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Ground warming leads to changes in carbon cycling in northern fen peatlands: implications for carbon storage

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Abstract

Northern peatlands store one third of the world's soil carbon (C), as they remove more C from the atmosphere via photosynthesis than they release to the atmosphere through ecosystem respiration and methane (CH_4) production. Climate change threatens this function by stimulating C release from peatland stores as peat temperatures warm and soil moisture is reduced. Ground heating of +4 ºC above ambient peat temperatures was initiated in a *Sphagnum* moss-dominated, nutrient poor fen and a *Carex* sedge-dominated, intermediate nutrient fen. Over one growing season, *Carex* fen heated plots had increases in photosynthesis (+23%), ecosystem respiration (+22%), and CH_4 production (+57%). While gas fluxes did not change at the *Sphagnum* fen, belowground organochemical properties revealed heated plots contained more phenolics, which are associated with belowground sedge root growth. Although *Sphagnum* fens may take longer to respond to climate change, both fen types are at risk for becoming weaker C sinks in the future.

Keywords

Boreal peatlands, carbon dioxide, methane, carbon cycling, FTIR, climate change, sedge, moss

Summary for Lay Audience

Greenhouse gases, such as carbon dioxide (CO_2) and methane (CH_4) are molecules in the atmosphere that trap heat, warming the Earth. Peatlands are globally widespread ecosystems that accumulate dead plant matter ("peat") because the waterlogged conditions and cool temperatures slow down decomposition. Peatland plants remove CO_2 from the atmosphere through photosynthesis and store it in the ground, which acts as a cooling mechanism for Earth's surface temperature. As climate change warms the planet, plants in peatlands may grow more and therefore remove even more CO_2 from the atmosphere, but if soil warms up and dries out the carbon stores in peatlands may break down and be released to the atmosphere as CO_2 and CH_4. In this thesis, ground heating rods were used to warm up the soil of two peatland types, a moss-dominated and a sedge-dominated peatland, to determine if future peatlands might lose their carbon stores. I found that in the sedge peatland, plants grew more under warmer conditions and therefore removed more CO_2 from the atmosphere, but soil microbes were more active and also released more CO_2 and CH_4 to the atmosphere. In the moss peatland, low soil nutrients resulted in no change in the amount of greenhouse gases released to the atmosphere, but sedges began to establish communities at this peatland. Since sedges provide ample nutrients to the soil, in the future there will likely be enough soil nutrients to fuel more CO_2 and CH_4 release to the atmosphere. Therefore, both peatland types may begin storing less carbon over the next century and instead begin emitting more greenhouse gases, which could increase the amount of greenhouse gases trapping heat in the atmosphere and further the rate of global warming through a positive feedback effect.

Co-Authorship Statement

Chapters 2 and 3 of this thesis are planned manuscripts for submission to a peer-reviewed journal. The field experiment in chapters 2 and 3 was conceived and designed by Dr. Brian Branfireun and Dr. Zoe Lindo, with collaboration from Dr. James McLaughlin and the Ontario Ministry of Natural Resources and Forestry. The gas flux field sampling method in chapter 2 was developed by Dr. Richard Petrone and Dr. Jing Tian. The sampling and analysis method in chapter 3 was developed by Ericka James and Dr. Brian Branfireun. The leaf area index and vegetation survey data in chapter 2 was collected by Caitlyn Lyons (2018) and Aejah Blesch (2019); Ericka James collected the remainder of the data. Ericka James analyzed the data, interpreted results, and wrote the manuscript. Manuscripts developed from this work will be credited to Ericka James, Dr. Brian Branfireun, Dr. Zoe Lindo, and Dr. James McLaughlin.

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Chapter 1

1 Introduction

1.1 The role of greenhouse gases in global climate change

Greenhouse gases in the atmosphere, which include water vapour (H_2O), carbon dioxide (CO_2), methane (CH_4), nitrous oxide (N_2O), and ozone (O_3), absorb and re-emit longwave infrared radiation that warms the Earth to habitable temperatures. Carbon dioxide is the most abundant greenhouse gas in the atmosphere after water vapour, with an estimated atmospheric stock of 828 Pg C (10^{15}; Ciais *et al.*, 2013). The atmosphere represents the smallest of three actively cycling carbon (C) stocks, following the ocean (37 000 Pg C) and terrestrial ecosystems (3650 – 4750 Pg C; Ciais *et al*, 2013). Much of the C in terrestrial ecosystems is stored in plant litter, soils, and live vegetation until it is released to the atmosphere through plant and root respiration (Post *et al.*, 1990). Plants remove CO_2 from the atmosphere via photosynthesis, allowing terrestrial landscapes to act as a C sink of 3 Pg C yr^{-1} (Ciais *et al.*, 2013). Fossil fuel emissions are the largest anthropogenic sources of CO_2 to the atmosphere (IPCC, 2007). Since the Industrial Revolution, human extraction and use of the large belowground stocks of oil, gas, and coal has been rapidly depleting these usually permanently buried stocks (IPCC, 2014). This has contributed to an increase in the atmosphere CO_2 stock by 4 Pg C yr^{-1} since the mid-1700s (Ciais *et al.*, 2013).

Global warming potential (GWP) measures the ability of greenhouse gases to absorb infrared radiation relative to the amount absorbed by the same mass of CO_2. Although CO_2 has an atmospheric lifetime of up to 200 years (Lashof & Ahuja, 1990), other greenhouse gases have a significantly greater ability to absorb infrared radiation, resulting in a greater GWP over short time scales. Methane and N_2O have GWPs of 25x and 298x greater than CO_2 over 100 years, respectively (Lashof & Ahuja, 1990; Soloman *et al.*, 2007), despite having shorter atmospheric lifetimes of 14 and 160 years (Ciais *et al.*, 2013; Lashof & Ahuja, 1990). As the third most abundant greenhouse gas in the atmosphere, CH_4 poses specific concern. The majority of CH_4 stocks are located in subsurface ocean hydrates and fossil fuel reserves (Wahlen, 1993). Anthropogenic sources of CH_4 to the atmosphere are dominated by agriculture, waste management, and energy production (IPCC, 2007), while wetlands are the largest natural source of CH_4. The atmosphere acts as the main sink for CH_4: the oxidation reaction of hydroxyl radicals (OH) with CH_4 in the troposphere forms carbon monoxide (CO), and eventually CO_2 and water vapour (Wahlen, 1993). Terrestrial sinks also remove CH_4 from the atmosphere, predominantly by the aerobic oxidation of CH_4 by bacteria in wetlands and lakes (Ciais *et al.*, 2013; Wahlen, 1993).

As anthropogenic emissions of greenhouse gases continue to increase, natural atmospheric and terrestrial sinks that remove excess CO_2 and CH_4 are unable to maintain pre-industrial atmospheric concentrations. Atmospheric concentrations of CO_2 and CH_4 have reached record highs, with CO_2 rising from pre-industrial concentrations of 280ppm to an average of 407ppm in 2018 (Blunden & Arndt, 2019; Soloman *et al.*, 2007), and CH_4 more than doubling from 730ppb to 1858ppb (Blunden & Arndt, 2019; Soloman *et al.*, 2007). Positive radiative forcing due to excess greenhouse gases in the atmosphere has been steadily increasing global temperatures and thus altering the global climate, affecting complex natural ecosystems and their natural C cycle.

1.2 Boreal Peatlands and Carbon Storage

Wetlands are persistently water-saturated ecosystems that cover approximately 4% of the world's land area (Bridgham *et al.*, 2006), widespread across North America, Russia, and northern Europe (Hu *et al.*, 2017). Wetlands can be broadly subdivided into two categories based on the amount of organic matter present within the soil: mineral-based wetlands include swamps and marshes, whereas organic-rich wetlands are broadly referred to as peatlands (Warner & Rubec, 1997). In the Canadian Wetland Classification System, peatlands are defined by a build-up of decomposing organic matter (peat) to a thickness of 40cm or more (Warner & Rubec, 1997). Peat accumulation is driven by slow rates of decomposition relative to photosynthetic uptake. Waterlogged conditions slow oxygen diffusion downwards through the peat profile, creating anoxic conditions as microbes deplete remaining oxygen, consequently slowing decomposition and resulting in the storage of carbon (C) belowground (Blodau *et al*., 2004; Moore & Knowles, 1989). Northern fens are estimated to accumulate C in peat at a rate of 13 – 38 g C m^{-2} yr^{-1} (McLaughlin & Webster, 2014; Turunen *et al*., 2002). This net removal of C from the atmosphere by northern peatlands has exerted a regulating net cooling effect on the global climate for the past 11Kya (Frolking & Roulet, 2007), with a net radiative forcing of -0.2 to -0.5 Wm^{-2} lowering the average surface temperature by 0.1-0.2 ºC throughout the Holocene (Frolking *et al*., 2006; Frolking & Roulet, 2007). Although peatland formation also depends on local topography and hydrology, regions that are generally cooler in temperature result in low evapotranspiration rates relative to precipitation, generating a surplus of water on the landscape (Hu *et al*., 2017; Yu *et al*., 2001). For this reason, 97% of global peatlands are located in cool, wet boreal and subarctic regions (Tarnocai, 2006). Boreal and subarctic peatlands have been estimated to store 462 Pg C (Bridgham *et al*., 2006; Gorham, 1991), representing one third of the world's total soil C pool despite only covering 2.3% of land area (Gorham, 1991).

Bogs and fens comprise the main two peatland types. While bogs receive their water supply solely from precipitation, fens obtain water from both precipitation and runoff from the surrounding catchment (either surface or groundwater) (Warner & Rubec, 1997). In some cases, groundwater supply to a fen is restricted as peat accumulates over time (Kuhry *et al*., 1993), resulting in a transition from fen to bog. Fens exist along a nutrient gradient, and fens containing higher concentrations of dissolved minerals are often dominated by graminoids (sedges, grasses, and rushes) and other vascular plants such as shrubs. More nutrient-limited, moss-dominated fens are at the other end of the fen continuum (Kuhry *et al*., 1993). Mosses can out-compete vascular plants in low-nutrient environments as they have adapted to low nitrogen (N) and phosphorus (P) conditions through cyanobacteria that are able to fix atmospheric N_2 deposits into biologically available NH_4^+ (Li & Vitt, 1997; Limpens & Berendse, 2003). In contrast, vascular plants rely on mineralization of existing soil nutrients for acquisition of N and P (Malmer *et al*., 1994). Both fen types store C, with mosses playing a critical role in C storage: recalcitrant, slow-decomposing litter contributes to large portions of the belowground C pool (Del Guidice & Lindo, 2017; Malmer *et al*., 1994).

1.3 Controls on Greenhouse Gas Fluxes from Peatlands

The amount of CO_2 that a peatland removes from the atmosphere is a function of the net exchange of CO_2 between an ecosystem and the atmosphere. Although the magnitude of net ecosystem exchange (NEE) varies from year to year and depends on peatland location and interannual variability in weather, fens generally act as a net C sink during the growing season and a net C source during the winter months (Carroll & Crill, 1997; Glenn *et al*., 2006; Webster *et al*., 2013). Similarly, during the growing season fens follow a diurnal cycle of net CO_2 uptake during the day and net CO_2 loss at night (Humphreys *et al*., 2006).

Primary factors influencing CO_2 exchange with the atmosphere include air and soil temperature, soil moisture and depth to the water table, plant community composition, which governs aboveground biomass and total leaf area, and belowground soil organic matter (SOM) pool lability and size. Both flooding and drought can inhibit photosynthesis (gross ecosystem production; GEP), as flooding reduces soil oxygen and slows gas diffusion rates from plant to atmosphere (Carroll & Crill, 1997; Pezeshki, 2001), while drought-induced moisture stress has the same effect (Chivers *et al*., 2009; McLaughlin & Webster, 2014; Olefeldt *et al*., 2017). Sedges and shrubs have a large photosynthetic capacity due to their extensive leaf surface area and stomatal conductance (Busch & Lösch, 1998; Ward *et al*., 2009; Webster *et al*., 2013; Wu & Roulet, 2014), whereas mosses have lower photosynthesis rates (Ward *et al*., 2009). However, mosses are photosynthetically active for a longer period of the year as they a) do not require time to develop leaves in the spring and b) can continue photosynthesizing beyond vascular plant senescence in the fall (Bubier *et al*., 1999; Glenn *et al*., 2006).

Total ecosystem respiration (ER), or the release of CO_2 from a peatland to the atmosphere, comprises autotrophic respiration by plants and live roots, and heterotrophic respiration by belowground fungal and bacterial communities as they decompose SOM. Respiration rates are highest under warm, dry conditions (Bridgham & Richardson, 1992;

Carroll & Crill, 1997; Laine *et al*., 2019; Olefeldt *et al*., 2017), as microbial metabolism is directly affected by temperature and aerobic conditions accelerate decomposition (Blodau *et al*., 2004; Bridgham & Richardson, 1992; Clymo, 1984). Higher aboveground leaf area and biomass leads to more SOM inputs into soil (Humphreys *et al*., 2006; Laine *et al*., 2019), and easily decomposable plant matter such as sedges are associated with higher respiration rates (Bubier *et al*., 1999, Wu & Roulet, 2014). Generally, nutrient-poor fens are dominated by slower-cycling fungal decomposer communities while faster-cycling bacterial decomposers outcompete fungi in fens richer in nutrients that are dominated by vascular plants (Strickland & Rousk, 2010). Faster-cycling bacterial-dominated peatlands thus generally have higher ER rates, and slower-cycling fungal-dominated peatlands have higher C storage.

Although peatlands are generally atmospheric CO_2 sinks, they are one of the largest natural sources of CH_4. Globally, peatlands emit 26.6 Tg CH_4 per year with 3.2 Tg emitted from Canadian peatlands alone (Bridgham *et al*., 2006). Methanogenesis is an anaerobic process facilitated by a group of eukaryotic microorganisms (“methanogens”) in the domain *Archaea* (Serrano-Silva *et al*., 2014), resulting in the production of CH_4 below the water table. As CH_4 diffuses upwards in the soil profile it is partially oxidized by methanotrophic bacteria in the aerobic zone (Jerman *et al*., 2017); some *Archaea* and sulfate-reducing bacteria are able to use an alternative electron acceptor, such as sulfate, to oxidize CH_4 anaerobically (Caldwell *et al*., 2008; Gupta *et al*., 2013). The dominant methanogenic pathways in peatlands are either acetoclastic (the conversion of acetate to CO_2 and CH_4) or hydrogenotrophic (the conversion of CO_2 and hydrogen to water and CH_4; Serrano-Silva *et al*., 2014). Acetoclastic methanogenesis is more dominant in nutrient-rich peatlands, largely due to the acetate in root exudates from vascular plants in sedge fens; hydrogenotrophic methanogenesis is more prominent in less productive peatland types (Bellisario *et al*., 1999; Godin *et al*., 2012). CH_4 fluxes have been directly correlated with aboveground sedge biomass in a multitude of field and laboratory studies (eg. Bellisario *et al*., 1999; Godin *et al*., 2012; Jerman *et al*., 2017; Moore *et al*., 2011; Robroek *et al*., 2015). Sedges and other graminoids facilitate the direct transport of CH_4 from the production zone to the atmosphere through porous aerenchyma tissue, allowing

CH_4 to bypass the CH_4 oxidation zone (Bellisario *et al.*, 1999). Root exudates from extensive graminoid rooting systems also provide labile C in the form of organic acids, amino acids, and sugars to methanogens (Jerman *et al.*, 2017). Water table depth and peat temperatures are also important controls on CH_4 fluxes. High water tables reduce the size of the aerobic CH_4 oxidation zone while simultaneously increasing methanogenesis (Crill *et al.*, 1988). However, this relationship is not consistent throughout field studies: the opposite relationship of CH_4 to water table has been found in some cases (Bellisario *et al.*, 1999; Carroll & Crill, 1997), and some have found water table to not be a predictor of total CH_4 fluxes at all (Godin *et al.*, 2012). Higher rates of methanogenesis occur under warmer soil temperatures in both *in situ* field experiments and laboratory studies (Crill *et al.*, 1988; Carroll & Crill, 1997; Dunfield *et al.*, 1993; Krumholz *et al.*, 1995; Moore *et al.*, 2011). Field observations have observed maximum mid-summer CH_4 fluxes as high as 500-1000 mg CH_4 m^{-2} d^{-1} in northern fens (Bellisario *et al.*, 1999; Moore *et al.*, 2011), although average growing season CH_4 fluxes are more moderate and tend to fall between 20-200 mg CH_4 m^{-2} d^{-1} (Bellisario *et al.*, 1999; Bubier *et al.*, 1995; Crill *et al.*, 1988; Roulet *et al.*, 1992).

1.4 Impacts of Climate Change on Peatlands

Average global temperatures are expected to reach 1.5 ºC above pre-industrial values by 2040, with northern latitudes warming faster than the global average (Allen *et al.*, 2018). Reduced soil moisture through increased evapotranspiration is also expected to occur at higher latitudes (Allen *et al.*, 2018; Kirtman *et al.*, 2013). As a result of these future changes in temperature and precipitation regimes and the resulting impacts on plant and microbial communities, the ability of peatlands to continue acting as a net C sink is uncertain. It has thus become increasingly important to simulate the separate and combined effects of warming and drying on CH_4 and CO_2 fluxes from peatlands. Many studies have used open top chambers (OTC) to initiate greenhouse-like passive warming, ground heating rods and infrared lamps to heat peat to a greater degree, and drainage ditches to lower the water table.

As the mechanisms and microorganisms responsible for CH_4 and CO_2 fluxes differ, they are often examined separately. Multiple experiments have focused on how CH_4 production via methanogenesis, and CH_4 consumption via methanotrophy are affected by warming and drying. Direct ground warming has been shown to increase net CH_4 fluxes in peatland field experiments (Wilson *et al*., 2016). However, separating methanogenesis and methanotrophy in the field is difficult, with field experiments measuring the total net CH_4 flux. Incubations of bog and fen peat have noted greater temperature response from methanogens when compared to methanotrophic bacteria (Dunfield *et al*., 1993; Krumholz *et al*., 1995), suggesting that warming may contribute to higher CH_4 fluxes from peatlands. A series of field experiments in sedge fens found that simultaneous warming and drying of plots leads to a slight decrease in overall CH_4 fluxes, attributed to lowered water table levels, and thus a larger zone of potential CH_4 consumption (Pearson *et al*., 2015; Peltoniemi *et al*., 2016). Similar results have been found in bog field experiments: a continental bog subjected to water table drawdown and passive OTC warming found that water table drawdown reduced CH_4 fluxes by 50% over 3 years, and by 76% over 13 years (Munir & Strack, 2014), even when accompanied by warming. Similarly, in an Alaskan rich fen, the largest CH_4 fluxes were found in heated, wet plots with elevated water levels increasing CH_4 fluxes by 30-180% (Turetsky *et al*, 2008; Olefeldt *et al*., 2017). However, it is important to note that passive OTC warming generally only increases air temperature by 0.5-1 ºC, with little effect on peat temperature; higher degrees of warming (+13 ºC) applied to bog and fen peat has shown that CH_4 production prevails over CH_4 consumption even when the water table is lowered (Moore & Dalva, 1993).

Methane fluxes can also be indirectly influenced through changes in plant community composition (White *et al*., 2008). Although the response of vegetation to climate change is largely dependent on peatland type, nutrient content, biogeochemistry, and microtopography (Strack *et al*., 2006), it is widely accepted that vascular plant cover will increase in peatlands. Warming and water table drawdown, both combined and alone, have been shown to benefit shrubs and sedges while reducing moss cover (Dieleman *et al*., 2015; Fenner *et al*., 2007; Mäkiranta *et al*., 2018; Weltzin *et al*., 2003). Plant removal experiments have demonstrated that extensive, deep rooting systems in vascular plants as well as porous aerenchyma (in sedges) allow for survival in both waterlogged and drought conditions, whereas mosses are easily desiccated and subject to moisture stress in areas of water table fluctuation (Fenner *et al*. 2007; Potvin *et al*., 2015). Although mosses outcompete vascular plants in low nutrient environments, vascular plants are able to grow taller and therefore outcompete mosses for light once well-established (Malmer *et al*., 1994). The combination of direct plant transport, and labile C from vascular plant biomass and root exudates increases methanogenesis (Basiliko *et al*., 2007; Bellisario *et al*., 1999; Fenner *et al*., 2007; Ward *et al*., 2013). In a bog vegetation removal experiment, sedge removal lowered potential CH_4 production by 32% (Robroek *et al*., 2015). Model projections indicated doubled CH_4 emissions with warming as little as +4.5 ºC above ambient temperatures (Ma *et al*., 2017), driven by supply of fresh substrate. Increases in CH_4 oxidation due to drier conditions did not offset CH_4 production in any case (Gong *et al*., 2013; Ma *et al*., 2017).

Similar to how CH_4 fluxes are determined by the combination of CH_4 production and consumption, photosynthesis and ER together determine the direction and magnitude of CO_2 fluxes in an ecosystem. In the future, it is possible that higher temperatures and atmospheric CO_2 will lead to more plant growth and thus increase CO_2 uptake through photosynthesis, but the simultaneous increases in substrate, microbial activity, and a larger aerobic zone may also increase decomposition rates. In addition, the expected lengthening of a snow-free season may extend the photosynthetic period of plants earlier into the spring (Allen *et al*., 2018; Bubier *et al*., 1998; Syed *et al*., 2006), but ER and soil surface temperatures are closely linked and less time with frozen ground may lead to more C losses from an ecosystem (Bubier *et al*., 1998). Greater leaf area and higher photosynthetic capacity of vascular plants compared to mosses leads to more photosynthesis (Busch & Lösch, 1998; Ward *et al*., 2009). However, *in situ* experiments measuring photosynthetic responses to climate change are relatively limited. One series of sedge fen experiments have shown that over a 4-year period, the combined effects of passive OTC warming of 1.5 ºC and water table drawdown increased photosynthesis rates (Pearson *et al*., 2015; Laine *et al*., 2019). Similarly, a bog and fen monolith experiment observed increased productivity in warmed peat directly related to an increase in plant and root growth, largely driven by the growth of graminoids (Weltzin *et al*., 2000).

It is generally accepted that warming and drying increase rates of ER, leading to more release of CO_2 into the atmosphere, although there have been contrasting results on whether temperature or water table is the main driver (Bridgham *et al*., 2008; Dieleman *et al*., 2016; Laine *et al*., 2019; Wu *et al*., 2011). Soil warming has been demonstrated to increase ER by up to 47% in field experiments (Schindlbacher *et al*., 2009; Ward *et al*., 2013), but other studies have found no changes in ER with warming and drying (Chivers *et al*., 2009; Pearson *et al*., 2015). The lack of consistent ER response to experimental warming may be due to a) a simultaneous increase in heterotrophic (fungi, bacterial, and animal) respiration and decrease in autotrophic (plant) respiration, offsetting any net changes in ER (Chivers *et al*., 2009; Laine *et al*., 2019) or b) fast turnover of labile organic matter under warm temperatures, depleting substrate quickly (Kuzyakov *et al*., 2007; Wu *et al*., 2011).

The response of peatlands to climate change is dependent on peatland type and location. Mesocosm experiments have shown fen peat to both lose more soil C through decomposition and uptake more C through photosynthesis than bog peat in warm, dry conditions, primarily due to the availability of labile C through vascular plant growth (Bridgham *et al*., 2008; Weltzin *et al*., 2000). As bogs are typically moss-dominated, little fresh substrate limits decomposition, and a thick aerobic layer limits CH_4 production rates even under warming scenarios (Gong *et al*., 2013; Wu & Roulet, 2014). Fens are well-connected to local hydrology and are thus more sensitive to changes in the hydrology (White *et al*., 2008). Large-scale modelling exercises predict that fens will become a weaker CO_2 sink and an increasing CH_4 source in the future, whereas bogs at the same latitude are predicted to change less over the next century (Gong *et al*., 2013; Wu & Roulet, 2014). The McGill Wetland Model has shown that lower rates of photosynthesis in dry conditions will lead to respiration exceeding photosynthesis with a 3 ºC increase in temperature or a 15cm water table drawdown (St-Hilaire *et al*., 2010; Wu *et al*., 2013; Wu *et al*., 2014), predicting a decline in CO_2 sink strength over the next century (Gong *et al*, 2013). Despite strong evidence that fens are at risk for becoming a C source in the future, the majority of field experiments investigating ecosystem-scale CO_2 and CH_4 responses to climate change are bog experiments; in addition, few studies investigate how fens of varying nutrient status respond differently to climate change despite vast differences in belowground chemistry and vegetation.

1.5 Rationale and Objectives

Fens are relatively understudied compared to bogs, and no studies use direct heating of the peat profile to simulate future climates in fens despite the high likelihood that northern peatlands will warm to a greater degree than is reflected in most passive OTC experiments. Little information exists on how different fen types will respond to climate change despite massive physical, biogeochemical, and vegetation differences between the two. The main objective of this thesis is to determine how future, warmer climates will affect carbon cycling in fen peatlands, and how this response differs between fen types.

The objectives of the research chapters in this thesis were to:

1) Determine how the direction and magnitude of CH_4 and CO_2 (GEP, ER, and NEE) greenhouse gas fluxes respond to direct ground warming over a growing season, and how this response differs between two fen types (Chapter 2).

2) Identify how belowground peat composition changes between heated and control chambers at the two fens by comparing the quantity and type of major organic molecules found in the peat and establishing relationships between gas fluxes and belowground organic chemistry (Chapter 3).

As peatlands are a significant part of the global C cycle, examining how net greenhouse gas fluxes and the belowground environment respond to field-scale warming will give improved insight into future global CO_2 and CH_4 budgets.

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Chapter 2

2 Contrasting responses of greenhouse gas fluxes to ground warming at two northern fen peatlands

2.1 Introduction

Despite only covering 2-3% of the world's land area, boreal and subarctic peatlands store up to one third of the global soil carbon (C) stock (Gorham, 1991), with Canadian peatlands alone storing 150 Pg C (Tarnocai, 2006). Water saturated, anaerobic conditions and cool temperatures result in slow decomposition rates, allowing organic material to build up over time (Kayranli *et al*., 2010). Peatlands remove more carbon dioxide (CO_2) from the atmosphere through photosynthesis than they release through decomposition, which maintains a net cooling effect on the global climate (Frolking & Roulet, 2007). Peatlands also act as a large natural source of methane (CH_4) to the atmosphere; although the atmospheric lifetime of CH_4 is shorter than that of CO_2, the global warming potential is 25x greater than CO_2 over short (100-year) time scales (Lashof & Ahuja, 1990). Methane is produced anaerobically below the water table by methanogenic *Archaea* and is partially consumed by methanotrophic bacteria as it passes through the aerobic layer on its way to the atmosphere (Serrano-Silva *et al*., 2014).

Climate change threatens peatland C sink function through both increased temperature and reduced soil moisture, weakening two important constraints on decomposition. Global temperatures have already reached 0.8-1.2 ºC above pre-industrial values (Allen *et al*., 2018), with mid-to-northern latitudes experiencing more extreme temperature increases than low latitudes (Allen *et al*., 2018; Kirtman *et al*., 2013). Warming temperatures may stimulate vegetation growth and increase photosynthesis, and thus CO_2 uptake from the atmosphere (gross ecosystem production; GEP), but the combination of more plant residue in the soil and a warmer, more aerobic environment may also stimulate the microbial community (Bridgham & Richardson, 1992), increasing decomposition and thus CO_2 release to the atmosphere (ecosystem respiration; ER).

Similarly, CH_4 production may increase due to higher temperatures and the availability of labile C, but CH_4 consumption may also increase as the aerobic zone grows with a lower water table. This poses the risk of both weakening the CO_2 sink strength of peatlands and increasing the CH_4 released from peatlands, but the magnitude of this effect is uncertain.

Photosynthesis is largely driven by both the plant community composition and vegetation biomass. Multiple field and laboratory experiments have shown that vascular plant cover in peatlands, particularly shrubs and graminoids (sedges, grasses, and rushes), increases under warming (Dieleman *et al*., 2015; Fenner *et al*., 2007; Walker *et al*., 2015; Weltzin *et al*., 2000; Wiedermann *et al*., 2007) and with water table drawdown (Makiranta *et al*., 2018; Weltzin *et al*., 2000). Simultaneously, mosses such as *Sphagnum* spp. decline due to vascular plants gaining a competitive advantage over mosses under warmer and drier conditions (Fenner *et al*., 2007; Dieleman *et al*., 2015; Makiranta *et al*., 2018; Wiedermann *et al*., 2007). The potential future increase in vascular plant cover in peatlands could increase ecosystem photosynthesis, and thus GEP, as sedges and shrubs have a higher photosynthetic capacity and greater leaf area than mosses (Bubier *et al*., 1999; Ward *et al*., 2009).

Vascular plants also have the potential to increase ER rates from peatlands by providing more labile C to the soil through a) more easily decomposable organic matter than the recalcitrant cell walls of mosses (Verhoeven & Toth, 1995), and b) root exudates acting as an additional substrate for microbes (Hutsch *et al*., 2002; Jerman *et al*., 2017). Low concentrations of root exudates, composed of organic acids, amino acids, and sugars, have been found to increase ER (de Graaff *et al*, 2010). Thus, peatlands with more vascular plants often have the highest respiration rates. (Humphreys *et al*., 2006; Laine *et al*., 2019; Lindroth *et al*., 2007). Warming and drying of the soil is expected to exacerbate this by increasing both rates of microbial metabolism and the depth of the aerobic zone where the majority of decomposition takes place (Bradford, 2013; Bridgham & Richardson, 1992). Both fens and bogs generally have higher ER rates under higher temperatures and lower water tables (Bridgham *et al*., 2008; Dieleman *et al*., 2016; Laine *et al*., 2019; Lindroth *et al*., 2007; Olefeldt *et al*., 2017), but some studies have not observed a change in total ER due to simultaneous increase and decrease of autotrophic and heterotrophic components in the short-term (Chivers *et al*., 2009; Pearson *et al*., 2015). Comprehensive models including changes in both GEP and ER have predicted that the rate of C sequestration will increase initially due to more C uptake from plants, but by the end of the century peatlands will become a C source to the atmosphere (Fan *et al*., 2013). Field experiments investigating both GEP and ER in sedge fens found that modest warming alone did not affect the C balance: however, even slightly lower water table elevations resulted in an increase in ER, exceeding GEP (Laine *et al*., 2019; Pearson *et al*., 2015).

A transition to sedge-dominated peatlands is especially of concern for CH_4 fluxes. Porous aerenchyma tissue in sedges, an oxygen transport adaptation to water-saturated environments (Visser *et al*., 2000), allows CH_4 to diffuse from the anaerobic zone of CH_4 production to the atmosphere (Serrano-Silva *et al*., 2014), bypassing the aerobic CH_4 consumption zone and resulting in larger amounts of CH_4 reaching the atmosphere (Moore *et al*., 2011; Ward *et al*., 2013). Combined with root exudates acting as a substrate, high sedge abundance results in significantly higher CH_4 fluxes (Bellisario *et al*., 1999; Godin *et al*., 2012; Moore *et al*., 2011). Higher temperatures are likely to result in higher CH_4 fluxes (Crill *et al*., 1988; Serrano-Silva *et al*., 2014), but reductions in water table may negate this effect as the size of the aerobic layer where CH_4 is consumed grows (Olefeldt *et al*., 2017; Peltoniemi *et al*., 2016; Roulet *et al*., 1992), leading to uncertainty in how CH_4 fluxes may change in the future. The SPRUCE bog field experiment has found that CH_4 fluxes increased with warming treatments (Gill *et al*., 2017); a model based on this experiment predicts an increase in CH_4 emissions by 100% under warming of +4.5 ºC above ambient (Ma *et al*., 2017).

Although multiple ongoing field and mesocosm experiments have been conducted on precipitation-fed bog peatlands (eg. Hanson *et al*., 2016; Kane *et al*., 2019; Moore *et al*., 2011; Potvin *et al*., 2015), minerotrophic fens (fed by both precipitation and groundwater) remain relatively understudied despite potentially responding more quickly than bogs to climate change (Bridgham *et al*., 2008), and covering up to 50% of Canada's peatland area (Tarnocai, 2006; Vitt *et al*., 2000; Wu & Roulet, 2014). Fen models predict that an increase of +3 ºC above ambient temperatures will change fens from a C sink to a C source (Wu *et al*., 2013), potentially as early as 2060 (Wu & Roulet, 2014), making them a critical focus for comprehensive field experiments. Fens exist along a natural nutrient gradient, ranging from moss-dominated, nutrient-poor fens to vascular plant-dominated, nutrient-rich fens (Warner & Rubec, 1997). Greenhouse gas fluxes vary widely between fen types: nutrient-poor fens typically emit lower CH_4 fluxes than vascular-dominated fens (Crill *et al*., 1988; Webster *et al*., 2013) and different respiration and photosynthesis rates based on water table levels, belowground chemistry, and plant community composition, thus making it critical to understand how climate change will impact each fen type.

Although open top chambers (OTCs) are commonly used to passively warm to 0.5-1 ºC above ambient air temperatures in peatlands, few experiments directly heat the peat profile. Heating above 1 ºC in large-scale field experiments have been performed in bogs (eg. Hanson *et al*., 2016; Gill *et al*., 2017; Potvin *et al*., 2015), but there are no similar studies in fens. The objective of this study was to determine how greenhouse gas fluxes (CO_2 and CH_4) respond to warming in two fen types, with the aim to further understanding of how fen C stores may change under future climates. As part of a large-scale collaborative field experiment, passive warming was initiated using large OTCs for two years at a *Sphagnum spp.* moss-dominated, nutrient poor fen, and a *Carex spp.* sedge-dominated fen with intermediate nutrient levels, followed by active warming (+4 ºC above ambient peat temperatures) through direct ground heating. I hypothesized that:

a) At both fens, heated plots would have higher values of both GEP and ER when compared with control plots, but with ER increasing to a greater degree than GEP, resulting in a larger value of NEE (more CO_2 release to the atmosphere).

b) Warming would result in a greater increase in CH_4 production by *Archaea* than consumption by methanotrophic bacteria, resulting in net increase of CH_4 fluxes at both fens.

2.2 Materials and Methods

2.2.1 Study Area

The study area was located near White River, Ontario (48 º21’ N, 85 º21’W) and is part of a long-term research site operated by the Ontario Ministry of Natural Resources and Forestry. The mean annual precipitation and temperature (1989-2019) were 970 mm and 2.1 ºC respectively from a nearby climate station in Wawa, ON. The growing season ranges from 70-100 days long with snow cover from December to March (McLaughlin, 2009). The study was conducted in two fens along a nutrient gradient approximately 2km apart: one a nutrient-poor, *Sphagnum*-dominated fen and the other a *Carex*-dominated fen with intermediate nutrient levels.

The *Sphagnum* fen is dominated by mosses including *Spagnum fuscum*, *S. magellanicum,* and *S. angustifolium*. Shrubs are also abundant, with leatherleaf (*Chamaedaphne calyculata*), blueberry (*Vaccinium angustifolium*), and cranberry (*Vaccinium oxycoccos*) being the most common. Other vegetation includes sundew (*Drosera sp.*), three-leaf Soloman’s seal (*Maianthemum trifolium*), and soft-leaf sedges (*Carex disperma*). The tree overstory over the peatland mainly consists of black spruce (*Picea Mariana*) and tamarack (*Larix laricina*) (Webster & McLaughlin, 2010). The *Carex* fen is dominated by multiple species of sedges, most notably *Carex oligosperma*, *Carex lasciocarpa*, and *Carex stricta*. Rosemary (*Andromeda polifolia*) and bog myrtle (*Myrica gale*) are abundant shrubs; violet (*Viola palustris*), St-John’s wort (*Triadenum fraseri*), and moss (*Spagnum angustifolium*) are less common but present. Adjacent upland vegetation consists of a 70-year boreal mixed-wood forest dominated by black spruce, balsam fir (*Abies balsamea*), and white birch (*Betula papyrifera*) (McLaughlin, 2009). On average, between June and October the water table at the *Sphagnum* fen is 19.8 cm below the peat surface, while at the *Carex* fen it is 5.6 cm below the peat surface.

2.2.2 Experimental Design

Sixteen collars (~1m dia) were installed at each fen in 2015, organized into four experimental blocks to account for natural spatial heterogeneity in vegetation, water chemistry, and microbial communities. The collars were connected by boardwalks to lessen disturbance of the surrounding environment. Eight plots in each fen were fitted with clear open-top polycarbonate chambers in 2017 approximately 1 metre in height and diameter. Prior to heating treatments, passive warming due to the placement of OTCs took place throughout the 2017-18 growing seasons, with average chamber daytime air temperatures 0.95-1.8 ºC warmer than ambient (Lyons *et al*., 2020). For the active ground warming treatments in the same 8 chambers, six evenly spaced vertical heating rods (60W Watlow FireRod® immersion heaters) were installed circumferentially penetrating to a depth of 50cm below the peat surface. Heating rods were powered on in late June 2019, programmed through Watlow EZ-ZONE® Configurator software to gradually ramp up to a target temperature of +6.75 ºC above ambient peat temperatures over two weeks. Due to more rapid warming of the peat profile than expected in the first week of heating, the target temperature was reduced to +4 ºC. For each chamber, one temperature sensor inside the collar and one reference sensor approximately two metres outside the collar were installed, both at a depth of 25cm; the heating system consistently monitored the temperature difference between the two sensors and automatically adjusted the heating rods as needed to maintain an constant offset of +4 ºC. Measured peat temperatures through the software were recorded two to three times per week and were also manually checked in multiple locations as part of the gas flux measurement routine.

2.2.3 CH_4 and CO_2 Flux Measurements

Gas flux measurements were taken with a portable GASMET^{TM} 4015X, with associated Calcmet software converting each intake of chamber air to ppm concentrations (accurate to ± 2%). Chambers were outfitted with a clear lid and a fan during sampling to maintain air circulation; control plots, which did not have a permanent chamber installation, were outfitted with a chamber for the duration of each measurement only. Approximately 10 minutes before each chamber was sampled, soil temperatures were taken at three different depths (5cm, 10cm, 25cm) at three random locations in the plot (Fisherbrand^{TM} Long-Stem Digital Thermometer). Soil moisture was also taken at 10cm depth at three different locations (Delta-T HH2 Moisture Meter). GASMET hardware was flushed with N_2 for 3-5 minutes at the beginning and end of each day to ensure no residual gases remained in the instrument, and a background spectrum of CO_2, CH_4, N_2O, CO, and H_2O vapour was collected before each sampling day. All measurements were taken within approximately four hours of solar noon (1:45pm) between 9am-4pm.

Measurements of CO_2 were taken over a three-minute period (as per Hanson *et al*., 2016), with 13 consecutive samples each of 15 seconds length. Two sets of CO_2 measurements were made per chamber. First, a measurement under natural light, representing the net CO_2 flux emitted from the chamber. This represents the net ecosystem exchange (NEE). Photosynthetically active radiation (PAR; Apogee MQ-200 Quantum Sensor) was recorded during light chamber CO_2 measurements. Sampling was ceased if PAR fell below 300µmol $m^{-2}s^{-1}$ as plant productivity significantly decreases below 194µmol $m^{-2}s^{-1}$ (Hanson *et al*., 2016). Following the light chamber measurement, the chamber lid was removed and allowed to re-equilibrate with the ambient atmosphere for 3-5 minutes. The second CO_2 measurement was made under a dark shroud fully extinguishing PAR to measure only CO_2 released by autotrophic and heterotrophic respiration (ER). The difference between NEE and ER values is GEP, representing gross photosynthesis.

Measurements of CH_4 were taken over a 30-minute period under a dark shroud, with 15s samples taken every 5 minutes for a total of 6 samples (Hanson *et al*., 2016). This longer measurement period was required as changes in CH_4 concentration over time are small. Air temperature inside the chambers was recorded simultaneously with gas measurements every 15 seconds (CO_2) or every 5 minutes (CH_4) throughout the sampling process (Fisherbrand Traceable Total-Range Thermometer). Raw CO_2 and CH_4 values were converted into a linear rate of change over time (in $gCO_2\ m^{-2}d^{-1}$ and $mgCH_4\ m^{-2}d^{-1}$, respectively) via the slope of the linear regression line, as a function of the average air temperature inside the chamber at the time of measurement and the chamber volume. Chamber volume varied slightly between chambers due to the chamber's microtopography; topography was measured biweekly in each chamber to account for variations between chambers and across the growing season. By convention, a negative flux value represents an uptake of C from the atmosphere by the peatland, while positive values represent a release of C from the peatlands into the atmosphere.

Overall, six sampling cycles were completed between June and August in 2018 (passive heating) and ten sampling cycles completed between June and October in 2019 (active heating). As a supplemental measurement, leaf area index (LAI) was recorded biweekly in each plot with an AccuPAR-LP-80 ceptometer (Decagon Devices Inc.). Project-level plant abundance and community composition data was obtained as an additional supplemental measurement, consisting of biweekly vegetation surveys using the point-intercept method to determine the density of individual plant species in each plot (Lyons *et al.,* 2020).

2.2.4 Statistics and Analysis

A repeated-measures analysis of variance (ANOVA) was first performed to analyze the overall effect of heating treatment on gas fluxes in 2018 and 2019 between fens and months, using the emmeans package in R for estimated marginal means post-hoc tests (Lenth *et al.,* 2020). Gas fluxes in 2019 were then analyzed for each fen separately with a linear mixed-effects model, using the lme4 package in R (Bates *et al*., 2015), which is able to incorporate the uneven increases in temperature among heated plots (i.e. most heated plots fluctuated between +3.5 and +5 ºC above ambient temperatures) and associated reductions in moisture. This analysis is thus able to identify whether gas fluxes differ between heated and control plots, as well as identifying whether the primary mechanism for observed changes was due to increased temperature, changes in soil moisture, or both. Gas fluxes (CH_4, ER, GEP, and NEE) were the response variables; fixed effects were temperature and soil moisture. Temperature values at 25cm peat depth were used for CH_4 fluxes, and at 5cm depth for CO_2 fluxes based on the best-correlated peat temperatures for each gas flux. Individual plots were the random effect in each model, accounting for differences in baseline gas fluxes among plots.

Temperature and moisture values were standardized to ensure valid comparison between parameters. Variance inflation factors (VIFs) between temperature, moisture, and month were tested using the “car” package to examine if strong interactions existed between variables and deemed insignificant if <4 (Fox *et al*., 2020). If VIF was >4, the variable was excluded from the model: month as a fixed-effect was removed from the statistical models for each individual fen for this reason. Models incorporating only temperature values were compared with models including both temperature and moisture values using Akaike Information Criterion (AIC) values and maximum likelihood ratio tests in order to test if the inclusion of moisture improved the model fit. Each model was followed by an ANOVA function to further analyze fixed effects (Bates *et al.*, 2015). The statistics reported in the results reflect the model of best fit, with the analysis repeated for all four gas fluxes.

Simple linear regressions between gas fluxes and environmental variables (i.e. LAI, vegetation densities collected by Lyons *et al.,* 2020) were performed to further explain variation in gas fluxes between sites, treatments, and years. As 2018 data only extended from June to August, regressions on 2019 data only included these months to allow comparison between the two years. Results for all statistical tests were considered significant if the *P*-value was less than 0.05, or if absolute value of t-statistic was greater than 1.96. Early June 2019 data was collected and used to examine baseline patterns of C fluxes at each site; however, since active heating was not switched on until mid-June it was not used in statistical analysis.

2.3 Results

2.3.1 Chamber Peat Temperature and Moisture

Passive warming in 2018 had no effect on peat temperatures (Table 2.1). Once active heating was initiated, heated plots from June to September in 2019 were, on average, 4.8 ºC warmer at 25cm depth than control plots at the *Sphagnum* fen and 3.7 ºC warmer at the *Carex* fen (Table 2.1). The temperature difference between heated and control plots at 5cm and 10cm depth at the *Sphagnum* fen were +2.1 ºC and +3.2 ºC, respectively, and at the *Carex* fen were +2.1 ºC and + 2.7 ºC. Three heated plots at the *Sphagnum* fen and two plots at the *Carex* fen failed to heat to the desired offset of +4 ºC due to technical malfunction and were thus excluded from analysis.

Table 2.1: Average peat temperature (± standard deviation) at three depths from the peat surface from June to August at each fen in 2018 and 2019 (ºC). Peat temperature measurements are midday (10am-2pm) values.

Site	Year	Plot	5cm Temperature	10cm Temperature	25cm Temperature
Carex	2018	Heated	15.0 ± 2.1	13.9 ± 1.6	12.9 ± 1.1
		Control	15.6 ± 2.3	14.2 ± 1.7	13.1 ± 1.2
	2019	Heated	16.8 ± 2.8	16.7 ± 2.5	16.2 ± 2.5
		Control	14.9 ± 2.2	14.0 ± 1.5	12.8 ± 1.0
Sphagnum	2018	Heated	16.8 ± 3.3	14.2 ± 2.0	12.9 ± 1.7
		Control	18.1 ± 3.6	14.6 ± 2.5	12.6 ± 1.8
	2019	Heated	18.4 ± 3.5	17.9 ± 2.8	18.3 ± 1.7
		Control	15.6 ± 3.3	14.0 ± 2.0	12.5 ± 1.0

There were no differences in soil moisture between passively heated and control chambers in 2018. However, 2019 was a drier year than 2018. Throughout the peak growing season in 2019 (June-August), soil moisture in the control chambers was, on average, 5.6% lower in the *Carex* fen and 3.9% lower in the *Sphagnum* fen compared to 2018 (Fig. 2.1a). Active heating had a slight drying effect: in the *Carex* fen, after active heating commenced, the average soil moisture in heated chambers was 32.2% compared to 39.9% in control chambers. In the *Sphagnum* fen, soil moisture was 14.7% in heated chambers and 16.9% in control chambers (Fig. 2.1b).

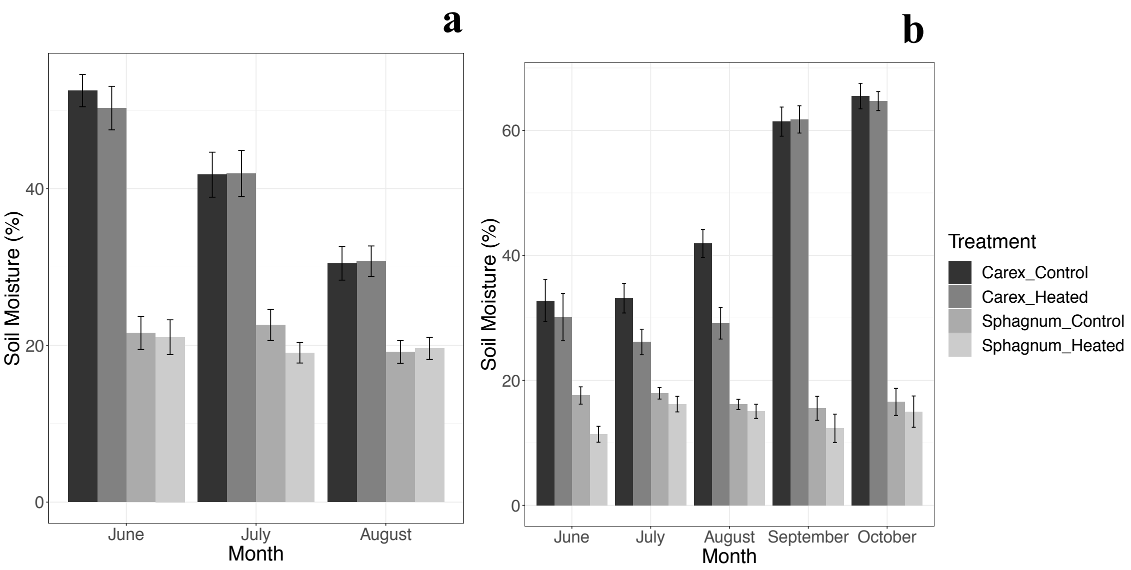

Figure 2.1: Average monthly soil moisture (± standard error) at each fen for 2018 (a) and 2019 (b).

2.3.2 CH_4 Fluxes

In both years, CH_4 fluxes were significantly higher in the *Carex* fen than the *Sphagnum* fen (2018 site: $F_{1,\,28} = 69.3$, $P < 0.001$; 2019 site: $F_{1,\,26} = 37.5$, $P < 0.001$; Table 2.2; Fig. 2.2); in 2018, the average CH_4 flux from the *Carex* fen during the growing season (June-August) was 144% higher than that from the *Sphagnum* fen, and in 2019 was 106% higher. Seasonal patterns were evident throughout the 2018 growing season at both fens (2018 month: $F_{2,\,56} = 18.88$, $P < 0.001$; Table 2.2), with the *Carex* fen reaching a peak CH_4 flux of 91.64 mg CH_4 m^{-2} d^{-1} in July and the *Sphagnum* fen reaching a peak flux of 36.22 mg CH_4 m^{-2} d^{-1} slightly later, in August. Passive warming had no effect on CH_4 fluxes at either site (2018 treatment: $F_{1,\,52} = 0.013$, $P = 0.91$).

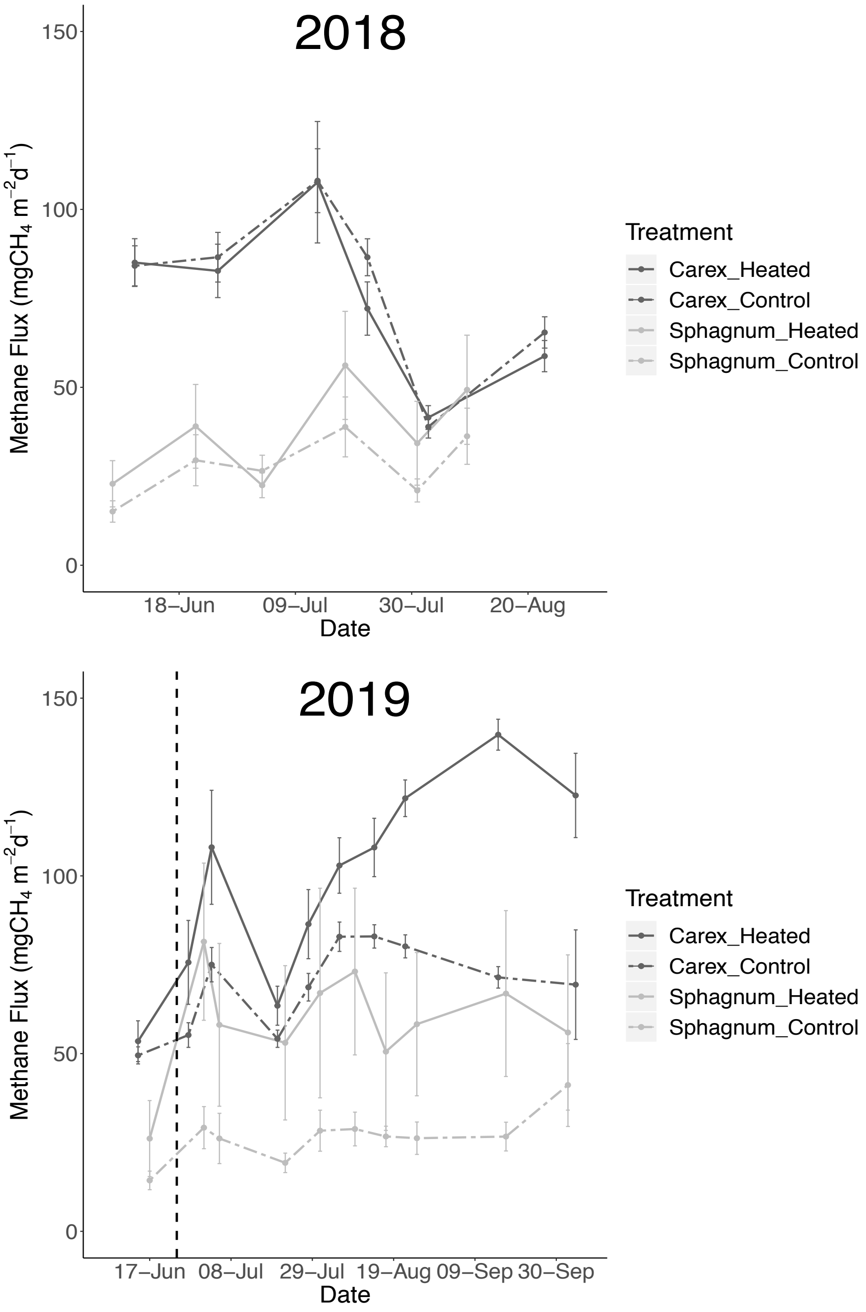

Figure 2.2: Time series of the average methane fluxes (± standard error) at each fen in passively heated and control plots in 2018, and actively heated (+4 ºC) and control plots in 2019. The vertical dashed line indicates the start of active heating.

At the *Carex* fen, actively heated plots produced significantly higher CH_4 fluxes than control plots from June to October ($F_{1, 52}$= 4.81, $P = 0.033$; Fig. 2.2). The mean seasonal CH_4 flux in heated chambers was 57% greater than that of control chambers. Based on *post hoc* tests, differences between the heated and control plots were minimal in June directly after heating commenced and greatest in August through to October. Heated plots also reached their seasonal maximum later in the year than control plots, peaking in mid-September (mean= 139.72 mg CH_4 m^{-2} d^{-1}) whereas control plots reached their seasonal maximum in mid-August (mean= 82.01 mg CH_4 m^{-2} d^{-1}). When incorporated into the mixed model, moisture content was deemed to have an insignificant effect on CH_4 fluxes ($F_{1, 51}$= 1.18, $P = 0.28$), although temperature and moisture interacted strongly ($F_{1, 51}$= 42.7, $P < 0.001$).

At the *Sphagnum* fen, actively heated plots had 114% higher mean seasonal CH_4 fluxes than controls (Fig. 2.2); however, fluxes were highly variable between chambers, with one heated chamber in particular producing much higher CH_4 fluxes than the rest of the plots (mean= 148.17 mg CH_4 m^{-2} d^{-1}). Pre-treatment fluxes from this chamber in June were similar to what they were in 2018 (64.17 and 67.46 mg CH_4 m^{-2} d^{-1} in 2018 and 2019, respectively), but one month after the heating treatment began the flux was more than double what it had been in 2018 (76.86 and 179.56 mg CH_4 m^{-2} d^{-1} in 2018 and 2019, respectively). With this chamber removed from analysis, the remaining heated chambers only produced 42% more CH_4 than control chambers ($F_{1, 46}$= 0.119, $P = 0.73$). Soil moisture had an insignificant effect on CH_4 fluxes ($F_{1, 48}$= 1.76, $P = 0.19$).

The relationship between sedge density in each plot with CH_4 fluxes varied depending on the fen type (Fig 2.3). There was no relationship between sedge density and CH_4 fluxes at the Carex fen ($F_{1,88}$= 0.065, $P = 0.799$, R^2= 0.0007), while at the *Sphagnum* fen there was a weak positive correlation ($F_{1,94}$= 6.353, $P = 0.013$, $R^2 = 0.0633$). When individual sedge species were investigated, counts of broadleaf sedge species (*Carex magellanica* and *Carex oligosperma*) were well-correlated to CH_4 fluxes at the *Sphagnum* fen (2018: $F_{1,14}$= 18.4, $P < 0.001$, $R^2 = 0.57$; 2019: $F_{1,25}$= 144.2, $P < 0.001$, R^2= 0.85), explaining the uncharacteristically high CH_4 fluxes in Chamber 16 (Fig. 2.4). At the *Carex* fen there was no relationship between individual sedge species and CH_4 fluxes.

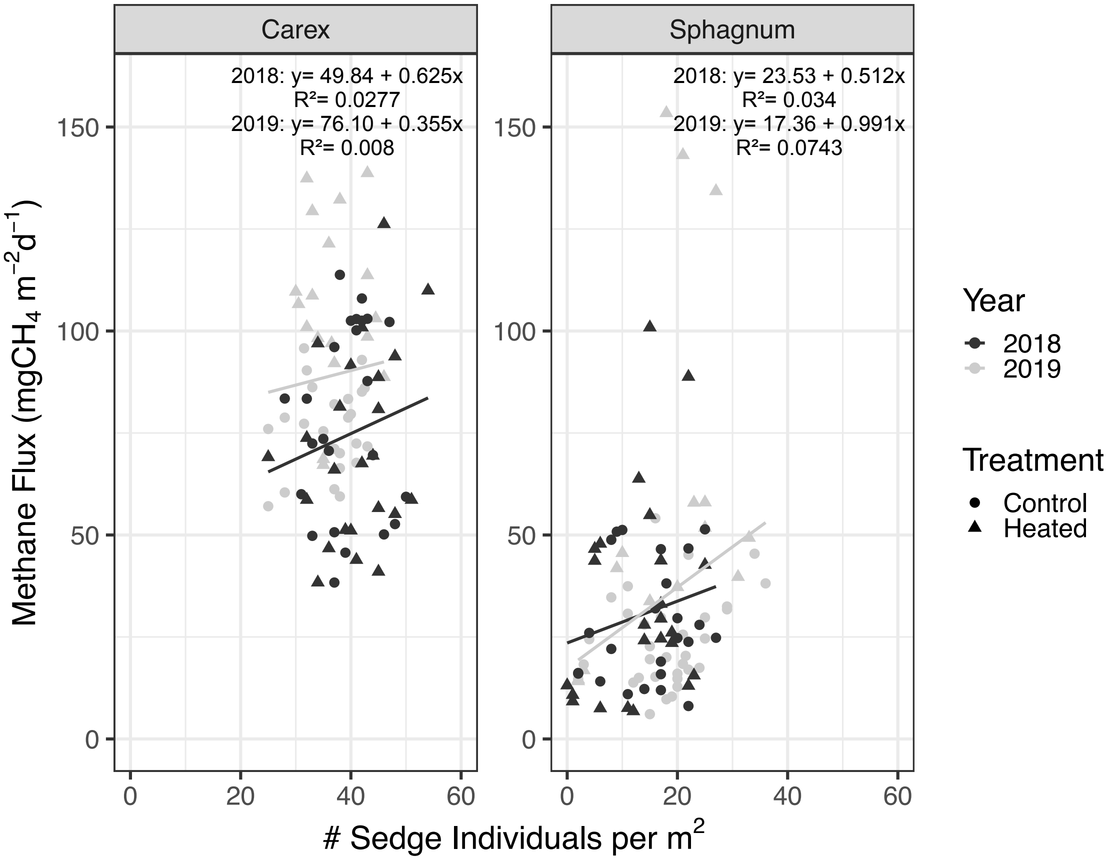

Figure 2.3: Correlation between plot-level sedge density (# individuals per square metre) and methane fluxes at each fen in 2018 (passive heating) and 2019 (active heating), from June to August. Each point represents one time point, at one plot.

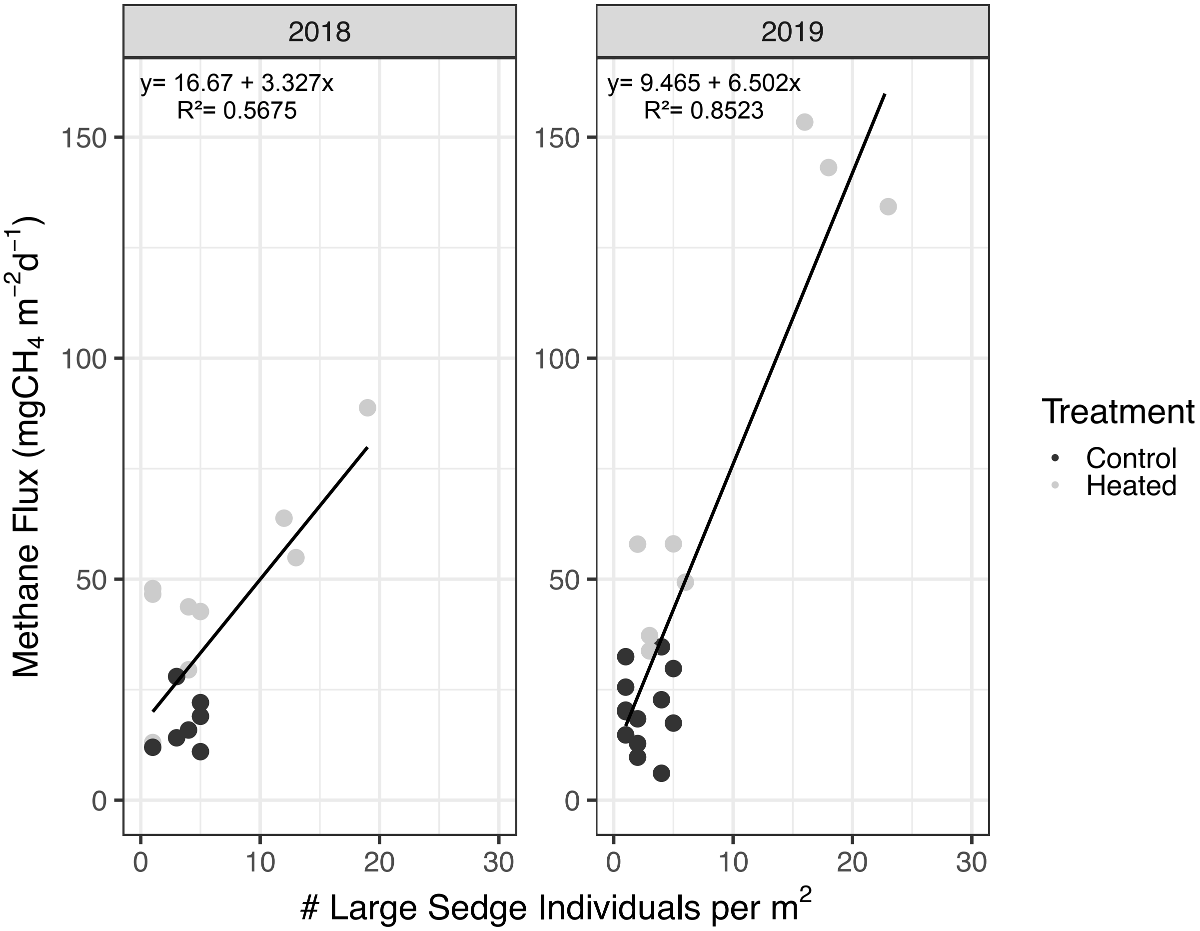

Figure 2.4: Correlation between broad leaf sedge density (*Carex magellanica* and *Carex oligosperma*) and methane fluxes at the *Sphagnum* fen in 2018 (passive heating) and 2019 (active heating), from June to August. Each point represents one time point at one plot.

Table 2.2: Statistical results summary for 2019 gas fluxes. Results reflect a repeated-measures ANOVA, identifying differences between the two sites (*Carex* and *Sphagnum*), between actively warmed (+4 ºC) and control chambers, and across five months (June – October). Significant p-values ($p < 0.05$) are in bold.

		CH_4				ER	
Effect	**df**	**F**	**P**	**Effect**	**df**	**F**	**P**
Fen	1, 24	33.04	**<0.001**	Fen	1, 24	1.903	0.1804
Month	4, 86	9.32	**<0.001**	Month	4, 95	111.5	**<0.001**
Treatment	1, 24	17.98	**<0.001**	Treatment	1, 24	8.86	**0.007**
Fen * Month	4, 86	5.077	**0.001**	Fen * Month	4, 95	9.037	**<0.001**
Fen * Treatment	1, 24	0.358	0.555	Fen * Treatment	1, 24	1.686	0.207
Month * Treatment	4, 86	5.402	**<0.001**	Month * Treatment	4, 95	2.516	**0.046**
Fen * Month * Treatment	4, 86	6.523	**<0.001**	Fen * Month * Treatment	4, 95	0.618	0.651

		GEP				NEE	
Effect	**df**	**F**	**P**	**Effect**	**df**	**F**	**P**
Fen	1, 31	8.50	**0.007**	Fen	1, 31	17.08	**<0.001**
Month	4, 83	102.03	**<0.001**	Month	4, 83	55.24	**<0.001**
Treatment	1, 31	9.11	**0.005**	Treatment	1, 31	3.912	0.057
Fen * Month	4, 83	7.10	**<0.001**	Fen * Month	4, 83	4.138	**0.0032**
Fen * Treatment	1, 31	2.52	0.123	Fen * Treatment	1, 31	2.765	0.107
Month * Treatment	4, 83	0.590	0.671	Month * Treatment	4, 83	0.857	0.494
Fen * Month * Treatment	4, 83	1.96	0.108	Fen * Month * Treatment	4, 83	3.294	**0.0148**

2.3.3 CO_2 Fluxes

Gross Ecosystem Productivity

Passive warming alone had no effect on GEP in 2018 (2018 treatment: $F_{1,\,30} = 0.205$, $P = 0.654$). Photosynthesis rates varied slightly between sites, with average GEP at the *Sphagnum* fen 17% higher than the *Carex* fen throughout the 2018 measurement period (2018 site: $F_{1,\,28} = 7.520$, $P = 0.011$). Photosynthesis rates peaked in July at both sites and followed similar seasonal patterns in 2019 (2018 month: $F_{2,\,55} = 6.251$, $P = 0.004$; Fig 2.5; Table 2.2).

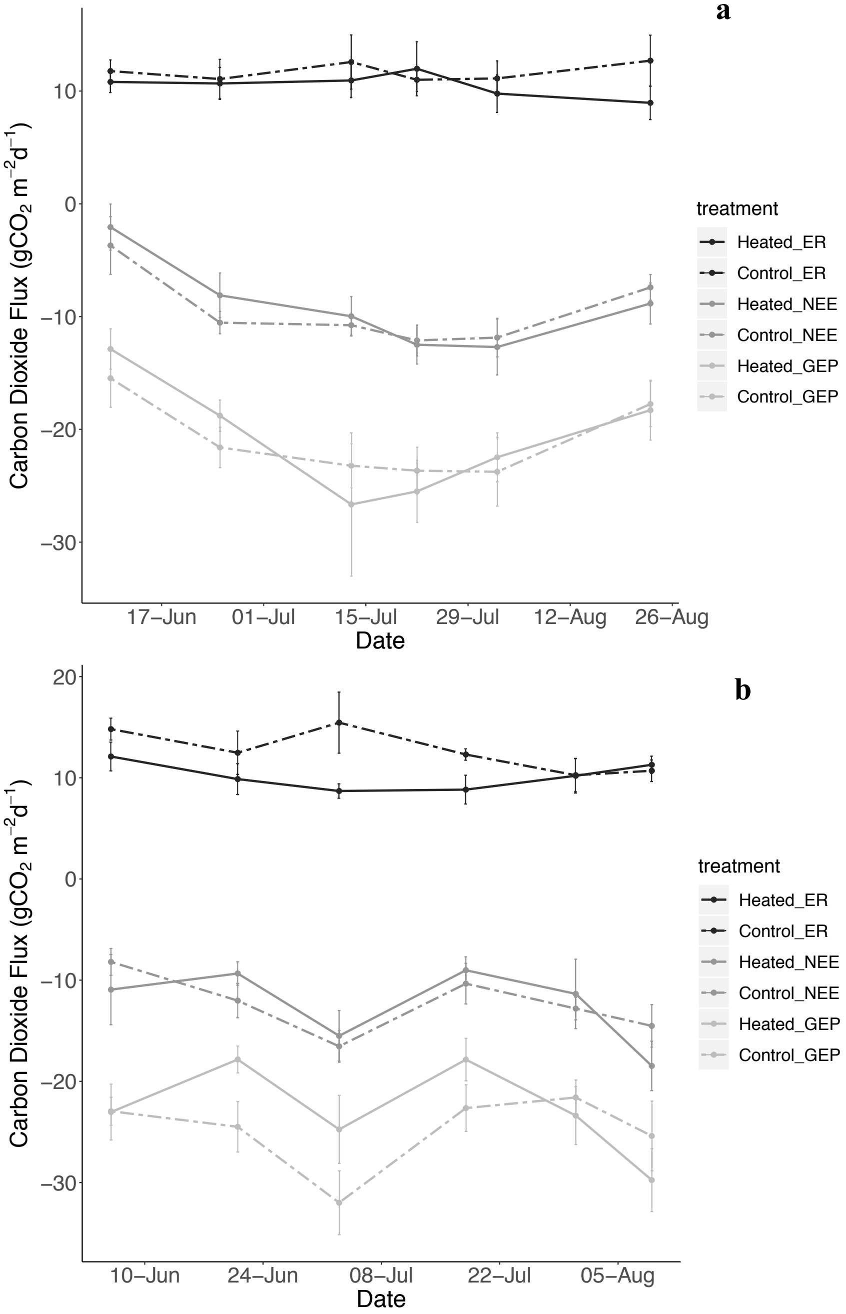

Figure 2.5: Time series of the average CO_2 fluxes (± standard error) at the *Carex* fen (5a) and *Sphagnum* fen (5b) in passively warmed (+1-2 ºC air temperature) and control plots across the 2018 growing season. Positive values represent a release of CO_2 to the atmosphere; negative values represent an uptake of CO_2 into the peatland.

Actively heated plots at the *Carex* fen had an average of 22.6% higher GEP than control plots over the growing season and reached a seasonal maximum of -59.42 g CO_2 m^{-2} d^{-1} compared to the control plot maximum of -49.12 g CO_2 m^{-2} d^{-1} (temperature: $F_{1, 53} = 36.72$, $P < 0.001$). Differences between heated and control plots were largest in July and August with minimal differences late in the season (Fig. 2.6a). When incorporated into the mixed model moisture was found to have a significant effect on photosynthesis (moisture: $F_{1, 55} = 28.81$, $P < 0.001$), although a moisture-GEP relationship was limited to July and August with highest photosynthesis rates in drier, warmer plots.

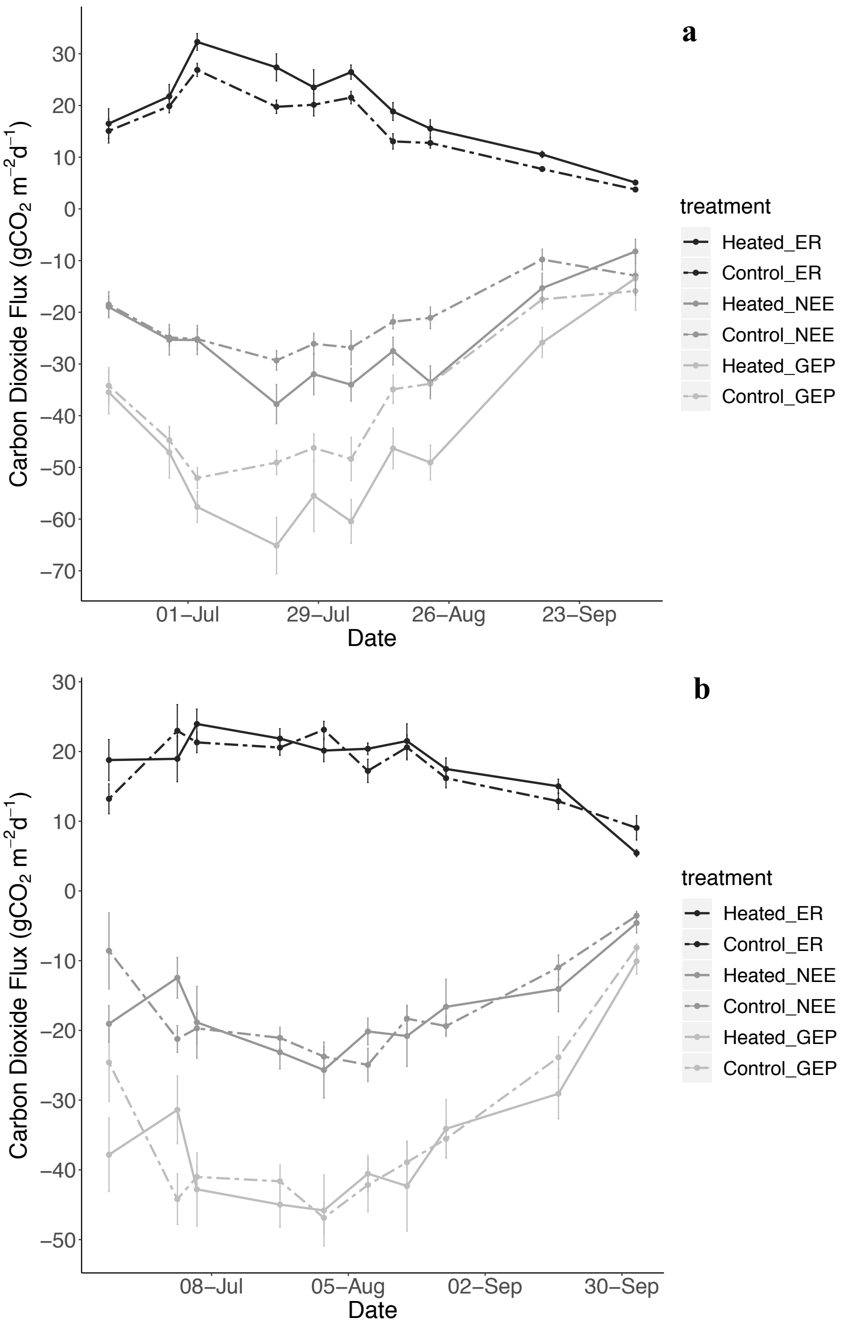

Figure 2.6: Time series of the average CO_2 fluxes (± standard error) at the *Carex* fen (6a) and *Sphagnum* fen (6b) in heated (+4 ºC) and control plots across the 2019 growing season. Positive values represent a release of CO_2 to the atmosphere; negative values represent an uptake of CO_2 into the peatland.

In contrast, at the *Sphagnum* fen in 2019 there was no change in GEP with soil temperature ($F_{1, 53} = 3.13$, $P = 0.083$; Fig. 2.6b), and surface soil moisture was not found to play a significant role in photosynthesis rates. Seasonal averages between heated and control plots were similar (-36.81 g CO_2 $m^{-2}d^{-1}$ and -38.55 g CO_2 $m^{-2}d^{-1}$, respectively).

Photosynthesis was strongly correlated with LAI in 2019 at the *Carex* fen ($F_{1, 40}= 16.0$, $P < 0.001$, $R^2 = 0.29$; Fig. 2.7), and poorly correlated with LAI in 2018 and at the *Sphagnum* fen in both years. Across both fens, GEP was on average 85% higher in 2019 than 2018 (2019 mean = -41.9 gCO_2 $m^{-2}d^{-1}$; 2018 mean = -22.6 gCO_2 $m^{-2}d^{-1}$), and LAI was 84% higher in 2019 than 2018 (2019 mean = 1.40; 2018 mean = 0.76). A basic one-way ANOVA test showed that actively heated plots at the *Carex* fen had a higher LAI and shrub density throughout the season than control plots did in 2019 (LAI: $F_{1,54}=5.17$, $P = 0.027$; Shrub density: $F_{1, 62} = 4.858$, $P = 0.031$), but they did not differ at the *Sphagnum* fen (LAI: $F_{1,50}= 2.612$, $P = 0.112$; Shrub density: $F_{1, 50}= 3.255$, $P = 0.077$). Other vegetation densities (sedges, herbs, and mosses) did not differ among plots at either site.

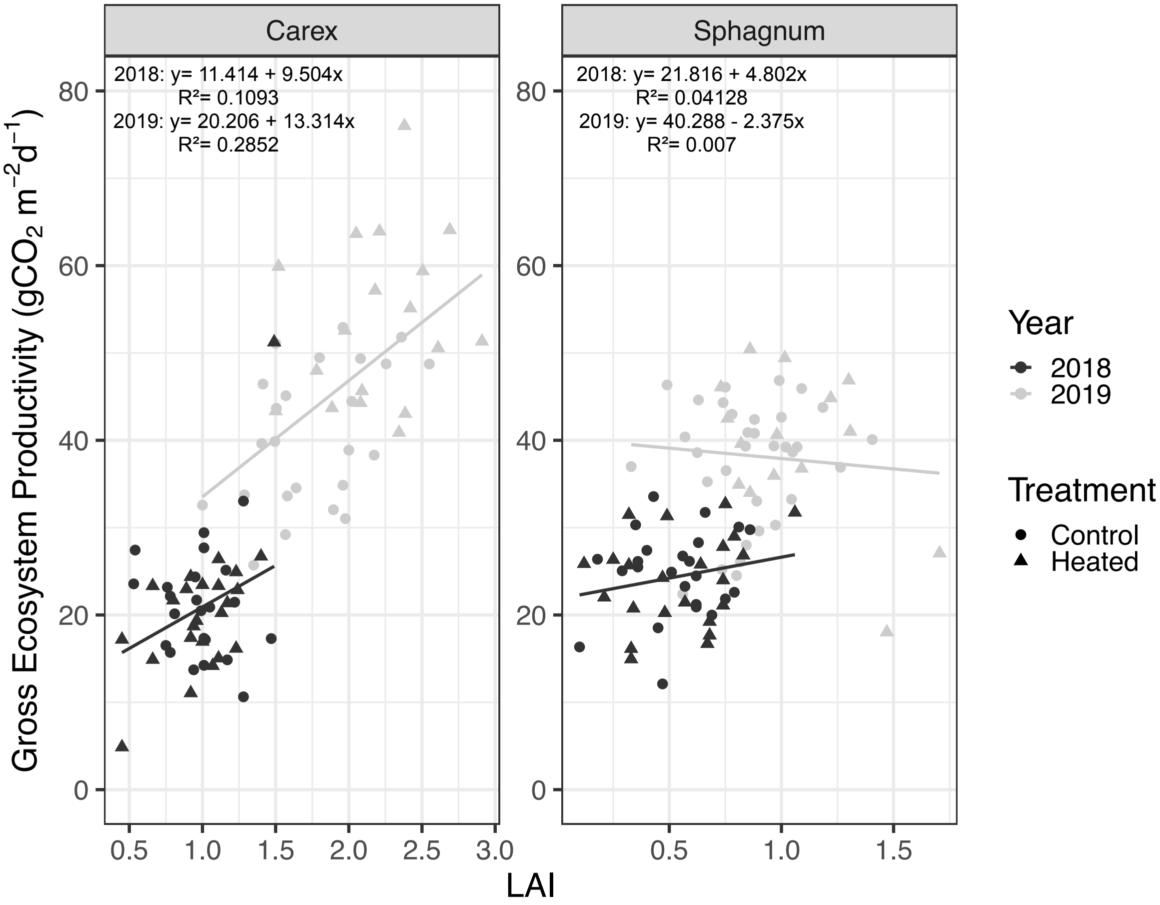

Figure 2.7: Correlation of leaf area index (LAI) with photosynthesis rates (GEP) across both fens, and across two years (2018 passive heating and 2019 active heating) from June to August. Each point on the graph represents one chamber measurement.

Ecosystem Respiration

There were no differences in ER between sites, and between passively warmed and control chambers in 2018 (2018 site: $F_{1, 28}$= 0.421, $P = 0.522$; 2018 treatment: $F_{1, 30}$= 2.677, $P = 0.11$; Fig. 2.5). Although there were no statistically significant seasonal patterns in 2018, ER peaked in the *Carex* fen in mid-July (mean= 12.31 g CO_2 m^{-2} d^{-1}) and in the *Sphagnum*-dominated fen slightly earlier in late June (mean= 12.67 g CO_2 m^{-2} d^{-1}).

Active warming significantly increased ER in 2019 (Table 2.2; Fig. 2.6). At the *Carex* fen, heated plot ER was significantly higher than control plot ER (temperature: $F_{1, 62}$= 146.8, $P < 0.001$); heated plots released an average of 21.8% more CO_2 into the atmosphere than control plots. Clear seasonal patterns were evident in 2019 likely due to the sample period extending two months longer than in 2018. Peak ER was reached in early July (M= 32.30 g CO_2 m^{-2} d^{-1} in heated plots; M= 26.88 g CO_2 m^{-2} d^{-1} in control plots), followed by a decline in ER through to October. Elevated ER was most evident in heated plots in June and July, with minimal effects of active warming on ER in June and October (Fig. 2.6a). Moisture improved the model fit ($F_{1, 60}$= 2.92, $P = 0.093$), with effects of moisture most visible in July when warm, dry plots released the most CO_2 to the atmosphere through respiration.

Active warming had no statistically significant effect on ER at the *Sphagnum* fen. Heated chambers released slightly more CO_2 to the atmosphere in July, August, and September, but control chambers had a higher ER in June and October, resulting in similar seasonal averages between heated and control plots. Seasonal patterns were evident: heated plots peaked in early July, nine days after warming was initiated (M= 23.95 g CO_2 m^{-2} d^{-1}), while control plots peaked in late July (M= 23.12 g CO_2 m^{-2} d^{-1}; Fig. 2.6b).

Leaf area index (LAI) was a poor predictor of ER in 2018 but was positively correlated with ER in 2019 at the *Carex* fen ($F_{1, 40}$ = 14.1, $P = 0.001$, $R^2 = 0.25$; Fig. 2.8). Photosynthesis and ER were positively correlated in both years and at both fens (2018:

$F_{1, 92} = 31.3$, $P < 0.001$, $R^2 = 0.25$; 2019: $F_{1, 88} = 115.5$, $P < 0.001$, $R^2 = 0.57$; Fig. 2.9). In general, higher LAI and GEP values in 2019 explained the higher ER throughout the 2019 growing season compared to 2018.

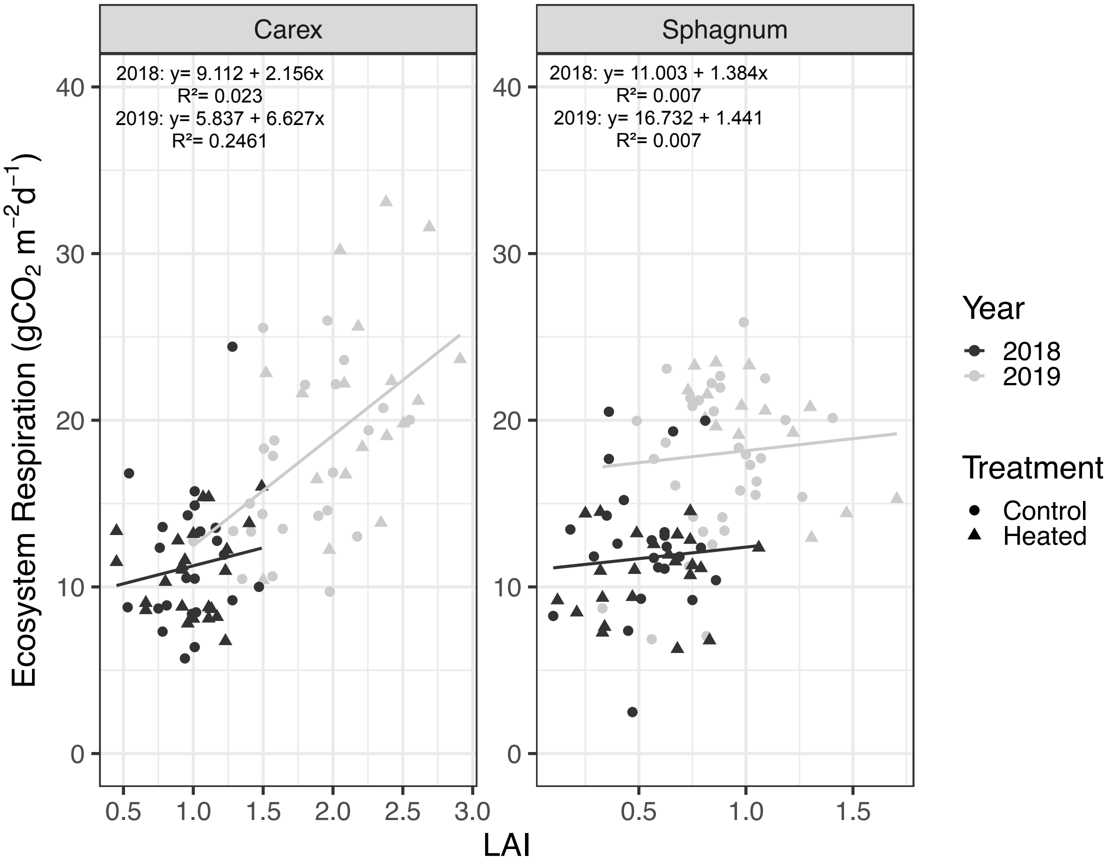

Figure 2.8: Correlation of leaf area index (LAI) with ecosystem respiration (ER) across both fens, and across two years (2018 passive heating and 2019 active heating) from June to August. Each point on the graph represents one chamber measurement.

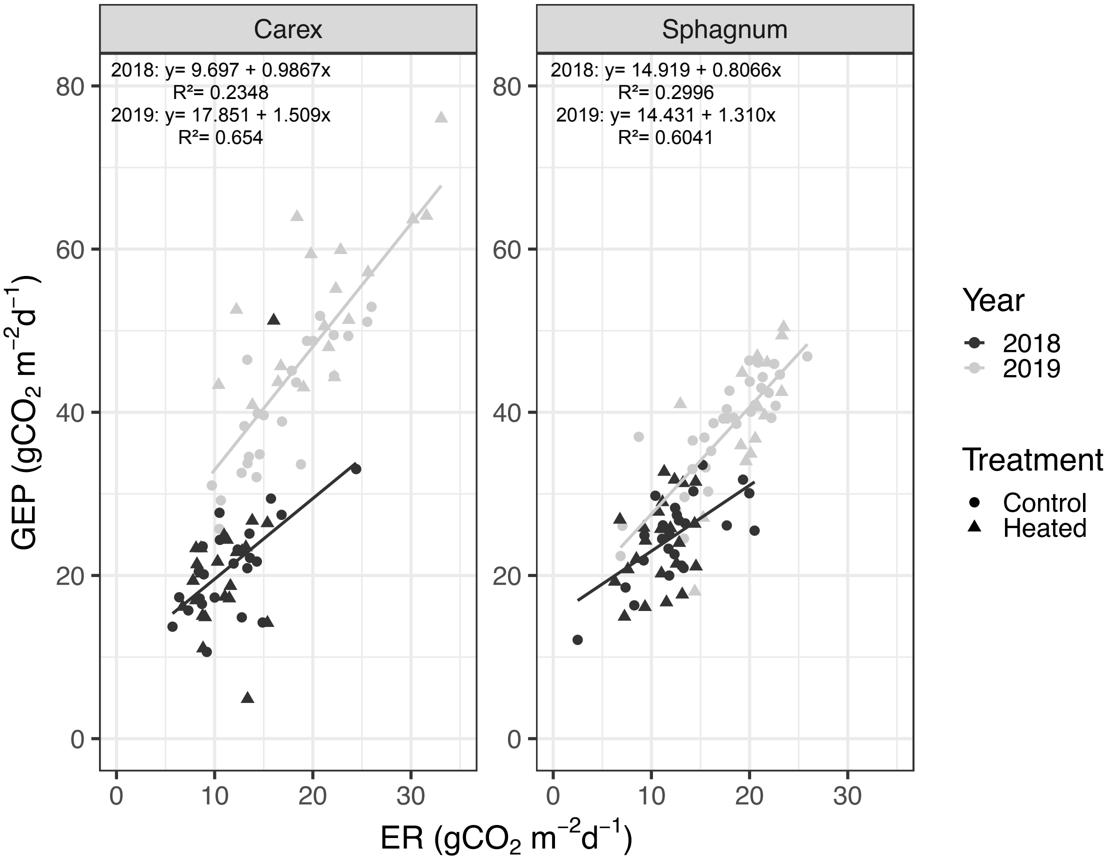

Figure 2.9: Correlation of GEP with ER across both fens, and across two years (2018 passive heating and 2019 active heating) from June to August. Each point on the graph represents one chamber measurement.

Net Ecosystem Exchange

Over the 2018 growing season, NEE at the *Sphagnum* fen was 38.9% higher than at the *Carex* fen, acting as a stronger CO_2 sink (2018 site: $F_{1, 27}$= 13.18, *P* = 0.001; Fig 2.5). This is in contrast to 2019, where *Carex* fen NEE was 32.4% higher than the *Sphagnum* fen. Following similar patterns to GEP and ER, the *Carex* fen acted as the strongest CO_2 sink in late July, whereas the *Sphagnum* fen peaked slightly later in early August (2018 month: $F_{2, 54}$= 15.72, *P* < 0.001; Table 2.2). Passive warming had no effect on NEE in 2018 at either fen (2018 treatment: $F_{1, 30}$= 0.206, *P* = 0.65).

In 2019, heated plots at the *Carex* fen acted as a significantly stronger CO_2 sink, with 22.8% higher NEE than control plots from June to October (temperature: $F_{1,52}$= 4.26, *P* = 0.044). The majority of this was due to August and July fluxes, with minimal differences between plots in June, September, and October. Both heated and control plot NEE peaked in mid-July, at -37.76 g CO_2 m^{-2} d^{-1} and -29.31 g CO_2 m^{-2} d^{-1} respectively, but heated plots remained strong CO_2 sinks into the fall. Control plot CO_2 uptake sharply declined in late August (Fig. 2.6a). The addition of moisture improved the model fit in the *Carex* fen, with drier, warmer plots acting as the strongest CO_2 sinks (similar to patterns of GEP and ER). At the *Sphagnum* fen, there were few differences in CO_2 sink strength between heated and control plots ($F_{1,54}$= 0.77, *P* = 0.38). Strong seasonal patterns showed that all plots had the highest NEE in late July, with heated and control plots reaching maximums of -25.68 g CO_2 m^{-2} d^{-1} and -24.95 g CO_2 m^{-2} d^{-1} respectively. However, heated plots showed signs of sustaining their CO_2 sink strength later into the fall: control plot fluxes sharply declined in September, while heated plot fluxes remained relatively close to the seasonal average (Fig. 2.6b).

2.4 Discussion

The significant variation in CH_4 fluxes between sites was consistent with results from a multitude of other studies reporting high CH_4 fluxes from sedge-dominated communities (eg. Bellisario *et al*., 1999, Crill *et al*., 1988, Moore *et al*., 2011, Ward *et al*., 2013). As each plot at the *Carex* fen had high sedge density, there was no correlation observed between CH_4 fluxes and sedge counts in individual plots. Higher nutrient levels in the *Carex* fen are provided by labile C through root exudates and easily decomposable sedge litter (Hutsch *et al*., 2002; Verhoeven & Toth, 1995), combined with a direct pathway for CH_4 to travel from peat to atmosphere through aerenchyma (Smith *et al*., 2003; Visser *et al*., 2000). This along with the higher water table, and thus a smaller aerobic zone of CH_4 consumption, resulted in consistently greater CH_4 fluxes from the *Carex* fen (Krumholz *et al*., 1995; Moore & Knowles, 1989; Moore & Dalva, 1997).

While sedge abundance explained some of the variation between CH_4 fluxes at the two fen types, peat temperature acted as a primary control on CH_4 fluxes within each individual fen. Active heating resulted in a significant increase in CH_4 fluxes at the *Carex* fen in just a few months of active heating, despite a slight reduction in soil moisture. Previous studies have shown that the highest CH_4 production occurs in warmed, wet plots with water table acting as the dominant control over fluxes when lowered significantly (i.e. over 5cm of water table drawdown; Turetsky *et al*., 2008; Pearson *et al*., 2015; White *et al*., 2008); we find here that within each individual month, the highest CH_4 fluxes did indeed come from the warmest, wettest plots. Aboveground sedge abundance (and thus sedge-facilitated gas transport) did not change between heated and control plots, pointing to belowground processes being responsible for increased CH_4 fluxes in the short term. Fenner *et al*. (2007) found an increase in vascular plant root biomass under heating treatments, as well as increased root exudation potential. The methanogenic *Archaea* community is resilient to change, with no changes in abundance or community structure observed with heating treatments (Peltoniemi *et al*., 2016; Wilson *et al*., 2016), so it is likely that a combination of increased belowground root biomass and stimulated root exudation were responsible for higher CH_4 fluxes under higher temperatures. Despite the heating system being turned off in mid-September, and peat temperatures returning to ambient levels by October, the higher CH_4 fluxes in heated chambers were sustained through October. Relatively dry conditions throughout the growing season likely led to a build-up of organic material in the top layer of peat, but was inaccessible to methanogens until the water table rose to the surface in September: *Archaea* are able to lay dormant for long periods of time under aerobic conditions, but are able to recover as soon as the area becomes water-saturated (Angel *et al*., 2012).

In strong contrast to the *Carex* fen, the *Sphagnum* fen had minimal increases in CH_4 fluxes with heating. Previous studies at this site have confirmed that the fen has lower substrate quality due to the dominance of decomposition-resistant *Sphagnum* (Godin *et al*., 2012; Palozzi *et al*., 2017; Verhoeven & Toth, 1995), and has a lower water table. In nutrient limited systems, readily available organic matter can be depleted in a matter of weeks upon temperature increases (Jerman *et al*., 2017), pointing to fast usage of much of the labile C in the *Sphagnum* fen in the first two weeks of treatment and supported by the sharp spike in CH_4 fluxes after heating was initiated. Activity of CH_4 oxidizing bacteria (methanotrophs) responsible for CH_4 consumption generally increases with temperature (Serrano-Silva *et al.*, 2014; Szafranek-Nakonieczna & Bennicelli, 2010), and this combined with the minor reductions in soil moisture may have stimulated the methanotroph community (Peltoniemi *et al.*, 2016), offsetting any increases in CH_4 production occurring with heating. The heterogeneous nature of the site resulted in high CH_4 fluxes from one chamber, surpassing even the CH_4 fluxes from the heated plots at the *Carex* fen. Although base values of CH_4 fluxes from this chamber have always been relatively high, heating treatment stimulated a substantial spike in CH_4 fluxes that was sustained throughout the season. At the *Sphagnum* fen, soft-leaf sedges (*Carex disperma*) are common, but this anomalous chamber contains broader-leaf sedges similar to those at the *Carex* fen (*Carex magellanica* and *Carex oligosperma*). Structural differences in these sedges, such as a more extensive rooting system and larger aerenchyma for transport due to the larger leaf area, may have resulted in more root exudates and more efficient CH_4 transport to the atmosphere. Although *Sphagnum* fen methanogenesis typically follows a hydrogenotrophic pathway (Bellisario *et al.*, 1999), with methanogens using H_2 and CO_2 to produce CH_4, acetoclastic methanogenesis utilizes acetate as found in root exudates, and could have been stimulated here as an additional pathway. Since moss fens are predicted to act as a larger C sink than sedge fens due to *Sphagnum*-driven slow turnover rates (Kuhry *et al.*, 1993; Lyons & Lindo, 2020), a shift to sedge-dominated communities as predicted with climate change may result in moss fens becoming larger CH_4 sources due to their large stores of belowground C.

While the CH_4 response to heating at the fens differed in magnitude but remained similar in direction, they differed completely in CO_2 flux response. Vegetation at the *Carex* fen responded rapidly to heating treatment, resulting in a higher LAI and photosynthesis rates, and a higher shrub count in heated plots. Previous studies on this same site found that after two years of passive OTC warming, LAI and thus aboveground vascular plant biomass at the *Carex* fen increased in heated plots (Lyons *et al.*, 2020). Vascular plants have a higher maximum photosynthetic rate than mosses do due to their large leaf area and efficient water conductance, leading to more gas exchange between leaf and atmosphere (Syed *et al.*, 2006). Drying in heated plots and sedge-driven rhizosphere oxidation may have stimulated nutrient uptake (Chivers *et al*., 2009; Kane *et al*., 2019; Laine *et al*., 2019), furthered by higher peat temperatures increasing root exudation and providing more nutrients for vascular plant growth.

Neither *Sphagnum* fen LAI nor GEP changed with heating. Many studies have found that moss cover declines under warming treatments (Fenner *et al*., 2008; Walker *et al*., 2015), with even minor changes in water table level detrimental to moss growth (Makiranta *et al*., 2018; Potvin *et al*., 2015). The combination of small soil moisture reductions and increased temperatures may have been enough to limit moss growth; they are easily subject to desiccation stress which results in low photosynthesis rates (Bridgham *et al*., 2008). Even if moss growth were to occur, photosynthetic capacity is lower compared to vascular plants (Syed *et al*., 2006; Wu *et al*., 2013), and as moss lays low to the ground, it does not typically contribute to the LAI measured with the ceptometer used in this study. Changes in vascular plant growth at this site is likely limited due to the nutrient-poor environment and short time frame of the study; the exception to this was the single outlier chamber with high CH_4 fluxes, which had higher sedge abundance and GEP rates than the other heated chambers did. The response of this chamber was likely a function of the sedge community that was already established in the years prior to heating treatments, providing a belowground environment richer in nutrients through plant litter and root exudates and thus allowing more rapid plant growth with heating.

The ER response followed similar trends to GEP, with significant increases occurring in heated plots at the *Carex* site, but no response at the *Sphagnum* site. Although plots with a higher aboveground LAI had higher respiration rates at the *Carex* fen, new vegetation growth stimulated from heating treatments would not have been available as litter this growing season (Gu *et al*., 2004); the increase in respiration can thus be linked to belowground factors rather than aboveground. Root growth under heating has been observed to lead to more root exudation (de Graaff *et al*., 2010; Kuzyakov *et al*., 2007), providing more substrate for decomposition. Both fen models and other direct peat heating experiments have demonstrated the highest increase in heterotrophic respiration (compared to autotrophic) due to stimulated root activity (Wilson *et al*., 2016; Wu &

Roulet, 2014), supporting that heterotrophic respiration at the *Carex* fen was likely responsible for the changes. Lack of labile substrate and vascular plants at the *Sphagnum* fen limited the response of ER to temperature, as most of the belowground C pool is composed of recalcitrant *Sphagnum* litter. The *Sphagnum* fen has been established as dominated by a fungal decomposer community whereas the *Carex* fen's decomposer community is predominantly bacterial (Lyons & Lindo, 2020). Fungal decomposer communities turn over C at a slower rate than bacterial communities and respond more slowly to changes in temperature and moisture (Strickland & Rousk, 2010), and thus may be less likely to respond to warming in the short term.

Contrary to my hypothesis, GEP at the *Carex* fen increased to a greater degree than did the respiration rates in heated chambers, resulting in more CO_2 uptake. Generally, short-term studies have had no impact of passive heating on NEE until 2+ years after heating initiation (Pearson *et al*., 2015; Laine *et al*., 2019; Makiranta *et al*., 2018; Wiedermann *et al*., 2007). Over 2-3 years of OTC passive warming, warming has commonly resulted in an increase in shrub and graminoid cover, a decline in moss cover, and an eventual increase in decomposition rates (Fenner *et al*., 2007; Laine *et al*., 2019; Walker *et al*., 2015). My results were even more rapid than this, with a significant increase in photosynthesis and respiration one month after warming was initiated. This may be a function of the direct ground heating: few studies have warmed peat directly, and passive OTC warming does not usually translate to warming in the peat profile. Other studies applying deep (25cm+) peat heating found similar rapid responses in greenhouse gas fluxes (eg. Wilson *et al*., 2016). Multiple models simulating future greenhouse gas fluxes have predicted an eventual stabilization of fluxes from peatlands, suggesting that over time microbes will either acclimate to elevated temperatures or labile C will become limiting (Crowther & Bradford, 2013; Rustad & Fernandez, 1998; Wilson *et al*., 2016; Wu *et al*, 2011). However, increased plant growth may add to the respiration response over time, eventually resulting in ER exceeding GEP. This agrees with model projections from Fan *et al*. (2013) that the overall rate of C sequestration will increase initially with warming but will eventually be offset by rising respiration rates. Although GEP > ER over one growing season, stimulated vascular plant growth has not yet contributed to the belowground litter pool – after new vegetation growth has made its way into the soil and down the peat profile it may result in higher decomposition rates and CH_4 fluxes in the future. Although it is likely that CH_4 and CO_2 fluxes from the *Carex* fen will continue to increase at a consistent degree due to the high amounts of labile litter, the *Sphagnum* fen contains larger belowground stores of C as recalcitrant moss litter (Lyons & Lindo, 2020). This puts moss-dominated fens at risk of becoming exponentially larger CO_2 and CH_4 sources once vascular plant communities are established: as demonstrated by the CH_4 flux response of one outlier chamber to heating, a sedge community in a moss fen is capable of producing extremely high CH_4 fluxes, and high decomposition rates may be to follow. As the response of fens to climate change is transient from year-to-year, long-term studies are necessary to examine how these changes develop over time.

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Chapter 3

3 Spectroscopic indicators of changes in peat organic matter chemistry under experimental warming

3.1 Introduction

Northern peatlands play a critical role in cooling Earth's surface temperature, sustaining slow decomposition rates relative to photosynthetic uptake year-round to maintain their large belowground carbon (C) stores. Although they cover just 3% of land surface area, they store approximately 32% of global soil C (Bridgham *et al*., 2006; Gorham, 1991). Climate change, however, threatens their C sink function by warming and drying the landscape, removing temperature and moisture constraints on decomposition and thus risking release of the large belowground C stores. Fen peatlands are at particular risk for becoming C sources in the future; as they have higher soil nitrogen (N) and nutrient content than bogs, plant growth and microbial activity respond to warming to a greater degree (Gong *et al*., 2013; Wu & Roulet, 2014). Increased vascular plant growth that is predicted for a warmer climate has the potential to either reduce this effect through increased photosynthesis (Dieleman *et al*., 2015; Walker *et al*, 2015), or enhance the release of C to the atmosphere by supplying fresh plant substrate to the microbial community, stimulating decomposition. Fens also naturally act as a large source of methane (CH_4) (Crill *et al*., 1988; Matthews & Fung, 1987), produced below the water table by methanogenic *Archaea*, and the amount of CH_4 released to the atmosphere is expected to increase under climate change based on both field experiments and models (eg. Ma *et al*., 2017; Moore & Dalva, 1993; Wilson *et al*., 2016)

Fens exhibit a large degree of variability in their belowground microbial communities, nutrient and soil organic matter (SOM) quality, and plant community. Greenhouse gas fluxes from fens are in part dependent on the plant community, with nutrient-rich sedge-dominated fens having significantly larger CH_4 fluxes than nutrient-poor moss-dominated fens do (Basiliko *et al*., 2007; Robroek *et al*., 2015; Ward *et al*., 2013). In addition, low

N, nutrient-poor, moss-dominated peatlands tend to have a decomposer communities dominated by fungi while high N, nutrient-rich, sedge peatlands are more likely to have a predominant bacterial decomposer community (Myers *et al*., 2012; Strickland & Rousk, 2010; van der Heijden *et al*., 2008), each having implications for C storage rates. Fungal communities are slower to turnover C (Ingwersen *et al*., 2008; Lyons *et al*., 2020; Six *et al*., 2006; Strickland & Rousk, 2010), enhanced by the presence of the recalcitrant *Sphagnum* litter that typically dominates peatlands with fungal decomposer communities (Del Giudice & Lindo, 2017). Comparatively, sedge-dominated peatlands have greater decomposition, and thus C turnover rates, due to their faster-cycling bacterial decomposer community and labile sedge litter (Del Giudice & Lindo, 2017). Root exudates from *Carex spp.* rooting systems provide additional nutrients to the soil and have been found to contribute to positive priming effects where decomposition is stimulated by the sugars and organic acids released from sedges' extensive rooting systems (Fenner *et al*., 2007; Dieleman *et al*., 2016). Although sedge fens may be able to respond quickly to climate change due to the readily available C as a nutrient source, moss fens have a larger potential store of C that could be released in the future as well as a fungal decomposer community that is able to degrade more recalcitrant plant residue, such as lignin and the lignin-like phenolic compounds present in *Sphagnum* mosses (Ingwerson *et al*., 2008; van der Heijden *et al*., 2008; Verhoeven & Toth, 1995).

Soil organic matter (SOM) quality is determined by the type of plant litter entering the peat profile, and it influences decomposition and CH_4 production rates (Duval & Radu, 2018; Limpens & Berendse, 2003). A common technique in peatland research to determine SOM quality and degree of decomposition is Fourier-transform infrared spectroscopy (FTIR), an analytical technique that passes a mid-infrared beam of light through a sample; based on the vibrational response of molecular bonds at specific wavelengths, qualitative information is obtained about the functional groups present in a sample and the relative abundance of each chemical property based on the absorption intensities (Zhou *et al*., 2011). Enrichment of recalcitrant matter (eg. lignin, carboxylic acids, aromatics, proteins, waxes, and lipids) relative to labile polysaccharides indicates a greater degree of decomposition due to the preferential decomposition of polysaccharide molecules (Artz *et al*., 2008; Biester *et al*., 2014; Zaccheo *et al*., 2002). The ratio of recalcitrant band intensities to polysaccharide band intensities is frequently used as a humification index. Peat containing lower amounts of polysaccharides compared to recalcitrant aromatic and aliphatic compounds has been related to lower microbial biomass and enzyme activity and is therefore considered to be low quality (Könönen *et al*., 2018). Peat quality is a relevant tool in many areas of peatland research: depending on local hydrology and belowground chemistry, humification indices generally increase with depth from the surface (Artz *et al*., 2008; Biester *et al*., 2014; Broder *et al*., 2012; Cocozza *et al*., 2003; Haberhauer *et al*., 1998). Humification indices are also used to compare the peat quality and composition between peatland types. Multiple studies have compared ombrotrophic, precipitation-fed bog FTIR spectra to groundwater and precipitation-fed minerotrophic fens (Heller *et al*., 2015; Krumins *et al*., 2012). Degree of drainage along with the aboveground plant community has often been cited as a main source of spectral variation between peatlands (Broder *et al*., 2012; Chapman *et al*., 2001; Heller *et al*., 2015; Palozzi & Lindo, 2017).

Large differences in peat quality and composition exist between fen types of differing dominant vegetation (Lyons *et al*., 2020; Palozzi & Lindo, 2017), and the CH_4 and CO_2 fluxes of each fen type respond differently to warming (Chapter 2 of this thesis). By examining how peat has been altered at a molecular level in response to warming, we are able to detect small-scale changes in peat quality and SOM utilization (Artz *et al*., 2008). This in turn aids in understanding the implications climate change may have on C storage and cycling. This field experiment aims to determine how direct ground heating at a *Sphagnum* moss-dominated nutrient-poor fen, and a *Carex* sedge-dominated fen with intermediate nutrient levels, alters belowground peat composition, as well as examining how differences in aboveground gas fluxes between fen types are reflected in the belowground organic chemistry. I hypothesize that the *Carex* fen, with a relatively fast-cycling bacterial decomposer community, will have a higher degree of decomposition in heated plots, reflecting the aboveground ecosystem respiration (ER) rates measured with gas fluxes, while control plots will contain less recalcitrant decomposition products. From the *Sphagnum* fen, I hypothesize no change in peat properties between heated and control plots due to the slow-cycling fungal decomposer community and the absence of gas flux response to warming over one growing season.

3.2 Materials and Methods

3.2.1 Study Site

The study area, described in detail in Chapter 2 and in other sources (McLaughlin & Webster, 2010; Webster & McLaughlin, 2010), was two boreal fens near White River, Ontario (48º21' N, 85º21'W). The cool, temperate climate has a mean annual temperature of 2.1 ºC and receives approximately 970mm of precipitation annually (Environment Canada, 1989-2019). The nutrient poor fen is dominated by *Sphagnum spp.* mosses, shrubs, herbs, and soft-leaf (*Carex disperma*) and broad-leaf sedges (*Carex oligosperma, Carex magellanica*). The intermediate-nutrient fen is located approximately 2km away and is dominated by *Carex spp.* sedges (mainly *Carex lasiocarpa, Carex oligosperma*, and *Carex stricta*), shrubs, and some mosses (*Spagnum angustifolium*). Both are located in a boreal mixed-wood forest containing black spruce (*Picea mariana*), balsam fir (*Abies balsamea*), and white birch (*Betula papyrifera*) (McLaughlin, 2009).

Sixteen collars penetrating 50cm into the soil were installed at each fen in 2015, and half of the collars at each fen were outfitted with clear open-top chambers (OTCs) in 2017. Passive heating through OTCs took place from 2017-2018, and active heating of the soil profile through 50cm-deep ground heating rods commenced in June 2019. Heating rods were set to heat the peat profile to +4 ºC above ambient temperatures, shutting off automatically when an offset of over 4 ºC was reached. Temperatures were recorded through Watlow EZ-ZONE® Configurator software 2-3x per week. Minor daily fluctuations throughout the growing season (June – September) resulted in heated plots at the *Sphagnum* fen averaging 4.8 ºC warmer than control plots at 25cm peat depth, and heated plots at the *Carex* fen averaging 3.7 ºC warmer than control plots. Three plots at the *Sphagnum* fen and two plots at the *Carex* fen failed to heat properly and were considered "passive" heating chambers for 2019. A small decline in soil moisture was observed in heated plots: at the *Sphagnum* fen, the soil moisture of heated plots was 2.2% lower than control plots, and at the *Carex* fen was 7.7% lower.

3.2.2 FTIR and C:N

Five 1cm^3 peat samples at 25cm depth per plot were collected using a 50 cm long flexible steel pickup tool at random locations in both the *Carex* and *Sphagnum* fens in October. Locations were chosen to ensure that samples were taken from both hummocks and hollows, and from both the edges and the center of the plot to ensure that a representative spectral profile was created. Peat samples were freeze-dried, coarse woody material > 2mm in size was removed, and the remainder was ground to a powder in a mortar and pestle. Absorbance measurements were made using a Nicolet 380 FTIR spectrometer and OMNIC^{TM} Series Software (Thermo Fisher Scientific Inc., WI, USA) equipped with a Smart MIRacle^{TM} Single Reflection ATR accessory and a ZnSe crystal plate (PIKE Technologies, Inc., WI, USA). Three absorbance spectra were obtained for each of the 32 plots by analyzing three separate subsamples of the homogenized peat. For each subsample, the average of 32 scans at a 4cm^{-1} resolution over a wavenumber range of 400-4000 cm^{-1} were used to determine an absorbance spectrum, and the three subsamples averaged to obtain a final representative spectrum for the plot. Using OMNIC software, corrections were applied for ATR, atmospheric CO_2 and H_2O, and to the baseline in order to obtain easily comparable spectra. Total C and N content of each sample was measured on a CHNS elemental analyzer (Vario ISOTOPE Cube, Elementar) and used to calculate the ratio of %C to %N.

3.2.3 Statistics and Analysis

Peak absorption intensities were obtained using OMNIC software, excluding peaks below 700 cm^{-1} due to the amount of noise in low wavenumber regions. First and second derivatives of the spectra were used to identify peaks located on the shoulders of larger peaks. Peaks were classified according to Table 3.1. Four different humification indices were calculated: the phenolic index (1515/1030), aromatic index (1632/1030), carboxylic index (1720/1030) and lipid index (2920/1030). The polysaccharide band (1030-1080 cm^{-1}) is used in the indices rather than the broad cellulose band (3340 cm^{-1}) due to other organic components interacting with the broad cellulose band (Boeriu *et al*., 2004). Higher humification indices represent a greater degree of decomposition due to the relative enrichment of recalcitrant components compared to polysaccharides. Spectra were analyzed for differences in individual spectral bands and humification indices between fens, and between heated and control chambers at each fen using a one-way analysis of variance (ANOVA). Linear regression models were used to relate spectral bands and indices to CH_4 fluxes, and the ecosystem respiration (ER) averaged over the 2019 growing season, as well to C:N.

Table 3.1: Classification of FTIR absorbance bands based on the wavenumber (cm^{-1}; inverse wavelength).

Wavenumber (cm^{-1})	Classification	Source
720	Long chain alkanes	Ibarra *et al*., 1996
835	Lignin	Zaccheo *et al*., 2002
900	Cellulose	Kačuráková *et al*., 2000
1030-1080*	Polysaccharides	Cocozza *et al*., 2003; Kačuráková *et al*., 2000; Zaccheo *et al*., 2002
1151	Polysaccharides	Boeriu *et al*., 2004; Kačuráková *et al*., 2000; Zaccheo *et al*., 2002
1265	Lignin backbone	Boeriu *et al*., 2004; Niemeyer *et al*., 1992, Zhou *et al*., 2011
1371	Phenolic (lignin) and aliphatic structures	Boeriu *et al*., 2004, Zhou *et al*., 2011
1426	Carboxylic structures (humic acids)	Boeriu *et al*., 2004
1450	Phenolic (lignin) and aliphatic structures	Zhou *et al*., 2011
1475	Waxes	Niemeyer *et al*., 1992
1515	Lignin backbone	Boeriu *et al*., 2004; Zaccheo *et al*., 2002, Zhou *et al*., 2011
1550	Amide II proteins	Zaccheo *et al*., 2002
1632	Lignin, and aromatic/aliphatic carboxylates	Niemeyer *et al*., 1992; Haberhauer *et al*., 1998
1650	Amide I proteins	Zaccheo *et al*., 2002
1720	Carboxylic acids	Cocozza *et al*., 2003; Niemeyer *et al*., 1992
2853/2922	Fats, waxes, lipids	Niemeyer *et al*., 1992; Zaccheo *et al*., 2002
3340	Cellulose	Ciolacu *et al*., 2011; Cocozza *et al*., 2003

*The polysaccharide band appears at the *Carex* fen at 1070-1080cm^{-1}, and at the *Sphagnum* fen at 1030-1040cm^{-1} due to variation in cellulose components (Kačuráková *et al.*, 2000).

3.3 Results

3.3.1 Peat Composition Between Fens

Both individual FTIR bands and calculated indices differed significantly between the two fen types (Table 3.2; Fig. 3.1). The *Sphagnum* fen had higher absorption intensities in the main cellulose band at 3340 cm^{-1} and its corresponding peak at 900 cm^{-1}, but the *Carex* fen had higher intensities in the two polysaccharide bands at 1151 cm^{-1} and 1030-1080 cm^{-1}. The *Carex* fen had higher intensity of three lignin bands (1632, 1515, and 1450 cm^{-1}) but the three other lignin bands (1371, 1265, and 835 cm^{-1}) were not different between the two fens. Both bands representing amide I and II proteins were higher at the *Carex* fen (1650, 1550 cm^{-1}) as well as one wax marker (1475 cm^{-1}). The *Sphagnum* fen had higher carboxylic acids (1720 cm^{-1}) compared to the *Carex* fen. The *Sphagnum* fen showed higher intra-site variability, with significant block effects present for three different bands (1650 cm^{-1}: $F_{3,12}$= 4.70, P = 0.036; 900 cm^{-1}: $F_{3,12}$= 5.50, P = 0.013; 835 cm^{-1}: $F_{3,12}$= 4.63, P = 0.023). The phenolic and aromatic humification indices were higher in the *Carex* fen, indicating that the peat contained more aromatic compounds and lignin than it did polysaccharides, while the carboxylic and lipid indices were higher in the *Sphagnum* fen. The *Sphagnum* fen had higher C:N (higher % C and lower % N) relative to the *Carex* fen. The *Carex* fen had significantly higher CH_4 fluxes, and slightly higher respiration rates over the growing season than the Sphagnum fen (Fig. 3.2).

Table 3.2: Mean (± standard deviation) band absorbance intensities, indices, and C:N of peat at each fen, with the results of one-way ANOVA tests between components at each fen. Significant results are in bold ($p < 0.05$).

Band (cm^{-1})	***Sphagnum* Fen**	***Carex* Fen**	**F**	**p**
720	0.013 (± 0.004)	0.009 (± 0.001)	9.49	**0.006**
835	0.008 (± 0.004)	0.009 (± 0.001)	0.866	0.364
900	0.010 (± 0.004)	0.008 (± 0.001)	3.35	0.083
1030-1080	0.102 (± 0.013)	0.127 (± 0.021)	15.09	**<0.001**
1151	0.044 (± 0.006)	0.063 (± 0.007)	58.88	**<0.001**
1265	0.033 (± 0.005)	0.036 (± 0.007)	1.089	0.320
1371	0.032 (± 0.005)	0.031 (± 0.003)	0.252	0.620
1426	0.028 (± 0.004)	0.031 (± 0.003)	7.79	**0.01**
1450	0.024 (± 0.004)	0.031 (± 0.003)	32.9	**<0.001**
1475	0.022 (± 0.004)	0.029 (± 0.003)	38.33	**<0.001**
1515	0.019 (± 0.003)	0.034 (± 0.003)	136.59	**<0.001**
1550	0.018 (± 0.004)	0.036 (± 0.003)	220.9	**<0.001**
1632	0.039 (± 0.006)	0.056 (± 0.004)	86.17	**<0.001**
1650	0.034 (± 0.007)	0.052 (± 0.004)	56.23	**<0.001**
1720	0.031 (± 0.006)	0.022 (± 0.002)	35.44	**<0.001**
2853	0.038 (± 0.006)	0.039 (± 0.002)	0.319	0.579
2922	0.052 (± 0.008)	0.052 (± 0.003)	0.061	0.808
3340	0.086 (± 0.013)	0.068 (± 0.005)	28.43	**<0.001**
Index				
Phenolic	0.192 (± 0.024)	0.274 (± 0.052)	30.58	**<0.001**
Aromatic	0.379 (± 0.037)	0.450 (± 0.074)	10.60	**0.004**
Carboxylic	0.308 (± 0.037)	0.182 (± 0.034)	92.82	**<0.001**
Lipid	0.511 (± 0.046)	0.422 (± 0.060)	20.05	**<0.001**
C:N	55.56 (± 1.215)	19.87 (± 0.303)	811.68	**<0.001**
%C	45.37 (± 0.15)	42.20 (± 0.40)	44.54	**<0.001**
%N	0.823 (± 0.018)	2.124 (± 0.019)	2138.8	**<0.001**

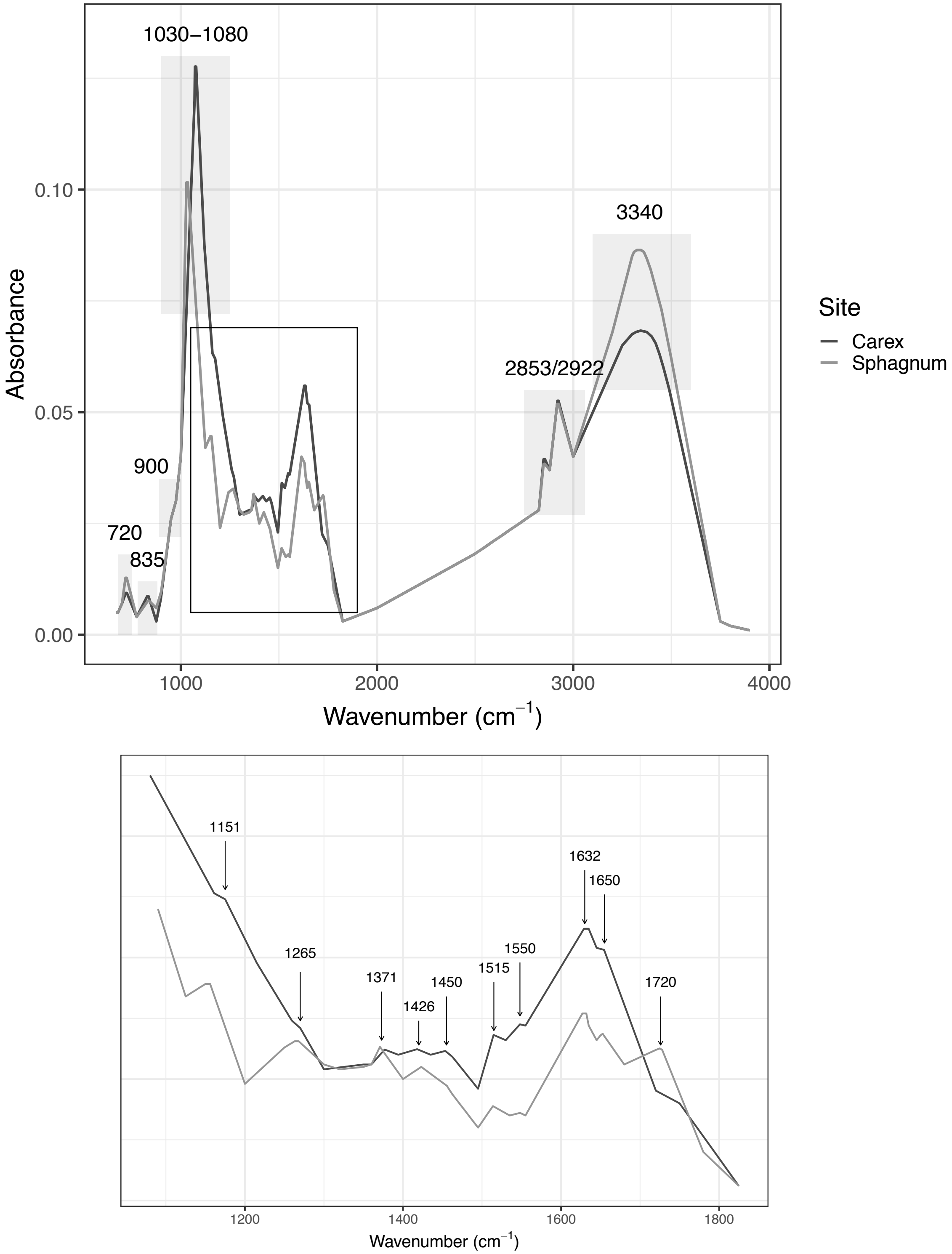

Figure 3.1: Absorbance spectra from Sphagnum and Carex fens, representing the average of all absorption values at each site. Major spectral bands are labelled, and peaks classified according to Table 3.1. The inset provides a closer view of the 1100-800cm^{-1} wavelength region.

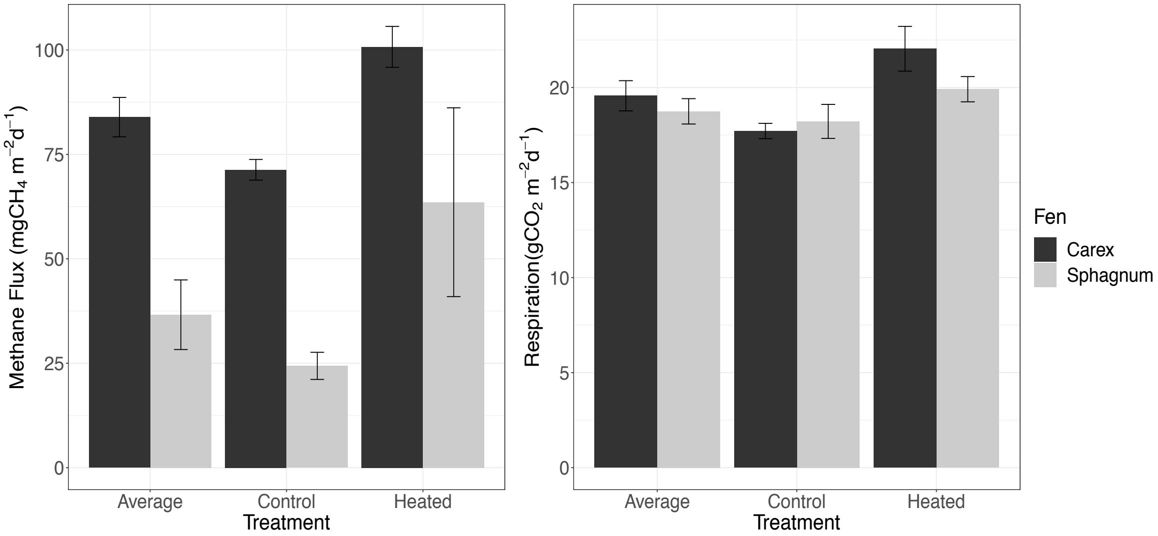

Figure 3.2: Average methane (CH_4) fluxes and ecosystem respiration (ER) from each fen treatment group across the 2019 growing season (June - September). Bars represent seasonal averages ± standard error.

3.3.2 Peat Composition Between Treatments

Both the phenolic and carboxylic humification indices were significantly higher in the heated plots of the *Sphagnum* fen than in the control plots (phenolic: $F_{1,14}$=8.238, p=0.012; carboxylic: $F_{1,14}$=6.981, p=0.019; Fig. 3.3) Aromatic and lipid indices also were higher in heated plots (Fig. 3.3). This is supported by trends observed in individual spectral bands: heated plots had higher amounts of recalcitrant material such as lignin, waxes and lipids, carboxyl groups, and proteins, but contained less labile components of cellulose and polysaccharides (3340 and 1030 cm^{-1}) when compared to the control plots. In the *Carex* fen there were minimal differences between indices or individual bands between heated and control plots, and there were no consistent patterns (Fig. 3.4). C:N ratios and overall percentages of C and N did not differ between treatments at either site. The *Carex* fen had both significantly higher CH_4 fluxes and respiration rates in heated plots compared to control plots; the *Sphagnum* fen had higher CH_4 fluxes in heated plots with no change in respiration rates (Fig. 3.2).

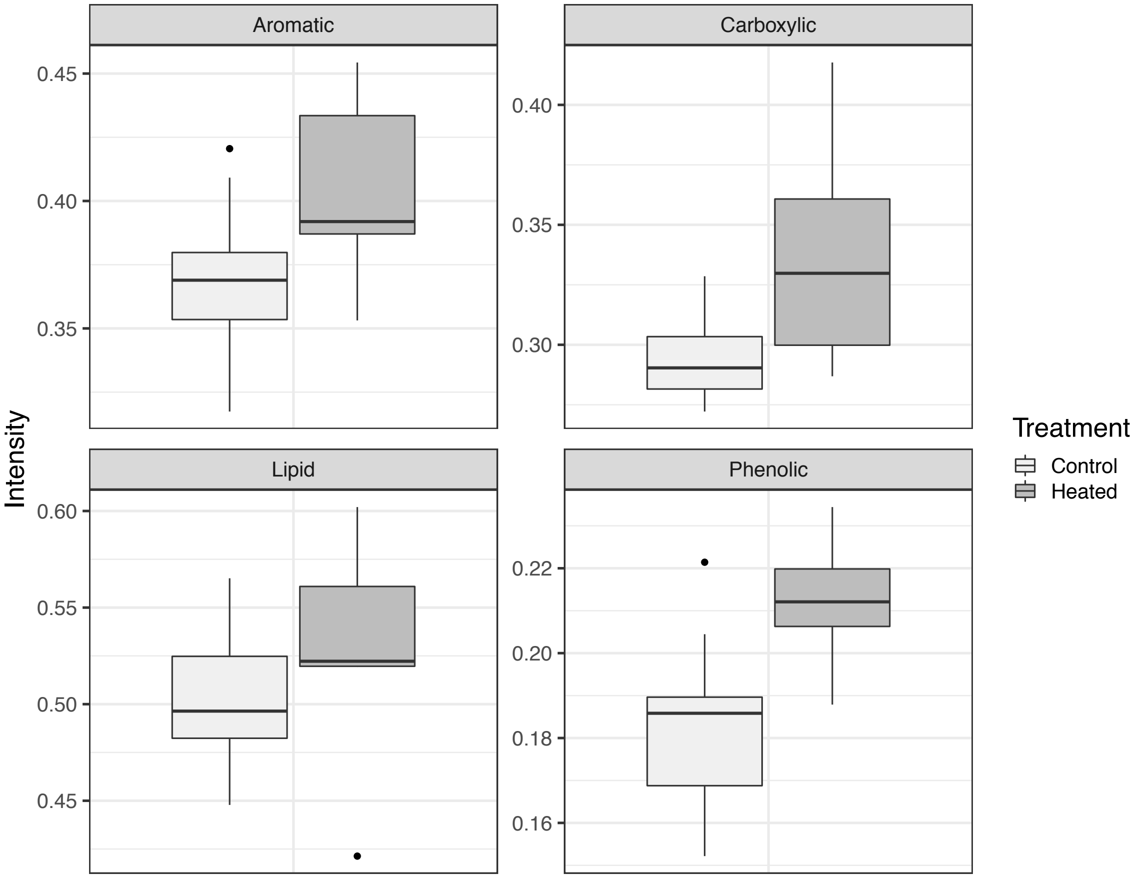

Figure 3.3: Box plot of humification indices at the *Sphagnum* fen between heated (+4 ºC peat temperature) and control plots. A higher index indicates higher proportions of aromatics, carboxylic acids, lipids, or phenolics compared to polysaccharide band absorbance (1030-1080 cm^{-1}).

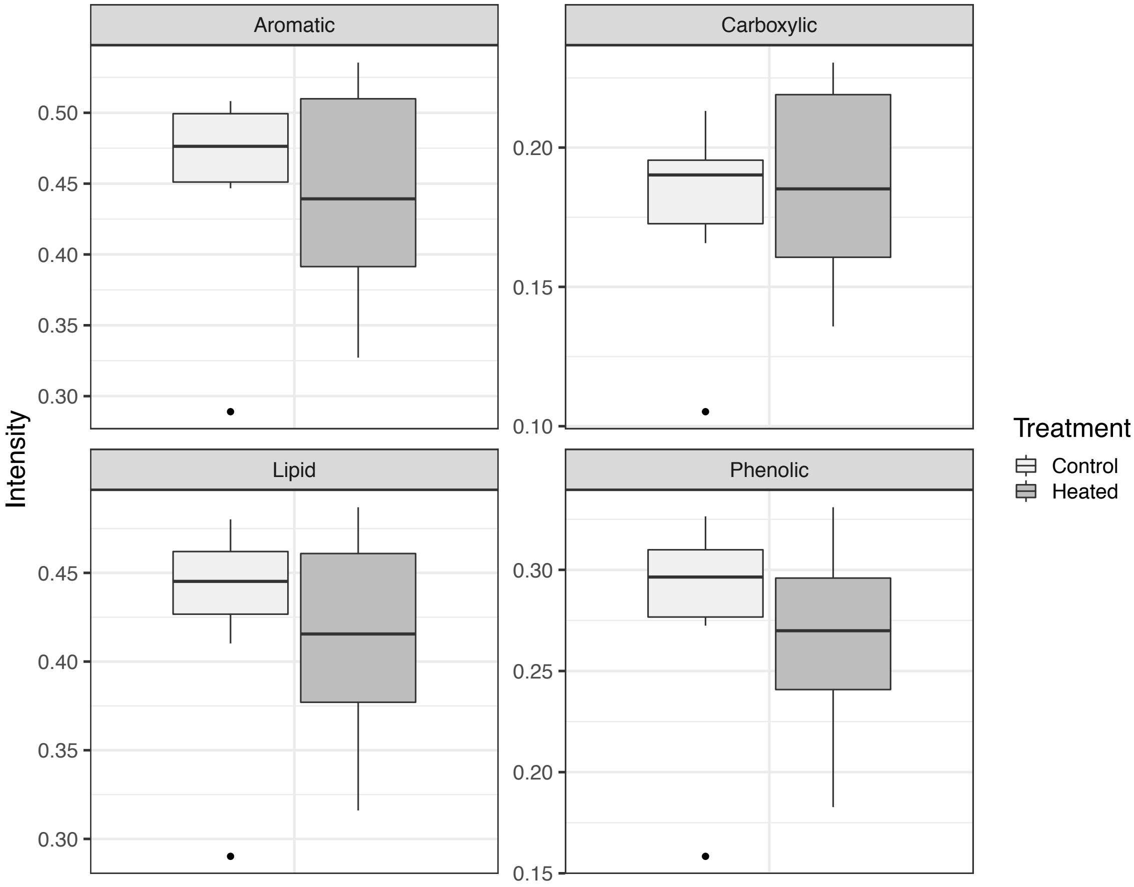

Figure 3.4: Box plot of humification indices at the *Carex* fen between heated and control plots.

3.3.3 Peat Properties and Greenhouse Gas Fluxes

At the *Sphagnum* fen, average growing season CH_4 flux from each plot was positively correlated with bands representing recalcitrant compounds (carboxylic acids, amide II proteins, lignin, and waxes), and with phenolic and carboxylic indices (Table 3.3). However, these relationships were largely driven by a single chamber that had higher CH_4 fluxes and recalcitrant band intensities than the others, and the relationships became insignificant when this chamber was removed from analysis. A negative correlation existed between C:N and CH_4 fluxes ($F_{1, 14}$= 6.96, P = 0.020, R^2 = 0.33; Fig. 3.5), primarily due to %N rather than %C: plots with lower %N produced lower CH_4 fluxes. At the *Carex* fen, no bands or indices were predictors of CH_4 flux.

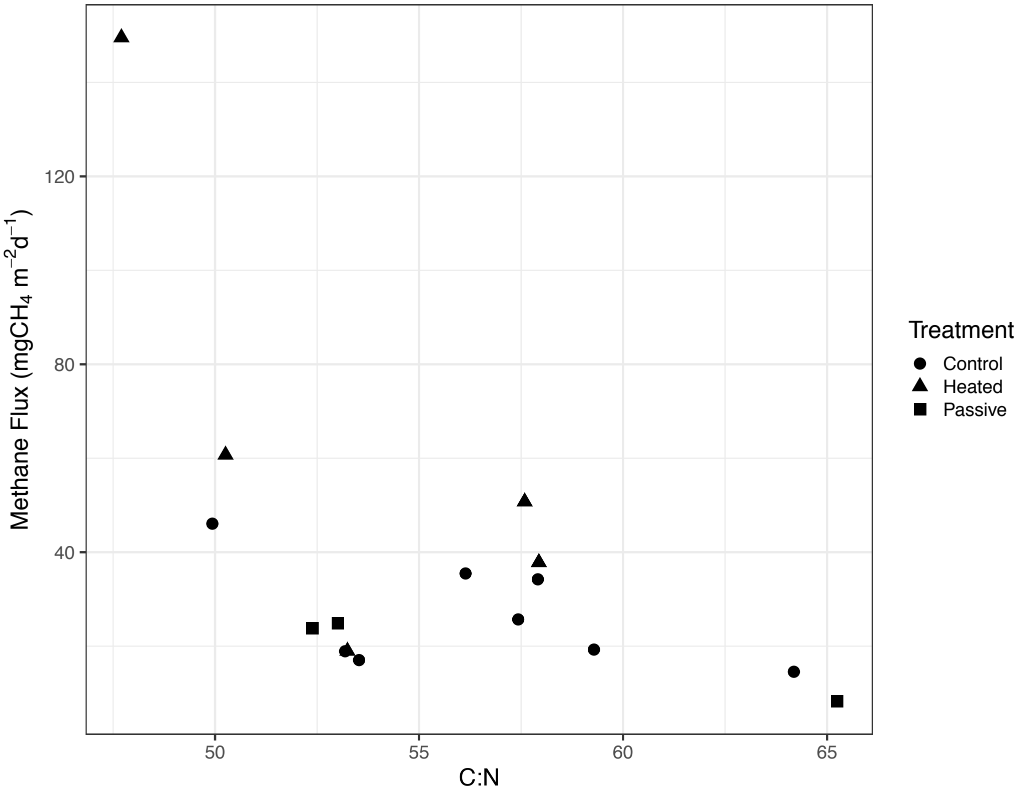

Figure 3.5: Average seasonal methane (CH_4) fluxes vs. C:N ratio at the *Sphagnum* fen at heated, control, and passively warmed chambers. "Passive" chambers represent plots that have had consistent OTCs placed since 2017 but have no active heating system.

Table 3.3: Regression analysis between average seasonal gas fluxes (CH_4 and ER) and select belowground FTIR band intensities at each plot for the *Sphagnum* fen. Unlisted bands and indices have p-values > 0.08. *Carex* fen is not included in this table due to low statistical significance. A "-" sign indicates a negative relationship; all other relationships are positive.

Gas Flux	Band (cm^{-1})	F	P	df	R^2
CH_4	1720	7.043	**0.0189**	1, 14	0.3347
	1550	5.221	**0.0043**	1, 11	0.3219
	1515	4.473	0.0529	1, 14	0.2421
	1475	5.396	**0.0358**	1, 14	0.2782
	Phenolic Index	4.662	**0.0487**	1, 15	0.2498
	Carboxylic Index	10.55	**0.006**	1, 14	0.4297
	C:N (-)	6.957	**0.0195**	1, 14	0.3320
ER	3340	4.109	0.062	1, 14	0.2269
	2922	4.680	**0.048**	1, 14	0.2505
	2850	4.265	0.058	1, 14	0.2335
	1720	8.536	**0.011**	1, 14	**0.3788**
	1650	7.442	**0.021**	1, 10	**0.4267**
	1632	4.588	0.050	1, 14	0.2468
	1515	3.828	0.071	1, 14	0.2147
	1475	5.449	**0.035**	1, 14	0.2802
	1450	3.811	0.071	1, 14	0.2140
	1426	5.474	**0.035**	1, 14	0.2811
	1371	6.657	**0.022**	1, 14	**0.3233**
	1265	5.955	**0.029**	1, 14	0.2984
	1151	6.896	**0.020**	1, 14	**0.3300**
	1030-1080	5.250	**0.038**	1, 14	0.2727

Rates of ecosystem respiration at the *Sphagnum* fen were positively correlated with a number of bands (Table 3.3) but were most related to band intensities of 1720cm^{-1} (carboxylic acids), 1650cm^{-1} (amide I proteins), 1151cm^{-1} (polysaccharides), and 1371cm^{-1} (lignin). No relationships existed between C:N and respiration rates. Again, the *Carex* fen did not have a relationship between spectral bands and respiration rates, but respiration and C:N were negatively correlated primarily due to the %N content rather than %C ($F_{1,12}$= 7.8, *P*= 0.016, R^2= 0.39; Fig. 3.6), contrary to the lack of relationship between C:N and respiration at the *Sphagnum* fen.

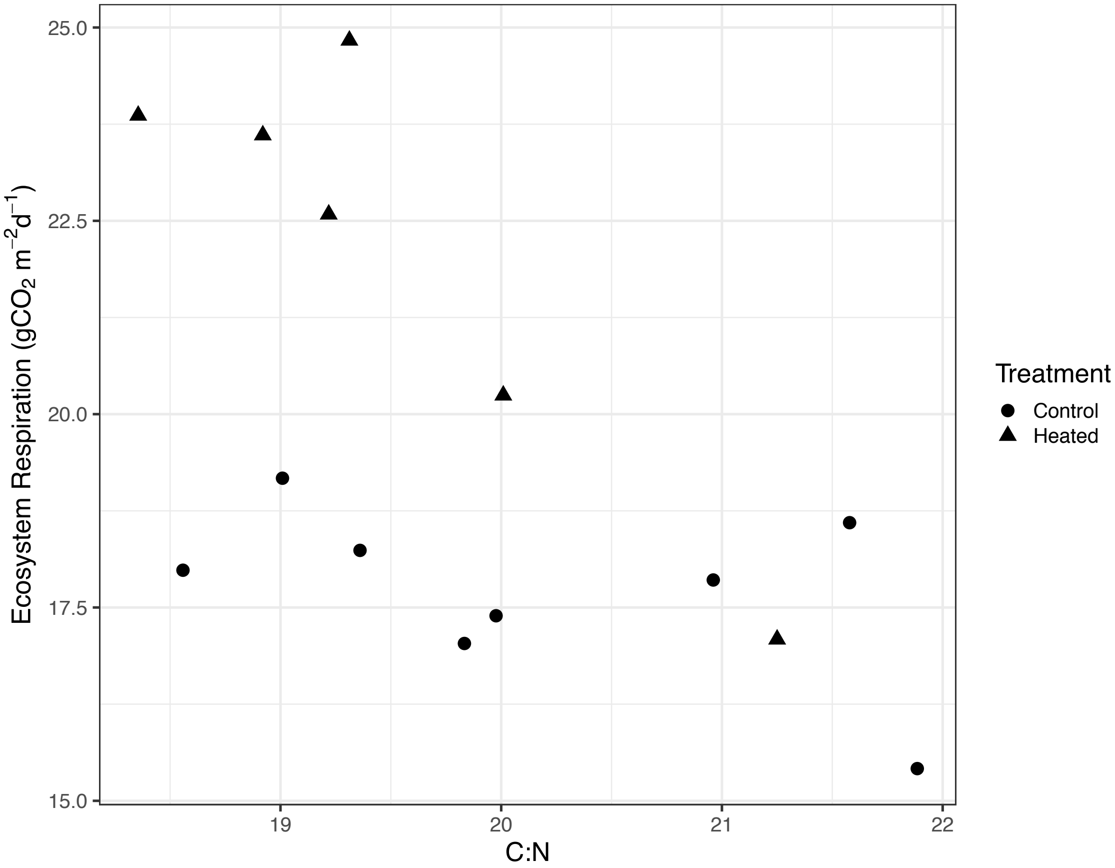

Figure 3.6: Relationship between C:N and ER at the *Carex* fen. Each point represents the average C:N and ER at one plot.

Humification indices were a direct reflection of the C content of each plot, correlating positively with C:N at both sites primarily due to the %C (Fig. 3.7). This relationship held true for both fens, but was only statistically significant at the *Carex* fen (phenolic: $F_{1,12}$= 8.03, P= 0.015, R^2= 0.40; aromatic: $F_{1,12}$= 5.82, P= 0.033, R^2= 0.45; lipid: $F_{1,12}$= 9.84, P= 0.009, R^2= 0.45).

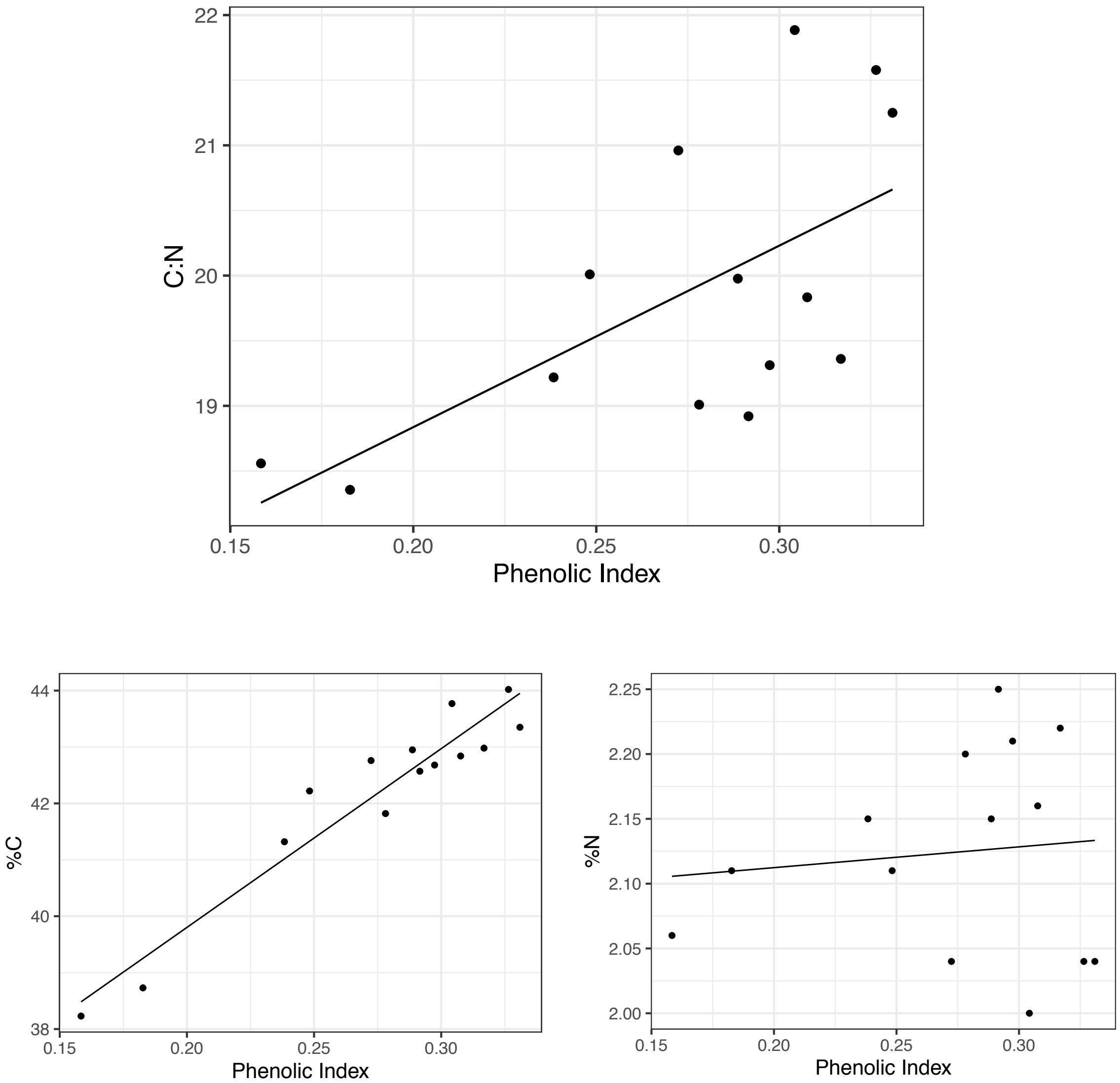

Figure 3.7: Relationship between humification indices and C:N. The phenolic index at the *Carex* fen is used as a representative example, but similar trends exist across all indices and fens. Insets separate the components of %C and %N from the C:N ratio.

3.4 Discussion

Spectral properties of peat reflected the differing degrees of decomposition and peat quality, belowground decomposer communities, and aboveground vegetation found at the two fens. The organic properties found were consistent with previous background FTIR spectral analysis on peat from these same sites by Palozzi & Lindo (2017). Multiple FTIR studies have found that recalcitrant components of peat are enriched as decomposition occurs, resulting in higher amounts of lignin-like molecules, aromatics, and proteinaceous compounds and lower amounts of easily decomposable cellulose and polysaccharide molecules (Artz *et al*., 2008; Biester *et al*., 2014; Zaccheo *et al*., 2002), as well as a lower C:N ratio (Broder *et al*., 2012). More decomposition products, and a lower C:N, were found at the *Carex* fen with peat similar in composition to deeper, more humified peat (Artz *et al*., 2006; Biester *et al*., 2014; Haberhauer *et al*., 1998), while a large portion of "undecomposed" materials and a high C:N were found at the *Sphagnum* fen, consistent with the lower respiration rates measured here. The low %N found at the *Sphagnum* fen compared to the *Carex* fen is consistent with an N-limited environment and "poor" quality peat that limits potential decomposition rates (Aerts *et al*., 2001; Limpens & Berendse, 2003). Spectroscopically derived humification indices can be used as a proxy for peat C content, as they were strongly related.

Aboveground vegetation played an important role in the peat composition and quality at each fen. Despite hosting multiple plant functional groups, the belowground peat composition reflected the dominant functional group; this varied at the plot level, as one sedge-dominated chamber at the *Sphagnum* fen had belowground chemistry and CH_4 fluxes that were more similar to the *Carex* fen. Biester *et al*. (2014) found that higher lignin content in peat was related to more vascular plants, as woody shrubs contain more true lignin than sedges (Dorrepaal *et al*., 2005), and *Sphagnum* mosses do not contain true lignin but rather lignin-like compounds (Dorrepaal *et al*., 2005; Schellekens *et al*., 2012). This pattern is mirrored by N content, with woody shrubs containing high amounts of available N and mosses containing the lowest amount of available N. My results confirm this, with the high-N content and lignin markers in the *Carex* fen reflecting the aboveground dominance of shrubs and sedges. Low amounts of phenolics in the

Sphagnum fen also reflect the belowground decomposer community's ability to degrade these recalcitrant compounds; fungal decomposers, making up the bulk of the decomposer community at the *Sphagnum* fen (Lyons *et al*., 2020), have the ability to degrade lignin and other phenolics unlike the bacterial decomposer community found at the *Carex* fen (Ingwersen *et al*., 2008), although this ability does not result in any tangible increase in decomposition rates. The high amounts of carboxylic acids and lipids at the *Sphagnum* fen can be attributed to the chemical composition of *Sphagnum* mosses, as both are components of Sphagnum cell walls (Eppinga *et al*., 2009; Verhoeven & Liefveld, 1997).

Despite few differences between observed rates of ER at heated vs. control plots, heated plots at the *Sphagnum* had significantly higher amounts of phenolic and carboxylic compounds; contrary to my hypothesis, spectral properties among heated and control plots at the *Carex* fen did not differ. Although heated plots released more CO_2 and CH_4 to the atmosphere, the belowground peat chemistry of heated vs. control plots was indistinguishable, and no relationships existed between spectral bands and C fluxes due to little within-fen variation in peat chemistry. Krumins *et al*. (2012) found that degree of decomposition was related to the proportion of recalcitrant vs. labile spectral bands in heterogenous, slow-decomposing bog peat but fen peat did not have the same relationship, attributed to stable and high decomposition rates. Although baseline rates of ER at the *Carex* fen are not significantly higher than at the *Sphagnum* fen, over time the high amount of labile litter present, as well as less variation in aboveground plant communities, has resulted in a well-decomposed, spatially homogeneous environment. Instead, N availability governed decomposition rates among individual plots, with high-N plots producing more CO_2. The lack of changes in heated plot peat biogeochemistry despite obvious changes in ER and CH_4 fluxes may point to utilization of "new", mobile C from root exudates rather than the "old" solid phase C pool (Kane *et al*., 2014).

In contrast, there were significant differences in belowground C chemistry between *Sphagnum* fen control and heated plots despite no observable change in CO_2 and CH_4 fluxes. Related studies have observed carboxylic acids being degraded as decomposition occurs (Krumins *et al*., 2012), the opposite to what was found here. It is possible that the microbial community was able to begin stimulating the release of acidic compounds from *Sphagnum*, but the process of decomposing recalcitrant *Sphagnum* litter is slow, and thus did not result in any changes in measured decomposition rates. Carboxylic acids in peat have previously been related to more free acid release with humification (Artz *et al*., 2008). As *Sphagnum* is acidic by nature (Verhoeven & Liefveld, 1997), very slight increases in *Sphagnum* litter decomposition with heating could release more organic acids into the soil.

Vascular plant root exudates and lignin in plant litter are the main sources of phenolic compounds in peatlands (Dorrepaal *et al*., 2005; Badri & Vivanco, 2009). Multiple studies have predicted an increase in vascular plant abundance in fens as surface temperatures continue to warm (Dieleman *et al*., 2015; Fenner *et al*., 2007; Mäkiranta *et al*., 2018). Dieleman *et al*. (2016) found that increasing phenolic compound concentrations in porewater was an “early warning” sign of sedge expansion as both root biomass and root exudates contribute to belowground phenolics. As sedges reproduce belowground via rhizomes that spread into new shoots the following spring (Bernard, 1990), one growing season of warming treatment is not likely to increase sedge abundance aboveground at the *Sphagnum* fen: since warming was initiated in June after the plant community was already established, changes in belowground C phenolics could reflect early root expansion with aboveground shoots to follow in the near future. Fine root biomass was likely captured in the solid samples as *Carex* roots extend deep into the soil profile, and the increase in carboxylic acids and phenolics could also reflect increased amino and organic acids through root exudation. Although root exudation releases C compounds into porewater, rapid dissolved organic matter (DOM) sorption onto the solid phase has been observed in soils as organic and amino acids from root exudates form stable complex with metal ions (eg. Al^{3+}, Mn^{2+}, Ca^{2+}) (Jones *et al*., 1994; Jones & Brassington, 1998; Jones & Edwards, 1998). Since sedge expansion is likely proportional to the amount of sedges already present in a plot, it was limited to the heated chambers with a previously established community of these sedges. As FTIR does not distinguish between root exudate-derived and lignin-derived phenolic compounds, an additional explanation for the increase in phenolic compounds seen in *Sphagnum* fen heated plots is the slow decomposition of "old" organic material deep in the peat profile. Small amounts of root exudation as seen in fens with few sedges contribute to positive priming effects (de Graaff *et al.,* 2010; Kuzyakov, 2010), which stimulates decomposition of both newly released root exudates and older peat. This may have resulted in the enrichment of phenolics in *Sphagnum* fen heated plots as older organic material is broken down, leaving recalcitrant lignin behind. This is in contrast to the *Carex* fen, where the high amount of root exudates produced in heated plots may have been enough to cause negative priming effects (de Graaff *et al.,* 2010); newly released root exudates are preferentially decomposed, limiting decomposition of older organic matter and thus resulting in no change between the concentration of phenolics in heated and control plots.

Average global surface temperatures are likely to exceed +1.5 ºC above pre-industrial values by the end of the century (IPCC, 2014), with more extreme temperature increases at northern latitudes. Rising temperatures have consistently been linked to more above-and-belowground vascular plant biomass in peatlands: increased vascular plant litter and root exudation under warming conditions provides additional N to peat, removing the nutrient limitation on vascular plant growth that is typically present in nutrient-poor *Sphagnum* fens (Eppinga *et al*., 2009; Dorrepaal *et al*., 2005). This allows for vascular plants to eventually outcompete *Sphagnum* mosses, as vascular plants have more extensive roots and grow much taller (Eppinga *et al*., 2009; Limpens & Berendse, 2003). As the fungal decomposer community found at the *Sphagnum* fen thrives on low-nutrient peat (Scheffer *et al*., 2001), there is also a possibility that this community will be outcompeted by bacterial decomposers. Early warning signs of vascular plant expansion in nutrient-poor fens occur with moderate degrees of warming in this study, which has significant implications for future C cycling. Shrubs and sedges are known to contribute to higher decomposition and CH_4 production rates due to their labile litter, leading to more greenhouse gases released from vascular-dominated fens; this is supported by the higher rates of ER and CH_4 production at the *Carex* fen, as well as the homogenous, highly decomposed organic peat chemistry. *Sphagnum* fens are particularly critical for C storage as mosses act as a regulator of belowground decomposition rates, allowing peat build-up and directly inhibiting vascular plant growth (Turetsky *et al*., 2012; Verhoeven & Liefveld, 1997; van Breemen, 1995). Changes to aboveground vegetation with warming thus poses the risk of diminishing peatland resiliency and their role as C stores. With early warning signs of both dominant vegetation shift and increasing decomposition visible after just one year of active warming, there is large potential for an eventual shift in peatland types to vascular plant dominated, resulting in the eventual degradation of the large C stores found in *Sphagnum* fens.

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Chapter 4

4 Thesis Synthesis and Conclusions

4.1 The role of fen peatlands in carbon cycling

Peatlands play a continuously important role in removing CO_2 from the dynamic atmospheric pool, regulating Earth's surface temperature by incorporating this potent greenhouse gas into plant matter and storing it belowground. They also act as a large natural source of CH_4 due to the anaerobic environment. A warmer, drier climate and the resulting cascade of changes in vegetation and belowground biogeochemistry introduces uncertainty into the ability of fens to maintain a C sink function. Although differences in C dynamics between peatlands and other wetland types (e.g. swamps), and between bog and fen peatlands has been established in the literature (Bubier *et al.*, 1999; Gong *et al.*, 2013; Heller *et al.*, 2015; Weltzin *et al.*, 2000), the substantial biogeochemical differences between fen types makes them crucial to examine separately as they may differ in their responses to climate change.

I found that direct peat warming (+4 ºC) in a sedge-dominated fen resulted in a rapid increase in CH_4 fluxes, ER, and GEP (Chapter 2). Over a single growing season, GEP increased more than ER which resulted in heated plots sequestering more C than control plots. In contrast, there were few changes in C fluxes at the moss-dominated fen due to a smaller pool of labile soil C and the slow-responding fungal decomposer community. However, the presence of broad-leaf sedge species in some plots contributed to larger CH_4 fluxes and pointed to moss fens acting as a potentially large source of CH_4 to the atmosphere in the future if vascular plant expansion continues.

Soil organic matter composition characterized using FTIR reflected the dominant vegetation type at each fen (Chapter 3). The sedge fen had lower C:N than the moss fen, driven mainly by the higher N found here. Recalcitrant molecules (i.e. lignin, aromatics) were more abundant than labile molecules (cellulose), an organic composition similar to deep, well-decomposed peat. The moss fen, in comparison, had lower N and more abundant labile molecules, similar in composition to poorly decomposed surficial peat. Active heating had little measurable effect on sedge fen peat chemistry in the short-term likely due to rapid utilization of root exudates as a primary nutrient source. Comparatively, FTIR spectra of moss fen peat from the heated treatments indicated higher phenolics and carboxylic acid fractions, indicative of belowground sedge expansion and increased decomposition of older organic material.

4.2 Implications and the trajectory of future peatlands under climate warming

Models predict an eventual weakening of the C sink in peatlands due to increased decomposition and higher CH_4 fluxes (Fan *et al*., 2013; St-Hilaire *et al*., 2010; Wu & Roulet, 2014). An initial increase in photosynthesis has been predicted by multiple models as nutrient cycling is stimulated and an expanded rhizosphere increases peat oxygenation (Green *et al*., 2019; Kane *et al*., 2014; Wu *et al*., 2011; Wu & Roulet, 2014). The relatively higher concentrations of N in sedge fens may further exacerbate this by stimulating further nutrient cycling and plant growth (Bengton *et al*., 2012; Kane *et al*., 2014). However, both fine root biomass and root exudation have been observed to increase with temperature (Bragazza *et al*., 2013; Kane *et al*., 2014; Malhotra *et al*., 2020), which contributes to increased decomposition and CH_4 fluxes through priming effects (Basiliko *et al*., 2012; Dieleman *et al*., 2016; Kuzyakov *et al*., 2007). Priming effects stimulate microbial metabolic activity, and thus ER, through fresh organic matter inputs (Bengton *et al*., 2012; Bragazza *et al*., 2013; de Graaff *et al*, 2010; Kuzyakov *et al*., 2010). This can result in degradation of the deep C stores that are usually kept stable due to a lack of fresh C supply (Fontaine *et al*., 2007), and an eventual weakening of the peatland C sink due to increased losses of CO_2 and CH_4 to the atmosphere. My research provides evidence that the speed at which this occurs depends on the peatland type. Sedges are an important regulator of the belowground environment as they provide labile litter and root exudates to the peat profile (Dorrepaal *et al*, 2005; Jones, 1998; Verhoeven & Toth, 1995), and thus potential CO_2 and CH_4 production in sedge-dominated peatlands are not usually restricted by substrate availability. As microbial activity has long been shown to increase with temperature (Lloyd & Taylor, 1994; Malhotra *et al*., 2020; Stres *et al*., 2008; White *et al*., 2008; Wilson *et al*., 2016), the bacterial decomposer community and *Archaea* at sedge-dominated fens are able to use this labile substrate immediately to fuel ER and CH_4 production upon an increase in peat temperature. Previous studies using passive heating via open top chambers have not observed a response from greenhouse gas fluxes for multiple years after heating was initiated (e.g. Chivers *et al*., 2009; Laine *et al*., 2019; Ward *et al*., 2013), but when the peat profile is heated directly, plant photosynthesis, ER, and CH_4 production all increase within a matter of weeks. This has important implications for future C storage as extreme short-duration heat events have been increasing in frequency since the 1950's (Easterling *et al*., 2000; IPCC, 2014), and the ability of microbes at sedge fens to respond quickly to heating may result in short-term bursts of CO_2 and CH_4 release to the atmosphere. In addition, predicted increases in mean global surface temperatures are only expected to accelerate further throughout the next century (Allen *et al*., 2018; IPCC, 2014), and priming effects from increased root exudation are likely to continue to increase rates of ER.

Since *Sphagnum* provides recalcitrant litter to the soil (van Breeman, 1995; Verhoeven & Toth, 1995), it is conducive to C storage and is considered an ecosystem engineer due to the organic matter buildup that occurs in *Sphagnum*-dominated peatlands. This in turn contributes to peatland resiliency (Turetsky *et al*., 2012), as even direct peat heating had little effect on greenhouse gas fluxes from *Sphagnum* peatlands. Although the presence of *Sphagnum* limits the response of gas fluxes to heating in the short-term, evidence for expanding sedge communities at moss fens could have serious implications for deep C stores. Increased temperatures and the associated reduction in water table has been shown in multiple studies to increase vascular plant cover at the expense of mosses (Dieleman *et al*., 2015; Makiranta *et al*., 2018; Potvin *et al*., 2015; Walker *et al*., 2006). Even small increases in vascular plant productivity can lead to a proportional expansion of their rooting systems (Lindroth *et al*., 2007; Wu *et al*., 2011) leading to a competitive advantage over mosses and eventually outcompeting them for light (Berendse *et al*., 2001; Bragazza *et al*., 2013). Although this occurs at different temperatures based on the peatland location, Dieleman *et al*. (2015) observed a transition from moss-to-sedge communities at peat temperatures between +4 ºC and +8 ºC above ambient. Peat heating at +4.5 ºC above ambient was sufficient in my field experiment to produce phenolic markers of belowground sedge expansion. In following growing seasons, as sedges continue to expand, the fresh labile litter and root exudates provided to the microbial community may begin to remove the substrate constraint on decomposition and CH_4 production at moss peatlands. Evidence of priming effects as seen at the moss fen site may further stimulate decomposition of older organic material as low levels of root exudates are continuously released from the expanding sedge community. As sedges also provide a conduit from CH_4 production zone to atmosphere, these fluxes are also expected to increase. Although *Carex* fens may respond to future warming with steady increases in GEP, ER, and CH_4 production, *Sphagnum* fens could eventually reach a tipping point where vascular plants outcompete mosses and result in degradation of the large belowground C stores, releasing CO_2 and CH_4 to the atmosphere. Although multiple models have examined greenhouse gas fluxes from fens (Gong *et al.*, 2013; Wu *et al.*, 2012; Wu & Roulet, 2014), it is apparent that fens show large variability in how they respond to heating due to the differences in aboveground vegetation community and belowground biogeochemistry. Separating fen types in models is crucial for predicting the future of the C sink in peatlands, as moss-dominated fens take longer to respond to changes in temperature but eventually may become a weaker C sink than sedge fens. The overarching consequence of increased CO_2 and CH_4 release to the atmosphere are the resulting positive feedbacks (IPCC, 2014). If even a small proportion of peatlands cease to act as a major C sink and instead become weak C sources, the resulting excess greenhouse gases in the atmosphere serve to amplify future climate change.

4.3 Limitations and future research

Carbon cycling is a dynamic and multi-system process, with the magnitude of C released to the atmosphere or stored belowground depending on multiple factors. Plant and microbial responses to warming change over time, exacerbated by potential reductions in soil moisture that occur after prolonged heating. Field experiments applying passive open top chamber warming to fens have observed minimal response from vegetation biomass and community composition in the first three to four years of treatment (Laine *et al*., 2019; Peltoniemi *et al*., 2016; Yang *et al*., 2015). Microbial metabolism responds quickly to heating stimulus (Bradford, 2013), but ecosystem-level community structure is slower to adapt and may change the response of the decomposer and methanogen communities over time (Munir & Strack, 2014; Wilson *et al*., 2016). Furthermore, large interannual variation in CO_2 and CH_4 fluxes in peatlands is common, governed by a variety of biotic and abiotic factors from year to year (Moore *et al*., 2011). I observed significant changes in both C fluxes and belowground peat chemistry after just one growing season of active heating, but it is important to note that this study is part of a long-term field experiment. Examining initial responses to warming is crucial as it provides insight on the potential short-term impacts of heating on peatlands: an increased frequency of temperature extremes is expected under climate change (IPCC, 2014), and my results from one year of active heating show that even one anomalously hot growing season has major implications for peatland C storage. However, continuation of this field experiment will simulate longer-term responses to climate change.

Belowground FTIR data analyzed in Chapter 3 represented an end-of-season snapshot of peat composition after four months of active heating had taken place. Microorganisms have been shown to consume the most labile organic matter in decomposition first, followed by more recalcitrant organic matter after the supply of fresh substrate has been depleted (Ingwerson *et al*., 2008; Zaccheo *et al*., 2002); depending on the peatland, this can occur as quickly as two weeks after incubation is initiated (Ingwerson *et al*., 2008). It is possible that unknown changes in the type of organic substrate used and in the rate of utilization occurred in our study, and future measurements should include peat samples taken at multiple time points across the growing season. It is also important that future studies sample peat from a variety of depths as processes at the peat surface (i.e. the top 10cm) differ from processes below the water table. Factors such as soil moisture, microbial biomass, root biomass, and other organic matter are strongly stratified by depth (Artz *et al*., 2008; Urbanova *et al*., 2018), and therefore the effects of warming may present differently at different depths in the peat profile. The ground heating rods used in Chapters 2 and 3 penetrated to 50cm depth, resulting in a consistent degree of heating throughout the peat profile and making a sampling depth of 25cm fairly representative of the peat's response to heating, but sampling from different depths would provide a clearer picture of small-scale processes.

Based on the discernable contrasts between fen types in their response to heating, it is important in future research to include a nutrient-rich fen to examine a full trophic gradient. Previous research on a nearby nutrient-rich fen site revealed significantly higher CH_4 fluxes and methanogen diversity, shallower water tables, higher N content, and greater aboveground biomass (Godin *et al*., 2012; Webster & McLaughlin, 2010). Although the two fen types examined here capture two differing vegetation and belowground communities, the differences between the two in their potential response to climate change highlights the importance of including a wider range of fen types.

4.4 Conclusions

As global temperatures continue to warm, a multitude of impacts to the vegetation and microbial communities are predicted to increase CO_2 and CH_4 released from peatlands with the eventual risk of becoming a C source to the atmosphere rather than their current state as a C sink. While they are often grouped together, fen types differ greatly in their responses to climate warming based on their dominant vegetation type, which in turn influences the belowground biogeochemistry, microbial community, and C storage capabilities. Sedge fens contain abundant labile C and are not restricted by substrate in their response to climate warming, which results in a faster response to warming than initially thought. Moss fens are slower to respond to climate warming as they are limited by available nutrients, but a community shift from moss-to-sedge peatlands could release the large C stores found here, and the resulting positive feedbacks pose a risk of further exacerbating future climate warming.

4.5 References

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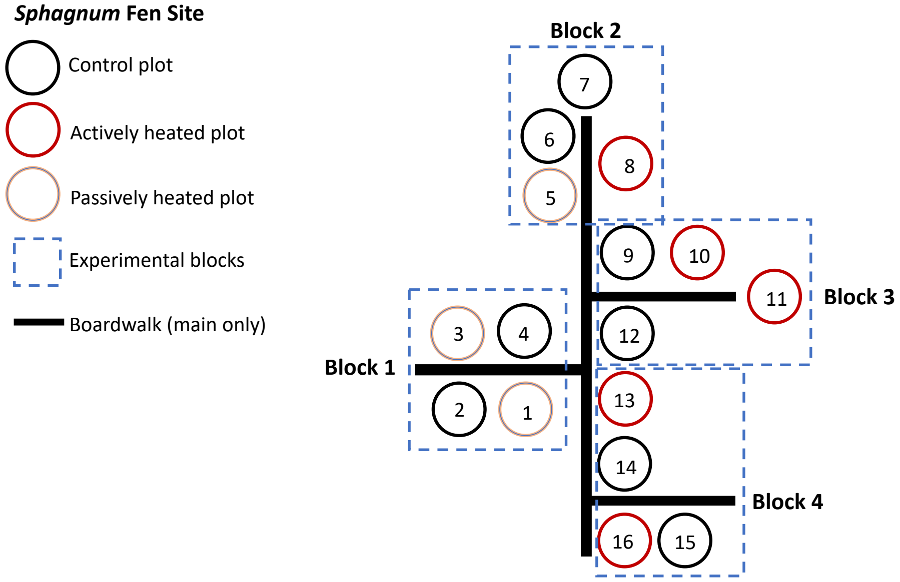
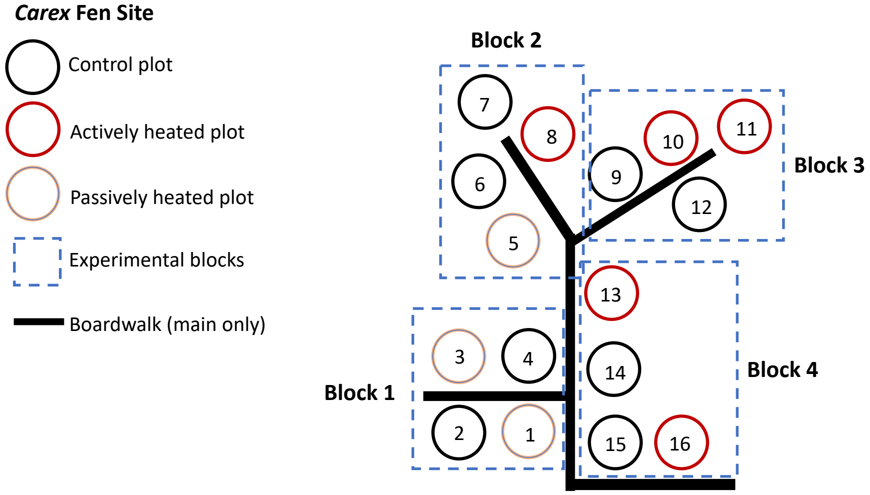
Appendices





Appendix A: Experimental site diagrams illustrating the locations of experimental plots and block configurations.

Curriculum Vitae

Name: Ericka James

Education: University of Western Ontario
MSc Geography, Environment & Sustainability collaborative
London, Ontario, Canada | 2018 - present

University of Alberta
BSc Environmental Earth Sciences
Edmonton, Alberta, Canada | 2013-2017

Awards: Environment & Sustainability Travel Award, $500
University of Western Ontario | 2019

Alexander Rutherford Entrance Scholarship, $2500
University of Alberta | 2013

Teaching Experience: Teaching Assistant
Introduction to Physical Geography, Geography of Canada, and Geography of Hazards.
University of Western Ontario | 2018-2020

Work Experience: Environmental Research Assistant
University of Alberta Centre for Earth Observation Sciences | 2016-2018

Volunteer: Centre for Environment and Sustainability EnviroCon Planning Committee
University of Western Ontario | 2018-2020

P.S. Warren Geological Society Environmental Representative
University of Alberta | 2016-2017

Association of Professional Engineers and Geoscientists of Alberta (APEGA) Student Liaison Committee
University of Alberta | 2015-2016