006; Dorrepaal *et al.*, 2009; Gill *et al.*, 2017; Lafleur *et al.*, 2005; Leroy *et al.*, 2017; Treat *et al.*, 2014; Updegraff *et al.*, 2001; Voigt *et al.*, 2017; Wilson *et al.*, 2016). Lafleur *et al.* (2005) suggested that soil temperature was a more critical control of peatland ER than the water table elevation. Dorrepaal *et al.* (2009) found that peatland ER increased up to 60% with only 1°C increase in temperature, and 69% of this increase was due to enhanced heterotrophic respiration in the subsurface peat horizons. If this increase is applied to all northern peatlands, there could be approximately 38 to 100 megatons of additional CO_2 lost via ER in the next few decades due to global warming (Dorrepaal *et al.*, 2009). Similarly, in another northern peatland, ER significantly increased under warming conditions regardless of peatland type (e.g., bog and fen) or water table level, which indicated that soil temperature was the primary control when predicting climate-induced increases in ER from northern peatlands (Updegraff *et al.*, 2001).

The temperature sensitivity of soil respiration is strongly governed by substrate quality, microbial physiology, and plant-soil interactions in peatlands. Weedon *et al.* (2013) suggested that in comparison to its direct effect on microbial metabolism, increased temperatures had a more pronounced impact on soil respiration and CO_2 release by regulating the C substrate supply of decomposition. Also, warming was shown to stimulate decomposer activity by shortening the microbial food chain with a reduction in top predators (Jassey *et al.*, 2013). Under warming conditions, an increased decomposer activity led to a destabilization of peatland C storage with the increased C loss from the accelerated decomposition (Jassey *et al.*, 2013). Moreover, with the depletion of biodegradable C under long-term warming, the carbon use efficiency of microbes decreased, which led to slower response of CO_2 emissions to warming (Allison *et al.*, 2010). Temperature is a critical control on peatland CO_2 emissions, but the response of

CO_2 emission to temperature highly depends on other factors such as microbial physiology and C substrate quality and quantity. Since *Sphagnum*-dominated and sedge-dominated peatlands are different in terms of vegetation-induced C substrate, pH and microbial community, ecosystem reparations between two peatlands types may respond differently to increased temperature.

Climate warming will also increase the length of the active growing season with the earlier start of the growing season in the spring and the later senescence of plants in the fall (Piao *et al.,* 2008). The warmer spring and fall results in increases in both plant photosynthesis and ecosystem respiration in peatlands; however, the balance of increased plant photosynthesis and respiration would vary between seasons. More specifically, in the spring, the increases in the plant photosynthesis could offset the increase in C loss from soil respiration (Piao *et al.*, 2008). By contrast, the warmed fall could lead to the net C loss by the greater increase in the soil respiration than plant photosynthesis (Li *et al.*, 2017; Piao *et al.*, 2008).

Even though CH_4 emission is a relatively small component in the peatland C cycle (Gill *et al.*, 2017; Rinne *et al.*, 2018; Treat *et al.*, 2014), CH_4 is 34 times more powerful as a greenhouse gas than CO_2 (IPCC, 2014). Hence, it is imperative to take CH_4 into account when estimating global warming potential (GWP) of greenhouse gas emissions of peatlands. The net CH_4 emission from peatlands is the balance between CH_4 production and CH_4 oxidation and both processes are highly temperature-dependent (Dunfield *et al.*, 1993). Recent studies indicated that in an ombrotrophic bog, CH_4 emissions were more sensitive to increased temperature than CO_2 emissions (Gill *et al.*, 2017; Wilson *et al.*, 2016), with the Q_{10} of CH_4 and CO_2 emissions ranging from 2.12 to 32.16 and 1.88 to 3.46, respectively (Gill *et al.*, 2017). Warming conditions could increase rates of both CH_4 production and oxidation, but the overall response of these two processes to increased temperature is dependent on some other environmental variables. For example, Munir & Strack (2014) found that the water table was an important control on opposite responses of CH_4 emissions from hollows and hummocks. More specifically, warming increased the CH_4 emission at the wetter hollow by up to 26% whereas it decreased the CH_4 emission at the drier hummock by up to 56% (Munir & Strack, 2014). Considering significant differences in vegetation and physical conditions, it is expected that CH_4 emissions from *Sphagnum*- and vascular plants-dominated peatlands would respond differently to rising temperatures.

In northern peatlands, increased temperature can also indirectly affect C cycling since the dominant vegetation community is expected to shift towards a higher proportion of vascular plants under climatic warming (Bragazza *et al.*, 2013; Day *et al.*, 2008; Dieleman *et al.*, 2015; Weltzin *et al.*, 2000). In comparison to moss, vascular plants are more competitive for nitrogen (N) acquisition (especially protein–N), which facilitate their proliferation in the N–limited ecosystem as temperature increases (Hill *et al.*, 2011). As vascular plants grow taller, they start to create shading effects on moss, which can further impede the moss growth owing to the shade-intolerant nature of moss (Walker *et al.*, 2006). The shift in aboveground vegetation dynamics may also have cascading effects on belowground C processes. First, vascular plants, especially graminoids, can produce C substrate (e.g., litter and root exudates) with greater biodegradability, which has the potential to fuel the microbial decomposition (Mastný *et al.*, 2018; Ward *et al.*, 2009, 2015). Secondly, labile C pool in root exudates from vascular plants can also initiate the “priming effect” of microbial activity, where microbes can invest more energy into the decomposition of recalcitrant organic matter, which has been previously “locked-up” in deeper peat horizon (Basiliko *et al.*, 2012; Gavazov *et al.*, 2018; Walker *et al.*, 2016; Zhu & Cheng, 2011). Additionally, the accelerated downward leaching of DOC can also cause an increase of decomposition within the deep peat horizon (Voigt *et al.*, 2017). Overall, there is a general trend of increasing C substrate quality and decomposition rates with the shift of vegetation towards vascular plants under climate change.

1.4.2 Effects of Increased Atmospheric Carbon Dioxide

Elevated atmospheric CO_2 (referred to as elevated CO_2 after this) can affect the peatland C cycling by altered vegetation community composition, productivity, and physiology. Elevated CO_2 can increase both above- and belowground plant biomass (Fenner *et al.*, 2007b; Kang *et al.*, 2001). Increases in aboveground biomass or plant productivity could increase the C substrate supply for microbial decomposition, and as a result, elevated CO_2 can lead to an increase in the greenhouse gas release including CO_2, CH_4 and nitrous oxide (N_2O) as well as pore water DOC concentrations in peatlands (Dijkstra *et al.*, 2012; Freeman *et al.*, 2004a; Kang *et al.*, 2001). In addition, the vegetation community in peatlands can shift towards a greater abundance of vascular plants under elevated CO_2. Previous studies reported that there was a concurrent increase in the vascular plant cover and a decrease in *Sphagnum* moss cover in British peatlands under elevated CO_2 (Fenner *et al.*, 2007b; Freeman *et al.*, 2004a). This shift in vegetation community can fuel the microbial decomposition by the increased supply of labile C substrate (e.g., increased root exudation and higher litter quality of vascular plants) and result in a greater C loss from peatlands. Fenner *et al.* (2007b) found there was an increase in the proportion of recently assimilated C in the pore water DOC under elevated CO_2, indicating the increased contribution of plant productivity or root exudates to the DOC pool. Likewise, the increased root exudation has been found to be responsible for the increased DOC concentration in peatlands under elevated CO_2 (Freeman *et al.*, 2004a). Again, with the presence of labile C substrate, rates of microbial decomposition can be further stimulated via the “priming effect” of microbial activity.

Belowground C processes such as methanogenesis, have been shown to be more responsive to elevated atmospheric CO_2 in relation to the aboveground plant productivity. It was well-established that plant productivity was a critical control on the CH_4 production and emission from peatlands (Dacey *et al.*, 1994; Lai, 2009; Ström *et al.*, 2003, 2012; Whiting & Chanton, 1993). Elevated CO_2 was shown to significantly increased CH_4 emissions from peatlands, which was attributed to increasing C substrate supplies for methanogenesis from plant productivity (Dacey *et al.*, 1994; Megonigal & Schlesinger, 1997). The increased allocation of vegetation biomass to plant roots (Nie *et al.*, 2013) and faster turnover rates of roots (Megonigal & Schlesinger, 1997) under elevated CO_2 also contribute to a larger labile C pool for microbial decomposition. The increased root exudation of labile C under elevated CO_2 leads to a shift of microbial community structure towards a higher proportion of heterotrophic bacteria and CO_2 emissions from peatlands (Mitchell *et al.*, 2003). Moreover, elevated CO_2 resulted in decreased water table levels of peatlands by increasing plant evapotranspiration rates (Fenner *et al.*, 2007a). Thicker aerobic zones that are caused by lower water tables increased the oxidation of CH_4 and subsequently reduced the net CH_4 emission from peatlands (Fenner *et al.*, 2007a; Megonigal & Schlesinger, 1997).

Taken together, elevated CO_2 can affect the belowground C cycling in peatlands leading to enhanced C loss from peatlands in both gaseous (e.g., CO_2 and CH_4) and dissolved (e.g., DOC) forms, although aboveground plant productivity was also shown to increase under elevated CO_2. Increases in labile C pools from plant productivity and vascular plant root exudation also could potentially increase the "priming effect" of microbial decomposition (Freeman *et al.*, 2004a), but more studies on the "priming effect" under elevated CO_2 are required to reach a firm conclusion. Furthermore, elevated CO_2 can help plants preserve water during the growing season by increasing their water use efficiencies, which will eventually lead to a delay in the canopy senescence in the fall (Morison, 1985; Reyes-Fox *et al.*, 2014). Overall, elevated CO_2 and warming could interactively extend the length of plant growing season by about two weeks each year (Reyes-Fox *et al.*, 2014). The extension in the length of plant growing season have implications on net seasonal C uptake of peatlands and, therefore, should be included in the seasonal C modelling of peatlands at a regional or global scale under future climate change.

1.4.3 Vegetation Community Composition

As previously discussed, vegetation community composition is tightly coupled with peatland C cycling through its determinant role on C uptake via plant photosynthesis and C release as CO_2, CH_4 and DOC via microbial decomposition (e.g., Glenn *et al.*, 2006; Ward *et al.*, 2009). *Sphagnum* productivity is low in comparison to vascular plants such as shrubs and sedges (Armstrong *et al.*, 2015; Ward *et al.*, 2013). However, as a non-vascular plant, *Sphagnum* photosynthesis starts earlier in the spring than vascular plants, immediately after the snow thaw (Moore *et al.*, 2002, 2006). Vascular plants, in particular sedges, senesce earlier in the fall than *Sphagnum*, leading to a longer photosynthetic period for *Sphagnum*. For instance, Kivimäki *et al.* (2008) reported that peatlands that contained a mixture of sedges and *Sphagnum* were larger CO_2 sinks by between 63 and 226% than peatlands with pure sedge communities.

Sphagnum moss acts as the ecosystem engineer and plays a key role in peatland C accumulation owing to its low litter decomposability, antibiotic properties, and organic acids released from decaying *Sphagnum*, which may inhibit the microbial decomposition and, therefore, releases of CO_2 and CH_4 from *Sphagnum*-dominated peatlands (Hájek *et al.*, 2011; Scheffer *et al.*, 2001; Siegel *et al.*, 2006; van Breemen, 1995). *Sphagnum* litters are protected by the polymeric phenolic network in their cell walls, which facilitate the recalcitrant nature of *Sphagnum* (Scheffer *et al.*, 2001; van Breemen, 1995). *Sphagnum* cells contain a large amount of polyphenol compounds, including *Sphagnum* acids that can have a direct toxic effect on microbes (Verhoeven & Toth, 1995). Also, given its high cation exchange capacity, *Sphagnum* is responsible for the acidic condition in the surrounding environment, which suppresses microbial decomposition (van Breemen, 1995). Moreover, the extensive presence of *Sphagnum*-associated methanotrophic bacteria is responsible for ~10 to 30% of the CH_4 oxidation, resulting in lower CH_4 emissions from *Sphagnum*-dominated peatlands than vascular plant-dominated peatlands (Larmola *et al.*, 2010).

Fast decomposition of sedge litters leads to higher CO_2 emissions from sedge-dominated peatlands (Leroy *et al.*, 2017), and DOC can be consumed at a higher rate, resulting in lower DOC concentrations in those peatlands (Palozzi & Lindo, 2017; Scheffer *et al.*, 2001; Webster & McLaughlin, 2010). Also, root exudates from vascular plants provide more easily degradable C substrates (e.g., acetate and formate) for methanogenesis (Koelbener *et al.*, 2010; Ström *et al.*, 2003, 2012), which contribute to larger CH_4 emissions from vascular plant-dominated peatlands. For example, Ström *et al.* (2003) showed faster CH_4 production rates within the rhizosphere of sedges due to the delivery of acetate in root exudates.

With climate change, the decreased growth of *Sphagnum* moss may weaken the C sink capacity in northern peatlands via enhanced C loss from microbial decomposition in more vascular plant-dominated peatlands. Despite potential increases in plant productivity under warming condition (Day *et al.*, 2008), vascular plants are tightly coupled with higher decomposability of plant litter and plant leachate (Del Giudice & Lindo, 2017; Dorrepaal *et al.*, 2005; Pinsonneault *et al.*, 2016; Scheffer *et al.*, 2001) as well as a greater amount of labile C from root exudates (Bragazza *et al.*, 2013; Walker *et al.*, 2016), which may ultimately lead to stimulated decomposition and a negative feedback on C storage in peatlands. The net effect of climate change on aboveground plant productivity and belowground microbial decomposition require further investigations towards a better understating on how peatland C cycling will respond to future climate changes.

1.5 Predicting Peatland Carbon Storage under Climate Change

Experimental studies, including small-scale incubation, mesocosm and field manipulation, provide valuable information on controls of C cycling in peatlands and potential responses of peatland C cycling to changes in environmental variables. However, experiments have typically focused only on *Sphagnum*-dominated ombrotrophic bogs or poor fens (Dorrepaal *et al.*, 2009; Fenner *et al.*, 2007b; Juutinen *et al.*, 2018; Ward *et al.*, 2015) with fewer studies conducted in peatlands that are dominated by both *Sphagnum* mosses and vascular plants/trees (Chivers *et al.*, 2009; Flanagan & Syed, 2011). To the best of my knowledge, no manipulative field experiment has been conducted in sedge-dominated intermediate fens to date. Since vascular plants would be increasingly prevalent with future climate changes (Dieleman *et al.*, 2015; Fenner *et al.*, 2007b; Weltzin *et al.*, 2003), a more in-depth understanding of processes and controls on C fluxes in vascular plant-dominated peatlands is required to increase the accuracy on predicting the peatland-climate feedback. More long-term manipulative field experiments on different peatland types are called to solve this knowledge gap for three reasons. First, results from small-scale incubation studies cannot be directly transferred to field conditions since the living vegetation is always excluded from the experiment (e.g., Duval & Radu, 2018; Reiche *et al.*, 2010). Second, incubation and mesocosm experiments usually fail to manipulate the *in situ* environmental conditions such as precipitation, water table or natural expansion of vegetation (Agethen *et al.*, 2018; Dinsmore *et al.*, 2009). Lastly, short-term incubation and mesocosms studies hardly capture the year-year variations of peatland C fluxes, which become less accurate for prediction of the long-term C fluxes in peatlands (e.g., Gill *et al.*, 2017; Turetsky *et al.*, 2008).

Although unable to replace long-term field monitoring, modelling is an important approach that provides valuable insights on responses of peatland C cycling to climate changes at a broader scale (Webster *et al.*, 2013). Peatlands are still being largely neglected in many global C assessments despite its critical role in global C cycling, mainly owing to their unique local hydrology (Limpens *et al.*, 2008). However, significant progress has been made to improve peatland-climate models in the past two decades. For example, the first processed-based peatland C model, Peatland Carbon Simulator (PCARS), that was developed by Frolking *et al.* (2002) successfully modelled the plant photosynthesis in an ombrotrophic bog over three years, although it was biased with respect to ecosystem respiration. At the same time, Zhang *et al.* (2002) developed the wetland-DNDC model to predict both CO_2 exchanges and CH_4 emissions based on complex processes of hydrology, soil temperature and vegetation dynamics in wetland ecosystems. A newer process-based model — McGill Wetland Model (MWM) — has been developed based on the structure of PCARS (St-Hilaire *et al.*, 2010), which successfully modelled plant photosynthesis and ecosystem respiration as separate processes from the net ecosystem exchange of CO_2 in northern peatlands (St-Hilaire *et al.*, 2010).

Significant improvements in current peatland C models are still required to increase their power in predicting peatland C cycling under future climate change. A majority of current peatland C models were on the site-scale, and most of them were validated against measurements from ombrotrophic bogs (St-Hilaire *et al.*, 2010; Zhang *et al.*, 2002), while largely neglecting vascular plant-dominated fen peatlands (but see Wu *et al.*, 2013), even though fen peatlands account for more than half of the peatland area in Canada (Tarnocai, 2006). Also, despite its importance in peatland C cycles, DOC dynamics were not included in most peatland C models (St-Hilaire *et al.*, 2010; Wu *et al.*, 2013). Last but not least, different plant functional groups and peatland types that represent different biogeochemical processes have not been parameterized separately in peatland C models (Wu, 2009; Wu & Roulet, 2014). As a result, in order to apply current peatland C models to regional- or global-scales, more C flux components (e.g., DOC) should be incorporated and different peatlands types should be modelled separately in peatland C models.

1.6 Rationale and Objectives of the Dissertation

Although multiple studies have explored the effects of increased temperature or elevated CO_2 on northern peatland C storage, few studies focused on interactive effects of warming and elevated CO_2 on C storage function of northern peatlands, and there have been no studies in sedge-dominated fen peatlands. **The overall objective** of my dissertation is to evaluate the C storage function in two contrasting types of understudied but widespread fen peatlands in the Canadian boreal ecozone — the *Sphagnum*-dominated poor fen and the sedge-dominated intermediate fen. There are three studies (presented in three research chapters in an integrated manuscript format) in this dissertation that explore different aspects of carbon balance in fen peatlands under climate change. The objectives of these three studies are:

1) Using a laboratory mesocosm approach, to measure the independent and interactive effects of increased temperature and elevated atmospheric carbon dioxide on above- and belowground plant biomass allocation and C fluxes (CO_2 and DOC) in the sedge-dominated fen peatland over a growing season (Chapter 2).

2) Use the multi-year field-based experimental measurement of carbon dioxide and methane fluxes to quantify differences and main controls on annual C fluxes from two different fen peatland types (*Sphagnum*-dominated and sedge-dominated) and investigate the effects of a passive warming treatment on greenhouse gas fluxes between these two contrasting peatland types (Chapter 3).

3) Examine the differences in the quantity and quality of dissolved organic carbon pools between a *Sphagnum*-dominated poor fen and sedge-dominated intermediate fen, and quantify the changes in this quantity and quality under an experimental passive warming treatment (Chapter 4).

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Chapter 2

2 Climate Change Alters Peatland Carbon Cycling Through Plant Biomass Allocation

2.1 Introduction

Despite their low productivities, northern peatlands are important carbon (C) storage systems, due to extremely low decomposition rates under a cool climate and wet soil conditions (Gorham, 1991). Although boreal peatlands only cover about 3% of the Earth's land surface, they are estimated to store approximately 450 Pg of C, which is approximately one-third of all terrestrial soil C stocks (Gorham, 1991). Maintaining C storage of northern peatlands is vital for moderating increasing atmospheric carbon dioxide (CO_2) concentrations and lessening further warming. However, northern peatlands are vulnerable to current climate change as northern latitudes are warming faster than low latitude systems (IPCC, 2014) and small changes in temperature or atmospheric CO_2 could alter C storage in northern peatlands (Tarnocai, 2006).

Temperature is an important control on peatland C cycling. Ecosystem respiration (ER) is dependent on temperature, and warming is well-documented to increase microbial activity and decomposition rates leading to a higher release of respired CO_2 from these organic-rich peat soils (Carey *et al.*, 2016; Davidson & Janssens, 2006; Dorrepaal *et al.*, 2009; Lafleur *et al.*, 2005; Updegraff *et al.*, 2001; Ward *et al.*, 2013). The warming-induced increase in decomposition is also linked to increased dissolved organic carbon (DOC) production and export from northern peatlands (Dieleman *et al.*, 2016; Freeman *et al.*, 2001; Leroy *et al.*, 2017), further suggesting that warming will lead to greater C loss from northern peatlands.

Documented shifts in plant community structure favouring fast-growing vascular plants versus slow-growing *Sphagnum* mosses (Dieleman *et al.*, 2015; Weltzin *et al.*, 2003) could potentially increase the C storage in northern peatlands through increases in primary productivity (Wang *et al.*, 2016a). However, vascular plants may also supply more labile C to the peat-soil system (Del Giudice & Lindo, 2017; Gavazov *et al.*, 2018), fueling microbial metabolism and further increasing decomposition rates and C loss from northern peatlands (Basiliko *et al.*, 2012). The balance between C uptake via aboveground plant productivity and C loss through belowground microbial decomposition leads to a significant uncertainty on evaluating effects of climate warming on C dynamics in northern peatlands (Jiang *et al.*, 2018).

Elevated atmospheric CO_2 may also destabilize the peatland C storage through microbial “priming” effects. Elevated CO_2 is expected to increase root biomass more strongly than warming (Fenner *et al.*, 2007), increasing the supply of labile root exudates to the C pool in peat soils (Phillips *et al.*, 2011). This increasing labile soil C pool may stimulate microbial activity and growth, leading to an enhanced decomposition of more recalcitrant soil organic C, and an increased C release as CO_2 and DOC (Fenner *et al.*, 2007; Freeman *et al.*, 2004; Gavazov *et al.*, 2018). Several studies have correlated increased vascular plant productivity with increased DOC export (Dieleman *et al.*, 2016; Fenner *et al.*, 2007; Freeman *et al.*, 2004; Gavazov *et al.*, 2018) suggesting recent fixed C from plant productivity can be quickly transported to the belowground system. Thus, direct inputs of root exudates combined with increased decomposition products increase the potential of DOC production and export from ecosystems with high hydrological conductivity, such as fen peatlands.

Both increased temperature and elevated atmospheric CO_2 are anticipated to affect the C cycling in northern peatlands; however, whether these factors will increase or decrease the C storage potential of northern peatlands is still unclear. Additionally, the few experimental studies that have addressed interactive climate change effects were conducted on moss-dominated peatlands (Berendse *et al.*, 2001; Dieleman *et al.*, 2015, 2016; Fenner *et al.*, 2007), without considering vascular plants-dominated peatlands, even though more than half of the of the peatland area in continental Canada is sedge-dominated (Yu, 2006). Recent studies suggest that sedges are highly responsive to warming and are likely to gain a competitive advantage over more shallow-rooting shrubs with climate warming (e.g., Wang *et al.*, 2016b). To date, no study has quantified the combined effect of increased temperature and elevated atmospheric CO_2 on plant biomass allocation and C fluxes (e.g., CO_2 and DOC) in a sedge-dominated peatland. This is the first mesocosm study that considers interactive effects of warming and elevated CO_2 on intact sedge-dominated intermediate fen monoliths. The objective of this study was to examine responses of sedge-dominated fen-peatlands to independent and interactive warming and elevated CO_2 treatments in terms of plant biomass and C fluxes over ten months. I hypothesized that: 1) increased temperature and elevated CO_2 will independently and interactively increase the C uptake into the peat system via increased aboveground plant productivity, 2) warming would increase the C loss from the peat system via the direct increase of belowground microbial activity lead to 3) a relatively unchanged net C balance due to concurrent increases in aboveground plant productivity and belowground microbial decomposition.

2.2 Materials and Methods

2.2.1 Study Site

Intact peat monoliths were collected from a 10.2 ha intermediate-nutrient fen peatland near White River, Ontario, Canada (48°21′ N, 85°21′ W). The mean annual temperature and precipitation (1981 – 2010) measured at nearby Wawa station (47°58′ N, 84°47′ W) were 2.1°C and 970 mm (319 mm was snowfall), respectively (Environment Canada). This fen supports predominately sedges (*Carex* spp.) with shrubs such as sweet gale (*Myrica gale* L.) and leatherleaf (*Chamadeaphne calyculata* (L.) Moench), and sporadic patches of bryophytes including *Sphagnum* spp. (Palozzi & Lindo, 2017).

2.2.2 Peat Collection and Experimental Design

Twenty-four cylindrical intact peat monoliths (approximately 30 cm diameter × 35 cm deep) were collected in August 2014 from the study peatland. Monoliths were transported in 20 L plastic pails back to the Biotron Institute for Experimental Climate Change at Western University, London, Ontario where they were maintained under ambient temperature and light conditions (London's) from August to December 2014. Mesocosms were connected with PVC drainpipes through ABS barbed fitting ports at the bottom of plastic pails that allowed pore water sampling and monitoring of the water level. Mesocosms were maintained during this 6-month recovery period by being watered twice a week with 700 ml diluted Rudolph's Solution (by a factor of 4 with pH adjusted to 5.8) that simulated the nutrient input through natural precipitation under the field condition

(Dieleman *et al.*, 2016; Faubert & Rochefort, 2002). Plants in the mesocosms were fully senesced by November and were placed under experimental conditions while still senesced.

In January 2015, the 24 mesocosms were allocated at random to one of six greenhouses with temperature, atmospheric CO_2 concentrations, and relative humidity, controlled by a computerized environmental control system (ARGUS®). Relative humidity was set at no less than 60%, while temperature and CO_2 settings followed a full factorial design for treatments, with three levels of temperature manipulation (control, control plus 4°C and control plus 8°C) and two levels of CO_2 concentration (430 ppm and 750 ppm). Temperature conditions followed two pre-set regimes: non-growing and growing season. During the non-growing season (November – April) the control temperature was set to 11.5°C, the average growing season temperature for the field site from which the peat monoliths were sampled, 15.5°C (+4) and 19.5°C (+8). During the growing season (May – October) the temperature was set to the daily average of maximum and minimum temperatures for the London area over the past five years, with corresponding +4 and +8°C offsets implemented in the other temperature treatments (see Lindo, 2015). The average ambient CO_2 concentrations (derived from outside ambient air) over the course of the experiment was 430 ppm, and the elevated CO_2 treatment was set at 750 ppm represents an expected near doubling of CO_2 for the next 50-100 years (IPCC, 2014). Water levels were maintained in the mesocosms weekly with diluted Rudolph's Solution and additional water level top-ups were added during warmer periods as necessary to maintain the water table ~7.5 cm below the soil surface. Mesocosms were maintained in experimental conditions for ten months before being destructively sampled. Net CO_2 flux, pore water carbon quantity (DOC), and pH were measured monthly, with vegetation biomass (root and shoot) and peat C to nitrogen (N) ratio (from the top and bottom 5 cm of the mesocosms) quantified at the end of the experiment.

2.2.3 Carbon Dioxide Fluxes

Dark and clear static chamber techniques were used to measure the net ecosystem exchange (NEE) and ecosystem respiration (ER), respectively, using custom-fit chambers and a LiCor LI-8100A infrared gas analyzer monthly from January to October 2015.

Before each NEE and ER measurement, the chamber was sealed and purged for 90 seconds, and the CO_2 concentration was then recorded every 0.5 seconds during a 60 second period. The volumes of the dark and clear chamber were ~26 L and ~19 L, respectively, and each had an internal fan to mix gas within chamber heads during measurements. Photosynthetically active radiation (PAR) was measured every 15 seconds after 60 seconds (unstable period) from the start of each measurement simultaneously with NEE measurements using a quantum sensor (Apogee MQ-200) outside the chamber just above the vegetation. Final CO_2 flux values were corrected in the LiCor LI-8100A for soil temperature, chamber volume, air moisture as well as initial CO_2 concentrations and pressure. Both NEE (average flux clear chamber) and ER (average flux dark chamber) values are presented as $g\ C\ m^{-2}\ d^{-1}$. While ER is always a positive value, negative NEE numbers represent net CO_2 uptake whereas positive numbers indicate net CO_2 release. Both NEE and ER measurements were conducted within five minutes for the same mesocosm; therefore ER, as measured under dark conditions, was assumed to be equal to the respiration under light conditions (ER_{light}) that occurred simultaneously with plant photosynthesis during NEE measurements. As a result, gross ecosystem production (GEP) was calculated as:

$$GEP = ER - NEE$$

If the NEE is a negative number, there is a net CO_2 input into the mesocosm, and by contrast, a net CO_2 loss from the peat system is indicated by a positive NEE value (Moore *et al.*, 2006).

2.2.4 Pore Water and Peat Analyses

Pore water samples (~ 150 mL) were collected monthly from the bottom drain pipe of each mesocosm from January to October 2015 using a GeoPump (Geotech Ltd., North Aurora, ON, Canada) equipped with a pre-acid washed tube. Water samples were filtered through 0.5 μm glass filters into 50 mL HDPE bottles and stored in the dark at 4°C before analysis. The pore water pH was measured before filtering. Pore water dissolved organic carbon (DOC) concentrations were determined using an Aurora iTOC 1030 (OI Analytical, College Station, TX, USA) using the persulfate wet oxidation method

(Osburn & St-Jean, 2007). In addition, the specific UV absorbance of DOC at 254 nm ($SUVA_{254}$) was measured for each pore water at the end of the experiment (October 2015) on a Spectramax® M2 spectrophotometer. I ran a blank (using Milli-Q water) and a duplicate every ten samples for absorbance measurements. Absorbance values were divided by DOC concentrations to determine $SUVA_{254}$ as a measure of DOC aromaticity. A higher $SUVA_{254}$ value indicates a greater DOC aromaticity and therefore a lower DOC quality (Weishaar *et al.*, 2003).

2.2.5 Peat Properties and Vegetation Biomass

At the end of the experiment, peat soils collected from the top and bottom 5 cm of the mesocosms were dried at 60°C until constant weights were achieved. Total C and N contents in peat samples were measured using a combustion elemental analyzer (vario MAX Cube, Elementar, Langenselbold, Germany), from which the C:N ratio was calculated for each peat sample.

Total aboveground vegetation and belowground root biomass from each mesocosm were measured. The aboveground vegetation, which had not yet senesced, was clipped at the peat surface (root: shoot interface) and dried in the oven at 60°C until a constant weight was achieved. For root biomass, peat monoliths were removed from their mesocosms, and the soil washed from the vascular plant root systems. Roots were also dried at 60°C until constant weights were achieved.

2.2.6 Statistical Analysis

A two-way, repeated measures analysis of variance (RM-ANOVA) was used to test the effects of temperature and atmospheric CO_2 concentrations on flux rates (NEE, ER, GEP) and pore water chemistry (DOC, pH) over the ten-month experiment. The effects of temperature and CO_2 on total plant biomass was determined by a two-way multivariate analysis of variance (MANOVA) with a Tukey *post hoc* test for both aboveground and belowground measurements, while a two-way analysis of variance (ANOVA) was used to test the effect of temperature and CO_2 on pore water $SUVA_{254}$ values at the end of the experiment. The C: N ratio of the top and bottom of the peat within mesocosms were analyzed using a full-factorial spatial RM-ANOVA. All statistical analyses were conducted using Statistica 13.3 (TIBCO Software Inc., 2017).

2.3 Results

2.3.1 Vegetation Biomass

Both increased temperature (Wilks = 0.226, $F_{4, 34} = 9.389$, $P < 0.001$) and elevated atmospheric CO_2 (Wilks = 0.686, $F_{2, 17} = 3.889$, $P = 0.041$) increased aboveground and belowground biomass in the mesocosms over the ten-month experiment period, with a significant interaction among those two variables (temperature × CO_2: Wilks = 0.214, $F_{4, 34} = 9.866$, $P < 0.001$; Figure 2.1). The increased temperature and elevated CO_2 significantly increased the total vegetation biomass (temperature × CO_2: $F_{2, 18} = 17.568$, $P < 0.001$), with the total vegetation biomass significantly increased by 12.8% and 21.1% under +4°C and +8°C warming, respectively (temperature: $F_{2, 18} = 5.972$, $P = 0.010$), while significantly increased by 13.8% under elevated CO_2 (CO_2: $F_{1, 18} = 8.236$, $P = 0.010$).

Increases in total vegetation biomass were driven by both increases in aboveground and belowground biomass under elevated temperatures and CO_2 conditions. Univariate results of the MANOVA demonstrated that the aboveground biomass generally increased under warming conditions (temperature $F_{2, 18} = 23.723$ $P < 0.001$), with elevated CO_2 conditions decreasing aboveground biomass under control temperatures but increased belowground biomass under +8°C temperatures leading to a significant main effect of CO_2 on increasing the belowground biomass by 17.5% (CO_2: $F_{1, 18} = 7.607$, $P = 0.013$; Figure 2.1). Although temperature did not significantly affect the belowground biomass (temperature: $F_{2, 18} = 1.130$, $P = 0.345$), there was a slight increase in belowground biomass under increased temperatures by 11% under the +8°C warming in relative to the control temperature.

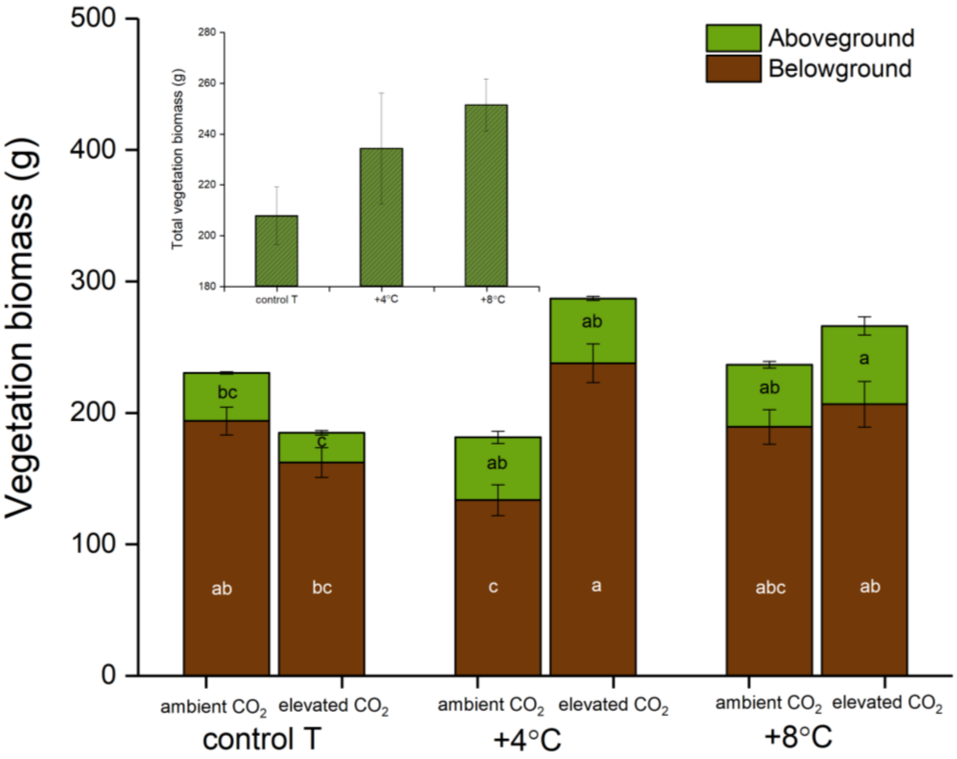

Figure 2.1 Interactive effect of increased temperature (control, +4°C, +8°C) and elevated atmospheric CO_2 (ambient (430 ppm), elevated (750 ppm)) on aboveground, belowground and total vegetation biomass in a sedge-dominated peatland mesocosm experiment after ten months. Letters denote significant differences of aboveground (inside green bars) and belowground (inside brown bars) biomass between treatments; each value represents the mean ± SE (n=4). The inset figure on the left top shows the main effect of increased temperature on total vegetation biomass in mesocosms after ten months as the central figure does not intuitively illustrate this effect. All values are the means (n=8 for each value); error bars are standard errors.

2.3.2 Carbon Dioxide Fluxes

2.3.2.1 Net Ecosystem Exchange (NEE)

During the sampling campaign in August, most NEE values under ambient CO_2 were not measured under optimal PAR conditions due to a rain event, so the August GEP values were discounted when analyzing treatment effects among mesocosms. NEE showed a clear seasonal pattern in the mesocosms throughout the experiment (Figure 2.2; Table 2.1), where NEE was near zero during the non-growing season (April – June) and then was strongly negative (C uptake) in July. NEE in the mesocosms remained negative from July to September before increasing again in October (Figure 2.2). NEE was lower under increased temperatures in September ($F = 8.608$, $P = 0.002$) and October ($F = 12.212$, $P < 0.001$). Temperature had a significant effect on NEE during the spring with NEE values that were more negative under increased temperature in May ($F = 5.329$, $P = 0.015$) but less negative under warming in June ($F = 4.829$, $P = 0.021$).

Elevated CO_2 significantly decreased NEE values (more negative) in the mesocosms (Figure 2.2; Table 2.1); however, this effect was partially attributed to the significantly lower NEE values (more negative numbers) under the elevated CO_2 in August. However, when the August data were excluded, NEE values were still considerably lower under elevated CO_2 (CO_2: $F_{1, 18} = 3.068$, $P = 0.097$) across all temperature treatments in particular under +4°C, even though the interactive effect between temperature and CO_2 was not significant. Similar to the temperature effect, elevated CO_2 had a more pronounced effect on NEE during the non-growing season with NEE values were significantly decreased by elevated CO_2 in September ($F = 8.163$, $P = 0.010$).

Table 2.1 RM-ANOVA analyses on the effects of increased temperature and elevated CO_2 on pore water DOC concentration and ER from January to October as well as on NEE and GEP from April to October in 2015.

Source of variation			DOC		ER	
	df	Error *df*	*F*	*P*	*F*	*P*
temperature	2	18	57.406	**< 0.001**	26.777	**< 0.001**
CO_2	1	18	1.144	0.299	2.259	0.159
temperature × CO_2	2	18	2.075	0.155	0.674	0.522
time	9	162	109.460	**< 0.001**	102.900	**< 0.001**
time × temperature	18	162	8.425	**< 0.001**	5.924	**< 0.001**
time × CO_2	9	162	0.450	0.905	1.467	0.164
time × temperature × CO_2	18	162	0.673	0.834	1.159	0.302

Source of variation			NEE		GEP	
	df	Error *df*	*F*	*P*	*F*	*P*
temperature	2	18 (15)[a]	0.490	0.621	11.271	**0.001**
CO_2	1	18 (15)	15.808	**0.001**	18.312	**0.001**
temperature × CO_2	2	18 (15)	2.560	0.105	2.454	0.120
time	6	108 (90)	121.810	**< 0.001**	98.034	**0.001**
time × temperature	12	108 (90)	6.628	**< 0.001**	2.526	**0.006**
time × CO_2	6	108 (90)	12.676	**< 0.001**	7.813	**< 0.001**
time × temperature × CO_2	12	108 (90)	4.224	< 0.001	2.472	**0.008**

[a] numbers in brackets represent error degree of freedom for GEP; few numbers not measured under full PAR conditions were discarded in the calculation.

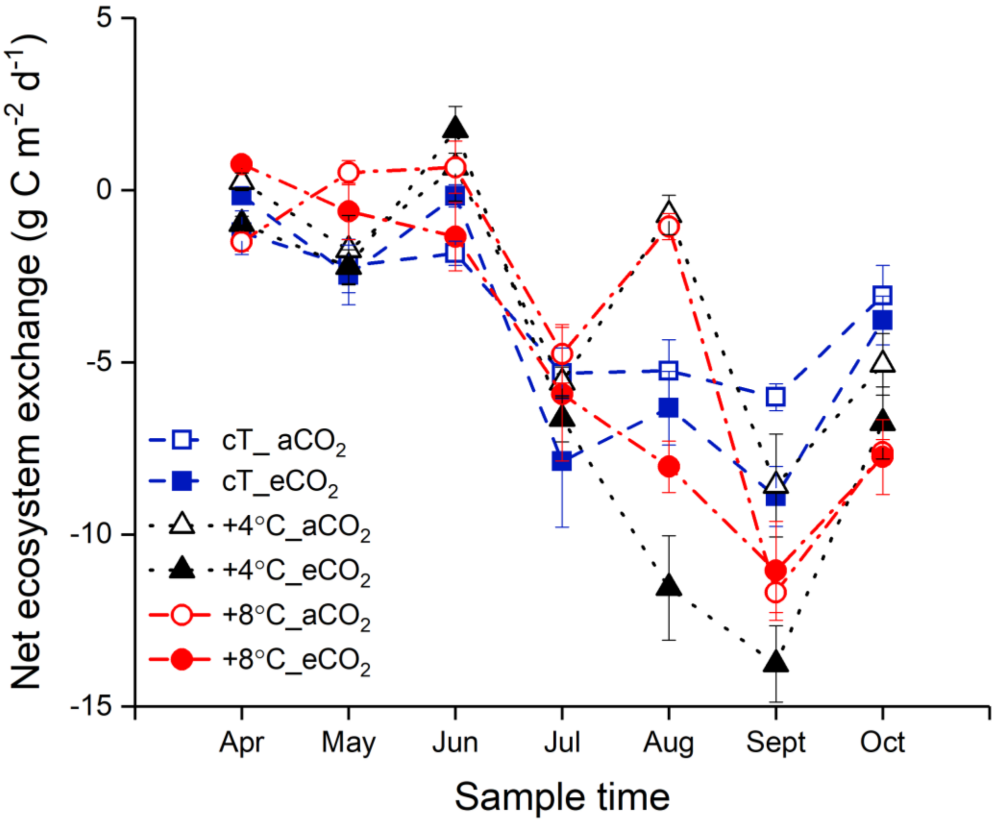

Figure 2.2 Net ecosystem exchanges (NEE, g C m^{-2} d^{-1}) in sedge-dominated peatland mesocosms placed under increased temperature (control (cT), +4°C, +8°C) and elevated atmospheric CO_2 (ambient (430 ppm; aCO_2), elevated (750 ppm; eCO_2)) over ten months. Negative NEE values indicate net uptake of CO_2 into mesocosms. Each value represents the mean ± SE (n=4).

2.3.2.2 Ecosystem Respiration (ER)

Elevated temperature significantly increased ER from mesocosms, with ER increasing under +4°C and +8°C temperature treatments as early as February (Figure 2.3), even prior to the transition of growing season greenhouse conditions. The switch to growing season conditions in May increased ER under the +8°C treatment, but control and +4°C treatments did not show substantial increases in ER until the peak growing season in July. Conversely, the control temperature treatment ER dropped significantly in August, while ER under the +4°C temperature treatment remained elevated until September. Indeed, ER under all six treatments was elevated relative to the start of the experiment with this trend more pronounced under increased temperatures. Although ER was 10% higher under elevated CO_2, there was no significant effect of CO_2 or interactive effect of temperature and CO_2 on ER throughout this experiment (Table 2.1).

2.3.2.3 Gross Ecosystem Productivity (GEP)

The pattern of GEP values followed the seasonal pattern of ER closely with peak GEP occurring from July to September (Figure 2.4; Table 2.1). GEP significantly increased under increased temperatures with the effect more pronounced during the non-growing season (e.g., September and October; Figure 2.4; Table 2.1). Elevated CO_2 also significantly increased GEP in the mesocosms with or without August data, and the greatest increase of GEP with elevated CO_2 occurred under +4°C. Likewise, elevated CO_2 exerted the most substantial impact on GEP after the peak growing season in September ($F = 18.391$, $P < 0.001$). An overall interactive effect of temperature and CO_2 on GEP was not observed in this experiment, but there was an interactive effect of increased temperature and elevated CO_2 on GEP in September ($F = 7.187$, $P = 0.006$) as suggested by univariate results.

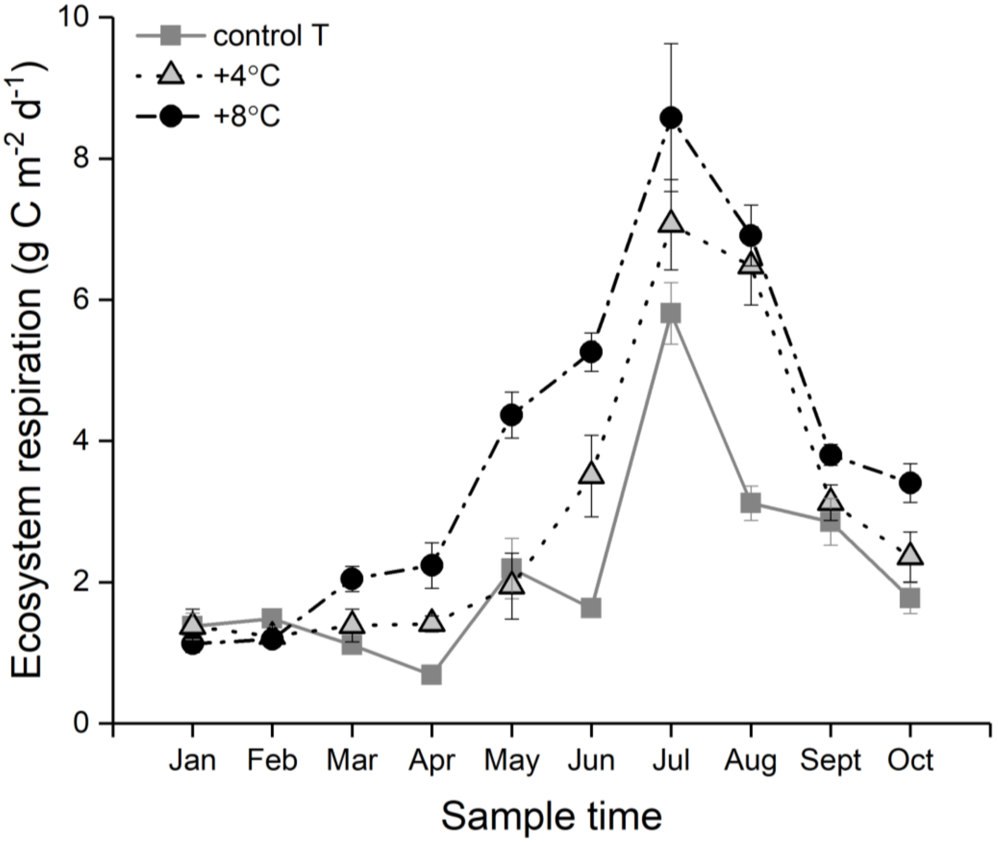

Figure 2.3 Effect of increased temperature (control T, +4°C, +8°C) on ecosystem respiration (ER, represented by positive numbers (g C m^{-2} d^{-1})) from sedge-dominated fen peatland mesocosms over ten months (January to October) in 2015. ER was plotted only for temperature treatments as there was no significant elevated CO_2 effect on ER (Table 2.1). Each value represents the mean ± SE (n=8).

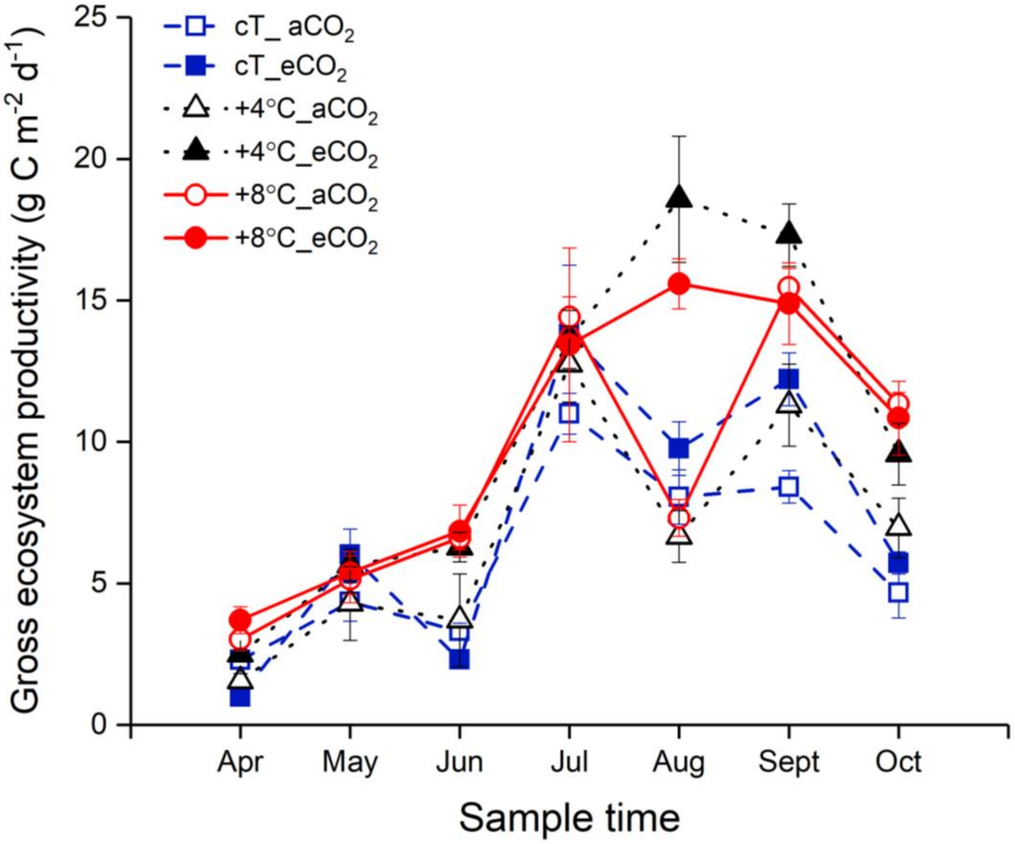

Figure 2.4 Gross ecosystem productivity (GEP, g C m^{-2} d^{-1}) of sedge-dominated peatland mesocosms placed under increased temperature (control (cT), +4°C, +8°C) and elevated atmospheric CO_2 (ambient (430 ppm; aCO_2), elevated (750 ppm; eCO_2)) over ten months. Each value represents the mean ± SE (n=4).

2.3.3 Pore Water and Peat Chemistry

Pore water DOC concentrations significantly increased under increased temperatures, with the increase most pronounced during the peak growing season (from June to September) when DOC concentrations were approximately twice as high as the pre-growing season (Figure 2.5; Table 2.1). DOC concentrations were not significantly different at the start of the experiment (January 2015) but started to separate among the three temperature treatments as early as February and continued to increase until the end of the experiment (October 2015). During the main growing season（from May until September), the pore water DOC concentration increased by 39% and 91% respectively under the +4°C and +8°C treatments, in comparison to the control treatment. In addition, DOC concentrations under both control and +4°C treatments returned to their pre-growing season level (or lower) after the growing season, while the DOC concentration under +8°C temperature remained elevated during the fall (Figure 2.5). There was no significant effect of elevated CO_2 on pore water DOC concentrations (Table 2.1); however, there was a notable but non-significant decrease of pore water DOC under the elevated CO_2 and +4°C temperature during the peak growing season in July ($F = 4.094$, $P = 0.058$).

Mean pore water pH values of the mesocosms varied significantly through the time (time: $F_{9,162} = 69.724$, $P < 0.001$), which peaked at ~5.82 during the main growing season (in July and August) across all temperature treatments. All pH values were in the range of 4.90 to 6.15 throughout the sampling period. There was a slight but significant increase in pore water pH under +8°C temperature treatment especially during the peak growing season (temperature × time: $F_{18,162} = 7.156$, $P < 0.001$; control = 5.77 (0.08), +4°C = 5.82 (0.16), +8°C = 5.90 (0.17)).

Neither increased temperature nor elevated CO_2 had an effect on $SUVA_{254}$ values of pore water DOC as measured at the end of the experiment (temperature: $F_{2, 18} = 2.892$, $P = 0.081$; CO_2: $F_{1, 18} = 0.263$, $P = 0.614$) with all values ranged between 3.93 and 4.45. The C:N ratios of peat soils at the top of the mesocosms were significantly higher than those at the bottom of the mesocosms (Spatial: $F_{1, 18} = 5.249$, $P = 0.034$), but there were no significant effects of increased temperature or elevated CO_2 on C:N values of the top and bottom peat soils (temperature: $F_{2,\,18} = 0.748$, $P = 0.928$; CO_2: $F_{1,\,18} = 0.302$, $P = 0.590$).

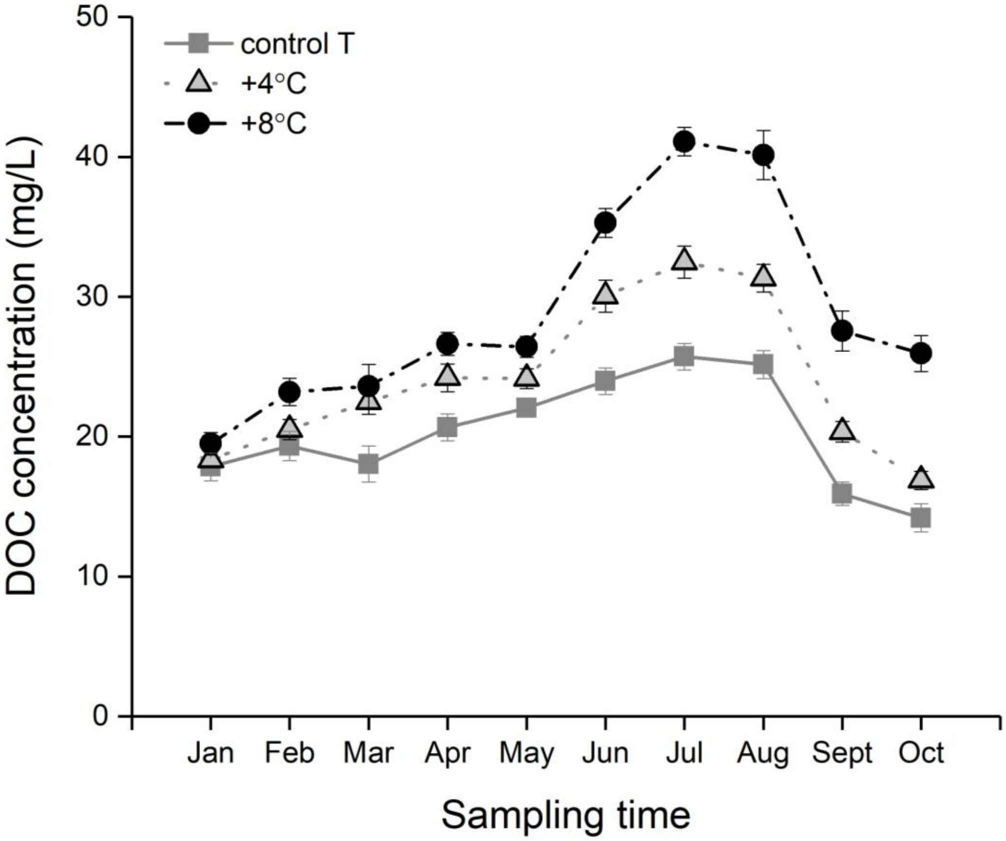

Figure 2.5 Effect of increased temperature (control T, +4°C, +8°C) on pore water dissolved organic carbon (DOC) concentrations (mg/L) from sedge-dominated fen peatland mesocosms over ten months (January to October) in 2015. Pore water DOC concentrations were only plotted for temperature treatments as there was no significant elevated CO_2 effect on DOC concentration (Table 2.1). Each value represents the mean ± SE (n=8).

2.4 Discussion

The results from this experiment show that under increased temperature and elevated atmospheric CO_2, sedge-dominated fens may remain a CO_2 sink through a balance between increases in both aboveground plant productivity and belowground microbial decomposition. However, the increased temperature also substantially increased the pore water DOC concentration, thus, the future climate change could weaken the C storage potential, which is determined by the difference between C uptake by plant productivity and C release in both gaseous (e.g., CO_2) and liquid (e.g., pore water DOC) forms via microbial decomposition, in this sedge-dominated intermediate fen.

I found that increased temperature and elevated CO_2 increased both aboveground and belowground plant biomass, with effects of increased temperature most pronounced in aboveground biomass, while the elevated CO_2 increased the allocation of biomass belowground. Wang *et al.* (2016a) found similar results in a meta-analysis for tundra systems; aboveground biomass significantly increases with increased temperature, whereas the belowground biomass is less sensitive to the increases in temperatures. Elevated CO_2 increased root biomass in numerous studies (Pregitzer *et al.*, 2000; Nie *et al.*, 2013), which is attributed to increases in root length and root diameter (Pregitzer *et al.*, 2000; Nie *et al.*, 2013). However, elevated CO_2 can also increase the root mortality, especially during the late growing season, which potentially leads to a net reduction of root biomass (Pregitzer *et al.*, 2000). In this study, a greater increase in root mortality than root production might be the explanation of the observed decrease in root biomass with elevated CO_2 under the control temperature treatment.

It is well established that decomposition rates are highly dependent on temperature, and warming conditions could directly increase the microbial activity in peatlands (Davidson & Janssens, 2006; Dorrepaal *et al.*, 2009; Lafleur *et al.*, 2005). In this experiment, observed increases in CO_2 emissions via ER under increased temperatures follow this ‘first order control’ of the temperature on microbial activity and decomposition.

Both increased temperature and elevated CO_2 have been found to increase peatland DOC export in previous studies. I found no significant effect of elevated CO_2 on DOC concentration in this experiment. Increased temperature significantly increased the pore water DOC concentration, which I mainly attributed to the enhanced microbial decomposition under warming conditions, rather than direct inputs from root exudates, which would have also coincided with an increase in the lability of the DOC (i.e., decreased SUVA values, which were not observed). However, at the start of the experiment (January 2015), there was no difference in DOC concentration despite differences among temperature treatments (Figure 2.5), suggesting the growth of sedges that provides labile C for microbial activity might also play a role in DOC production.

This study suggested that climate warming might extend the growing season by delaying the plant senescence during the fall, as I observed a higher proportion of green area in the mesocosms under increased temperature in October (see an example in Appendix A). Richardson *et al.* (2018) also found that in an ombrotrophic bog, soil warming of up to 9°C resulted in an extension of the growing season by one to two weeks with an earlier growth of plants in the spring and delayed plant senescence during the fall. Although warming did not affect the seasonal NEE, Li *et al.* (2017) found that the growth of sedges was stimulated under the warming condition during the early growing season. With increased water use efficiency of plants, elevated CO_2 can also cause a delay of plant senescence in the fall, which further increase the length of the growing season by about seven days (Reyes-Fox *et al.*, 2014). In this study, elevated CO_2 significantly decreased the NEE during the late growing season (e.g., September), which was mainly because of the increased GEP under elevated CO_2. Increases in plant productivity due to this extended growing season significantly increased the net CO_2 uptake in the mesocosms under elevated CO_2 condition. Additionally, I observed a substantial increase in pore water DOC under the +8°C temperature treatment in October, possibly derived from the decomposition of litter due to the higher productivity of this treatment.

In this experiment, I also observed a decreased NEE (increased net CO_2 uptake) under elevated CO_2, with the greatest increase under +4°C temperature treatment. Since the elevated CO_2 effect on root biomass was also more pronounced under +4°C, I argue that instead of directly increasing the aboveground plant productivity, the decreased NEE under elevated CO_2 was possibly driven by the alleviated nutrient stress for plant growth with stimulated root growth in the sedge-dominated mesocosms.

Nie *et al.* (2013) found that the root quality greatly decreased under elevated CO_2 with increased C:N, and this decrease in root quality can impede the decomposition of the root litter and increase the net C storage in peatlands. Although I did not directly measure the C:N of roots in this study, I observed decreases of peat C:N ratios from both the top and bottom of the mesocosm under the elevated CO_2 with +4°C temperature. This suggested that elevated CO_2 could potentially increase the C storage potential in peatlands via decreased root quality and lower rates of decomposition.

Increases in root biomass have been shown to be tightly coupled with increases in CO_2 release via ER as well as increases in DOC production via root exudation (Freeman *et al.*, 2004; Jackson *et al.*, 2009; Pregitzer *et al.*, 2008). Particularly in sedge-dominated ecosystems, fine roots of sedges contribute a considerable amount of respired CO_2 compare to their leaves and roots of shrubs (Crow & Wieder, 2005). Although I saw only a slight increase of ER under the elevated CO_2, the pore water DOC concentration decreased sharply under the elevated CO_2 with +4°C temperature, together with a decrease in SUVA value (e.g., higher DOC quality) and a slight decrease in pH. I suggest that the change in pore water chemistry under elevated CO_2 and +4°C temperature was linked with the increased root exudation of labile C with enhanced root growth. Taken together, results from this study are consistent with Freeman *et al.* (2004): elevated CO_2 tends to affect the peatland C cycling via changes in plant productivity rather than a direct effect on peatland decomposition.

This study highlighted the importance of examining changes in belowground biomass under climate change, notably when the belowground biomass accounted for the majority of the total vegetation biomass as in sedge-dominated peatlands (Saarinen, 1996). In *Sphagnum*-dominated bogs and poor fens, the presence of *Sphagnum* is often touted as the main reason for low decomposition rates due to low nutrient inputs from *Sphagnum* litters and the leaching of acidic compounds (e.g., phenols) from *Sphagnum* can inhibit the microbial activity (van Breemen, 1995). However, climate change is anticipated to shift plant community composition with increased vascular plant productivity in northern peatlands. In particular, *Sphagnum* has been shown to decrease and be largely replaced by sedges (e.g., *Carex* spp.) under increased temperature (Dieleman *et al.*, 2015; Weltzin *et al.*, 2003) and elevated atmospheric CO_2 concentrations (Fenner *et al.*, 2007; Freeman *et al.*, 2004). Vascular plants support substantially higher C turnover rates (Fenner *et al.*, 2007) and CO_2 emissions (Dieleman *et al.*, 2017) than *Sphagnum* moss; hence, increases in the prevalence of sedge-dominated intermediate fen would have significant impacts on CO_2 emissions and long-term C storage in northern peatlands under future climate change.

2.5 Conclusion

In this study, I experimentally examined the response of a sedge-dominated fen peatland to increased temperature and elevated atmospheric CO_2 regarding C and biomass dynamics. The sedge-dominated fen peatland can remain as a net C sink under simulated warming and elevated CO_2 over one growing season. Even though a shifted vegetation community is not expected, climate warming will increase the plant productivity and net CO_2 uptake in the sedge-dominated fen, which can offset the increased C loss via decomposition. This study, therefore, highlights the importance of incorporating the interactive effect of warming and elevated atmospheric CO_2 on C cycling in sedge-dominated fens into peatland C modelling. Future studies should investigate the net effect of altered root morphology and biomass on peatland C balances during the long-term period.

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Chapter 3

3 Greenhouse Gas Fluxes in Two Boreal Fens with Contrasting Vegetation Communities and Their Responses to *in situ* Passive Warming

3.1 Introduction

Owing to waterlogged and cool conditions that limit rates of decomposition, northern peatlands play disproportionately important roles as terrestrial organic carbon (C) sinks. Although occupying only about 3% of the global land area, northern peatlands store approximately 30% of global soil C (Gorham, 1991; Post *et al.*, 1982). The primary C input into peatlands is via photosynthesis and there are multiple pathways by which peatlands can lose C into either the atmosphere in gaseous forms (as carbon dioxide, CO_2 and methane, CH_4) or into receiving ecosystems, including lakes and rivers, as dissolved organic carbon (DOC) (Blodau, 2002). Peatlands C fluxes are subject to environmental disturbances (e.g., climate warming) that could potentially change the wet and cool environment (Davidson & Janssens, 2006). Thus, predictions of peatland C cycle under climate change are essential when estimating potential feedbacks between terrestrial ecosystems and the atmosphere.

Northern peatlands are mainly classified into bogs, poor fens, intermediate fens and rich fens based on local vegetation communities as well as physical conditions such as nutrient status, pH and water table position (Rydin & Jeglum, 2013). Generally, bogs and poor fens are dominated by *Sphagnum* mosses, and intermediate fens and rich fens are dominated by sedges such as *Carex* spp. (e.g., Myers *et al.*, 2012; Webster & McLaughlin, 2010). *Sphagnum*-dominated poor fens and the sedge-dominated intermediate fens are two main fen types peatland in Canada and account for over 50% of the peatland area in northern regions (Tarnocai, 2006). However, these two types of fen are very different from the more commonly studied moss-dominated bogs. *Sphagnum*-dominated fen peatlands are generally greater C sinks than vascular plants-dominated peatlands (Webster *et al.*, 2013; Wu & Roulet, 2014) because of their lower decomposition rates (Armstrong *et al.*, 2015) that are inhibited by antibiotic compounds (e.g., phenols) released from *Sphagnum* mosses (van Breemen, 1995).

Besides, sedge-dominated peatlands emit a significantly higher amount of CH_4 than *Sphagnum*-dominated peatlands (Godin *et al.*, 2012; Webster *et al.*, 2013) owing to the extensive presence of vascular plants (Ward *et al.*, 2013, 2015). Increases in vascular plant abundance, especially sedges, could substantially increase peatland CH_4 emissions (Joabsson *et al.*, 1999), and this is because sedges can provide labile C substrate for methanogenesis via their root exudates (Ström *et al.*, 2003). Positive relationships between sedge productivity and CH_4 emissions in wetlands have been reported in previous studies (Dacey *et al.*, 1994; Whiting & Chanton, 1993). Sedges also have higher capacities for transporting CH_4 via their aerenchyma tissues, which contribute considerably to higher CH_4 emissions from sedge-dominated peatlands (Bhullar *et al.*, 2013).

As predicted by a peatland C model, the C stored in fens could be more sensitive to future climate warming in comparison to bogs (Wu & Roulet, 2014). Owing to their differences in C cycling and potential responses to climate warming, different peatland types should be parameterized separately in peatland C models to increase the modelling accuracy. Moreover, it has been suggested that there would be a shift from the *Sphagnum*-dominated peatlands towards vascular plants-dominated peatlands (Dieleman *et al.*, 2015; Wang *et al.*, 2017; Weltzin *et al.*, 2000) under climate warming. This shift in vegetation will lead a substantial increase in the proportion of vascular plant-dominated peatlands under future climate warming. However, many previous experiments focused only on nutrient-poor, *Sphagnum*-dominated bogs, with much less data on minerotrophic, vascular plants-dominated fens, especially sedge-dominated fen peatlands (Chivers *et al.*, 2009; Mäkiranta *et al.*, 2018). The lack of data on fen peatlands leads to the failure to separate different peatland types in peatland C models, which can result in significant uncertainties on C fluxes in peatlands and their potential responses to future climate change.

Given the underrepresentation of fen peatlands in the scientific literature despite their importance on the northern landscape, the objective of this study was to quantify and compare the seasonal CO_2 and CH_4 fluxes in a *Sphagnum*-dominated poor fen and a sedge-dominated intermediate fen. Further, I investigated responses of CO_2 and CH_4 fluxes in those two fens to *in situ* passive warming over one growing season using a passive chamber approach. I hypothesized that: 1) the *Sphagnum*-dominated poor fen is a larger CO_2 sink due to a slower decomposition rate, 2) the sedge-dominated intermediate fen is a larger CH_4 source because of the extensive presence of sedge plants as well as the wetter condition, 3) in both fens, net ecosystem exchanges will remain unaltered under passive warming, owing to the concurrent increases in plant productivity and ecosystem respiration, and 4) passive warming will increase CH_4 emissions from both fens via direct increases of microbial activity.

3.2 Materials and Methods

3.2.1 Study Site

The study area contains two contrasting fen peatlands — a nutrient poor, *Sphagnum*-dominated poor fen peatland and a nutrient richer, sedge-dominated intermediate fen. The two fen sites are approximately 2 km apart, and they are a part of long-term research peatland complex that is monitored by the Ontario Ministry of Natural Resources and Forestry near the township of White River, Ontario, Canada (48˚21’N, 84˚20’W). The mean annual temperature (from 1981-2010) in this region was 2.1ºC, and the mean annual precipitation was 970 mm, of which 319 fell as snow (Environment Canada). The *Sphagnum*-dominated poor fen supports a relatively high diversity of plants including *Sphagnum* spp., ericaceous shrubs including labrador tea (*Rhododendron groenlandicum* Oeder) and leatherleaf (*Chamadephne calyculata* (L.) Moench), as well as multiple dwarf shrubs such as cranberry (*Vaccinium oxycoccus*) and wild blueberry (*Vaccinium angustifolium*). Also, the *Sphagnum*-dominated poor fen is partially treed with black spruce and tamarack. The sedge-dominated intermediate fen is overwhelmingly dominated by *Carex* spp. sedges (*C. oligosperma* Michx. and *C. stricta* Lam.) with sweet gale (*Myrica gale* (L.)) and scattered patches of *Sphagnum* spp. (Palozzi & Lindo, 2017).

3.2.2 Experimental Design

In 2015, sixteen 1 m diameter and 50 cm deep rigid collars were installed into the peat at each fen site. All collars were located within 20 m of each other and were assigned within four experimental blocks to account for any potential underlying spatial heterogeneity in vegetation composition, moisture variability, and biogeochemical processes at the two sites. Permanent boardwalks were installed to ensure access to the sampling plots and minimize disturbance during measurements. All plots recovered for one year prior to the first measurements in 2016. CO_2 and CH_4 fluxes were measured during the growing season (July – September) in 2016 and 2017. Additionally, a well was installed in the middle of each collar at the start of the growing season in 2016 for integrated pore water sampling. All wells were capped to minimize the transportation of gas from the soil. Gas fluxes data from this study are valid for analyzing treatment effects (e.g., peatland type and passive warming) but these data should be used with caution for representations of gas fluxes in natural peatland ecosystems. In June 2017, half the plots within each block (8 out of 16 collars at each site in total) were randomly assigned to a passive warming treatment using a transparent polycarbonate open-top chamber approximately 1m in diameter and 1m tall. The polycarbonate permitted 70 to 80% light transmission into the sampling plots.

3.2.3 Greenhouse Gas Fluxes

Greenhouse gas (CO_2 and CH_4) fluxes were measured using the closed-chamber technique with a Gasmet^{TM} DX 4015 for real-time gas measurements (Gasmet Technology, Helsinki, Finland), on a weekly to biweekly basis from July to October in 2016 and from May to October in 2017. During each sampling campaign, chambers at each fen site were sampled for gas fluxes in a randomized order during the day. The surface area and volume of the chamber used were ~0.68 m^2 and ~ 740 L, respectively. I calculated CO_2 (in g CO_2 m^{-2} day^{-1}) and CH_4 (in mg CH_4 m^{-2} day^{-1}) fluxes using a linear regression for changes of gas concentrations within the closed chamber as a function of time, corrected for the air temperature inside the chamber during each measurement according to the ideal gas law (Crill *et al.*, 1988). CO_2 fluxes were measured under clear and covered (dark) chambers to calculate net ecosystem exchange (NEE) and ecosystem respiration (ER), respectively. For ER measurements, the chamber was darkened with an opaque cloth shroud blocking all sunlight (PAR = 0 inside the dark chamber). Both clear and dark CO_2 measurements were made for 3 minutes, with averaged CO_2 concentrations (ppm) measured at a 15 s interval. CH_4 fluxes were also made under the dark condition to minimize the CH_4 oxidation caused by plant photosynthesis (Luan & Wu, 2014). CH_4 fluxes were calculated from concentrations (ppm) averaged over 5 min intervals for 30 minutes.

The air temperature (°C) inside the chamber was measured simultaneously with each gas concentration reading from Gasmet (e.g., every 15 s for CO_2 and every 5 min for CH_4 measurements) using a Fisherband ^{TM} Traceable^{TM} Total-Range Thermometer coupled with a Type-K thermocouple probe (Thermo Fisher Scientific, Waltham, Massachusetts, USA). Clear chamber measurements (NEE) were conducted between 10 a.m. and 4 p.m. during high sunlight (i.e., PAR > 1000) to ensure maximum plant photosynthesis; PAR was recorded simultaneously with each gas reading every 15 s using an Apogee MQ-200 quantum sensor (Apogee Instruments, Inc, Logan, UT, USA), which was placed on the middle of the chamber lid. Before the start of each sampling day, the Gasmet was zeroed with pure nitrogen gas (99.998% purity, Praxair Canada Inc., Mississauga, Ontario, Canada) as a background for gas concentration calculations. Soil moisture (vol%) within top ~10 cm peat soils were measured using HH2 Moisture Meter (Delta-T Devices, Burwell, Cambridge, UK). In 2016, soil temperatures were also measured ~10 cm below the peat surface using the HH2 Moisture Meter. In 2017, additional soil temperatures (°C) were made at 5, 10, 15, 20, and 25 cm below the peat surface using a Fisherband^{TM} Long-Stem Digital Thermometer (Thermo Fisher Scientific, Waltham, Massachusetts, USA). Within each plot, both soil temperature and soil moisture values were averaged with measurements made at three different spots (in the *Sphagnum*-dominated poor fen, measurements made at different microsites including hummock, hollow and lawns if applicable), and both measurements were made as close as to CO_2 and CH_4 fluxes measurements during each gas sampling date.

All NEE and ER measurements were made within 10 min of each for individual chambers so that dark respiration would be representative of the respiration under light condition. We, therefore, calculated the gross ecosystem production (GEP) as:

$$GEP = ER-NEE$$

When NEE is a negative number, it represents a net uptake of CO_2 from the atmosphere, while a positive NEE represents a net release of CO_2 into the atmosphere (Moore *et al.*, 2006).

3.2.4 Statistical Analysis

All graphics work and correlation analyses were completed in OriginPro 2017 (OriginLab, version 94E). All other statistical analyses in this chapter were conducted in TIBCO® Statistica^{TM} (version 13.3, 2017). Repeated measures analysis of variance (RM-ANOVA) of gas fluxes (including monthly averaged NEE, GEP, ER and CH_4, from July to October 2016) were used to test any initial block effect at each fen site. Two-way RM-ANOVA was also used to test differences in monthly averaged GEP, ER, NEE and CH_4 fluxes between two fen sites over two growing seasons in 2016 and 2017. Gas fluxes after June 18, 2017 (time of the initiation of passive warming) were tested for the effects of passive warming in different fen sites on NEE, ER, GEP and CH_4 fluxes using RM-ANOVA followed by Tukey HSD *post hoc* tests. The passive warming effect on the GEP-CH_4 relationship was evaluated using Analysis of covariance (ANCOVA).

3.3 Results

There was no significant block effect on most C fluxes in either the *Sphagnum*-dominated poor fen or the sedge-dominated intermediate fen in 2016, indicating the homogeneity of soils among the 16 plots at each fen site (Table 3.1). A significant block effect on CH_4 emissions from the *Sphagnum*-dominated poor fen was primarily driven by several large emissions from block 3 and 4 in October, but there was no significant block effect in the CH_4 emissions during the main growing season (July to September) (block: $F_{3,12} = 1.631$; $P = 0.234$).

Passive warming significantly increased the soil temperature from 0.6 to 1.0°C in the *Sphagnum*-dominated poor fen to the depth of 20 cm below the peat surface. In the sedge-dominated intermediate fen, the average soil temperature only slightly increased near the peat surface by 0.5°C under passive warming (see Appendix E). Soil moisture was not altered by passive warming in either fen site (see Appendix E).

Table 3.1 RM-ANOVA analyses of block effects on CH_4 and CO_2 fluxes in two fens using baseline data (without passive warming effect) from July to Sept/October in 2016.

Site	Variable	*df*	Total *df*	*F*	*P*
Sphagnum-dominated poor fen	CH_4	3	12	5.625	**0.012**
	NEE	3	12	2.233	0.137
	ER	3	9	1.074	0.408
	GEP	3	9	1.074	0.407
Sedge-dominated intermediate fen	CH_4	3	11	0.320	0.811
	NEE	3	12	2.889	0.079
	ER	3	6	0.409	0.752
	GEP	3	8	0.468	0.713

3.3.1 Carbon Dioxide Fluxes

3.3.1.1 Net Ecosystem Exchange (NEE)

Both the *Sphagnum*-dominated poor fen and the sedge-dominated intermediate fen were net CO_2 sinks (NEE < 0) during the periods of measurement in 2016 and 2017 (Figure 3.1). On average, the *Sphagnum*-dominated poor fen was a larger CO_2 sink than the sedge-dominated intermediate fen by 16% during the peak growing season in 2016 (July to September) and by 58% during the full growing season in 2017 (May to October). However, the difference of NEE between two fen sites was only significant in 2017 when spring and the fall NEE were included (Table 3.2).

Differences in NEE between the two fen sites illustrated expected seasonal patterns in both 2016 (time × site: $F_{2,60} = 7.387$, $P = 0.001$) and 2017 (time × site: $F_{5,65} = 3.274$, $P = 0.011$; Figure 3.1). NEE was lower in the *Sphagnum*-dominated poor fen throughout the growing season in 2017 except for June and July, when NEE were similar between two fen sites, after a decrease of NEE in the sedge-dominated intermediate fen (Figure 3.1). The lower NEE in the *Sphagnum*-dominated poor fen were more pronounced during the spring (May: $F = 6.856$, $P = 0.021$) and the fall (September: $F = 12.263$, $P = 0.004$; October: $F = 9.588$, $P = 0.009$).

There was no overall effect of passive warming on the seasonal NEE in either fen site (Table 3.3); however, passive warming increased September NEE in 2017 by 168% in the sedge-dominated intermediate fen and by 27% in the *Sphagnum*-dominated poor fen (passive warming in September: $P = 0.010$; Figure 3.1).

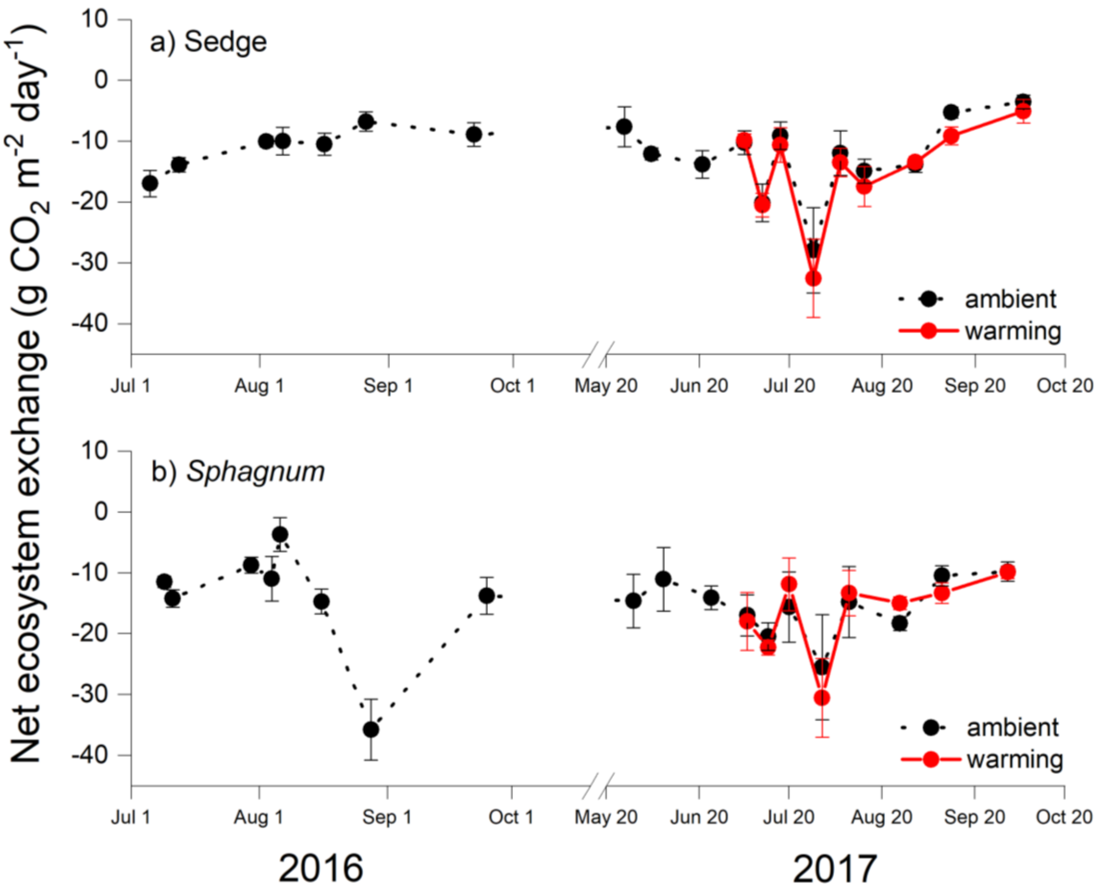

Figure 3.1 Seasonal patterns of net ecosystem exchanges (in the unit of g CO$_2$ m^{-2} day^{-1}) under ambient and passive warming (started on Jun 18 in 2017) in: a) sedge-dominated intermediate fen and b) *Sphagnum*-dominated poor fen over two field seasons in 2016 and 2017. Each value represents the mean ± standard error (n=16 before the start of passive warming; and n=8 for both "ambient" and "warming" treatments after the initiation of passive warming).

Table 3.2 RM-ANOVA results for differences in CO_2 and CH_4 fluxes between two fen sites in 2016 and 2017.

Year	**Variable**	**Sedge-dominated**	***Sphagnum*-dominated**	***df***	**Total *df***	***F***	***P***
2016	NEE (g CO_2 m^{-2} day^{-1})	-11.69 ± 1.22	-13.54 ± 1.22	1	30	1.153	0.292
	ER (g CO_2 m^{-2} day^{-1})	9.70 ± 0.79	8.46 ± 0.72	1	20	1.316	0.265
	GEP (g CO_2 m^{-2} day-1)	22.42 ± 1.20	24.31 ± 1.15	1	23	1.277	0.270
	CH_4 (mg CH_4 m^{-2} day^{-1})	49.06 ± 5.04	42.66 ± 4.88	1	29	0.833	0.369
	GWP_{100} (g eqv-CO_2 m^{-2} day^{-1})[a]	-10.02	-12.09				
2017[b]	NEE (g CO_2 m^{-2} day^{-1})	-9.05 ± 1.74	-14.28 ± 1.38	1	11	5.367	**0.038**
	ER (g CO_2 m^{-2} day^{-1})	8.99 ± 0.74	11.87 ± 0.56	1	20	9.599	**0.006**
	GEP (g CO_2 m^{-2} day^{-1})	18.99 ± 3.22	27.40 ± 1.97	1	9	4.958	0.053
	CH_4 (mg CH_4 m^{-2} day^{-1})	65.02 ± 3.23	27.82 ± 3.23	1	14	57.176	**< 0.001**
	GWP_{100} (g eqv-CO_2 m^{-2} day^{-1})	-6.84	-13.33				

[a] The global warming potential over 100 year time period (GWP_{100}) was calculated as NEE + (CH_4 * GWP_{100} of CH_4), where NEE is in g CO_2 m^{-2} day^{-1}, and the CH_4 is in g evq-CO_2 m^{-2} day^{-1}. GWP_{100} of CH_4 is 34 evq-CO_2 as suggested by IPCC (2014)

[b] only data from "ambient" plots were used for analyses

Table 3.3 RM-ANOVA analyses of passive warming effect on monthly averaged NEE, ER, GEP and CH_4 (July to October in 2017) between two fen sites. Block effect was tested and removed from the mixed model if it was not significant.

	NEE				ER			
Source of Variation	*df*	Total *df*	*F*	*P*	*df*	Total *df*	*F*	*P*
site	1	24	10.007	**0.004**	1	23	15.583	< **0.001**
warming	1	24	0.714	0.406	1	23	0.122	0.730
site × warming	1	24	0.415	0.526	1	23	0.548	0.467
time	3	72	21.005	< **0.001**	3	69	47.099	< **0.001**
time × site	3	72	0.707	0.551	3	69	2.439	0.072
time × warming	3	72	1.345	0.266	3	69	0.498	0.685
time × site × warming	3	72	0.181	0.909	3	69	0.449	0.719

	GEP				CH_4			
Source of Variation	*df*	Total *df*	*F*	*P*	*df*	Total *df*	*F*	*P*
site	1	19	9.877	**0.005**	1	28	35.02	< **0.001**
warming	1	19	0.104	0.751	1	28	0.490	0.490
site × warming	1	19	0.425	0.522	1	28	0.539	0.469
time	3	57	31.463	< **0.001**	3	84	36.58	< **0.001**
time × site	3	57	0.745	0.974	3	84	16.80	< **0.001**
time × warming	3	57	1.851	0.148	3	84	2.77	**0.046**
time × site × warming	3	57	0.460	0.711	3	84	0.452	0.717

3.3.1.2 Ecosystem Respiration (ER)

In 2016, ER was 13% lower overall in the *Sphagnum*-dominated poor fen than the sedge-dominated fen, which was largely driven by a considerably lower ER from this fen in October (1.05 g CO_2 m^{-2} day^{-1} in comparison to 6.80 g CO_2 m^{-2} day^{-1} in the sedge-dominated intermediate fen; Figure 3.2). The *Sphagnum*-dominated poor fen experienced a significantly higher ER (32%) than sedge-dominated intermediate fen in 2017 (Figure 3.2; Table 3.2). The two fen sites had similar seasonal patterns of ER with ER in both sites peaking July (time × site: $F_{5,100} = 0.544$, $P = 0.724$). Short-term passive warming did not significantly alter the ER in either of the fen sites in 2017 (Table 3.3).

Even though an effect of passive warming on ER was not observed, soil temperature and ER were strongly correlated at all measured depths in both 2016 (Figure 3.3) and 2017 (Figure 3.4) in the sedge-dominated intermediate fen, and soil temperature became an increasingly stronger predictor of ER at a deeper depth in this fen site (Figure 3.4). However, in the *Sphagnum*-dominated poor fen, only a small to moderate correlation was found between soil temperature and ER in 2016 and 2017 (Figures 3.3 and 3.4). Soil temperature at 10 cm and 15 cm best-predicted ER in the *Sphagnum*-dominated poor fen while there were only weak relationships between ER and soil temperature at a deeper depth (e.g., 25 cm; Figure 3.4). There was no relationship between passive warming on ER and soil temperature at any depth in either of the fen sites, based on ANCOVA analyses (Sedge: 5 cm: $P = 0.129$; 10 cm: $P = 0.173$; 15 cm: $P = 0.108$; 20 cm: $P = 0.086$; 25 cm: $P = 0.072$; *Sphagnum*: 5 cm: $P = 0.156$; 10 cm: $P = 0.117$; 15 cm: $P = 0.184$; 20 cm: $P = 0.236$; 25 cm: $P = 0.634$; Figure 3.4a-e).

Soil moisture was not strongly correlated with ER in either the sedge-dominated intermediate fen or the *Sphagnum*-dominated poor fen in 2016 (Figure 3.5a). In 2017, there were small to moderate negative correlations between soil moisture and ER in the sedge-dominated intermediate fen (Figure 3.5b). Likewise, passive warming did not alter the relationship between soil temperature and ER in either the sedge-dominated intermediate fen ($P = 0.197$) or the *Sphagnum*-dominated poor fen ($P = 0.619$) in 2017 (Figure 3.5b).

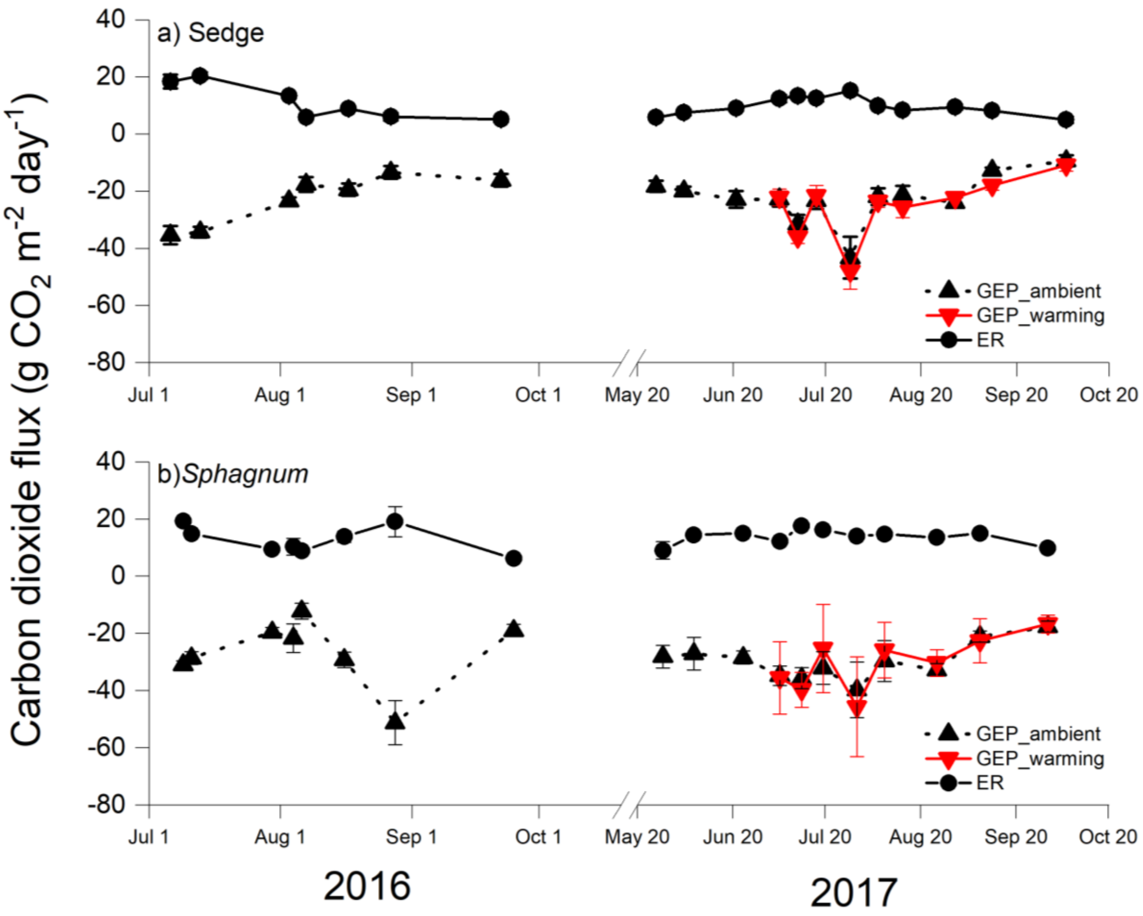

Figure 3.2 Seasonal patterns of gross ecosystem productivity (GEP) and ecosystem respiration (ER) under ambient and passive warming (started on Jun 18 in 2017) in: a) sedge-dominated intermediate fen and b) *Sphagnum*-dominated poor fen over two field seasons in 2016 and 2017. Each value represents the mean ± standard error (before the start of passive warming; n=16; n= 8 for both “ambient” and “warming” treatments after the initiation of passive warming). Both GEP and ER values are in units of g CO_2 m^{-2} day^{-1}.

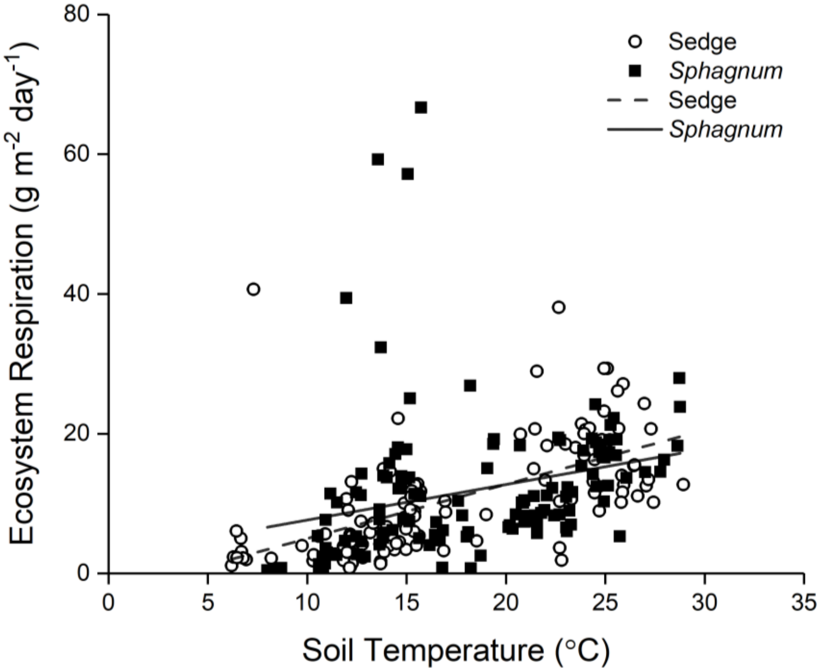

Figure 3.3 Correlations between soil temperature (~10 cm below the peat surface) and ecosystem respiration (ER) from the sedge-dominated intermediate fen (as indicated by hollow black circles) and the *Sphagnum*-dominated poor fen (as indicated by black filled squares) from July to October in 2016. The significant, strong positive linear correlation between soil temperature and ER were found both in the sedge-dominated intermediate fen (Pearson's r: 0.60, n = 113, $P < 0.001$) and the *Sphagnum*-dominated poor fen (Pearson's r: 0.27, n = 133, $P = 0.001$).

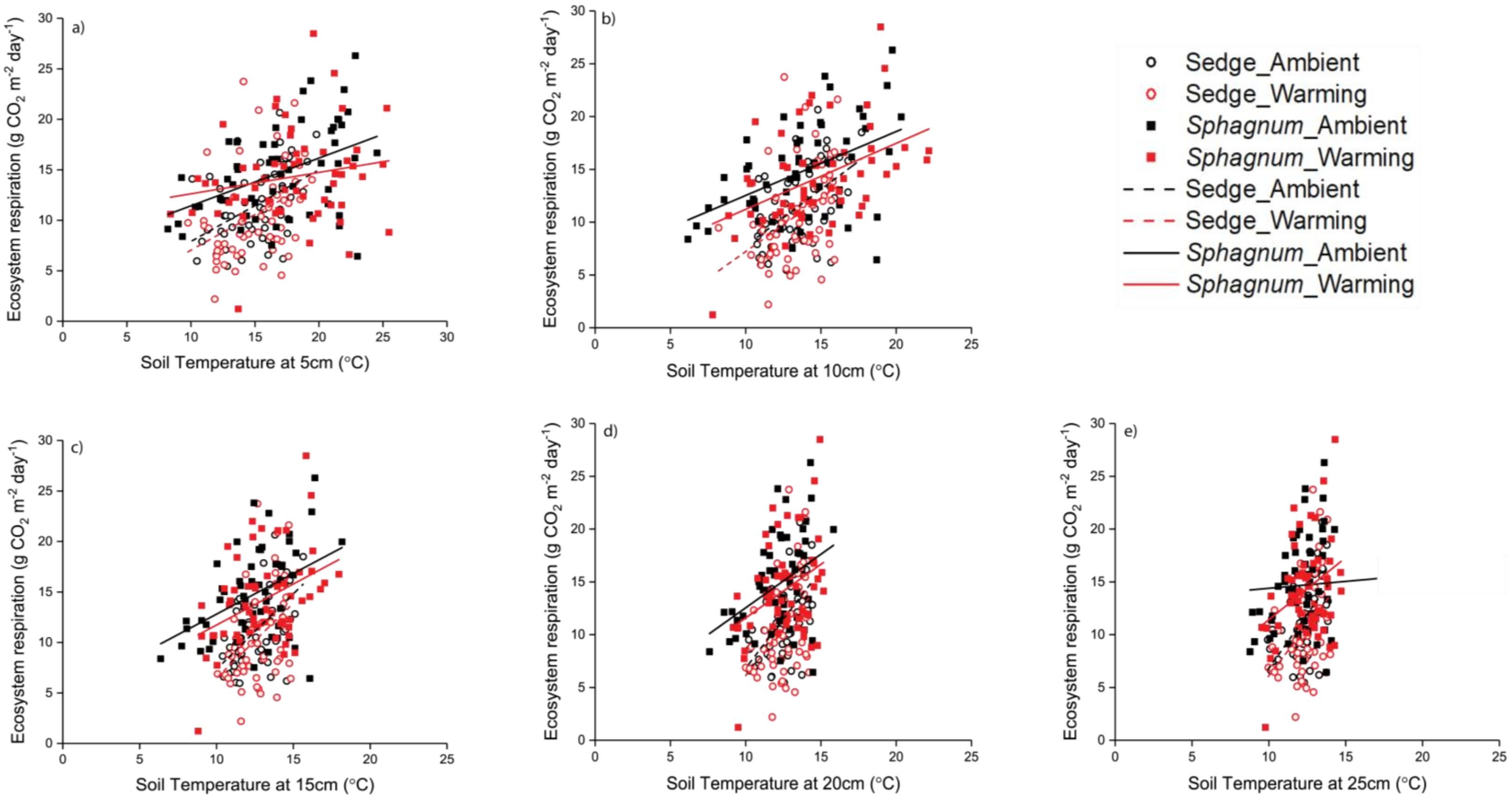

Figure 3.4 Correlations between ER and soil temperature at different depths under ambient and passive warming conditions from both sedge-dominated intermediate fen and *Sphagnum*-dominated poor fen during the growing season (July to September) in 2017. Figures 3.4 a) to e) represent ER and soil temperature correlations with soil temperature measured at 5, 10, 15, 20 and 25 cm. In the sedge-dominated intermediate fen, ER and soil temperatures were moderately to strongly correlated at different soil depths under both

ambient (5 cm: Pearson’s r: 0.46, $P < 0.001$; 10 cm: Pearson’s r: 0.53, $P < 0.001$; 15 cm: Pearson’s r: 0.57, $P < 0.001$; 20 cm: Pearson’s r: 0.59, $P < 0.001$; 25 cm: Pearson’s r: 0.58, $P < 0.001$) and passive warming conditions (5 cm: Pearson’s r: 0.38, $P < 0.004$; 10 cm: Pearson’s r: 0.40, $P = 0.003$; 15 cm: Pearson’s r: 0.42, $P = 0.001$; 20 cm: Pearson’s r: 0.43, $P < 0.001$; 25 cm: Pearson’s r: 0.43, $P < 0.001$). In the *Sphagnum*-dominated poor fen soil temperature and ER were moderately correlated at all depths under the ambient condition (5 cm: Pearson’s r: 0.44, $P < 0.001$; 10 cm: Pearson’s r: 0.47, $P < 0.001$; 15 cm: Pearson’s r: 0.43, $P = 0.001$; 20 cm: Pearson’s r: 0.39, $P= 0.004$; 25 cm: Pearson’s r: 0.17 $P = 0.228$) and passive warming, except the a small correlation at 5 cm under the warming condition (5 cm: Pearson’s r: 0.19, $P < 0.001$; 10 cm: Pearson’s r: 0.45, $P < 0.001$; 15 cm: Pearson’s r: 0.40, $P = 0.002$; 20 cm: Pearson’s r: 0.37, $P = 0.005$; 25 cm: Pearson’s r: 0.34, $P = 0.011$).

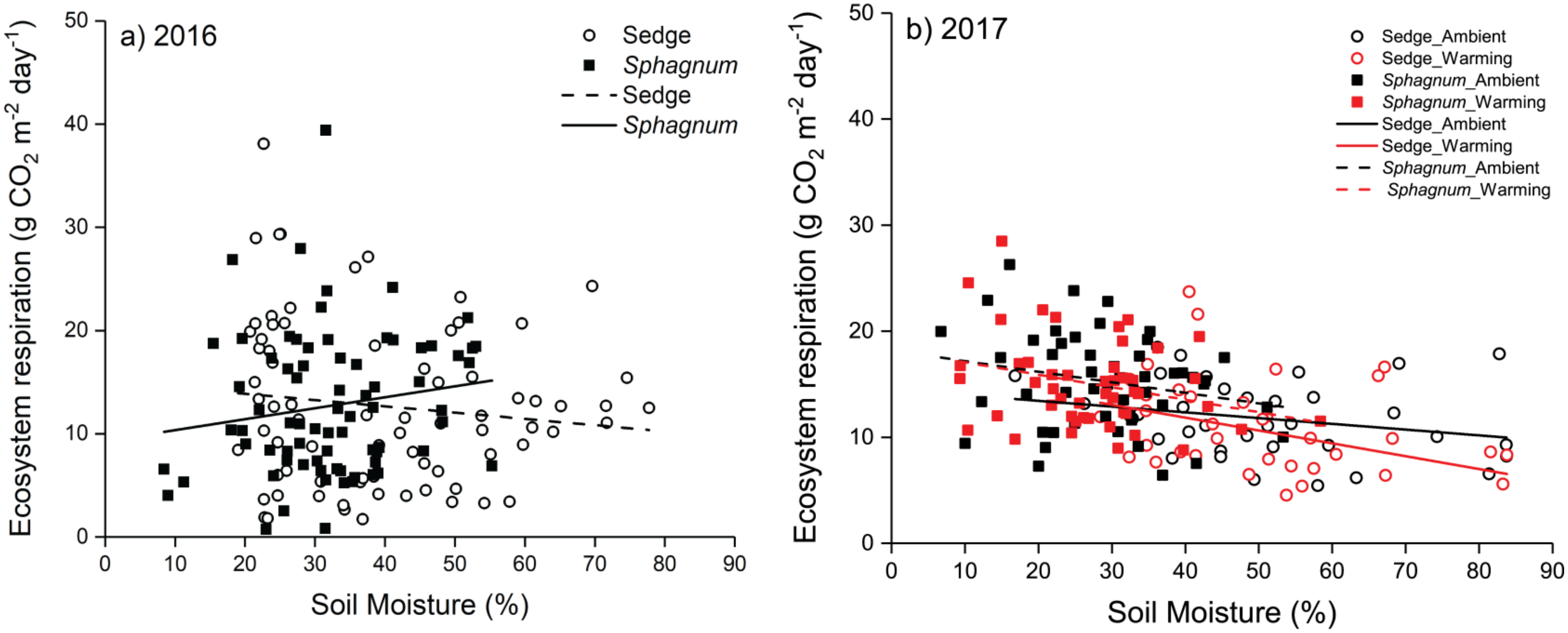

Figure 3.5 Correlations between soil moisture (~10 cm below the peat surface) and ER from the sedge-dominated intermediate fen (as indicated by black hollow circles) and the *Sphagnum*-dominated poor fen (as indicated by black filled squares) from: a) July to September in 2016 and b) July to October in 2017. In 2016, a small negative correlation was found between soil moisture and ER in the sedge-dominated intermediate fen (Pearson's r: -0.12, n = 76, *P* = 0.294), and there was a small positive correlation between soil moisture and ER in the *Sphagnum*-dominated poor fen (Pearson's r: 0.16, n = 75, *P* = 0.171). In 2017, soil moisture and ER moderately and positively correlated with ER in the sedge-dominated intermediate fen under both ambient (Pearson's r: -0.25, n = 36,

P = 0.135) and passive warming conditions (Pearson's r: -0.32, n = 36, *P* = 0.055). While in the *Sphagnum*-dominated poor fen, there are small negative correlations between soil moisture and ER under both the ambient (Pearson's r: -0.23, n = 48, *P* = 0.123) and passive warming condition (Pearson's r: -0.28, n = 48, *P* = 0.050).

3.3.1.3 Gross Ecosystem Productivity (GEP)

The GEP in the *Sphagnum*-dominated poor fen was 8.4% and 44.2% higher than the sedge-dominated intermediate fen during field seasons in 2016 and 2017, respectively. (Figure 3.2; Table 3.2). In 2016, GEPs in two fen sites showed seasonal patterns during the peak growing season (time × site: $F_{2,46} = 6.732$, $P = 0.003$). The GEP of the *Sphagnum*-dominated poor fen was significantly lower in July ($F = 5.343$, $P = 0.030$) but significantly higher in August ($F = 11.531$, $P = 0.002$) in comparison to the sedge-dominated intermediate fen, and GEPs were similar in September.

By contrast, in 2017, GEP between two fens did not change significantly throughout the growing season (time × site: $F_{5,40} = 0.244$, $P = 0.940$). More specifically, GEP of the *Sphagnum*-dominated poor fen was three times as high as that of the sedge-dominated peatland at the start of the growing season (e.g., May 2017; Figure 3.2), but GEP became closer between the two fen sites in June after an increase of GEP in the sedge-dominated intermediate fen. From July to October, GEP in the *Sphagnum*-dominated poor fen were ~ 4.98 g CO_2 m^{-2} day^{-1} to 9.26 g CO_2 m^{-2} day^{-1} higher than the sedge-dominated intermediate fen, with the difference only being significant in September ($F = 5.517$, $P = 0.047$) and October ($F = 8.520$, $P = 0.019$).

Similar to the NEE, passive warming did not significantly alter GEP in either fen site (Table 3.3). However, the September GEP was considerably higher (84%) under passive warming in the sedge-dominated intermediate fen (passive warming in September: $P = 0.068$; Figure 3.2), whereas GEP in the *Sphagnum*-dominated poor fen was only slightly higher (7%) under the passive warming in September (Figure 3.2).

3.3.2 Methane Fluxes

In 2016, the mean seasonal CH_4 emission was 15% greater from the sedge-dominated intermediate fen than that from the *Sphagnum*-dominated poor fen (peatland type: $F_{1,29} = 0.834$, $P = 0.369$, Figure 3.6) and by 134% in 2017 under ambient temperatures (peatland type: $F_{1,14} = 66.293$, $P < 0.001$, Figure 3.6). CH_4 emissions from the sedge-dominated intermediate fen showed clear seasonal patterns in both years (Figure 3.6). For example, in 2017, the mean CH_4 flux in the sedge-dominated intermediate fen increased sharply around mid-June before reaching the seasonal maximum at ~118 mg CH_4 m^{-2} day^{-1} in mid-July. After that, the mean CH_4 flux gradually decreased to 50 mg CH_4 m^{-2} day^{-1} by mid-September, and then remained relatively constant until early October (Figure 3.6). In contrast, the mean CH_4 flux from the *Sphagnum*-dominated poor fen did not show clear seasonal patterns in either year, although temperature and GEP changed over time (Figure 3.6).

There were strong positive correlations between soil temperature and CH_4 emission in the sedge-dominated intermediate fen at all soil depths except near the surface (5 cm) (Figures 3.7 and 3.8). I did not observe an effect of passive warming on CH_4-temperature correlations at all depths, as suggested by ANCOVA analyses (5 cm: $P = 0.680$; 10 cm: $P = 0.575$; 15 cm: $P = 0.620$; 20 cm: $P = 0.752$; 25 cm: $P = 0.726$). By contrast, in the *Sphagnum*-dominated poor fen, only small correlations between soil temperature and CH_4 were found in both 2016 and 2017 (Figures 3.7 and 3.8).

Unlike soil temperature, CH_4 emissions were not related to soil moisture in either the sedge-dominated intermediate fen or the *Sphagnum*-dominated poor fen in either 2016 (sedge: Pearson's r = 0.04, $P = 0.830$; *Sphagnum*: Pearson's r = - 0.18, $P = 0.351$; Figure 3.9a) or 2017 (sedge: Pearson's r = - 0.16, $P = 0.298$; *Sphagnum*: Pearson's r = 0.06, $P = 0.722$; Figure 3.9b). According to ANCOVA analyses, passive warming did not alter the relationship between soil moisture and CH_4 emissions in either the sedge-dominated intermediate fen ($P = 0.553$) or the *Sphagnum*-dominated poor fen ($P = 0.973$) (Figure 3.9b).

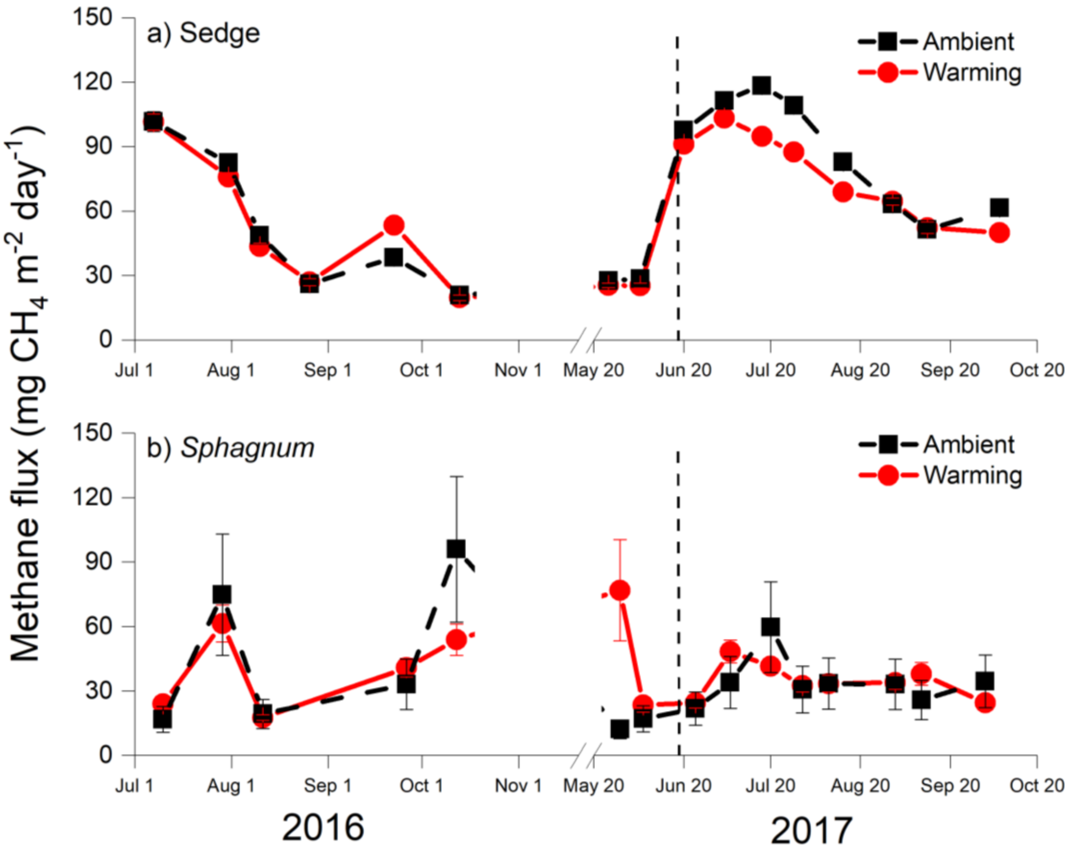

Figure 3.6 Seasonal patterns of CH_4 emissions from: a) sedge-dominated intermediate fen and b) *Sphagnum*-dominated poor fen over two field seasons in 2016 and 2017. Solid, black squares with dash lines indicate "ambient" plots in both Figures a) and b); solid, red circles with solid lines indicate "warming" plots in both Figures a) and b). Each value represents the mean ± standard error (n=8). The vertical black dash line indicates when the passive warming started in 2017.

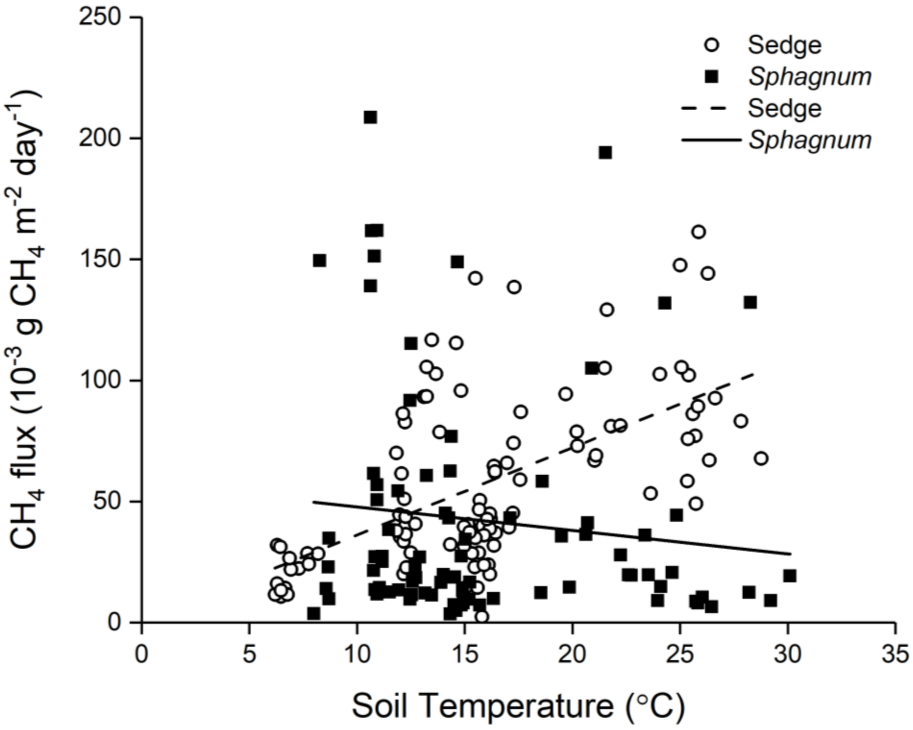

Figure 3.7 Correlations between soil temperature (~10 cm below the peat surface) and CH_4 emissions from the sedge-dominated intermediate fen (as indicated by hollow black circles) and the *Sphagnum*-dominated poor fen (as indicated by black filled squares) during July to October in 2016. The significant, strong positive correlation was found between soil temperature and CH_4 emissions in the sedge-dominated intermediate fen (Pearson's r: 0.59, n = 101, $P < 0.001$), whereas a non-significant, small negative linear correlation was observed in the *Sphagnum*-dominated poor fen (Pearson's r: -0.12, n = 86, $P = 0.29$).

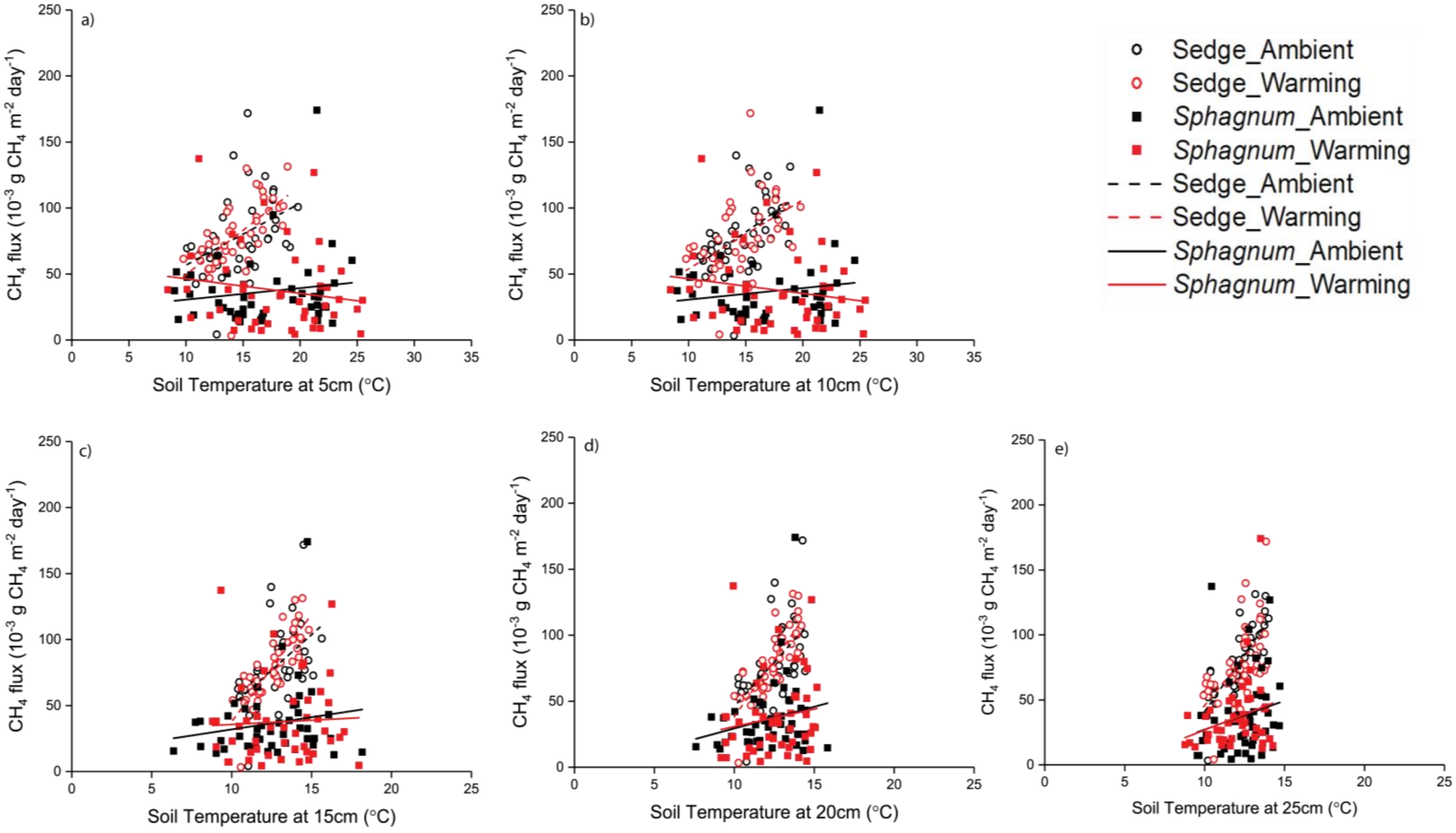

Figure 3.8 Correlations between soil temperature and CH$_4$ emissions at different depths under ambient and passive warming conditions from both sedge-dominated intermediate fen and *Sphagnum*-dominated poor fen during the growing season (July to September) in 2017. Figure 3.9 a) to e) represent soil temperature and CH$_4$ emissions correlations with soil temperature measured at 5

cm, 10 cm, 15 cm, 20 cm and 25 cm. Strong positive correlations between soil temperature and CH_4 emission were found in the sedge-dominated intermediate fen at different soil depths under both ambient (5 cm: Pearson's r: 0.40, $P = 0.010$; 10 cm: Pearson's r: 0.51, $P < 0.001$; 15 cm: Pearson's r: 0.53, $P < 0.001$; 20 cm: Pearson's r: 0.56, $P < 0.001$; 25 cm: Pearson's r: 0.78, $P < 0.001$) and passive warming conditions (5 cm: Pearson's r: 0.63, $P < 0.01$; 10 cm: Pearson's r: 0.46, $P < 0.002$; 15 cm: Pearson's r: 0.82, $P < 0.001$; 20 cm: Pearson's r: 0.81, $P < 0.001$; 25 cm: Pearson's r: 0.58, $P < 0.001$). By contrast, soil temperature and CH_4 emissions were not strongly correlated in the *Sphagnum*-dominated poor fen under either the ambient (5 cm: Pearson's r: 0.14, $P = 0.333$; 10 cm: Pearson's r: 0.14, $P = 0.333$; 15 cm: Pearson's r: 0.17, $P = 0.245$; 20 cm: Pearson's r: 0.22, $P = 0.132$; 25 cm: Pearson's r: 0.20, $P = 0.173$) or passive warming conditions (5 cm: Pearson's r: -0.16, $P < 0.291$; 10 cm: Pearson's r: -0.16, $P = 0.333$; 15 cm: Pearson's r: 0.05, $P = 0.743$; 20 cm: Pearson's r: 0.16, $P = 0.299$; 25 cm: Pearson's r: 0.26, $P = 0.083$).

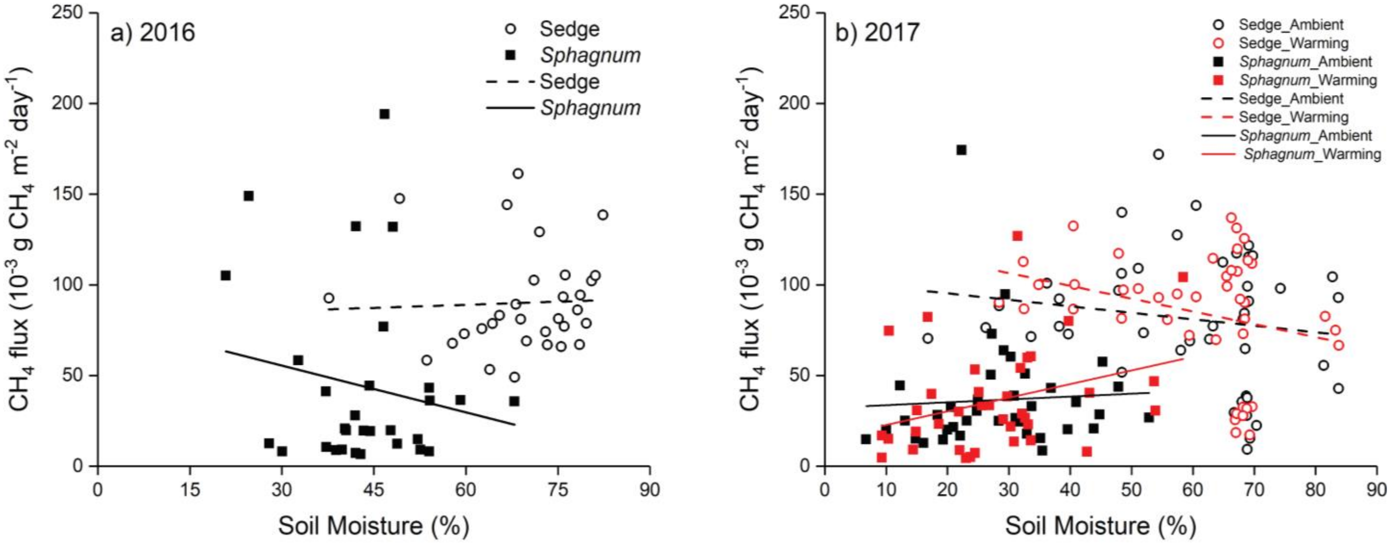

Figure 3.9 Correlations between soil moisture (~10 cm below the peat surface) and CH_4 emissions from the sedge-dominated intermediate fen (black hollow circle) and the *Sphagnum*-dominated poor fen (black filled squares) from: a) July to September in 2016 and b) July to October in 2017. In 2016, small correlations were observed between soil moisture and CH_4 emissions in both the sedge-dominated intermediate fen (Pearson's r: 0.04, n = 31, *P* = 0.830) as well as the *Sphagnum*-dominated poor fen (Pearson's r: -0.18, n = 30, *P* = 0.351). In 2017, under the ambient condition, there were small correlations between soil moisture and CH_4 emissions from both the sedge-dominated intermediate fen (Pearson's r: -0.15, n = 45, *P* = 0.298) and the *Sphagnum*-dominated poor fen (Pearson's r: 0.06, n = 39, *P* = 0.722). Under the passive warming condition, moderate correlations between soil moisture and CH_4 emissions were observed in the sedge-dominated intermediate fen (Pearson's r: -0.29, n = 42, *P* = 0.057) and the *Sphagnum*-dominated poor fen (Pearson's r: 0.32, n = 37, *P* = 0.053).

Passive warming did not significantly change the overall CH_4 emissions from either the sedge-dominated intermediate fen or the *Sphagnum*-dominated poor fen throughout July to October in 2017 (site × warming: $F_{1,28} = 0.527$, $P = 0.474$; Figure 3.6, Table 3.3). However, the mean CH_4 emission in the sedge-dominated intermediate fen decreased by 11.3% under the passive warming treatment, and this decrease occurred mainly during the peak growing season in July when the GEP was high in that peatland. In addition, in the sedge-dominated intermediate fen, there was a positive linear correlation between monthly averaged GEP and CH_4 emission over the growing season (July to September) (Pearson's r: 0.81, n = 23, $P < 0.001$; Figure 3.10a), and this correlation was significantly altered under the passive warming (Pearson's r: 0.55, n = 23, $P = 0.007$) as suggested by the ANCOVA analysis ($P = 0.009$; Figure 3.10a). Meanwhile, no linear correlations were found between GEP and CH_4 in the *Sphagnum*-dominated poor fen, but these correlations were not significant under both ambient (Pearson's r: -0.15, n = 24, $P = 0.48$) and passive warming conditions (Pearson's r: -0.05, n = 24, $P = 0.83$; Figure 3.10b).

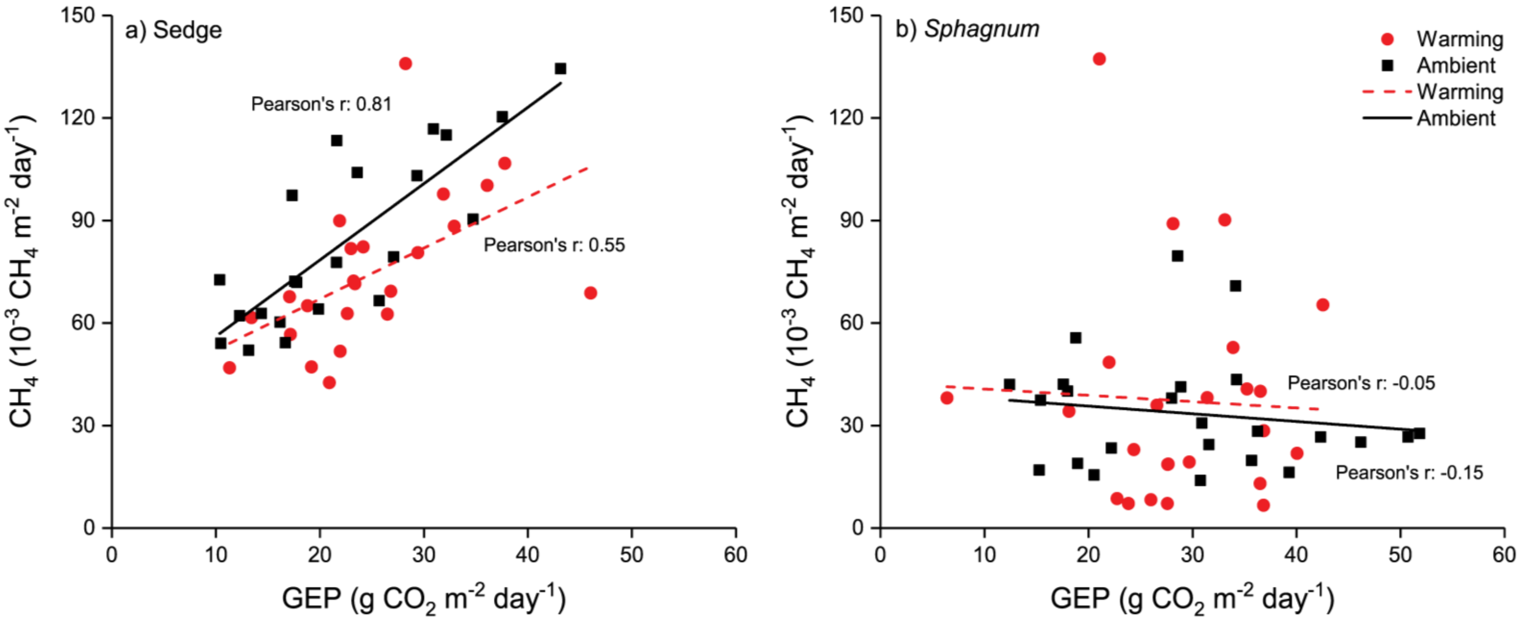

Figure 3.10 Short-term passive warming significantly altered the correlation between GEP and CH_4 emission: a) from the sedge-dominated intermediate fen (ambient: Pearson's r: 0.81, n = 23, $P < 0.001$; warming: Pearson's r: 0.55, n = 23, $P = 0.007$; ANCOVA: $P = 0.009$), but did not have significant effect on correlation between GEP and CH_4 emission b) from the *Sphagnum*-dominated poor fen (ambient: Pearson's r: -0.15, n = 24, $P = 0.48$; warming: Pearson's r: -0.05, n = 24, $P = 0.83$) during the peak growing season in 2017. Monthly averaged values (from July to September in 2017) in "ambient" and "warming" plots are represented by black filled squares and red filled circles, respectively. Linear fittings of GEP and CH_4 correlations in "ambient" and "warming" plots are represented by solid black lines and red dash lines, respectively.

3.4 Discussion

3.4.1 Carbon Dioxide Exchanges

Supporting my first hypothesis, the *Sphagnum*-dominated poor fen was a larger CO_2 sink than the sedge-dominated intermediate fen over a full growing season. This is also consistent with previous studies that suggested *Sphagnum*-dominated peatlands are usually greater CO_2 sinks, owing to their lower CO_2 emissions via ER (Glenn *et al.*, 2006; Lafleur *et al.*, 2005). I observed a lower ER in 2016, but a higher ER in 2017, from the *Sphagnum*-dominated poor fen. This indicates that a larger CO_2 sink in the *Sphagnum*-dominated poor fen is not always driven by its lower ER. In *Sphagnum*-dominated peatlands, lower C substrate quality impedes decomposition leading in part to lower CO_2 emissions (Reiche *et al.*, 2010). As indicated by the $SUVA_{254}$ data, the *Sphagnum*-dominated poor fen DOC was more aromatic in character than DOC from the sedge-dominated intermediate fen, supporting the lower substrate quality explanation.

I propose that different seasonal vegetation dynamics between different vegetation groups (e.g., sedges, shrubs and mosses) played an essential role in controlling the net CO_2 uptake in peatlands. Firstly, shrubs have longer growing periods than sedges by at least ten days, and this may contribute considerably to the higher seasonal plant production of shrubs (Sweet *et al.*, 2015). Secondly, in comparison to sedges, shrubs are more competitive in absorbing nutrients, especially during the early growing season in spring by virtue of their shallower root system (Wang *et al.*, 2016). In this study, the NEE of the *Sphagnum*-dominated poor fen was significantly higher than that of the sedge-dominated intermediate fen in the spring (e.g., May 2017). The NEE between two fen sites became similar throughout the growing season from June to August, after sedges started to grow in June. Furthermore, the considerably higher GEP in the *Sphagnum*-dominated poor fen greatly contributed to more negative NEE (C uptake) in this fen during the fall (September and October 2017). These findings suggest that the larger CO_2 sink in the *Sphagnum*-dominated poor fen is driven by plant productivity in the spring and the fall.

Although this study did not find any clear relationship between the 2017 passive warming treatments and C exchange, this is not inconsistent with previous studies. Previous work found that passive warming started to have more significant impacts on peatland CO_2 exchanges only after several growing seasons (Chivers *et al.*, 2009; Dorrepaal *et al.*, 2009; Wiedermann *et al.*, 2007). Chivers *et al.* (2009) started to see increases in both plant productivity and ER in a rich fen almost two and a half years after the initiation of passive warming. Similarly, Dorrepaal *et al.* (2009) reported a significant effect of passive warming on ER after four years from the start of the experiment in a *Sphagnum*-dominated peatland in Sweden. Wiedermann *et al.* (2007) suggested that a *Sphagnum*-dominated peatland was relatively stable under the passive warming condition for as long as nine years. These data suggest that deeper soil warming as a result of more prolonged climate warming may accelerate the destabilization of the C pool of northern peatlands.

I did observe a significantly more negative NEE in the sedge-dominated intermediate fen under passive warming. I hypothesized that warming could lead to an extended growing season for plants by delaying their senescence during the fall, and indeed the results presented here support this idea in vascular plant dominated peatlands. The initial photosynthetic activity and senescence of plants, and therefore the length of growing season, are defined by threshold temperatures (Mynenl *et al.*, 1997) and it has been predicted that the length of active growing season will increase by one to two weeks under climate warming conditions due to a fall extension (Richardson *et al.*, 2018). Thus, the warming-induced changes in growing season length will be increasingly important in predicting responses of peatland C cycling to climate warming.

3.4.2 Methane Fluxes

Net CH_4 emissions varied significantly among different peatland types, owing to differences in water table depths and vegetation communities among different type of peatlands. In this study, I found that the sedge-dominated intermediate fen was a significantly larger source of CH_4 than the *Sphagnum*-dominated poor fen, and this was consistent with results from previous studies at the same peatlands but with less intensive measurement programs (Godin *et al.*, 2012; Webster *et al.*, 2013). The water table is an important control on CH_4 emissions from peatlands, with lower water tables reducing CH_4 emissions (Blodau *et al.*, 2004; Turetsky *et al.*, 2014; Updegraff *et al.*, 2001) because of deeper aerobic zones and increased CH_4 oxidation (Updegraff *et al.*, 2001).

The average water table was significantly lower in the *Sphagnum*-dominated poor fen than sedge-dominated intermediate fen (Table 3.1) — decreased methanotrophy at least partially explains the significantly higher CH_4 emission from the latter fen.

Vascular plants also play an essential role in regulating net CH_4 emissions from peatlands, and the predominance of sedges in the intermediate fen may also drive an increase in CH_4 production. The removal of vascular plants (e.g., *Carex* spp. and *Eriophorum* spp.) decreased CH_4 emissions by 30% to 85% in a bog (Waddington *et al.*, 1996). Likewise, Turetsky *et al.* (2014) found increased CH_4 emissions from peatlands with greater graminoid abundance. Positive correlations between plant productivity and net CH_4 fluxes have been widely reported in previous studies (Lai *et al.*, 2014; Luan & Wu, 2014; Strack *et al.*, 2004; Waddington *et al.*, 1996; Whiting & Chanton, 1993). A positive correlation between GEP and CH_4 emission was also found here, but only in the sedge-dominated intermediate fen, and this may be due to the production of root exudates that are metabolized by methanogens, or the transport of CH_4 through aerenchyma of some peatland vascular plants, including *Carex* spp. (Joabsson *et al.*, 1999).

Temperature has long been recognized as one of the primary controls on peatland CH_4 emissions (Dunfield *et al.*, 1993; Duval & Radu, 2018; Gill *et al.*, 2017; Wilson *et al.*, 2016; Yvon-Durocher *et al.*, 2014). Increased temperature can directly stimulate peatland CH_4 emissions since temperature is the 'first order control' on the microbial community. Turetsky *et al.* (2008) found that increased CH_4 emission was associated with increased methanogen abundance in peat soils under warming condition. In this study, I did not directly measure methanogen activity, but I speculate that passive warming did not affect the microbial activity according to the unaltered ecosystem respiration under passive warming in both of the fen sites. I argue that, under passive warming, the decrease in growing season CH_4 emission from the sedge-dominated intermediate fen was mainly attributed to the indirect effect of warming on the aboveground plant community. Vegetation and temperature have been found to affect peatland CH_4 emissions interactively, and vegetation is a more important control on peatland greenhouse gas production than moderate increases in temperature (Ward *et al.*, 2013). A positive correlation between GEP and CH_4 emissions was also significantly altered under passive warming with the same GEP values supporting lower CH_4 emissions under warming in the sedge-dominated intermediate fen (Figure 3.10). There are two potential explanations for the warming-induced decrease in CH_4 emissions from the sedge-dominated intermediate fen. First, with increased plant productivity, there is enhanced internal oxygen transport via aerenchyma in vascular plants, which could lead to enhanced CH_4 oxidation and reduced net CH_4 emission from the sedge-dominated intermediate fen (Luan & Wu, 2014). Second, plant biomass tends to allocate more towards aboveground relative to belowground under the warming condition (Day *et al.*, 2008). I also found in the mesocosm experiment that warming was a primary control on increases in aboveground plant biomass (see Chapter 2; Figure 2.1). The decrease in the C allocation towards belowground root systems might result in decreases in C substrate supply for methanogenesis via root exudates (Joabsson & Christensen, 2001; Ström *et al.*, 2003).

Finally, I found that CH_4 emissions were strongly correlated with soil temperature at various depths (10, 15, 20 and 25 cm) in the sedge-dominated intermediate fen, indicating root exudates are supporting the methanogenesis throughout the peat horizon. However, there were only weak correlations between CH_4 emissions and soil temperatures at all depths up to 25 cm in the *Sphagnum*-dominated poor fen, and the lack of response of CH_4 emission to temperature could be derived from the substrate limitation for methanogenesis in this fen, as suggested by a previous study at the same site (Godin *et al.*, 2012). Shrubs such as leatherleaf were predominant vascular plants in the *Sphagnum*-dominated poor fen. Indeed, shrubs have relatively shallow rooting systems in comparison to sedges (Wang *et al.*, 2016), whose roots can penetrate 230 cm below the surface (Saarinen, 1996). Shallow roots of shrubs constrained the transport of labile C substrate via root exudates to anaerobic peat horizon below the water table, where methanogenesis occurred, and this could substantially limit the CH_4 production in the *Sphagnum*-dominated poor fen.

3.5 Conclusion

This chapter elucidates that CO_2 and CH_4 fluxes are significantly different between *Sphagnum*-dominated and sedge-dominated fens in terms of magnitudes, seasonal variations, and environmental controls. Also, C fluxes in the sedge-dominated fen are more sensitive to warming than the *Sphagnum*-dominated fen. While CH_4 fluxes from the *Sphagnum*-dominated fen remain unaltered, the sedge-dominated fen tends to negatively respond to climate warming with fewer CH_4 being released with rising temperatures. If *Sphagnum*- and sedge-dominated fens are not considered separately, peatland C models will likely to overestimate the global warming potential of northern peatlands under climate change. Overall, this work suggests that incorporating the peatland type as a parameter into peatland C models is essential to simulate ecosystem-atmosphere C exchanges accurately. Future research should further explore the control of sedge plants on net CH_4 emissions from northern peatlands under varying temperature regimes.

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Chapter 4

4 Dissolved Organic Carbon Characteristics in Two Contrasting Boreal Fens and Their Responses to *in situ* Passive Warming

4.1 Introduction

By containing ~ 30% of global soil carbon (C), northern peatlands are significant long-term C stores (Gorham, 1991; Post *et al.*, 1982). The accumulation of C in northern peatlands results from wet and cool environments at higher latitudes, which slows microbial decomposition leading to a net C accumulation despite low primary productivity (Gorham, 1991). However, changes in environmental conditions, such as increased temperature, elevated atmospheric carbon dioxide (CO_2) and or water table drawdown are expected to destabilize the C storage in northern peatlands (Bridgham *et al.*, 2008; Davidson & Janssens, 2006). As a result, northern peatlands are likely to experience increases in both greenhouse gases emissions (e.g., CO_2 and CH_4) (Dorrepaal *et al.*, 2009; Gill *et al.*, 2017; Turetsky *et al.*, 2008; Wilson *et al.*, 2016; Yvon-Durocher *et al.*, 2014) and dissolved organic carbon (DOC) production (Dieleman *et al.*, 2016; Fenner & Freeman, 2011; Freeman *et al.*, 2001a; Freeman *et al.*, 2004) under future climate conditions. Research has tended to prioritize studies of the impacts of climate change on greenhouse gas emissions from peatlands (Gill *et al.*, 2017; Voigt *et al.*, 2017; Ward *et al.*, 2013), and studies on peatland DOC dynamics under climate warming are more scarce. Since DOC is a critical C substrate for microbial decomposition, it is hypothesized that increasing DOC concentrations in peatland would greatly influence the water quality and decomposition processes in receiving ecosystems such as rivers and streams (Ritson *et al.*, 2014). The increase in DOC production from northern peatlands is undoubtedly an important and less well-studied pathway of future C loss from northern peatlands (Evans *et al.*, 2005).

In addition to the continued breakdown of peat soils through continued decomposition, living vegetation also contributes to DOC via inputs of fresh plant litter, root exudates as well as its impacts on microbial decomposition rates (Dieleman *et al.*, 2017; Gavazov *et* *al.*, 2018; Hodgkins *et al.*, 2014; Moore & Dalva, 2001; Palozzi & Lindo, 2017; Walker *et al.*, 2016; Zhu & Cheng, 2011). High-quality DOC contains a large portion of labile DOC that can be readily utilized by microorganisms, whereas DOC with low quality tends to more resistant to biodegradation (Kalbitz *et al.*, 2000). Both laboratory (Del Giudice & Lindo, 2017; Pinsonneault *et al.*, 2016) and field experiments (Armstrong *et al.*, 2012; Wickland *et al.*, 2007) have revealed the heterogeneous nature of plant-derived DOC. For instance, *Sphagnum* mosses are commonly associated with slow decomposition rates due to more decay-resistant structures and through the inhibition of microbial activity due to the presence of sphagnan — a type of polysaccharide in their cell walls (Hájek *et al.*, 2011; van Breemen, 1995). In contrast, vascular plants have more decomposable litters and more biodegradable DOC; Robroek *et al.* (2016) found that sedge-derived DOC had a 68% higher mineralization rate relative to *Sphagnum* mosses. Additionally, vascular plants can provide labile C substrate via leaf litter leaching and compounds released from living roots (Dieleman *et al.*, 2017; Mastný *et al.*, 2018; Wang *et al.*, 2015). These highly labile C inputs have been shown to enhance the decomposition of more recalcitrant organic C in deep peat horizon by "priming" microbial activity (Gavazov *et al.*, 2018; Walker *et al.*, 2016). It is not unexpected that peatlands with different dominant vegetation communities tend to exhibit distinct DOC pools in both quantity and quality (Webster & McLaughlin, 2010), and these differences in DOC quantity and quality may influence future decomposition rates and greenhouse gas emissions from northern peatlands in a warming world (Hodgkins *et al.*, 2014; Hoyos-Santillan *et al.*, 2016).

Temperature is also a vital control on peatland DOC quantity and quality. Higher temperatures can directly increase microbial activity and decomposition (Davidson & Janssens, 2006), resulting in higher pore water DOC concentrations (Dieleman *et al.*, 2016; Fenner *et al.*, 2007; Pastor *et al.*, 2003; Kane *et al.*, 2014). Under warming conditions, peatland DOC was found to be less aromatic in character (Dieleman *et al.*, 2016) and to decompose two times faster (Kane *et al.*, 2014). Increases in DOC quality can stimulate the decomposition and greenhouse gas emissions from peatlands, leading to positive feedback to climate warming (Hodgkins *et al.*, 2014). Moreover, climate warming was shown to substantially increase the vascular plant growth at the expense of

Sphagnum mosses (Dieleman *et al.*, 2015; Heijmans *et al.*, 2008; Jassey *et al.*, 2013; Walker *et al.*, 2015). Interactions between warming and the warming-induced vegetation shift can considerably alter the DOC quantity and quality in northern peatlands, making the peatland C cycling under climate change more difficult to predict.

Vegetation-derived DOC near the peat surface tends to be more responsive to climate warming since the rising temperature has a more significant influence on aboveground vegetation than belowground microbial processes (Day *et al.*, 2008; Wang *et al.*, 2016). The warming-driven increases in vegetation productivity or changes in vegetation community composition can potentially alter the DOC characterization near the peat surface. However, previous studies on peatland DOC dynamic have focused mainly on bulk pore water DOC sampled from wells or being exported in runoffs (Freeman *et al.*, 2001a; Kane *et al.*, 2014; Ritson *et al.*, 2014; Waddington & Roulet, 2000) with vertical changes of DOC within the peat horizon being largely neglected. Multiple studies regarding vegetation-derived DOC characterization primarily focused on vegetation leachate using incubation experiment in the laboratory (Del Giudice & Lindo, 2017; Hodgkins *et al.*, 2014; Mastný *et al.*, 2018; Wickland *et al.*, 2007), and there is yet no field-based study investigating the near-surface, vegetation-derived DOC that reflects more recently produced DOC with higher biodegradability, although this DOC pool is expected to be vulnerable to climate warming.

Despite the importance of understanding DOC quantity and quality in peatlands with different vegetation communities and their potential responses to climate warming, only a few studies have investigated this relationship in *Sphagnum*-dominated poor fens (Dieleman *et al.*, 2016; Kane *et al.*, 2014), and no study has yet been conducted in the sedge-dominated fen. In this study, two fen peatlands with contrasting vegetation communities, a *Sphagnum*-dominated poor fen and a sedge-dominated intermediate fen, were studied to:1) characterize the differences in quantity and quality of DOC in both near-surface and deeper bulk pore waters, and 2) investigate responses of DOC quantity and quality in shallow (near-surface) and deep (bulk) pore waters in response to experimental passive warming over one growing season. The hypotheses of this study were:1) the sedge-dominated intermediate fen would have higher concentrations of DOC with a more biodegradable character in shallow pore waters than *Sphagnum*-dominated poor fen due to the dominance of vascular plants; 2) deeper pore water DOC concentrations would be higher in the *Sphagnum*-dominated poor fen due to its more recalcitrant quality, and; 3) shallow pore water DOC would be more responsive to passive warming than the deep pore water DOC in both fen sites owing to faster responses of aboveground plant productivity to warming conditions.

4.2 Materials and Methods

4.2.1 Study Site

The study site locates at two contrasting fen peatlands, a poor fen and an intermediate fen, near White River, ON, Canada (48˚21’N, 84˚20’W). Both fen sites are in a peatland complex that has been studied since 2005 (Palozzi & Lindo, 2017; Webster & McLaughlin, 2010; Webster *et al.*, 2013). According to climate data from the nearest weather station (Wawa, 47°58′ N, 84°47′ W), the mean annual temperature in this area was 2.1˚C, and the total precipitation was 970 mm of which 319 mm was snowfall over the period 1981 to 2010 (Environment Canada). The poor fen is acidic, relatively nutrient-poor and dominated by *Sphagnum* mosses, with the presence of ericaceous shrubs including leatherleaf (*Chamadephne calyculata* (L.) and labrador tea (*Rhododendron groenlandicum* Oeder) as well as some short vascular plants including bog rosemary (*Andromeda polifolia*) and bog cranberry (*Vaccinium oxycoccos*). A scattered tree overstorey of black spruce (*Picea mariniana*) and tamarack (*Larix laricina*) is also present. The intermediate fen is less acidic and more nutrient-rich, with a much simpler vegetation community dominated by sedges (*Carex* spp.) and shrubs (dominantly sweet gale (*Myrica gale* (L.)) (Palozzi & Lindo, 2017).

4.2.2 Experimental Design and Set-up

As part of a broader long-term experiment investigating the impacts of climate change on northern fen peatlands, sixteen 1 m diameter, 50 cm deep rigid polyvinyl chloride (PVC) plastic collars were installed in each of the two peatlands in 2015 to create experimental plots and left to recover from this disturbance for a full year. At the same time, a fully penetrating well (~50 cm deep) made from Teflon® was installed in the middle of each collar for integrated pore water sampling. In June 2017, clear polycarbonate chambers (~740 L in volume) were installed on eight collars for passive warming in a random block design at each of the sites to account for environmental variations among collars. All collars were grouped into four blocks at each site, with two controls and two passively warmed collars within each block. In general, there were four treatments in the field experiment: poor fen ambient (non-warming), poor fen warming, intermediate fen ambient (non-warming) and intermediate fen warming.

4.2.3 Pore Water Sample Collection

Shallow pore water samples (between 10-15 cm relative to the peat surface) were collected using MacroRhizon® samplers installed vertically in each plot (Rhizosphere Research Products, Wageningen, Netherland). The membranes of the Rhizon samplers have a nominal 0.15 μm pore size, and as such, samples taken from the Rhizons are considered filtered and were not subjected to any further processing. Rhizon water samples were collected under vacuum weekly from June to October 2017 into 20 ml clean plastic syringes connected to the Luer-lock fitting on each Rhizon sampler. Once the syringe was filled, the sample was dispensed into a 20 ml-acid washed glass vial and stored in the dark at 4°C until analysis.

Deep pore waters were sampled from the Teflon wells through a ¼” clear Teflon tubing installed permanently in each well through a ¼” Teflon compression fitting fitted in a cap. Each well was covered by a cap to keep it free from contamination. Deep pore water samples were collected using a Geopump® (Geotech Environmental Equipment, Inc, Denver, CO, USA) that attached with a Masterflex® C-FlexUltra tubing (Core-Palmer Instrument Co., Vernon Hills, IL, USA). In 2016, after the wells were first installed, deep pore water samples were collected from the wells monthly from July to October as baseline data. The pore water samples from wells were collected into 500 ml PETG bottles and then filtered using 0.5 μm pore size filters into 60 ml HDPE bottles and 60 ml amber glass bottles for DOC quantity and quality measurements respectively. In 2017, pore water samples were sampled from wells on a weekly basis from May to October. Pore waters from deep well and shallow Rhizons were sampled within two days during each sampling trip. All filtered water samples were stored at 4°C in the dark before analysis.

4.2.4 Pore Water Analysis

All pore water samples were analyzed for DOC concentrations using an Aurora 1030 iTOC analyzer using the sodium persulfate wet oxidation method (Osburn & St-Jean, 2007). Samples were also analyzed for DOC quality using a Horiba Aqualog® spectrofluorometer with a xenon lamp (HORIBA Scientific, Ltd, Kyoto, Japan). Ultraviolet absorbance at 254 nm and excitation-emission fluorescence matrices (EEMs) were analyzed simultaneously. Final specific UV absorbance values ($SUVA_{254}$) were calculated from 254 nm absorbance values dived by the total DOC concentrations. Three commonly used fluorescence indices were calculated from the EEMs data — freshness index (BIX), fluorescence index (FI) and humification index (HIX) (e.g., Dieleman *et al.*, 2016; Fellman *et al.*, 2010), together with Peak A, C, B and T and Peak C/A_{340} (Coble, 1996) that indicates humic-like DOC (Peak A & C), protein-like DOC (Peak B & T) and DOC molecular weights (Peak C/A_{340}) using the R software x64 3.4.0 (R Core Team, 2013). All EEMs' fluorophores were produced with excitations ranging from 240 – 600 nm (5 nm increment) and emissions ranging from 245.60 – 827.72 nm (4.66 nm increment) with an integration time at 0.5 s. Raman analysis was used to normalize samples with the changes in the lamp intensity over time. For every ten samples, a blank (using Milli-Q water) and a duplicate were run for quality assurance.

4.2.5 Statistical Analysis

All statistical analyses were conducted in Statistica 13.3 (TIBCO Software Inc., 2017). The block effect was tested using the repeated-measures ANOVA (RM-ANOVA) and Tukey HSD *post hoc* test for all DOC quantity and quality indicators in the two fen sites. If there was a significant block effect, the "block" was included as a factor in subsequent analyses; otherwise, it was excluded from further analyses. The RM-ANOVA was also used for quantifying effects of fen type and passive warming on all DOC quantity and quality indices from both sources (shallow vs. deep pore waters) in two fen sites throughout the growing season in 2017. Monthly DOC concentration and $SUVA_{254}$

values in both fens from 2016 were tested using RM-ANOVA for any initial variation among blocks at each fen site. OriginPro 2017 (OriginLab, version 94E) was used for conducting the principal component analysis (PCA) and the production of all figures in this chapter.

4.3 Results

4.3.1 Dissolved Organic Carbon Quantity

The mean DOC concentration in shallow pore water was significantly higher in the *Sphagnum*-dominated poor fen (56.9 mg/L) than the sedge-dominated intermediate fen (32.7 mg/L; Figure 4.1a; Table 4.1). Shallow water DOC concentrations varied seasonally and differently between the two fen sites (Table 4.1). In the sedge-dominated intermediate fen, the shallow water DOC concentration slowly increased from the start of the growing season (mid-June) before reaching a peak at around late-August, following by a slight decrease towards the fall (Figure 4.1a). In contrast, there was a strong increase in shallow water DOC concentration in the *Sphagnum*-dominated poor fen from the start of the growing season, before reaching the first peak at around the start of August, followed by a decrease then a further increase until September, after which concentrations declined through the fall (Figure 4.1a). Passive warming did not have any effect on shallow DOC concentration in either fen site (Figure 4.1a; Table 4.1).

Likewise, the mean DOC concentration in deep pore water was also significantly higher in the *Sphagnum*-dominated poor fen (44.2 mg/L) than the sedge-dominated intermediate fen (27.7 mg/L; Figure 4.1b; Table 4.1). There was a seasonal pattern of deep water DOC concentration between the two fen sites that was different than for shallow water DOC (Figure 4.1b; Table 4.1). In the *Sphagnum*-dominated poor fen, deep water DOC concentrations increased consistently from the start of the growing season to the fall, while the sedge-dominated intermediate fen showed an increase in the deep water DOC concentration until reaching a maximum during late August, followed by a decline through the fall (Figure 4.1b). There was also no significant passive warming effect on the deep water DOC concentration in either fen (Figure 4.1b; Table 4.1), but there was a slight increase in deep water DOC concentration (from 42.4 mg/L to 46.1 mg/L) in the

Sphagnum-dominated poor fen under passive warming. However, this increase was mainly driven by the increased deep water DOC concentration in a single block (block 1) in the *Sphagnum*-dominated poor fen where the deep water DOC concentration was consistently lower than other blocks in both 2016 and 2017 (Table 4.2).

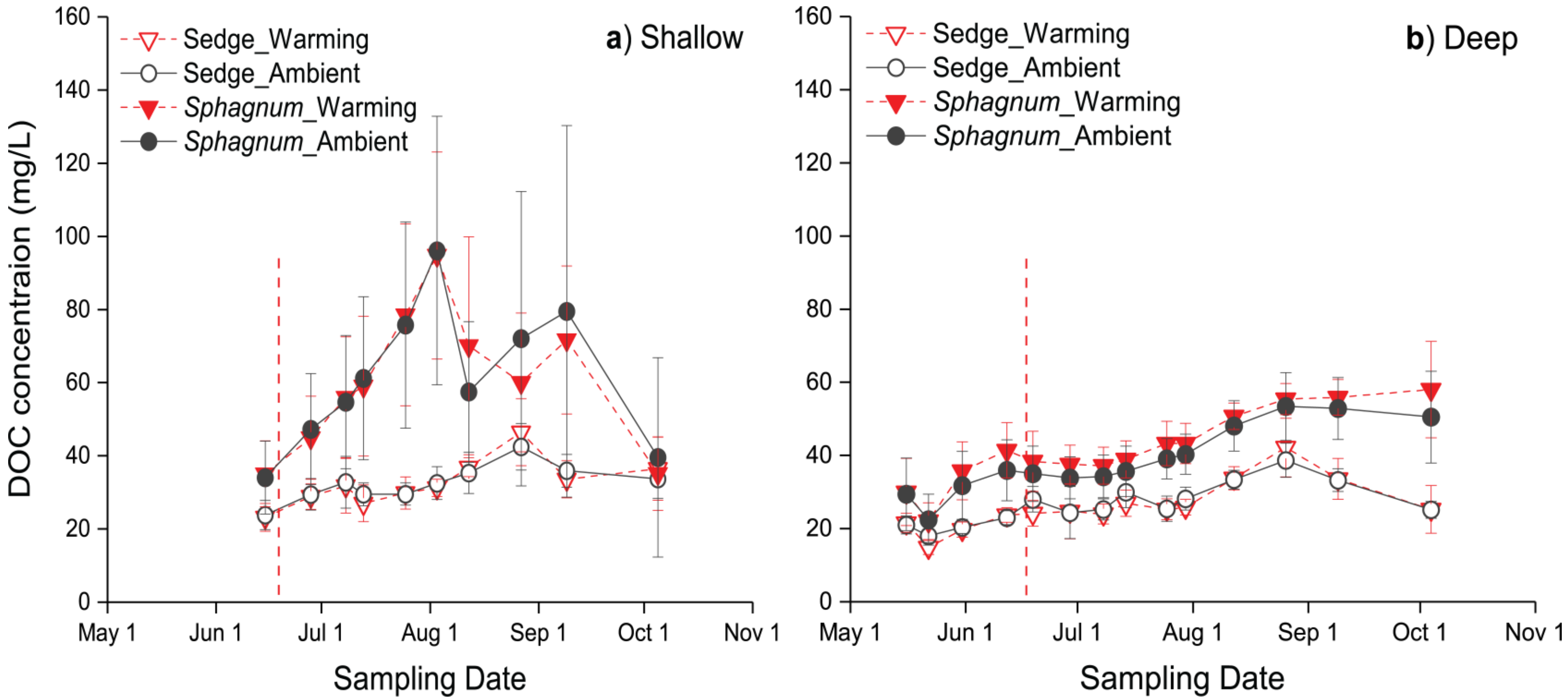

Figure 4.1 Seasonal patterns and passive warming effects on DOC concentrations in: a) shallow Rhizon and b) deep well pore waters between two fen sites throughout the full growing season in 2017. In both figures, vertical dash lines in red represent the time when passive warming begins. Each value represents the mean ± standard error.

Table 4.1 RM-ANOVA analyses on monthly averaged pore water DOC concentrations in two fen sites in 2017.

	Shallow pore water (Rhizon)				Deep pore water (well)			
Source of variation	*df*	Error *df*	*F*	*P*	*df*	Error *df*	*F*	*P*
site	1	27	27.135	< **0.001**	1	28	84.104	< **0.001**
warming	1	27	0.007	0.933	1	28	0.916	0.347
site × warming	1	27	0.007	0.935	1	28	1.169	0.289
time	4	108	21.856	< **0.001**	5	140	140.27	< **0.001**
time × site	4	108	13.262	< **0.001**	5	140	27.789	< **0.001**
time × warming	4	108	0.544	0.704	5	140	0.822	0.536
time × site × warming	4	108	0.537	0.709	5	140	0.858	0.511

Table 4.2 RM-ANOVA analyses of block effects on DOC concentration and $SUVA_{254}$ in two fen sites in 2016 and 2017.

		2016				2017			
Site	Variable	*df*	Error *df*	*F*	*P*	*df*	Error *df*	*F*	*P*
Sphagnum-dominated poor fen	DOC	3	12	11.855	**0.001**	3	12	4.956	**0.018**
	$SUVA_{254}$	3	12	4.872	**0.019**	3	12	4.303	**0.028**
Sedge-dominated intermediate fen	DOC	3	12	0.547	0.660	3	12	1.876	0.188
	$SUVA_{254}$	3	12	0.743	0.973	3	12	3.003	0.726

4.3.2 Dissolved Organic Carbon Quality

4.3.2.1 Specific UV Absorbance ($SUVA_{254}$)

The mean $SUVA_{254}$ of DOC in shallow pore waters was slightly lower in the sedge-dominated intermediate fen (3.33 L mg^{-1} m^{-1}), than that in the *Sphagnum*-dominated poor fen (3.55 L mg^{-1} m^{-1}), although this difference was not significant (Figure 4.2a; Table 4.3). The $SUVA_{254}$ in shallow pore waters changed significantly over the growing season, but the seasonal patterns were different between the two sites, which was mainly driven by the increase in shallow water $SUVA_{254}$ in the *Sphagnum*-dominated poor fen during the fall (Figure 4.2a; Table 4.3). There was no overall effect of passive warming on shallow pore water $SUVA_{254}$ in either fen (Table 4.3); however, in October shallow pore water $SUVA_{254}$ decreased by 28% in the sedge-dominated intermediate fen and increased by 38% in the *Sphagnum*-dominated poor fen under the passive warming (Figure 4.2a).

In deep pore waters, $SUVA_{254}$ values were similar in both sites at the start of the growing season (e.g., May) but diverged in June with deep pore water $SUVA_{254}$ becoming substantially higher in the *Sphagnum*-dominated poor fen than the sedge-dominated intermediate fen until the end of the growing season (Figure 4.2b; Table 4.3). Deep pore water $SUVA_{254}$ in both fens peaked around late August; however, deep water $SUVA_{254}$ in the *Sphagnum*-dominated poor fen remained elevated until early in October, whereas in the sedge-dominated intermediate fen, deep water $SUVA_{254}$ slowly decreased during the fall (Figure 4.2b). Passive warming did not significantly affect $SUVA_{254}$ values of deep pore waters in either fen site (Table 4.3), but I did observe subtle and different responses of deep water $SUVA_{254}$ to passive warming between two fens. Deep water $SUVA_{254}$ slightly decreased in the sedge-dominated intermediate fen and slightly increased in the *Sphagnum*-dominated poor fen under passive warming. In the sedge-dominated intermediate fen, the slight increase of deep pore water $SUVA_{254}$ under passive warming mainly resulted from a warming-driven increase in deep water $SUVA_{254}$ in October. By contrast, in the *Sphagnum*-dominated poor fen, passive warming slightly but evenly increased the deep water $SUVA_{254}$ in June, July and September throughout the growing season (Figure 4.2b).

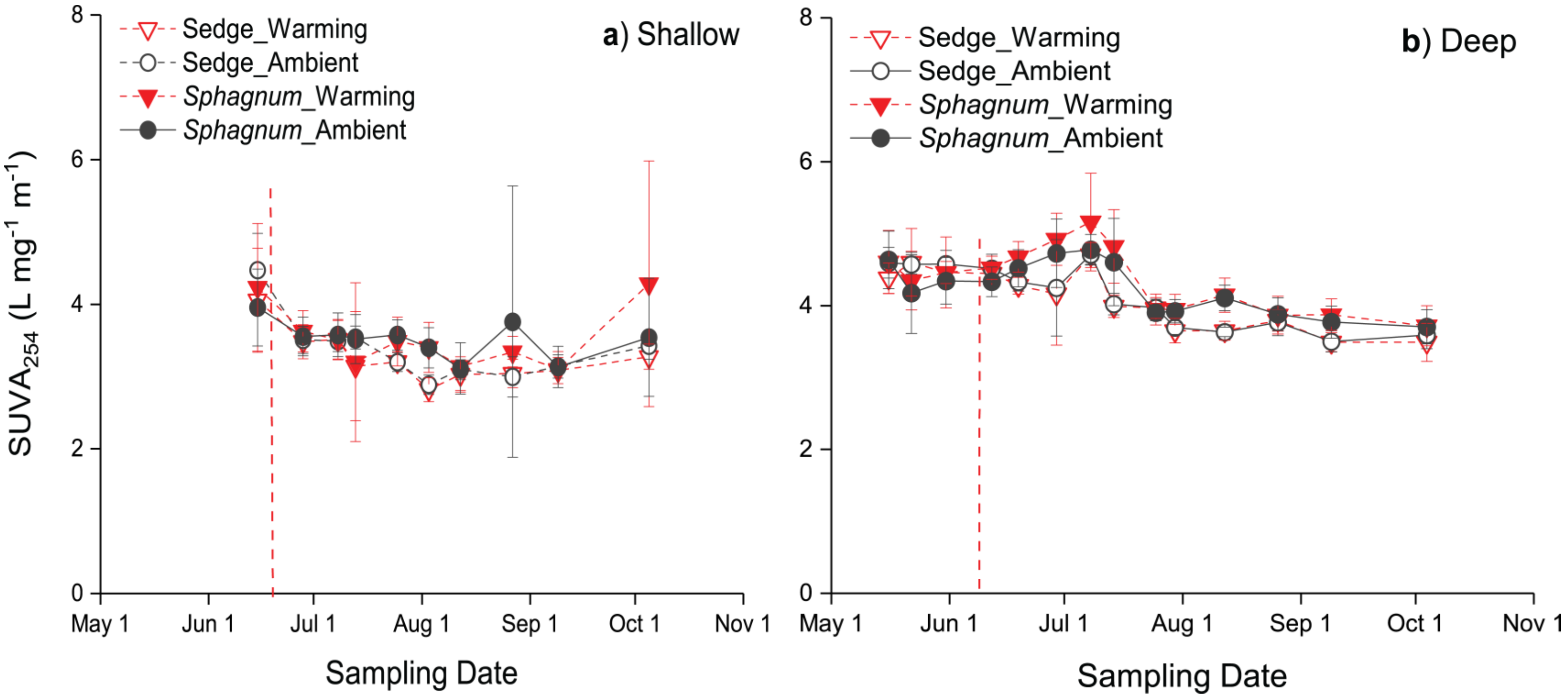

Figure 4.2 Seasonal patterns and passive warming effect on Specific UV Absorbance (SUVA) at 254 nm in: a) shallow Rhizon and b) deep well pore waters between two fen sites throughout a full growing season in 2017. In both figures, vertical dash lines in red represent the time when passive warming begins. Each value represents the mean ± standard error.

Table 4.3 RM-ANOVA analyses on monthly averaged $SUVA_{254}$ in two fen sites in 2017.

	Shallow pore water (Rhizon)				Deep pore water (well)			
Source of variation	*df*	Error *df*	*F*	*P*	*df*	Error *df*	*F*	*P*
site	1	25	3.332	0.080	1	28	13.095	< **0.001**
warming	1	25	0.043	0.837	1	28	0.146	0.705
site × warming	1	25	0.766	0.390	1	28	1.473	0.235
time	4	100	12.084	< **0.001**	5	140	156.86	< **0.001**
time × site	4	100	0.792	0.533	5	140	6.819	< **0.001**
time × warming	4	100	2.154	0.080	5	140	0.489	0.784
time × site × warming	4	100	1.409	0.237	5	140	0.509	0.769

4.3.2.2 Fluorescence Indices

In shallow pore waters, several EEMs indices including FI, BIX, Peak C/A_{340}, Peak B and Peak T were significantly higher in the sedge-dominated intermediate fen than the *Sphagnum*-dominated poor fen (Figures 4.3 and 4.4; Table 4.4). Although it was not evident in Figure 4.4d, the average Peak T value in the shallow pore water was about 28% higher in the sedge-dominated intermediate fen than the *Sphagnum*-dominated poor fen. Other EEMs indices such as HIX, Peak A and Peak C were not different between the two fen sites (Figures 4.3 and 4.4; Table 4.4). Passive warming did not significantly affect any fluorescence index of shallow pore water DOC in either fen site (Table 4.4).

In the deep pore waters, FI, BIX and Peak C/A_{340} indices were also significantly higher in the sedge-dominated intermediate fen than the *Sphagnum*-dominated poor fen, whereas Peak A and Peak C were significantly lower in the sedge-dominated intermediate fen than the *Sphagnum*-dominated poor fen (Figures 4.3 and 4.4; Table 4.4). There were no significant differences in HIX and Peak T between the two fen sites, and even though the peak B was significantly higher in the sedge-dominated intermediate fen, this difference was mainly driven by the substantially lower peak B value in “block 2” in the *Sphagnum*-dominated poor fen and should not be overinterpreted. The passive warming treatment did not significantly affect any of the derived fluorescence indexes of deep pore water DOC in either fen site (Table 4.4).

Additionally, in the principal component analysis of shallow pore waters, the first two principal components accounted for 63.79% of the variance (PC1: 38.70% and PC2: 25.09%), while 55.42% of the variance was explained by the first two principal components (PC1: 30.21% and PC2: 25.20%) in the PCA of deep pore waters (Figure 4.5). In shallow pore waters, the DOC concentration, Peak B and BIX were greatly correlated with the PC1, whereas the PC2 strongly controlled $SUVA_{254}$, FI, Peak A and Peak C. In deep pore waters, PC1 primarily drove Peak B, Peak T and HIX while the DOC concentration, Peak C and BIX were mainly controlled by PC2 (Table 4.5).

Table 4.4 RM-ANOVA analyses on monthly averaged EEMs indices in two fen sites in 2017.

Index	Source of variation	Shallow pore water (Rhizon)				Deep pore water (Well)			
FI		*df*	Error *df*	*F*	*P*	*df*	Error *df*	*F*	*P*
	site	1	28	42.129	< **0.001**	1	28	287.13	< **0.001**
	warming	1	28	0.22	0.643	1	28	0.034	0.855
	site × warming	1	28	3.797	0.061	1	28	0.319	0.577
	time	4	112	3.21	**0.016**	5	140	33.629	< **0.001**
	time × site	4	112	0.683	0.605	5	140	28.373	< **0.001**
	time × warming	4	112	0.321	0.863	5	140	1.409	0.225
	time × site × warming	4	112	2.857	**0.027**	5	140	1.378	0.236
BIX		*df*	Error *df*	*F*	*P*	*df*	Error *df*	*F*	*P*
	site	1	28	73.208	< **0.001**	1	28	443.46	< **0.001**
	warming	1	28	0.026	0.872	1	28	0.014	0.905
	site × warming	1	28	2.271	0.143	1	28	1.698	0.203
	time	4	112	3.603	**0.008**	5	140	11.976	< **0.001**
	time × site	4	112	1.993	0.100	5	140	14.814	< **0.001**

	time × warming	4	112	0.66	0.621	5	140	1.23	0.298
	time × site × warming	4	112	1.923	0.112	5	140	1.778	0.121
HIX		*df*	Error *df*	*F*	*P*	*df*	Error *df*	*F*	*P*
	site	1	28	0.041	0.841	1	28	2.401	0.132
	warming	1	28	0.694	0.412	1	28	0.402	0.531
	site × warming	1	28	3.051	0.092	1	28	0.800	0.379
	time	4	112	4.97	**0.001**	5	140	8.244	< **0.001**
	time × site	4	112	0.876	0.481	5	140	0.459	0.806
	time × warming	4	112	0.273	0.895	5	140	0.096	0.993
	time × site × warming	4	112	3.351	**0.012**	5	140	0.370	0.868
Peak C/A340		*df*	Error *df*	*F*	*P*	*df*	Error *df*	*F*	*P*
	site	1	28	2.401	0.132	1	28	75.830	< **0.001**
	warming	1	28	0.402	0.531	1	28	0.237	0.631
	site × warming	1	28	0.800	0.379	1	28	0.066	0.780
	time	4	112	8.244	< **0.001**	5	140	2.679	**0.036**
	time × site	4	112	0.459	0.806	5	140	13.106	< **0.001**

	time × warming	4	112	0.096	0.993	5	140	0.347	0.846
	time × site × warming	4	112	0.370	0.868	5	140	0.517	0.723
Peak A		*df*	Error *df*	*F*	*P*	*df*	Error *df*	*F*	*P*
	site	1	26	0.030	0.863	1	28	4.900	**0.036**
	warming	1	26	1.020	0.322	1	28	0.000	0.838
	site × warming	1	26	0.310	0.585	1	28	0.500	0.485
	time	4	104	12.960	< **0.001**	5	140	118.200	< **0.001**
	time × site	4	104	11.300	< **0.001**	5	140	28.500	< **0.001**
	time × warming	4	104	1.240	0.298	5	140	0.800	0.583
	time × site × warming	4	104	0.150	0.965	5	140	0.400	0.843
Peak C		*df*	Error *df*	*F*	*P*	*df*	Error *df*	*F*	*P*
	site	1	26	1.820	0.189	1	28	16.300	< **0.001**
	warming	1	26	1.570	0.221	1	28	0.100	0.733
	site × warming	1	26	0.310	0.581	1	28	0.300	0.604
	time	4	104	16.090	< **0.001**	5	140	208.500	< **0.001**
	time × site	4	104	11.690	< **0.001**	5	140	35.100	< **0.001**

	time × warming	4	104	1.260	0.291	5	140	0.700	0.589
	time × site × warming	4	104	0.120	0.973	5	140	0.200	0.962
Peak B		*df*	Error *df*	*F*	*P*	*df*	Error *df*	*F*	*P*
	site	1	26	14.960	< **0.001**	1	28	5.840	**0.022**
	warming	1	26	0.040	0.836	1	28	1.590	0.218
	site × warming	1	26	0.000	0.973	1	28	0.890	0.355
	time	4	104	5.010	< **0.001**	5	140	17.320	< **0.001**
	time × site	4	104	6.530	< **0.001**	5	140	14.370	< **0.001**
	time × warming	4	104	0.630	0.640	5	140	0.930	0.464
	time × site × warming	4	104	0.270	0.899	5	140	1.390	0.230
Peak T		*df*	Error *df*	*F*	*P*	*df*	Error *df*	*F*	*P*
	site	1	26	6.820	**0.015**	1	28	1.560	0.222
	warming	1	26	1.660	0.209	1	28	0.330	0.569
	site × warming	1	26	0.250	0.623	1	28	0.010	0.907
	time	4	104	8.760	< **0.001**	5	140	29.560	< **0.001**
	time × site	4	104	15.040	< **0.001**	5	140	2.100	0.069

time × warming	4	104	0.210	0.933	5	140	0.480	0.792
time × site × warming	4	104	0.100	0.983	5	140	0.390	0.854

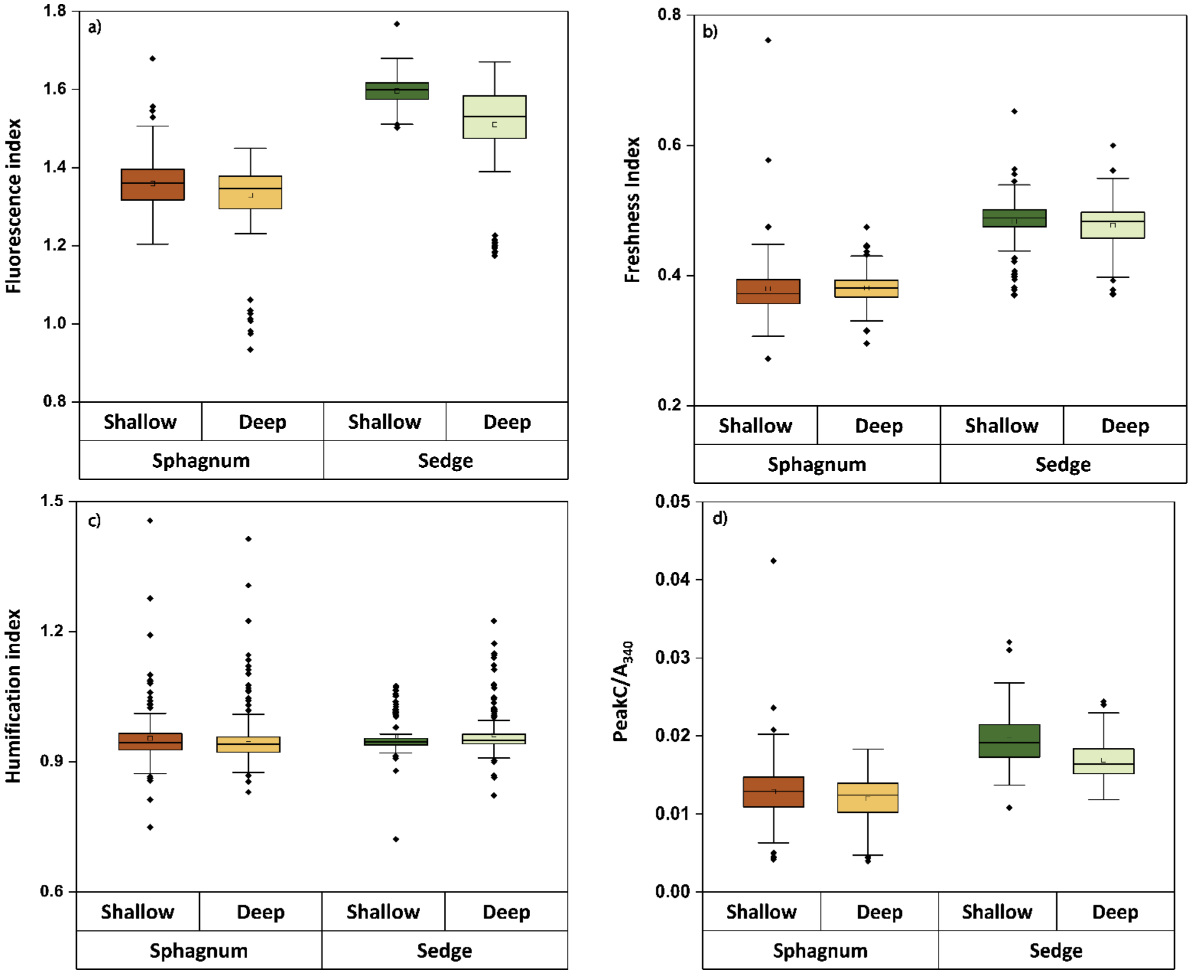

Figure 4.3 EEMs indices of DOC from both shallow and deep pore waters between the *Sphagnum*-dominated poor fen and the sedge-dominated intermediate fen in terms of: a) fluorescence index (FI), where low FI values (~1.2) indicate more plant-derived DOC and higher FI values (~1.8) indicating more microbial-derived DOC, b) freshness index (BIX), where higher BIX values represent more recently produced DOC, c) humification index (HIX), where higher HIX values suggest more degraded DOC and d) Peak C/A_{340}, which are reversely correlated to molecular weights of DOC. All index values are unitless.

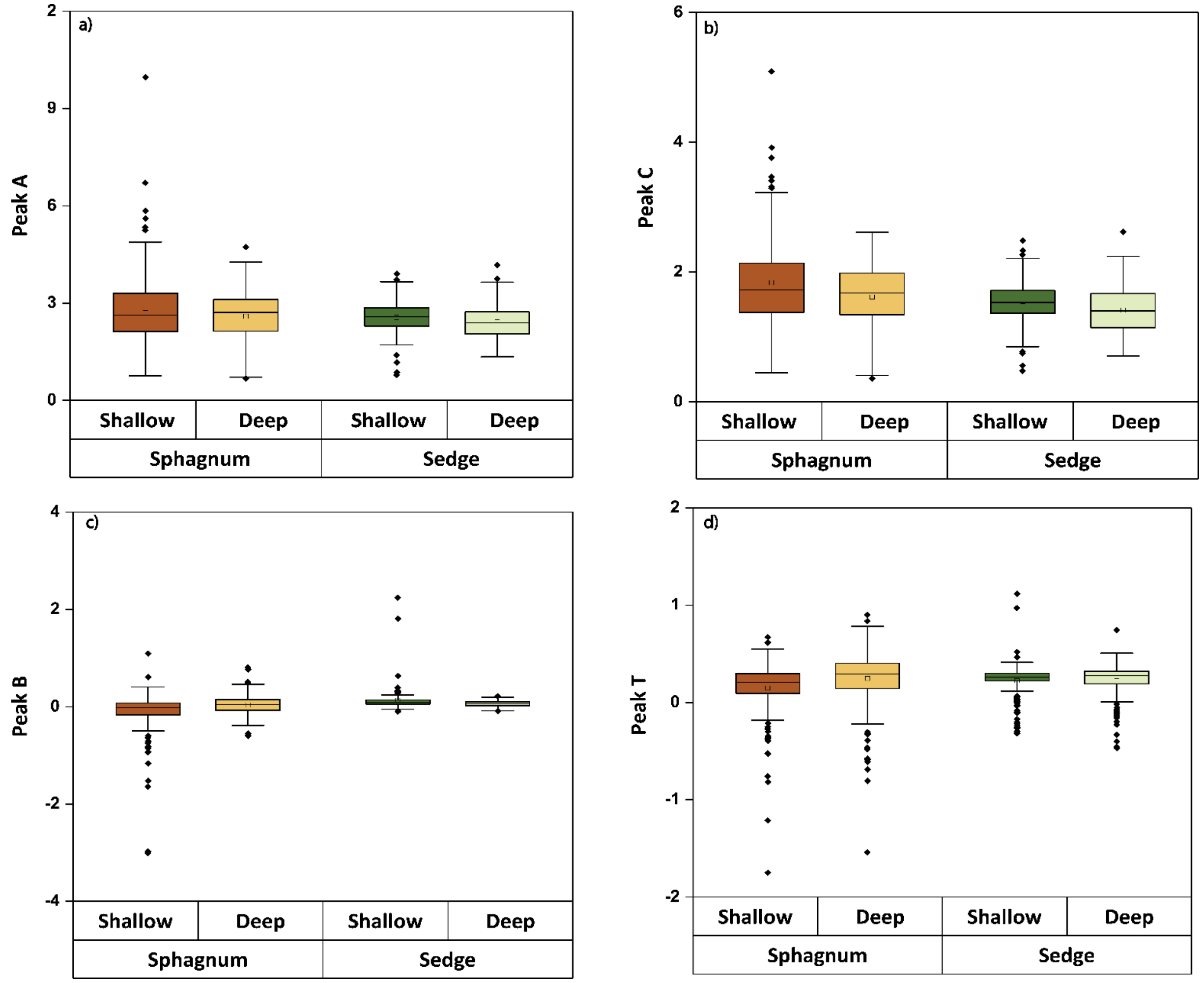

Figure 4.4 EEMs indices of DOC from both shallow and deep pore waters between the *Sphagnum*-dominated poor fen and the sedge-dominated intermediate fen of: a) Peak A, which is an indicator of humic-like C compounds, b) Peak C, which is another indicator of humic-like C compounds, c) Peak B, which is an indicator of protein-like C compounds and d) Peak T, which is also an indicator of protein-like C compounds. All index values are unitless.

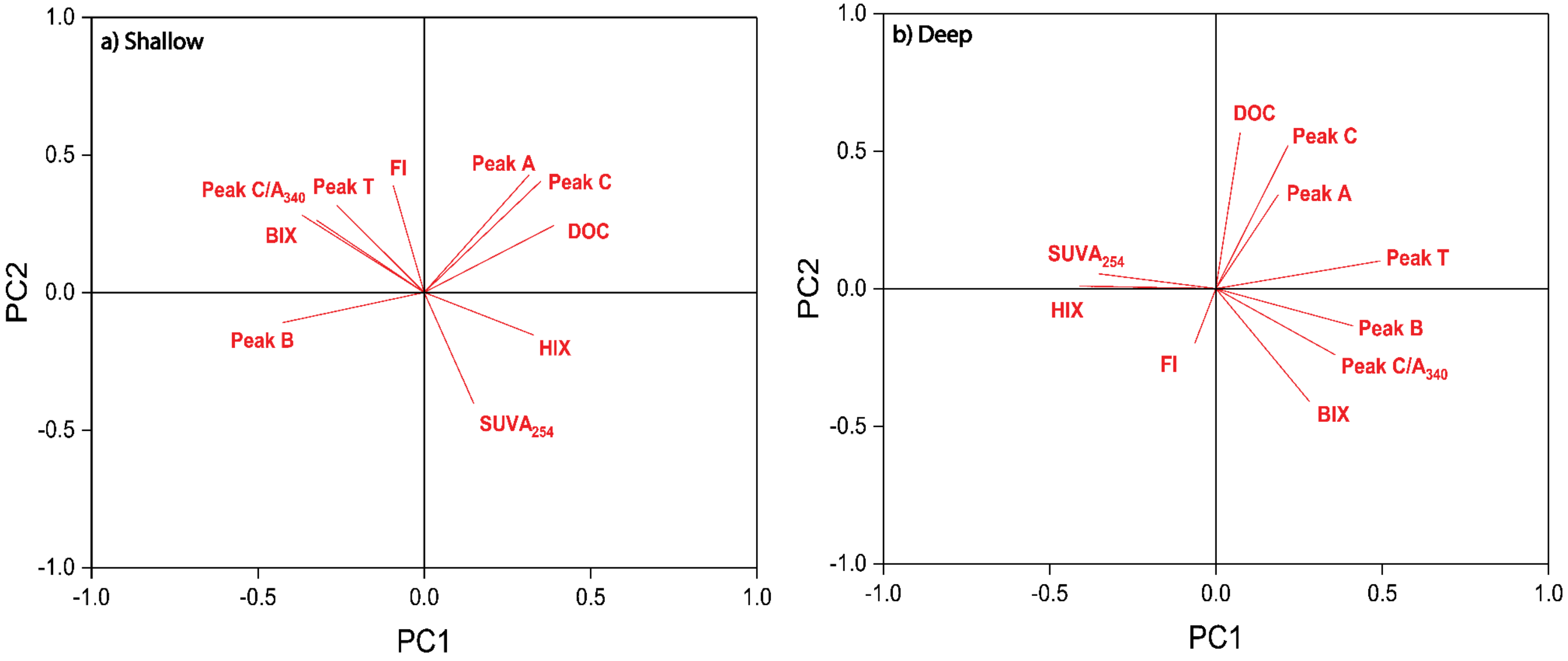

Figure 4.5 Principal components analysis (PCA) of DOC quantity and quality indices in: a) shallow and b) deep pore waters in the *Sphagnum*-dominated poor fen and the sedge-dominated intermediate fen. Coefficients of variables between PC1 and PC2 are shown in y-axis and x-axis, respectively. Variable loadings for each PC are shown as labelled lines.

Table 4.5 Coefficients of DOC quantity and quality indices with PC1 and PC2 in shallow and deep pore waters in two fen sites in 2017.

	Shallow pore water (Rhizon)		Deep pore water (Well)	
Variable	PC1	PC2	PC1	PC2
DOC	**0.39**	0.24	0.07	**0.57**
$SUVA_{254}$	0.15	**-0.40**	-0.35	0.05
FI	-0.09	0.39	-0.06	-0.20
BIX	**-0.37**	0.28	0.28	**-0.41**
HIX	0.33	-0.15	**-0.41**	0.01
Peak C/A_{340}	-0.32	0.26	0.36	-0.24
Peak A	0.31	**0.43**	0.19	0.34
Peak C	0.35	**0.40**	0.22	**0.52**
Peak B	**-0.42**	-0.11	**0.41**	-0.14
Peak T	-0.26	0.32	**0.49**	0.10

4.4 Discussion

Dissolved organic carbon is a significant component of C cycles in a number of natural soil ecosystems such as forests, grasslands and peatlands (Kindler *et al.*, 2011; Waddington & Roulet, 1997, 2000). Numerous studies have revealed the heterogeneous nature of plant-derived DOC at the surface of peatlands (e.g., Del Giudice & Lindo, 2017; Pinsonneault *et al.*, 2016); however, to the best of my knowledge, this is the first field-based experiment examining the difference of DOC quantity and quality between two contrasting boreal fen peatlands and their potential responses to *in situ* passive warming. Quantity and quality of DOC in peatlands may not only affect the *in situ* decomposition rate, but may also influence the temperature sensitivity of DOC, and ultimately have a significant impact on C storage function of northern peatlands under future climate warming (Zhu & Cheng, 2011).

4.4.1 Dissolved Organic Carbon Characterization in Two Contrasting Boreal Fens

I found that the DOC concentration in deep pore waters was considerably higher in the *Sphagnum*-dominated poor fen in relative to the sedge-dominated intermediate fen, which was in line with results from a previous study at the same site (Webster & McLaughlin, 2010) and another peatland complex (Pastor *et al.*, 2003). Owing to the decay-resistant C and low hydrological activity, it was hypothesized that DOC could accumulate in the *Sphagnum*-dominated poor fen towards a higher concentration than the sedge-dominated intermediate fen, where DOC was more biodegradable and could be readily utilized by microbes (Hodgkins *et al.*, 2016; Wickland *et al.*, 2007). These results highly support this hypothesis as I found two distinct DOC pools in deep pore waters between two fens; DOC compounds were highly plant-derived with higher molecular weights and aromaticity in the *Sphagnum*-dominated poor fen, whereas, in the sedge-dominated intermediate fen, DOC compounds were highly microbe-derived with lower molecular weights and aromaticity.

Specifically, although most FI values were lower than ~1.8 in both fens, indicating higher proportions of plant contributions than microbial-derived C to DOC pools (Fellman *et al.*, 2010), the average FI was significantly higher in the sedge-dominated intermediate fen compared to the *Sphagnum*-dominated poor fen, suggesting that more plant-derived C dominate the DOC pool in the *Sphagnum*-dominated poor fen. Deep water DOC in the sedge-dominated intermediate fen contained lower molecular weight compounds as indicated by a higher average Peak C/A_{340} value, which was negatively correlated with molecular weights of DOC (Fellman *et al.*, 2010). The $SUVA_{254}$ and Peak C values, which are indicators of plant-derived aromatic DOC (Fellman *et al.*, 2010), were significantly higher in deep water DOC from the *Sphagnum*-dominated poor fen, which further suggests a greater proportion of plant-derived DOC with higher aromaticity in the *Sphagnum*-dominated poor fen.

By contrast, in the sedge-dominated intermediate fen, a more microbial-derived DOC played a vital role in shaping the deep water DOC pool. The more humified DOC was indicated by lower HIX suggested a more advanced decomposition in the sedge-dominated intermediate fen. Besides, BIX values in both peatland sites were below ~0.6, indicating plants and peat soils (i.e., microbially modified organic components) were primary sources of those DOC (Fellman *et al.*, 2010). Furthermore, the higher BIX in the sedge-dominated intermediate fen suggested a higher proportion of freshly produced DOC compounds from microbes at the sedge-dominated fen site. Previous work at the same site determined that the carbon use efficiency (CUE) of microbes was higher in the sedge-dominated intermediate fen (Palozzi & Lindo, 2017), even though there was no significant difference in either the total microbial biomass (Palozzi & Lindo, 2017) or basal microbial activities (Myers *et al.*, 2012) between the two fen sites. Increases in CUE were found to relate to increases in the C substrate biodegradability (Allison *et al.*, 2010), which further supports the more labile and microbial source of DOC from the sedge-dominated intermediate fen. Also, the peat C:N ratio was significantly higher in the sedge-dominated intermediate fen in comparison to the *Sphagnum*-dominated poor fen

(Myers *et al.*, 2012). Since there was no difference in C:N from plant inputs (e.g., leaf C:N) to soils between the two fens (Palozzi & Lindo, 2017), the higher peat C:N in the sedge-dominated intermediate fen is highly suggestive of greater microbial activity in this fen.

Furthermore, the PCA analysis of deep water DOC further confirmed that the DOC consisted of two pools: the biodegradable DOC pool, which was primarily driven by PC1 and contained a greater amount of recently produced, protein-like C compounds, and a recalcitrant DOC pool, which was primarily explained by PC2, that was comprised of mainly terrestrial-derived, aromatic C compounds. Similarly, different DOC pools were found in shallow pore waters: PC1, which was highly correlated with DOC concentration, BIX and Peak B, was associated with the biodegradable DOC pool, and $SUVA_{254}$, Peak A and Peak C, which were driven by the recalcitrant DOC pool were correlated with PC2.

Additionally, these results showed that the DOC concentration from the shallow pore waters in the *Sphagnum*-dominated poor fen was significantly higher than that in the sedge-dominated intermediate fen. I argue that, except for shrub root exudates, the *Sphagnum* leachate also contributed considerably to the shallow DOC pool in this site. The enormous amount of DOC from *Sphagnum* leachate has been reported in a previous study (Shirokova *et al.*, 2017). In the *Sphagnum*-dominated poor fen, DOC from shallow pore waters had similar aromaticity with the sedge-dominated intermediate fen as indicated by $SUVA_{254}$ values, which were both significantly lower than those of deep pore water DOC. This was in agreement with results from previous studies that showed *Sphagnum* mosses could produce highly biodegradable DOC that was quickly used by microbes (Pinsonneault *et al.*, 2016; Wickland *et al.*, 2007). Besides, a higher proportion of fungi relative to bacteria in the *Sphagnum*-dominated poor fen (Lyons *et al. in prep.*) could be partially responsible for a more advanced decomposition of recalcitrant DOC, leaving the labile DOC accumulating within the surface area (Myers *et al.*, 2012). High quantity and biodegradability in the C substrate within the DOC pool can provide another explanation for higher CO_2 emissions from the *Sphagnum*-dominated poor fen than the sedge-dominated intermediate fen (Webster *et al.*, 2013).

Moreover, the DOC quality data in both shallow and deep pore waters suggested different vertical decomposition patterns between the two fen types. I argue that in the sedge-dominated intermediate fen, vascular plants significantly contributed to the DOC pool via root exudates, and in contrast, the DOC pool was shaped mainly by *Sphagnum* and peat leachate in the *Sphagnum*-dominated poor fen. In agreement with Hodgkins *et al.* (2016), the contribution of microbially-derived DOC was increasingly crucial in the sedge-dominated peatland, as suggested by higher BIX and FI values. Furthermore, the root biomass in the sedge-dominated intermediate fen was about ~ three times the value of that in the *Sphagnum*-dominated poor fen because of a significantly higher proportion of vascular plants (Palozzi & Lindo, 2017). Indeed, the depth of vascular plant roots could reach ~ 230 cm below the peat surface (Saarinen, 1996) and, thus, in the sedge-dominated intermediate fen, contributions of plants to the belowground DOC pool were relatively even throughout the whole vertical peat horizon. Roots of vascular plants can transport oxygen belowground and subsequently turn on the “enzymatic latch” by activating phenol oxidase activities (Freeman *et al.*, 2001b). Phenoloxidase is the only type of enzyme that can decompose phenolic compounds, which are recalcitrant and difficult for microbes to break down (Freeman *et al.*, 2001b). Thus, the removal of phenolic compounds can potentially stimulate microbial activates via increased DOC biodegradability. The deep rooting system can provide an explanation of the similarity of BIX and HIX indices between shallow and deep pore waters in the sedge-dominated intermediate fen, as labile C from root exudates can also cause the “priming effect” on microbial activities and stimulate the microbial decomposition of deep peat (Walker *et al.*, 2016; Zhu & Cheng, 2011). The lower molecular weight of DOC from the sedge-dominated intermediate fen, as shown by Peak C/A_{340}, indicated a higher microbial-derived DOC, which is in line with a greater amount of “decomposition” product from this site (Palozzi & Lindo, 2017). For example, in the fall, slight increases in deep DOC in both peatlands could be attributed to the falling leaves from vascular plants (Figure 4.1b), since fresh leaves from vascular plants could generate a greater amount of DOC relative to their roots and *Sphagnum* mosses, and so could stimulate microbial activities via the “priming effect” (Mastný *et al.*, 2018).

4.4.2 Peatland Dissolved Organic Carbon under Climate Warming

In this experiment, passive warming resulted in increases in soil temperature by ~ 0.5 °C and ~ 1.5 °C in the sedge-dominated intermediate fen and the *Sphagnum*-dominated poor fen, respectively. Contrary to my initial hypothesis, results from this experiment suggested that DOC quantity and quality in both fens could remain unchanged under passive warming during a relatively short period (e.g., one growing season). The stability of DOC pools to passive warming in this experiment could be explained by that the Q_{10} (a measure of the rate of change in a chemical or biological system per 10˚C increase in temperature, which represents changes in decomposition rates when the temperature increases by 10°C) of DOC (~1.6) was considerably lower than other decomposition processes that produce CH_4 (~5.63) and CO_2 (~1.98) (Gill *et al.*, 2017; Moore & Dalva, 2001). Although increased temperature was reported in numerous studies to be coupled with increases in DOC concentration (Dieleman *et al.*, 2016; Fenner *et al.*, 2007; Freeman *et al.*, 2001a; Kane *et al.*, 2014; Moore & Dalva, 2001) and altered DOC quality in peatlands (Dieleman *et al.*, 2016; Kane *et al.*, 2014), studies showing increasing DOC with warming were run for much longer periods (e.g., 12 years of data from (Freeman *et al.*, 2001a)) or under greater experimental temperature increases (e.g., at least 4°C in (Dieleman *et al.*, 2016)). Consistent with the findings here, Wilson *et al.* (2016) found in a short-term experiment that the pore water DOC concentration was not altered by *in situ* soil warming up to 9°C in an ombrotrophic bog.

The peatland DOC pool represents the balance between the DOC production and mineralization, and the unchanged DOC pool in this study could have resulted from the concomitant increases of both processes with higher temperatures. Specifically, in the sedge-dominated intermediate fen, I observed an increase in aboveground plant production as indicated by leaf area index (see Appendix F) under passive warming, and this increases in plant growth slight increased the Peak A and Peak C in shallow pore waters, which indicated greater aromatic compounds from vascular plant sources (Fellman *et al.*, 2010). Since the DOC concentration was not changed under warming, I hypothesize that the DOC decomposition was also increased under warming; however, *in situ* measurements of microbial activity is required to confirm this assumption.

4.5 Conclusion

This study showed that the DOC pool of the sedge-dominated intermediate fen contained a significantly higher proportion of microbial-derived labile C with lower molecular weight, relative to the *Sphagnum*-dominated poor fen. Thus, under a stronger or a more prolonged warming condition, a higher CO_2 emission would be expected from the sedge-dominated intermediate fen, owing to its greater biodegradability of C substrate supporting microbial decomposition. With a shift in the vegetation community from *Sphagnum* to sedges, northern peatlands may positively respond to climate warming with increased biodegradability and turnover in DOC decomposition. A better understanding of DOC characterization in different peatland types provides us with insights into decomposition dynamics and C storage functions in northern peatlands and their potential responses to future climate change.

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Chapter 5

5 General Discussion and Conclusions

5.1 Contributions to Current Knowledge

My doctoral work has contributed to the current knowledge of C dynamics in northern peatlands and their potential responses to future climate change in several ways:

1. The net C balance of sedge-dominated fens may not shift under future climate change, owing to concurrent increases in aboveground plant production and belowground microbial decomposition, driven by the interaction between warming and elevated atmospheric CO_2 (Chapter 2). Previous studies have predicted that with warmer temperatures, northern peatlands would become weaker C sinks (Deng *et al.*, 2015; Wu & Roulet, 2014). However, the interactive effect between warming and elevated CO_2 was not considered when examining the C balance of fen peatlands, especially in those are dominated by sedges. My findings suggest that elevated atmospheric CO_2 could offset the increase in temperature-driven ecosystem respiration via increased C storage in aboveground biomass coupled with increased plant C allocation to belowground root growth. The interaction of multiple environmental variables and the effects on the plant C allocation should be considered in peatland C models when predicting C fluxes between sedge fen peatland ecosystems and the atmosphere under future climate scenarios.

2. The length of growing season, which positively correlates with peatland net ecosystem exchange, is a critical control on seasonal CO_2 exchanges of peatlands (Sweet *et al.*, 2015). In the field manipulation, moderate, passive warming led to increased aboveground plant production in both sedge and *Sphagnum* fens, and the sedge fen responded more strongly to increases in fall temperatures (e.g., in September; Chapter 3). As indicated by results from the mesocosm experiment, increases in temperature by more than 4°C under the elevated CO_2 led to a greater significant increase in aboveground plant production in the sedge fen (Chapter 2). The resultant increase in plant production is

a key mechanism that helps explain the increased C input into peatlands under warmer conditions. Hence, spring and fall CO_2 exchanges should be fully characterized under warmer conditions, and the warming-induced longer growing season should be incorporated into the estimation of peatland C cycling in future climate change projections.

3. The results from my field-based research showed that C cycles between sedge and *Sphagnum* fens were significantly different in their magnitudes and environmental controls (Chapter 3 & 4). Despite previous studies that have treated different fen types together as simply ‘fen peatlands’ (e.g., Aerts *et al.*, 1999; Lin *et al.*, 2012; Sulman *et al.*, 2010), the *Sphagnum* fen was a significantly larger CO_2 sink and a significantly smaller CH_4 source compared to the sedge fen (Chapter 3). If the *Sphagnum* and sedge-dominated fens are not separated in peatland C models, peatland NEE may be overestimated by at least 16% and CH_4 emission underestimated by more than 15% from northern peatlands (Chapter 3). Furthermore, DOC in *Sphagnum* and sedge fens differed significantly in terms of quantity and quality (Chapter 4). In the sedge fen, DOC compounds were lower molecular weight and lower aromaticity while the *Sphagnum* fen DOC primarily comprises plant-derived high molecular weight, aromatic compounds (Chapter 4). Given significant differences in C cycles between two fen peatlands, the peatland type is an important parameter when simulating C dynamics from northern peatlands.

4. In the field experiment, C fluxes in both *Sphagnum* and sedge fens were unaltered under moderate passive warming during the short-term period (e.g., one growing season; Chapter 3 & 4). My study found that CO_2 exchanges (Chapter 3), together with DOC quantity and quality (Chapter 4), remained unaltered in both fens with temperature increases of ~1˚C. However, the sedge fen experienced a significant reduction in CH_4 emissions (11%) under warming during the peak growing season (Chapter 3). Several previous studies suggested that peatland CH_4 emission would significantly increase with rising temperatures (Gill *et al.*, 2017; Turetsky *et al.*, 2008; Voigt *et al.*, 2017; Wilson *et*

al., 2016); however, there would be an overestimation of warming-induced increases in peatland CH_4 emissions if the sedge control over CH_4 emissions is not well represented in peatland C models.

5.2 Predictions of Peatland Carbon Cycling Under Future Climate Change

The global average temperature is predicted to increase by 1 to 4°C by the end of the twenty-first century, and the average temperature increase is predicted to be much faster at higher latitudes (e.g., the boreal region) in relative to temperate and tropical regions (IPCC, 2014). There are concerns that the C sink strength of northern peatlands can potentially shrink under climate warming, or under more extreme conditions, northern peatlands can even become net C sources, which will further increase the atmospheric CO_2 concentration and global temperature. With small to moderate increases in temperatures (e.g., 0.3 to 3°C), the net C uptake can potentially increase in northern peatlands due to the increased aboveground plant biomass and productivity (Hollister *et al.*, 2005; Keenan *et al.*, 2014; Walker *et al.*, 2006). The longer growing season can also increase the annual C uptake into northern peatlands (Churkina *et al.*, 2005; Fridley *et al.*, 2016; Richardson *et al.*, 2018). Several C models have reached a consensus that northern peatlands could remain as C sinks until at least 2060 (Fan *et al.*, 2013; Green *et al.*, 2019; Wu & Roulet, 2014). After that, with greater increases in temperature, (e.g., 3 to 8°C), together with decreases in water table, the vegetation community may reorganize in northern peatlands with *Sphagnum* moss being replaced by vascular plants (Dieleman *et al.*, 2015; Keenan *et al.*, 2014; Mäkiranta *et al.*, 2018). Overall, there will be an increase in the respiration/photosynthesis ratio, which will lead to a net C loss from northern peatlands.

If sedge fens largely replace *Sphagnum* fens under future climate change, my research suggests that northern peatlands may become smaller CO_2 sinks owing to the lower aboveground primary productivity combined with the higher ecosystem respiration

(Chapter 3). The more dominant sedge fens will also emit a significantly higher amount of CH_4 than the moss-dominated systems further increasing their global warming potential (Chapter 3). Also, there will be a potential increase in decomposition and CO_2 releases from receiving ecosystems (e.g., rivers and lakes) owing to the higher DOC quality in sedge fens.

5.3 Knowledge Gaps and Future Research

Vascular plants are more productive than *Sphagnum* moss, but there are also higher decomposition rates and C loss from vascular plant-dominated peatlands. Thus, the C sink strength of northern peatlands will likely to shrink from 2060 to 2100, and some peatlands will even become net C sources by the end of this century (Fan *et al.*, 2013; Green *et al.*, 2019; Wu & Roulet, 2014). Despite this, C dynamics in sedge-dominated fens are generally less studied than *Sphagnum*-dominated bogs and fens, even though it is an important type of peatland in North America. The abundance and biomass of vascular plants in peatlands is currently a parameter that is held constant in the terrestrial C modelling (Fan *et al.*, 2013). Furthermore, DOC dynamics has largely been neglected in process-based C models of peatlands, and in particular, the DOC quality in the different type of peatlands have not been well-represented. Hence, large uncertainties still exist regarding peatland C dynamics and associated environmental controls, which prevents us from accurately modelling peatland C balances under future climate change.

There is growing evidence on the interactive effect of increased temperature and elevated atmospheric CO_2 on C fluxes in northern peatlands (including Chapter 2 in this dissertation), most of the experiments showing interactive effects of those two environmental stressors using small-scale mesocosm or incubation studies; *in situ* experimental manipulations of those two factors are still limited. Even though mesocosm or incubation studies provide us with insights into the treatment effect of environmental stressors, they fail to simulate the real condition in the natural environment with respect to precipitation, water table fluctuation or vegetation dynamics. Future research on responses of C fluxes in northern peatlands to future climate change should include both increased temperature and elevated atmospheric CO_2 as influencing factors in the field experiment. Since northern peatlands may shift towards a new state under persistent or stronger climate change (Dise, 2009), longer-term field manipulations are needed to capture the C balance associated with this state shift under future climate scenarios.

Although greenhouse gas flux measurements have been made in peatland ecosystems around the northern hemisphere, the majority of these were made during the growing season with many fewer studies reporting C fluxes during the winter (but see Rinne *et al.*, 2018). Winter CO_2 and CH_4 fluxes are important components of annual C budget in northern peatlands, but the mechanisms that control winter C exchanges are not well understood. Root biomass was suggested as a major control on winter CO_2 emissions from northern peatlands (Zhao *et al.*, 2016), and since the root biomass was predicted to increase warming and elevated CO_2 (e.g., the Chapter 2), winter CO_2 emissions from northern peatlands are likely to increase under future climate change. Future research should include the winter greenhouse gas fluxes in the annual estimate of C accumulation in northern peatlands.

Increased temperature and elevated CO_2 can greatly affect the plant biomass allocation in peatlands and thereby could considerably affect the long-term C accumulation in northern peatlands and their responses to climate change. Future research should provide more detailed evidence on how climate change would affect plant and root traits and litter quality in northern peatlands. Moreover, changes in plant traits or vegetation type can lead to significant changes in the quantity and quality of DOC in peatlands (Pinsonneault *et al.*, 2016). Thus, a more detailed study on effects of changing DOC characterization on decomposition rates and greenhouse gas production from northern fen peatlands is required to improve our understanding of decomposition potentials of northern peatlands in response to climate change.

The climate-derived changes in growing season length may have a cascading effect on seasonal C fluxes in northern peatlands. For example, an earlier start of spring melting may promote the growth of some vascular plant such as shrubs. Similarly, increased temperatures in the fall may extend the growing period of plants. Both the earlier growth and late senesce can increase the annual C uptake into peatlands (Keenan *et al.*, 2014). On the other hand, however, the earlier spring melting may trigger the water stress later during the growing season, which can impede the plant growth and C uptake into peatlands (Green *et al.*, 2019). Given that longer growing season may concurrently increase the C uptake and C release, the overall effect of an extended growing season on peatland C balance should be explored in future studies.

Lastly, even though not discussed in this dissertation, other environmental factors such as the increased fire frequency, which is caused by the warming-induced drier conditions, will put the large C stock in northern peatlands at risk (Turetsky *et al.*, 2015). Particularly, the increased fire disturbance will lead to a great loss of C as CO_2 from northern peatlands, especially from the "old" carbon that has been deeply buried in the peat horizon (Turetsky *et al.*, 2011). Additionally, an earlier spring melt under climate warming can potentially increase the fire frequency by increasing the severity of droughts in peatlands during the growing season (Green *et al.*, 2019). Hence, more research should focus on the effect of fire frequency on the C loss from northern peatlands to improve accuracy when predicting the peatland C dynamics under climate change.

5.4 Concluding Remarks

Northern peatlands play a significant role in sequestering atmospheric CO_2 and have had a net cooling effect on Earth over the Holocene. Since the northern hemisphere, in particular, will experience significant changes in climate over the coming century, it is a critical challenge to accurately predict the fate of C in peatlands under future climate scenarios at both regional and global scales. A better understating of environmental controls on various biogeochemical processes in northern peatlands at both community and ecosystem levels will lead to more reliable predictions on whether northern peatlands will remain carbon sinks or will become net carbon sources under changing climate.

5.5 References

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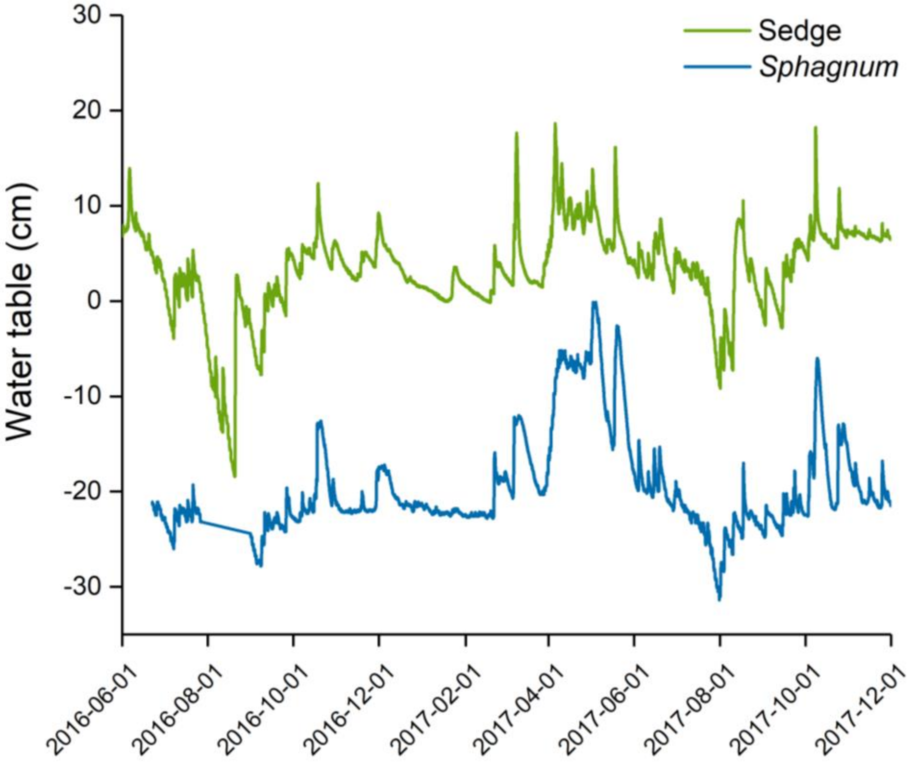
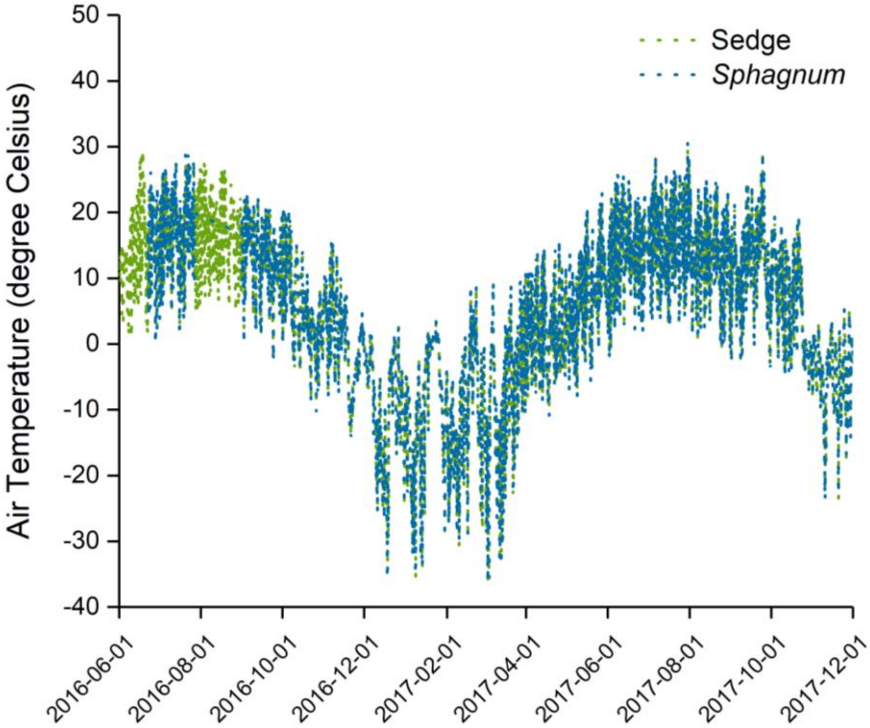
Appendices

Appendix A An example of the increased green area in the sedge-dominated mesocosm from: a) ambient T, b) +4°C to c) +8°C under the ambient CO_2 condition in October 2015 (Chapter 2).

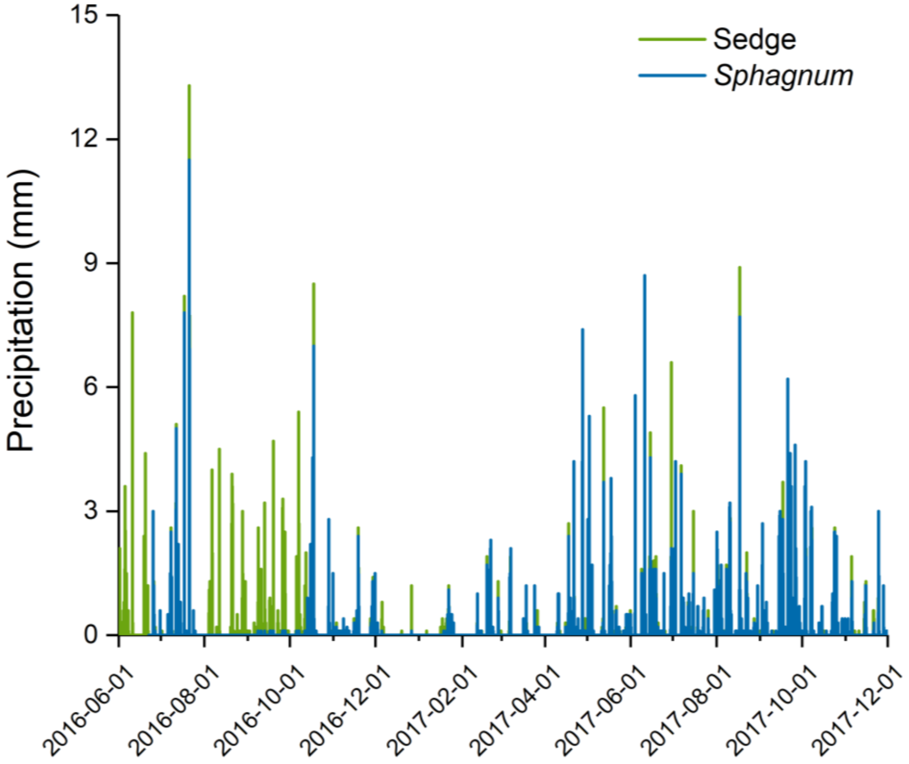
Appendix B Water table depths (cm) in the sedge-dominated intermediate fen (in green colour) and the *Sphagnum*-dominated poor fen (in blue colour) during field seasons in 2016 and 2017. Positive and negative numbers represent water tables above and below the peat surface, respectively.



Appendix C Air temperatures (degree Celsius) in the sedge-dominated intermediate fen (in green colour) and the *Sphagnum*-dominated poor fen (in blue colour) during field seasons in 2016 and 2017.



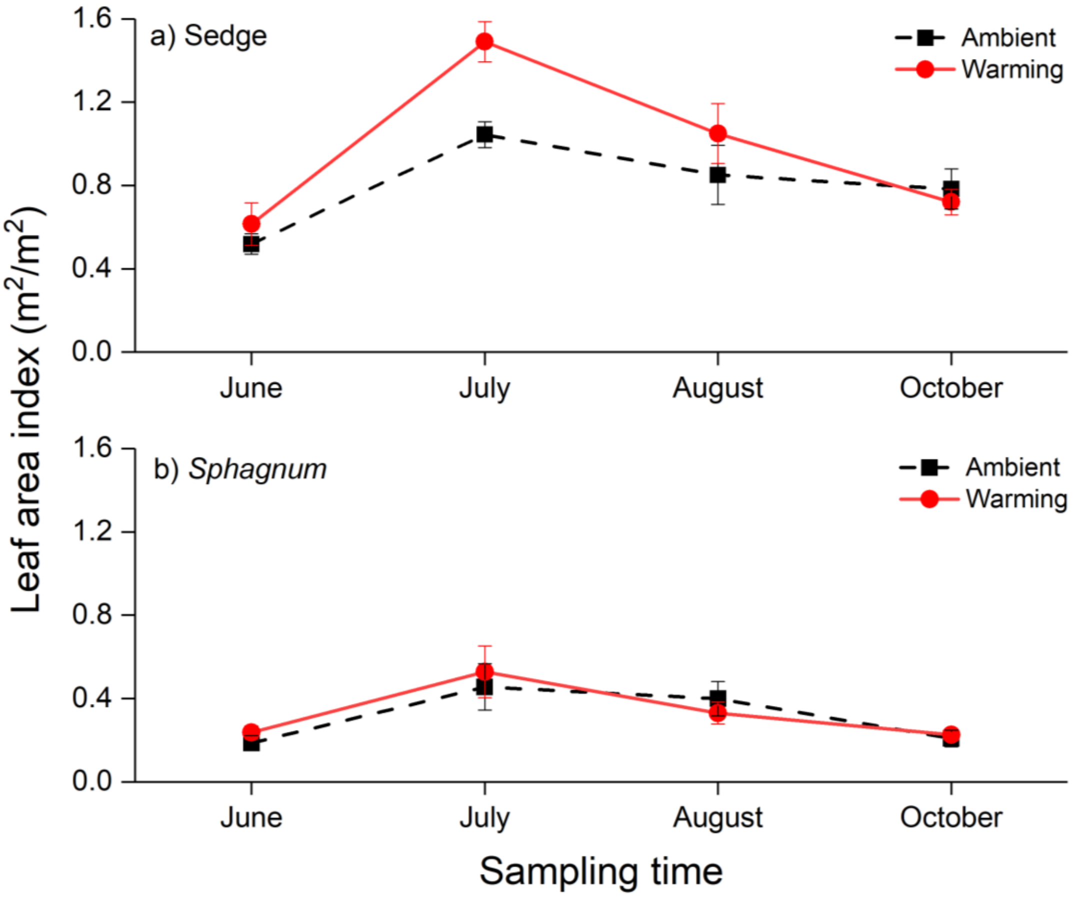
Appendix D The amount of precipitation (mm) in the sedge-dominated intermediate fen (in green colour) and the *Sphagnum*-dominated poor fen (in blue colour) during field seasons in 2016 and 2017.



Appendix E RM-ANOVA analyses of passive warming effects on soil temperature (°C) at 5 cm, 10 cm, 15 cm, 20 cm and 25 cm as well as soil moisture (%) (~10 cm below the peat surface) in the sedge-dominated intermediate fen and the *Sphagnum*-dominated poor fen. Data collected from each plot were averaged from three measurements during each filed campaign from late June to mid-October in 2017. Each value represents the mean ± standard error.

Variable	Sedge-dominated				*Sphagnum*-dominated			
	Ambient	Warming	*F*	*P*	Ambient	Warming	*F*	*P*
Soil Temp at 5 cm (°C)	15.04 ± 0.37	15.53 ± 0.37	0.875	0.366	16.07 ± 0.31	16.97 ± 0.31	4.324	0.056
Soil Temp at 10 cm (°C)	13.60 ± 0.15	13.67 ± 0.15	0.104	0.751	13.00 ± 0.19	14.00 ± 0.19	13.046	**0.004**
Soil Temp at 15 cm (°C)	12.95 ± 0.07	12.91 ± 0.07	0.171	0.690	11.94 ± 0.16	12.55 ± 0.16	7.431	**0.018**
Soil Temp at 20 cm (°C)	12.66 ± 0.07	12.58 ± 0.07	0.688	0.421	11.70 ± 0.33	12.65 ± 0.33	4.051	0.067
Soil Temp at 25 cm (°C)	12.40 ± 0.07	12.32 ± 0.07	0.761	0.398	12.12 ± 0.50	12.01 ± 0.50	0.028	0.870
Soil moisture (%)	52.68 ± 2.74	48.41 ± 2.74	1.210	0.313	30.28 ± 2.21	26.69 ± 2.38	1.218	0.293

Appendix F Monthly measurements of leaf area index (LAI) at both a) sedge-dominated intermediate fen and b) *Sphagnum*-dominated poor fen in 2017. Solid, black squares with dash lines indicate "ambient" plots; solid, red circles with solid lines indicate "warming" plots. Each value represents the mean ± standard error (n=8).



Curriculum Vitae

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- Tian, J., Lindo, Z., Petrone, R.M., McLaughlin J.M. & Branfireun B.A. (2018, Jun) Greenhouse gas fluxes and carbon storage function in two contrasting peatlands — implications for global warming. *Canadian Geophysical Union Annual Meeting*, Niagara Falls, Canada (*Oral*)

- Tian, J., Lindo, Z., Petrone, R.M., McLaughlin J.M. & Branfireun B.A. (2018, Mar) Greenhouse gas fluxes and carbon storage function in two contrasting peatlands — implications for global warming. *Student Canadian Geophysical Union Conference*, London, Canada (*Oral*)

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- Tian, J. & Hornibrook, E.R.C. (2015, Apr) Carbon storage in and beneath a British peatland. *Western University Earth Day Conference*, London, Canada (*Oral*)

- Hornibrook, E.R.C., Tian, J., Middleton, B., McAleer, A. & Smith, D. (2015, Mar) Greenhouse gas overview & Carbon storage in mires. *Exmoor Mires Project Conference*, Dulverton, United Kingdom (*Oral*)