

The effect of scale on the relative importance of climatic
and biotic variables influencing methane fluxes from an
Arctic wet sedge meadow

by

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Abstract

Methane fluxes (F_{CH_4}) from an Arctic wet sedge meadow at Daring Lake, NT, Canada were examined during the growing seasons of 2008-2017 over several temporal and spatial scales. The largest methane emissions (seasonal averages of 118 - 277 mg $\text{CH}_4 \text{ m}^{-2} \text{ d}^{-1}$) were recorded at the plot scale mid-summer using manual chamber methods and were associated with wetter locations with more sedges. Plot-scale F_{CH_4} were negligible where shrubby peat soils were raised above the water table. Ecosystem-scale F_{CH_4} measured on a quasi-continuous basis employing an eddy covariance technique were roughly 50% of plot-scale F_{CH_4} . Moisture, temperature and vegetation-related variables explained up to 80% of temporal F_{CH_4} variability ($p < 0.001$). Both magnitudes of F_{CH_4} and relationships with driving variables were not consistent between scales and measurement techniques, demonstrating both the importance of scale in deducing all processes influencing F_{CH_4} variability and the difficulties in upscaling F_{CH_4} at this heterogeneous wetland.

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List of Symbols and Abbreviations

Symbol	Definition	Symbol	Definition
C	carbon	OC	organic carbon
¹² C	carbon-12	OM	organic matter
¹³ C	carbon-13	P	atmospheric pressure
$\delta^{13}\text{C}_{\text{CH}_4}$	ratio of stable isotopes ¹³ C/ ¹² C to a standard reference material	PAR	photosynthetically active radiation
$\delta^{13}\text{C}_{\text{CO}_2}$		Pg	petagram
CO ₂	carbon dioxide	POC	particulate organic carbon
CH ₄	methane	ppmv	parts per million volume
DIC	dissolved inorganic C	R	ideal gas constant
DOC	dissolved organic C	SOM	soil organic matter
EC	eddy covariance	SUVA ₂₅₄	specific absorbance at $\lambda = 254$ nm
F _{CH₄}	methane flux	T _{air}	air temperature
F _{CO₂}	carbon dioxide flux	T ₂	soil temperature at 2 cm
H ₂	hydrogen	T ₅	soil temperature at 5 cm
H ₂ O	water	T ₁₀	soil temperature at 10 cm
cm	centimeters	T ₂₀	soil temperature at 20 cm
dx/dt	change in concentration over time	TD	thaw depth
°C	degrees Celsius	TN	total nitrogen
IRGA	infrared gas analyzer	V	chamber volume
LAI	leaf area index	VWC	volumetric water content
NPOC	non-purgeable OC	WMS	Wavelength modulation spectroscopy

1 Chapter: Introduction

Arctic terrestrial ecosystems play a large role in the global carbon (C) budget as permafrost soils contain approximately 1300 Pg of organic C (Hugelius *et al.*, 2014). With one third of the global terrestrial C pool in permafrost affected soils (McGuire *et al.*, 2009; Tarnocai *et al.*, 2009), Arctic terrestrial ecosystems have a great capacity to affect the global C cycle by contributing or mitigating emissions of carbon dioxide (CO₂) or methane (CH₄) to the atmosphere. Past studies have suggested that Arctic terrestrial ecosystems are an overall C sink, but the response of Arctic C dynamics to changes in climate and vegetation is uncertain (McGuire *et al.*, 2009). Shifts in Arctic environmental conditions could affect the balance between vegetation growth and decomposition such that Arctic ecosystems may become net sources of both CO₂ and CH₄ (Alm *et al.*, 1999; Lafleur *et al.*, 2001; Oechel *et al.*, 1995; Waddington & Roulet 1996).

Rising air temperatures in Arctic regions have been reported in recent decades (Chapman & Walsh, 1993; Overpeck *et al.*, 1997; Serreze *et al.*, 2000), demonstrating an enhanced greenhouse effect relative to other parts of the globe, otherwise known as Arctic amplification (Pachauri *et al.*, 2014), which has resulted in several climate-induced shifts in the biophysical environment. These include warmer soils and thawing permafrost (Schuur *et al.*, 2008), changes in winter snow cover (Welker *et al.*, 2000), tree (Danby & Hik, 2007) and shrub (Tape *et al.*, 2006) expansion, and earlier spring snowmelt and lengthening of the growing season (Høye *et al.*, 2007). These changes in ecological and abiotic characteristics influence the C cycle of Arctic environments with the potential to either enhance or mitigate climate change depending on the changes to

the relative rates of ecosystem sequestration vs emission of CO₂ and CH₄ (Pachauri *et al.*, 2014).

Wetlands are important contributors to terrestrial C cycles. They cover about 3% of land surface and contain one third of the global soil organic C (Frolking *et al.*, 2011; Limpens *et al.*, 2008; Page *et al.*, 2011). Arctic wetlands typically store a large amount of organic matter within their deep layers of water-logged peat, which decompose slowly due to cold and anoxic conditions. However, wetlands emit CH₄, a greenhouse gas 28.5 times more potent than CO₂ over a 100-year timeframe (Pachauri *et al.*, 2014). Wetlands account for 30% of global CH₄ emissions to the atmosphere with estimates of 142-208 Tg CH₄ yr⁻¹ between 2000 and 2009 (Kirschke *et al.*, 2013). Of the 500-600 Tg CH₄ emitted annually on a global scale (Dlugokencky *et al.*, 2011), Arctic wetlands alone contribute an estimated 10-150 Tg CH₄ yr⁻¹ (Gao *et al.*, 2013; McGuire *et al.*, 2012; Wik *et al.*, 2016). Wetlands with anaerobic conditions in saturated peat promote high rates of methanogenesis, the microbial production of CH₄ that occurs under reducing conditions (Joabsson *et al.*, 1999). Factors affecting the production, consumption, storage and transport of CH₄ in Arctic wetlands are important to consider when predicting future CH₄ fluxes (F_{CH4}) in a warming and wetting climate. With continued climate change, Arctic wetlands are expected to experience warming and changes in precipitation amount and timing (Houghton *et al.*, 2001). Some wetlands may experience drying due to greater rates of evapotranspiration and drainage due to permafrost thaw (Lafleur, 1993), while other landscapes may become wetter with subsidence of ice-rich permafrost (Jorgensen *et al.*, 2008; Smith *et al.*, 2005), all of which can potentially influence C cycling and CH₄ emissions. Arctic wetlands are likely to change in their structure, composition and

function (Pachauri *et al.*, 2014) and the combined effect of all these changes on CH₄ emissions is uncertain.

The soil-vegetation-climate interactions controlling F_{CH₄} can vary over temporal and spatial scales (Moore *et al.*, 2011; Treat *et al.*, 2007; Turetsky *et al.*, 2014). Comparing F_{CH₄} over multiple temporal and spatial scales can reveal underlying mechanisms that influence CH₄ production, storage and transport. Both emergent F_{CH₄} patterns and processes are necessary to better understand the sensitivity of F_{CH₄} to current and future climate and environmental change. Practically, this will provide insight into the transferability of relationships for predicting change in F_{CH₄} in space and over time. This study will employ the eddy covariance (EC) method and the manual chamber method to assess ecosystem- and plot-scale F_{CH₄} over 3 and 9 growing seasons, respectively within a Southern Arctic wetland at the Daring Lake Tundra Ecosystem Research Station. The main research objectives of this study are:

- 1) To characterize the temporal variability of F_{CH₄} at the Daring Lake wetland site over several growing seasons using both EC and chamber measurements and identify relationships between F_{CH₄} and environmental variables such as temperature, moisture, and vegetation.
- 2) To characterize the spatial variability of F_{CH₄} among plots and within the EC footprint and compare EC and chamber-derived F_{CH₄}.
- 3) To assess if the relationships between F_{CH₄} and environmental variables are similar across different time periods (half hourly, seasonally, interannually) and suggest the mechanisms of F_{CH₄} production, transport and storage that may explain variability in these relationships.

The organization of this thesis is as follows: Chapter 2 describes in detail some of the processes important to F_{CH_4} in the context of similar studies; Chapter 3 outlines the two methods of F_{CH_4} measurement, peat porewater sampling and ancillary measurements; Chapter 4 presents the results of this study; Chapter 5 discusses the processes driving F_{CH_4} based on the evidence and their dependence on scale; and finally the conclusion, Chapter 6, summarizes key considerations when interpreting similar research and predicting future F_{CH_4} from Arctic wetlands.

2 Chapter: Background

2.1 Carbon budgets

The C budget of an ecosystem is a result of the balance between vegetation growth (primary production) and respiration by heterotrophic and autotrophic organisms. Primary production consumes atmospheric CO₂ as it is sequestered through photosynthesis. Carbon is then reduced by plant metabolic processes and is both stored as energy for the plant and provides infrastructure for plant growth. Plant material makes its way into the soil through root growth, plant-animal interactions, and seasonal abscission events and may be stored in the soil as organic matter for short or long periods of time depending on rates of decomposition. Microbial decomposition releases several decomposition products including CH₄, CO₂, dissolved organic carbon (DOC), particulate organic carbon (POC) and dissolved inorganic carbon (DIC) (Davidson & Janssens, 2006). The gaseous exchange of C between the surface and the atmosphere includes fluxes of CO₂ (F_{CO_2}), CH₄ and volatile hydrocarbons, while DOC, DIC and POC represent sub-surface C storage and aquatic fluxes. Conditions that favour the net increase of belowground C over time vs. conditions that promote net losses to the atmosphere are important to identify when quantifying feedback effects of climate change on atmospheric concentrations of C (Pachauri *et al.*, 2014).

Soil organic C accumulates in wetlands through a small but persistent imbalance between vegetation growth and its decomposition (Ström *et al.*, 2003). Soil organic C decomposition is restricted by cold and moist conditions and the presence of permafrost and other protection mechanisms. The highest densities of soil organic C are found in wet boreal and tundra ecosystems (Post *et al.*, 1982). Permafrost soils underlie roughly

24% of exposed land in the Northern hemisphere, where continuous permafrost is dominantly distributed between 66°N and 84°N (Zhang *et al.*, 1999). These frozen soils inhibit decomposition rates of organic material by physically and thermodynamically isolating C.

2.2 Arctic wetlands

Peat accumulating wetlands are wetlands with at least 40 cm of peat and are classified as either bogs or fens, where the influence of groundwater or surface water movement is the primary differentiating property (Warner & Rubec, 1997). Fens are minerotrophic and tend to have a fluctuating water table (WT) due to local groundwater and surface water dynamics, whereas the acidic, nutrient-poor bog water is unaffected by ground or surface water movement (Warner & Rubec, 1997). Peatlands are ecosystems with poorly drained soils and hydrophytic vegetation and that contain biological features adapted for wet conditions (Warner & Rubec, 1997). Arctic plant species suited to peatlands include both hydrophytic vascular plants such as *Carex* spp. (Christensen *et al.*, 1998; Emmerton *et al.*, 2014; Joabsson & Christensen, 2001; Moore & Knowles, 1987; Schimel, 1995), *Eriophorum* spp. (Joabsson & Christensen, 2001; Nordstroem *et al.*, 2000; Schimel, 1995; Ström *et al.*, 2003) and non-vascular plants such as *Sphagnum* spp. and *Polytrichum* spp. (Christensen *et al.*, 1998; Emmerton *et al.*, 2014; Moore & Knowles, 1987; Nordstroem *et al.*, 2000). The presence of certain species is linked to the availability of nutrients. For example, with increasing *Sphagnum* moss coverage, wetlands tend to be more acidic due to the release of organic acids from decomposing *Sphagnum* material (Warner & Rubec, 1997). Vegetation associated with *Sphagnum* dominated wetlands in northern boreal and Arctic wetlands include Cotton grass

(*Eriophorum vaginatum*), ericaceous shrubs (*Kalmia*, *Ledum*, *Chamaedaphne*, *Vaccinium* and *Gaylussacia* spp.) and black spruce (*Picea mariana*) (Batzer & Baldwin, 2012).

Peatlands are typically characterized by microtopographic variation, where individual features are referred to as 'microforms'. These include shallow pools, low-lying, relatively wet and sparsely vegetated lawns, and raised, drier hummocks often densely packed with vascular plants (Sullivan *et al.*, 2008). In permafrost terrain, palsas are also possible. 'Palsa' is a Fennoscandian term that originally describes a raised hummock with a core of ice (Seppälä, 1972). More recently palsas have been defined as peat mounds with alternating layers of segregated ice and peat or mineral soil (ACGR-NRC, 1988). Palsas are often associated with the southern limits of discontinuous permafrost (Seppälä, 2011) due to the insulating property of dry peat, where otherwise conditions are too warm for perpetual ground ice. Palsas form in wet ecosystems and require at least 200-210 days a year with air temperatures below 0°C (Lundqvist, 1962). The segregation of ice into ice lenses (Berteaux *et al.*, 2016) results in heaving of soil and a raised surface. This surface supports plant communities less tolerant of saturated soils such as deciduous shrubs (Ackerman *et al.*, 2017; Myers-Smith *et al.*, 2015). Eventual collapse of the palsas results when moisture or warm air penetrates the ice core (Pissart, 2002), leaving a subsided, water-logged surface. These are known as collapse scars, where the standing dead remains of *Betula* or ericaceous shrubs indicate the former palsa microforms (Zuidhoff & Kolstrup, 2005). Other microforms or patterned ground that may occur in Arctic wetlands include frost or mudboils (Wilson and Humphreys, 2010), and low or

high-centered polygons with ice wedge margins degrading to wet troughs (Becker *et al.*, 2016; Mackay 2000).

Peatlands are a class of wetland where organic matter has accumulated based on geographic location and climatic conditions favouring peat growth over decomposition. Arctic peatlands developed during the Holocene around 8000-10000 years before present (BP) as determined using radiocarbon dating of basal peat (Tarnocai & Zoltai, 1988). Cool and moist conditions after the last deglaciation lead to the initial peat development of Arctic peatlands (Tarnocai, 1978). Peatland development may occur as a result of infilling and/or paludification (Tarnocai & Zoltai, 1988). Peatlands are distinguished by their geomorphology, chemistry, hydrology and vegetation. They may be patchy or extensive, fed by groundwater or perennial snowpack, coastal or within low-lying valleys, on ice wedge polygonal ground or underlain by glacial till (Woo & Young, 2006). Wet meadows in the Arctic are defined as wetlands receiving both overflow and subsurface flow and are thus often mineral rich. Meadows are covered in graminoid species (Woo & Young, 2006). Arctic wet sedge meadows as described by (Bliss and Matveyana, 1992; Christensen *et al.*, 2003; Christensen *et al.*, 1998; Christensen, 2001; Emmerton *et al.*, 2016; Emmerton *et al.*, 2014; Henry, 1998; Joabsson and Christensen, 2001; Joabsson *et al.*, 1999; Johnson *et al.*, 2000; McEwing *et al.*, 2015; Yu *et al.*, 2017) are usually characterized by sufficient peat accumulation to be classified as fens.

Canada contains one third of global peatlands (Rydin, 2006) with 16,000 km² of peatlands within the Arctic and most in the low Arctic (National Wetlands Working Group, 1986). The low Arctic, relative to the high Arctic, is comparatively warm and moist with higher mean annual temperatures, higher density of lakes and ponds (ECG,

2013) and longer growing seasons driven by latitudinal climatic gradients (Billings, 1973). In Canada, the Low Arctic is roughly defined as the region extending across the northern mainland between the Richardson Mountains in the Yukon to Ungava Bay in northern Quebec while the High Arctic includes the Canadian Arctic Archipelago and portions of the northeastern district of Keewatin and northern Quebec (ESWG, 1995). Low Arctic peatlands are abundant in the Mackenzie Delta and Yukon coast due to low lying, poorly drained topography densely packed with lakes (Tarnocai & Zoltai, 1988). On the Canadian shield, where this study takes place, peatlands are most common in the Keewatin district and southern Baffin Island but also occur throughout the region in low-lying areas such as shallow valleys, along drainage pathways, between bedrock outcrops, along the coast, within ponds, lakes or slow-flowing rivers or wherever high water table levels persist long enough for peat development through paludification or terrestrialization (Rydin, 2006). Wetlands and peatlands are scarcer in Canada's high Arctic/Arctic Archipelago due to an arid climate. But shallow peat accumulation occurs in lowlands sometimes fed by perennial snowpack and glacial meltwaters and along the coast (Emmerton *et al.* 2014; Tarnocai & Zoltai, 1988).

2.3 Methane fluxes

Methane fluxes span several orders of magnitude in northern wetlands (Emmerton *et al.*, 2014; Lai *et al.*, 2014; Moore *et al.*, 2011; Smemo & Yayitt, 2006), where wet sedge ecosystems are a dominant CH₄ source with an estimated average of 100 mg CH₄ m⁻²d⁻¹ based on a meta-analysis of subarctic and Arctic sites in Alaska, Russia and Sweden (Vourlitis & Oechel, 1997) (Table 1). The large range in F_{CH₄} reflects the large variability in environmental factors which affect methanogenesis and methanotrophy,

methane storage, and transport (Vourlitis & Oechel, 1997). Some of the environmental factors that correlate strongly with F_{CH_4} are depth to water table (Christensen *et al.* 2000; McEwing *et al.* 2015; Moore & Knowles 1987; Moore *et al.* 2011; Ström & Christensen 2007; Torn & Chapin 1993; Waddington & Roulet, 1996), soil/peat temperature (Christensen *et al.* 1995; Moore *et al.* 2011; Ström *et al.* 2012), vegetation composition (Bubier *et al.*, 1995; Christensen *et al.* 2000; Joabsson & Christensen 2001; Lai *et al.* 2014; Moore *et al.* 2011; Ström *et al.* 2012; Ström & Christensen 2007), net ecosystem exchange (NEE)/gross primary productivity (GPP) (Bubier *et al.*, 1995; Christensen *et al.*, 2000; Christensen *et al.*, 1996; Lai *et al.* 2014; McEwing *et al.* 2015; Ström *et al.* 2015; Waddington *et al.* 1996), and thaw depth (Emmerton *et al.* 2014; Stuartevant & Oechel 2013; Verville *et al.* 2008; Zona *et al.* 2009). However, the degree to which these variables are important depends on the key mechanisms important in limiting or enhancing CH_4 fluxes and the temporal and spatial scale at which these mechanisms are important.

Table 1. Mean, median and ranges for F_{CH₄} from wetlands, bogs, fens and wet sedge meadows. Units are converted to mg CH₄ m⁻² d⁻¹ and rounded to the nearest mg for comparisons across multiple datasets including the current study.

Region	Ecosystem	Method	Range	Mean	Median	Reference
Global	rich fen	chamber	-19 to 1328	93 ± 3	45	<i>Turetsky et al. (2014)</i>
High Arctic	wet sedge	EC	-8 ×10 ⁻¹ to 3	1 ± 2×10 ⁻¹	-	<i>Emmerton et al. (2014)</i>
		chamber	-5×10 ⁻² to 4×10 ⁻¹	2×10 ⁻¹ ± 1×10 ⁻¹	-	
		chamber	n/a	64 ± 2*	-	<i>Strom et al. (2015)</i>
Arctic	wet sedge	chamber	30 to 142 [#]	100	-	<i>Vourlitis & Oechel (1997)</i>
		EC	14 to 26 ^d	21 ± 5	-	<i>Euskirchen et al. (2017)</i>
		EC	-1 to 105	52	-	<i>Friborg et al. (2000)</i>
		chamber	n/a	61	66	<i>Schimel (1995)</i>
		EC	-10 to 166	54 ± 2	53	<i>current</i>
		chamber	-11 to 820	118 ± 3(112** ± 2)	108(98**)	
		chamber	6 to 638	144 ± 16, 70 ± 19***	-	<i>McEwing et al. (2015)</i>
Subarctic	wetland	chamber	-33 to 4114	112 ± 6	68	<i>Turetsky et al. (2014)</i>
	palsa fen	EC	42 to 180	-	-	<i>Hanis et al. (2013)</i>
Temperate	bog	chamber	-2 to >1000	-	-	<i>Moore et al. (2011)</i>
	treed rich fen	EC	0 to 111 ^d	68	-	<i>Long et al. (2010)</i>

^ddaily mean values *2013 mean **weighted mean and median values ***mean values for wet and dry sites, respectively [#]values based on a meta-analysis of 10 publications documenting wet sedge sites across Alaska, Russia and Sweden.

2.3.1 CH₄ production

Methanogenic archaea cannot breakdown complex molecules, and thus require several bacterial communities to supply more easily decomposable substrates (Zinder, 1993). The production of CH₄ begins with the hydrolysis of organic polymers by fermenting bacterial enzymes, producing alcohols, fatty acids and H₂ (Conrad, 1999). These are then further broken down into acetate, H₂ and CO₂; the main substrates required for methanogenesis (Conrad, 1999). CH₄ production is classified based on the reaction substrate, where hydrogenotrophic and acetoclastic methanogenesis require H₂/CO₂ and acetate, respectively.

Acetoclastic methanogenesis, also referred to as acetate cleavage, produces both CO₂ and CH₄. Hydrogenotrophic methanogenesis involves the reduction of CO₂ with H₂ (Krohn *et al.*, 2017). The production of CH₄ can be dominated by either reaction pathway, usually dependent on the amounts of H₂/CO₂, acetate and the unique blend of methanogenic archaea within reducing environments (Kotsyurbenko *et al.*, 2004). Hydrogenotrophic methanogenesis becomes increasingly important relative to acetoclastic methanogenesis with decreasing supply of labile organic matter (OM), such as with depth in the peat/soil profile, where hydrogenotrophic methanogenesis accounts for 50-100% of the total CH₄ production (Chasar *et al.*, 2000; Hornibrook *et al.*, 1997; Nakagawa *et al.*, 2002). The rates of methanogenesis of both pathways can be affected by redox potential, the availability of nutrients, substrates and terminal electron acceptors (Whiticar, 1999) where methanogens can be outcompeted by other bacteria, such as sulphate-reducing bacteria (Whiticar, 1999). Acetate fermentation dominates 70% of methanogenesis in low-sulphate environments, with increasing rates of carbonate

reduction when acetate concentrations are low (Whiticar, 1999). Originating from fresh organic matter, acetate becomes less available with depth in the peat/soil profile (Chasar *et al.*, 2000; Hornibrook *et al.*, 2000) and over time within a growing season (Avery *et al.*, 2003). Methanogenesis is associated with highly reduced conditions, where both pathways are inhibited by redox potentials that are too high (Wang *et al.*, 1993). Methanogenesis generates less energy than the reduction of alternate electron acceptors such as Fe^{3+} , SO_4^{2-} , NO_3^- and Mn^{4+} , and therefore is largely carried out once these electron acceptors have been reduced and sufficient substrate remains (Wang *et al.*, 1993). A soil redox potential of around -150 mV has been shown as the value below which methanogenesis may proceed (Masscheleyn *et al.*, 1993; Wang *et al.*, 1993).

When considering environmental controls on CH_4 production, soil temperature and depth of the water table are the most commonly mentioned variables (Dise *et al.*, 1993; Elberling *et al.*, 2008; Glaser & Chanton, 2009; Ström & Christensen 2007; Torn and Chapin 1993; Waddington *et al.*, 1996). Water table levels largely affect CH_4 production by controlling the location and depth of the anaerobic zone and the extent of the aerobic zone where CH_4 consumption occurs (Moore & Knowles, 1989). Increasing soil temperature increases reaction rates of both CH_4 production and CH_4 consumption (Dunfield *et al.*, 1993). Water table and soil temperature do not always correlate well with F_{CH_4} at the plot-level (Strom *et al.*, 2015; Zhu *et al.*, 2014). The isolation of these variables neglects the influence of substrate availability (Amaral & Knowles, 1994; Bahooin & Jones, 1992; Valentine *et al.*, 1994; Williams & Crawford, 1984) and quality (Schimel, 1995) on CH_4 production rates. Further, Schimel (1995) found that plant community structure that promotes plant-mediated transport, which allows CH_4 to bypass

aerobic zones where methanotrophic microbes consume CH₄ and reduce CH₄ emissions (described further below), was a strong predictor of F_{CH₄}.

2.3.2 CH₄ consumption

Low-affinity methanotrophy is the microbial consumption of CH₄ occurring at CH₄ concentrations higher than 40 ppm (Le Mer & Roger, 2001), and is characteristic of methanogenic ecosystems such as rice fields and wetlands (Le Mer & Roger, 2001). High-affinity oxidation of CH₄, occurring at near-atmospheric (2 ppm) CH₄ concentrations, contributes very little to overall consumption rates (Topp & Pattey, 1997). Methanotrophy can occur both aerobically and anaerobically, although the anaerobic mechanism is reported only for marine sediments (Alperin & Reeburg, 1985) and flooded rice fields (Chowdhury & Dick, 2013; Murase & Kimura, 1994). Variations in F_{CH₄} are sometimes exclusively attributed to variations in methanotrophy (Sass *et al.*, 1990; Schütz *et al.*, 1989), making it an important process to understand when considering CH₄ emissions from Arctic wetlands. Methanotrophy is highly dependent on soil oxygen and CH₄ concentrations (Segers, 1998), therefore in water-logged peat layers this is largely dependent on root respiration; transporting oxygen from the atmosphere to the rhizosphere (Hanson & Hanson, 1996). If the water table is below the surface, or surface soil moisture is low, a large aerobic layer is formed between the water table and the atmosphere. CH₄ travelling towards the surface via diffusion can then be oxidized to CO₂ by methanotrophs before reaching the soil surface. Similar to CH₄ production, CH₄ consumption reaction rates are dependent on soil temperature (Dunfield *et al.*, 1993), although methanotrophy has a wider range of optimal temperatures (Dunfield *et al.*,

1993).

2.3.3 CH₄ transport

CH₄ is transported to the atmosphere via three main pathways; diffusion, ebullition and plant-mediated transport. Diffusion of CH₄ is proportional to the concentration gradient of CH₄ between the peat and the atmosphere, which drives a slow upward movement of CH₄ in soils where CH₄ production exceeds consumption, at least at depth. Diffusion coefficients and subsequently, diffusion rates, are much higher for unsaturated peat layers than those below the WT (Walter & Heimann, 2000). This has to do with differences in molecule size, temperature and pressure of a given substance where dissolved gasses are slower-moving compared to those in gaseous states due to the higher viscosity of liquid (Motinsky, 2011). Ebullition is the release of CH₄ in the form of gas bubbles from deep, anaerobic layers of peat. Methane release as ebullition is comparatively much faster, as fluxes greater than 40 g CH₄ m⁻² can be released in short periods of time (Glaser *et al.*, 2004; Rosenberry *et al.*, 2013). If CH₄ concentrations are supersaturated in peat porewater, the pressure of the CH₄ will exceed hydrostatic pressure and bubbles are formed (Lai, 2009). These bubbles remain within the peat pores until a threshold pressure is reached and they are released to the atmosphere (Lai, 2009). This rapid ejection allows the CH₄ to bypass the methanotrophs within the aerobic zone.

Plant-mediated transport of methane release to the atmosphere has been documented in various Arctic wetlands (Andresen *et al.*, 2017; King *et al.*, 1998; Schimel, 1995; Ström & Christensen, 2012). Methane is transported by aerenchymatous tissues present in some hydrophytic vascular plants. These tissues allow for both diffusion of oxygen to the rhizosphere in water-logged environments and the transport of

CH₄ directly to the atmosphere. Aerenchymatous tissue transport is driven by pressure gradients between the plant and the atmosphere or due to diffusional gradients enhanced by plant respiration (Lai, 2009). Wet sedge meadows, often dominated by *Eriophorum vaginatum*, *E. scheuchzeri* and *Carex aquatilis*, can have enhanced F_{CH₄} due to both plant-mediated transport and plant productivity whereby labile C and substrates are produced at depth and exuded from plant roots. Waddington *et al.* (1996) found that vascular plant transport of CH₄ through aerenchymous tissues was positively correlated to the position of the water table throughout the growing season, suggesting that plant-mediated transport of CH₄ is dependent on high water table levels. The average contribution of plant-mediated CH₄ release is reported as high as 75% of total wetland CH₄ emissions (Schimel, 1995). The effect on F_{CH₄} is highly dependent on plant species type (Joabsson & Christensen, 2002; Schimel, 1995). Plant species that have shown significant effects on overall F_{CH₄} from Arctic wetlands include *Eriophorum* spp. (Frenzel & Rudolph, 1998; King *et al.*, 1998; Ström *et al.*, 2012; Schimel 1995), *Carex aquatilis* (Andresen *et al.*, 2017; King *et al.*, 1998; Schimel, 1995), and *Arctophila fulva* (Andresen *et al.*, 2017). Although plant-mediated methane release can be a dominant pathway for CH₄ release, the overall effect of vascular plant abundance is dependent on the competing process of plant CH₄ consumption. Methanotrophic microorganisms within the plant and in the rhizosphere can oxidize CH₄ before its release to the atmosphere (Bosse and Frenzel, 1997; Gibert and Frenzel, 1995).

2.4 Scale dependence

The relationships between environmental variables and F_{CH₄} can differ when considered at a range of spatial and temporal scales. At large spatial and temporal scales,

such as among ecosystems (Turetsky *et al.*, 2014) or among years (Smemo & Yavitt, 2006), the influence of water table depth is an important control on F_{CH_4} with wetter conditions resulting in greater CH_4 emissions. Over shorter time scales, such as within a single summer season, this relationship is less clear when CH_4 emissions may show hysteresis or even negative correlations with water table depth (Brown *et al.* 2014). At finer spatial scales, such as 1 x 1 m plot-scale measurements at a given site, microtopography (and its close relationship with water table position) and vegetation characteristics are associated with variations in F_{CH_4} (Fox *et al.* 2008; Sachs *et al.* 2010; Wickland *et al.* 2006). A study by Moore *et al.* (2011) examined scale-dependent CH_4 flux relationships at the Mer Bleue bog in eastern Ontario, Canada. Monthly mean F_{CH_4} were highly correlated with peat temperature (within season effect), seasonal means were correlated to water table (interannual effect) and multi-year spatial variation correlated best with vegetation characteristics, followed by peat temperature and water table levels (spatial effect). Moore *et al.* (2011) suggested that the relative importance of these variables is affected by their spatial and temporal range, where large ranges of temperature, water table levels, or vegetation composition explain a greater proportion of variance in F_{CH_4} .

2.5 Methods of measuring F_{CH_4}

Measurements of C fluxes between the surface and the atmosphere are determined using ‘top-down’ and ‘bottom-up’ approaches to the system (McGuire *et al.*, 2009). The ‘top-down’ approach considers the atmospheric concentration of either CO_2 or CH_4 as representative of the dynamic surface it overlies. The ‘bottom-up’ approach measures surface concentrations of CO_2 and CH_4 at micro- and ecosystem scales. These

measurements can be integrated to represent the surface-atmosphere C cycle for various scales of interest (McGuire *et al.*, 2009). The bottom-up approach is often used for C budget studies as it captures the spatial and temporal variation of processes that are driving the C cycle. The most commonly used techniques of measuring site-specific CH₄ fluxes from the ‘bottom-up’ perspective are the eddy covariance method and the chamber method.

Eddy covariance measures vertical turbulent fluxes based on the covariance of vertical wind speed and concentrations of gases of interest. Studies that have examined CH₄ ecosystem-atmosphere exchange in Arctic wetlands have used the eddy covariance technique to measure hectare-sized areas upwind of the towers/masts upon which the measurement systems are installed. These studies have examined wet sedge meadows in the High Arctic (Emmerton *et al.*, 2014), in Alaska (Johnson *et al.*, 2000; Euskirchen *et al.*, 2016), and Greenland (Joabsson & Christensen, 2001; Soegaard & Nordstroem, 1999; Ström *et al.*, 2003; Sullivan *et al.*, 2008). Chamber measurements of F_{CH₄} represent relatively small spatial scales. Chamber measurements F_{CH₄} have also been made in Arctic peatlands (Billings *et al.*, 1982; Christensen *et al.*, 1998; Joabsson & Christensen, 2001; Moore & Knowles 1987; Roulet *et al.*, 2007; Schimel *et al.*, 1995; Ström *et al.*, 2015).

The chamber method encloses a surface and monitors the gas of interest either manually or automatically over a given period of time. Non-steady state chambers are typically closed loop and the concentration change within the volume is proportional to the flux. This is contrasted by the steady state chamber method, where air is passed through the chamber and the difference in CH₄ between the inlet and outlet is monitored. The manual or static chamber technique has been used in many recent studies (Lai *et al.*, 2014; Moore *et al.*, 2011; Ström *et al.*, 2015) where remote field locations restrict the use of on-

site gas analyzers. Instead, discrete samples are collected for analysis later and there is typically no circulation within the chamber between measurements. The plots encompassed by the chambers typically cover 0.05-0.07 m². The non-steady state chamber technique can be criticized due to a lack of spatial representation of an ecosystem and due to ‘chamber effects’ (Mosier, 1990). During the time required to sample a given area, a minimum of 20 minutes, the chamber creates its own microclimate that has a different temperature and humidity than the surrounding area. It affects the gas concentration gradients required to drive F_{CH_4} and it negates the effect of wind turbulence on gas transport (Davidson *et al.*, 2002; Livingston & Hutchinson 1995; Lund *et al.*, 1999). When chambers are not automated, relatively few F_{CH_4} measurements are made and are unable to capture the temporal variability in F_{CH_4} . The discontinuity of temporal and spatial coverage of the chamber method is contrasted by the eddy covariance (EC) method, where vertical wind speed and gas concentrations are measured at high frequency (10 to 20 Hz) and a F_{CH_4} is obtained typically every 30 minutes. The EC method is most applicable when the terrain is flat and homogeneous and extensive such that environmental conditions and the vegetation cover vary little within the area of measurements and beyond (Baldocchi, 2003). The EC technique correlates vertical fluctuations in turbulent wind with fluctuations in gas concentrations and assuming no advection or storage, the surface-atmosphere exchange of the gas is representative of the source/sink strength of an upwind area known as the footprint (Baldocchi, 2003). A systematic bias often presented by the EC method is the underestimation of effluxes at night during low wind speeds and limited atmospheric

turbulence (Aubinet *et al.*, 2000; Baldocchi *et al.*, 2000; Black *et al.*, 1996; Goulden *et al.*, 1996).

Due to the advantages and limitations of both methods, a number of studies have compared EC and chamber F_{CH_4} from different ecosystems, including wetlands (Hendriks *et al.*, 2010; Meijide *et al.*, 2011; Sachs *et al.*, 2010; Schiler-Uijl *et al.*, 2010; Yu *et al.*, 2013). Yu *et al.* (2013) found the seasonal patterns of daily mean F_{CH_4} at an alpine wetland were similar across manual chamber, automated chamber and EC methods. There were also comparable correlations for all methods between hourly mean F_{CH_4} and soil temperature despite differences in diurnal patterns, where continuous chamber F_{CH_4} peaked between 22:00 and 24:00 with peak soil temperature and EC F_{CH_4} peaked around 13:30 with peak solar radiation (Yu *et al.*, 2013).

2.6 Methods to assess other factors influencing F_{CH_4}

There are several below-ground indices that provide insight on CH_4 production pathways, CH_4 transport and OM structure and composition. Peat porewater may be sampled and analysed for DOC, total nitrogen (TN: the sum of organic nitrogen, ammonia, nitrates and nitrites) (Chasar *et al.*, 2000; King *et al.*, 1998; Strack *et al.*, 2006), $SUVA_{254}$ (the specific UV absorbance at a wavelength of 254 nm divided by the concentration of DOC) (Herndon *et al.*, 2015), dissolved CH_4 and CO_2 , and their hydrogen (Chasar *et al.*, 2000; Hornibrook *et al.*, 1997; Whiticar *et al.*, 1986) and C isotope composition (Chasar *et al.*, 2000; Kotsyurbenko *et al.*, 2004). Dissolved organic and inorganic C represent subsurface C reservoirs (Kayranli *et al.*, 2009) along with soil organic matter. Nitrogen is a limiting nutrient to both plant and microbial growth. Therefore, TN can affect primary production and litter quality and can favour growth of

vascular plants over bryophytes (Berendse *et al.*, 2001; Heijmans *et al.*, 2002). The form of nitrogen is also important as nitrate can act as an alternative electron acceptor and limit methanogenesis. $SUVA_{254}$ is a proxy for aromaticity (Weishaar *et al.*, 2003), due to the light absorbance of aromatic compounds. The sp^2 hybridized C-C bonds, those that mix both s and p electron orbitals before sharing electrons, are more abundant in aromatic compounds relative to simpler, long chain C compounds with sp^3 bonds. The sp^2 bonds absorb a higher frequency of radiation (smaller wavelength) than the sp^3 bonds (Peacock *et al.*, 2014). The molecular aromaticity of the DOC is of interest in that lower weights or decreased aromaticity (lower $SUVA_{254}$) typically indicates fresh C, whereas higher $SUVA_{254}$ values are linked to the preferential removal of labile DOC and the associated increase in relative abundance of less labile compounds (Pinney *et al.*, 2000).

The conversion of C from parent organic material to CH_4 or CO_2 and transport to the atmosphere can be tracked using C isotope ratios ($^{13}C/^{12}C$). $\delta^{13}C$ values indicate the difference in $^{13}C/^{12}C$ of the sample to a Cretaceous marine fossil, Pee Dee Belemnite (PDB) equivalent standard used when characterizing isotopic signatures in parts per mil. Most natural C compounds have lighter or negative $\delta^{13}C$ values relative to the PDB standard. Because lighter C is preferentially used in many biological processes, CH_4 signatures are very light. Differences in these isotope signatures can help identify the dominant CH_4 production pathway, the relative rates of methanogenesis and methanotrophy, and CH_4 transport. Methane has a $\delta^{13}C_{CH_4}$ range of -110 ‰ to -50 ‰, with hydrogenotrophic methanogenesis ranging from -110‰ to -60‰ and acetate fermentation from -65‰ to -50‰ (Whiticar, 1999). Reaction pathways can also be differentiated by the ratios of $\delta^{13}C$ values between CO_2 and CH_4 . The difference between

$\delta^{13}\text{C}_{\text{CO}_2}$ and $\delta^{13}\text{C}_{\text{CH}_4}$ is significantly greater for carbonate reduction (49-95‰) than for acetate fermentation (39-58‰) (Whiticar, 1999), the result of different kinetic isotope effects of the two pathways (Mach *et al.*, 2015). For both reaction pathways, molecules with a lighter isotopic weight react and diffuse more rapidly, resulting in an increasing concentration of ^{12}C relative to ^{13}C in microbial decomposition products of CO_2 and CH_4 (Whiticar, 1999). As these reactions continue to occur, there is an ongoing removal of ^{12}C , leaving behind increasingly heavy C molecules. If fresh OM is not continuously introduced belowground, CH_4 and CO_2 isotopic signatures can become ^{13}C enriched, nearing the signatures of the original organic matter (Whiticar, 1999).

Processes of CH_4 transport also result in fractionation where isotopically lighter $^{12}\text{CO}_2$ and $^{12}\text{CH}_4$ are both consumed and transported faster compared to $^{13}\text{CO}_2$ and $^{13}\text{CH}_4$ (Chanton, 2005; Whiticar, 1999). The result is F_{CH_4} and F_{CO_2} with $\delta^{13}\text{C}$ depleted signatures relative to dissolved CH_4 or CO_2 in the porewater. This fractionation occurs for plant-mediated transport, ebullition and diffusion. Chasar *et al.* (2000) found that CH_4 emitted from a mid-latitude, sedge-dominated fen was ^{13}C depleted by 3-8‰ compared to porewater $^{13}\text{C}_{\text{CH}_4}$ whereas a bog site emitted CH_4 that was ^{13}C enriched by 5-8‰ compared to porewater CH_4 . Chasar *et al.* (2000) suggested that these enriched ^{13}C values could be due to decreased transport of CH_4 or increased rates of methanotrophy. Methanotrophs preferentially use lighter CH_4 isotopes, leaving behind ^{13}C enriched CH_4 . Methanotrophy can also result in lighter CO_2 as the ^{13}C of the CH_4 substrate is more

depleted than soil organic matter substrates. The fractionation of both CO₂ and CH₄ are important measures providing insight to rates of CH₄ transport and consumption.

Source $\delta^{13}\text{C}_{\text{CO}_2}$ and $\delta^{13}\text{C}_{\text{CH}_4}$ values can be determined using the ‘Keeling plot’ approach, based on a mass balance calculation using atmospheric and sample gas concentrations and isotope signatures (Keeling 1958; Keeling 1961). The method uses linear regression to solve a 2 member mixing model;

$$\delta^{13}\text{C}_a = c_b(\delta^{13}\text{C}_b - \delta^{13}\text{C}_s)(1/c_a) + \delta^{13}\text{C}_s \quad [\text{Eq. 1}]$$

where c_a , c_b and c_s represent the atmospheric concentration of CO₂ or CH₄, the background concentration of CO₂ or CH₄ and the source concentration of CO₂ or CH₄, respectively (Pataki *et al.*, 2003). Using measurements of atmospheric (from within the chamber enclosure at the end of a flux measurement) and background CO₂ or CH₄ concentrations, the resulting y-intercept ($\delta^{13}\text{C}_s$) is interpreted as the source isotope signature (Pataki *et al.*, 2003). The source isotope signature can then be used to suggest the production pathway of both CH₄ and CO₂, providing insight on possible production, consumption or transport limitations on F_{CH₄}.

3 Chapter: Methods

To characterize the temporal variability of F_{CH_4} at the Daring Lake wetland, measurements were conducted using both the chamber and EC technique over a variety of time periods. To characterize the spatial variability of F_{CH_4} , fluxes and variables were compared among plots (chamber) and by wind direction (EC). Chamber measurements were performed by the author on the same collars (e.g. plots) 8 times over the 2017 growing season, including a 24-hour period in mid-July. Various research assistants and graduate students (Hayne 2009; Vandewint 2010) performed chamber measurements on these and other plots within the fen during the growing seasons of 2008 through 2016 excluding 2011. Environmental variables which were measured at the collars included soil temperature and moisture for all seasons, and thaw depth, vegetation composition and water table depth for the 2017 growing season only. LAI measurements were also performed on five permanent plots along the boardwalk leading to the EC tower from 2008-2017. EC instrumentation measured half-hourly F_{CH_4} during the growing seasons of 2015-2017. Ancillary measurements at the same time step at the EC tower included water table depth, air and soil temperatures, net radiation, upwelling and downwelling photosynthetically active radiation (PAR) and atmospheric humidity. Linear regressions and mixed effect models were used to examine the relationships between F_{CH_4} and the fore mentioned variables. Relationships between F_{CH_4} and environmental variables were compared across multiple scales based on the coefficients resulting from linear regressions and mixed effect models. Temporal scales included diel, seasonal and multi-year periods and spatial scale was compared using the chamber (plot-level) and EC

(ecosystem-level) method. All measurements are described in detail in the following sections.

3.1 Site description

The field site is located at the Daring Lake Tundra Ecosystem Research Station (TERS), which is operated by the Government of Northwest Territories, Department of Environment and Natural Resources. TERS is located within the Southern Arctic ecozone, 300 km north east of Yellowknife and 100 km from the nearest Tłı̄chǫ community, Wekweètì (Figure 1). TERS is a research and monitoring facility established in 1995. The station also holds a tundra science and culture camp for youth in the area every year in August. The camp approaches learning from both scientific and Tłı̄chǫ traditional knowledge perspectives and showcases current Arctic research.

The Daring Lake fen is located at 64.965°N, 111.567°W, approximately 2 km south-east of TERS (Figure 1). The fen is described as a 48 ha Arctic wet sedge meadow and lies at the bottom of a shallow valley between an esker to the north and bedrock outcrops to the south. The fen receives overland and subsurface flow from approximately 1.5 km² of the surrounding area.

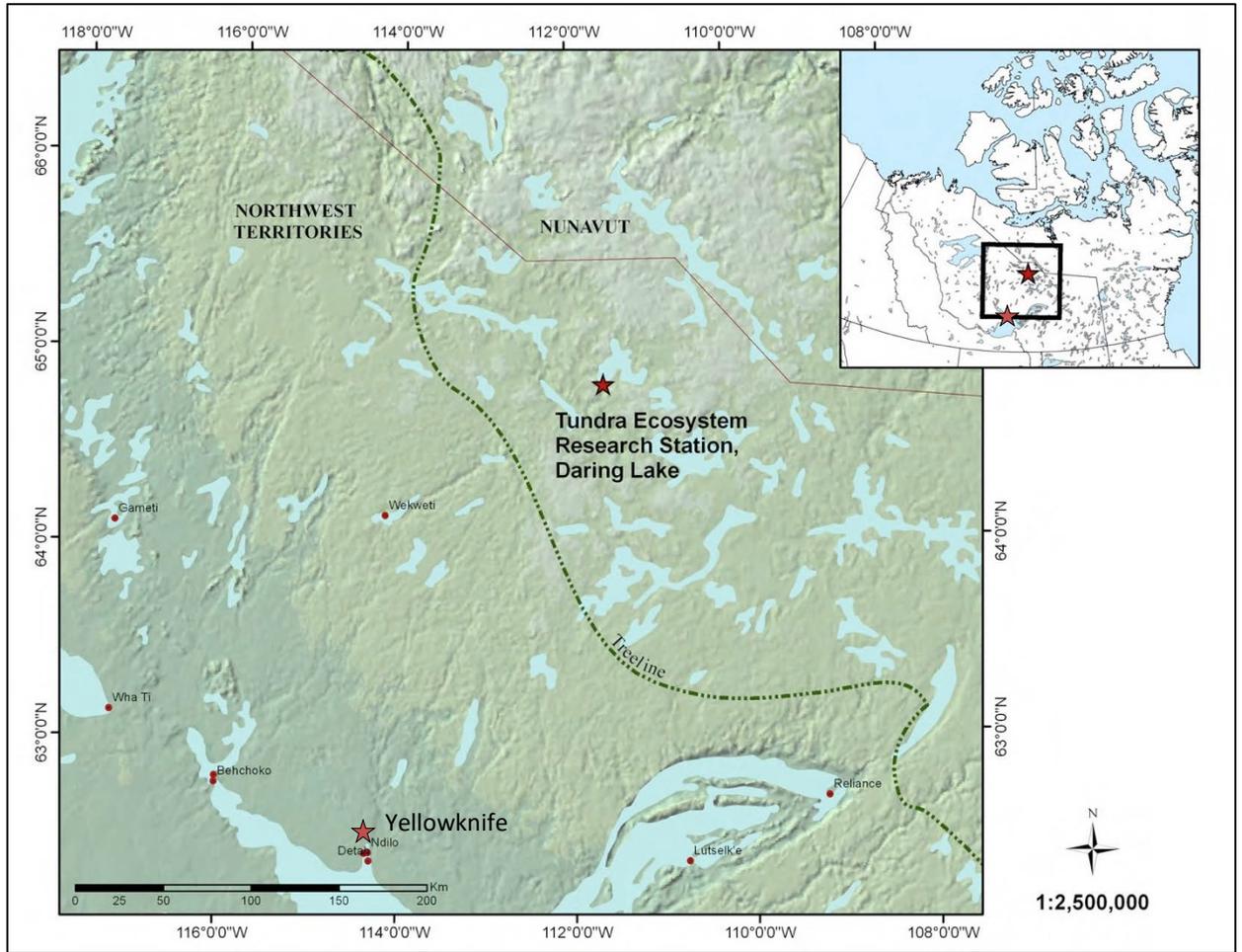


Figure 1. Daring Lake Tundra Ecosystem Research Station location in the Northwest Territories, relative to several Tłı̨chǫ communities and northern Canada (inset).

In the region, continuous permafrost extends to a depth of over 160 m (Dredge *et al.*, 1999). The peat soils in the fen have an active layer of approximately 0.70 m (Humphreys & Lafleur, 2011) while other areas within the valley have active layers ranging from 0.3-1.2 m as a result of varying soil texture, drainage and vegetation characteristics (Dredge *et al.*, 2012). The mineral soil underlying the fen peat is a fine-

textured silty loam while elsewhere in the research valley, soils are coarser with sand and sandy loam textures (Humphreys & Lafleur, 2011).

Using data from the Daring Lake weather station between 1995-2014, mean annual air temperature is -7.9°C , with mean January and July air temperatures of -29.1°C and 13.5°C , respectively. Mean summer precipitation is 141 mm (Skaarup, 2017).

The fen is characterized by different microforms (Figures 2 & 3). The lawns are flat and relatively low-lying, where the peat is almost always completely saturated. *Sphagnum* mosses dominate surface cover with sparse sedge cover. Within the lawns are tussocks, elevated mounds with drier conditions that have resulted in an increased growth of vascular plants such as sedges, bog rosemary and dwarf birch (Figure 3). Within the wetland small palsas, which are approximately 3-35 m wide and up to 70 m long and have peat soils approximately 30-50 cm above the water table due to ice lens development below within the finer-textured silty loam (Figure 4). This drier peat is dominated by *Betula nana*, *Ledum palustre*, *Vaccinium vitis-idea* and *Rubus chamaemorus* along with various sedges, lichen and moss underlain by a shallow active layer (Figure 3). Adjacent to the palsas are areas once populated with birch that have subsided, with dead birch stems and *Sphagnum* moss cover referred to here as ‘collapse scars’ in some locations fully saturated and in others, the surface is still above the water table (Figure 3).

The peat soils of the fen are mainly composed of sedge and *Sphagnum* plant materials (Figure 4), have a relatively low bulk density of $0.04 \pm 0.01 \text{ g cm}^{-3}$ between 0-10 cm (Piquette, 2009), the layer within which the water table usually remains, and a greater bulk density of $0.19 \pm 0.01 \text{ g cm}^{-3}$ for the 10-40 cm layer. The basal date is 1910

± 80 years BP with a long-term C accumulation rate of $17.3 \text{ g C m}^{-2} \text{ yr}^{-1}$ based on radiocarbon dating of a 40 cm peat core (Okolo, 2008).

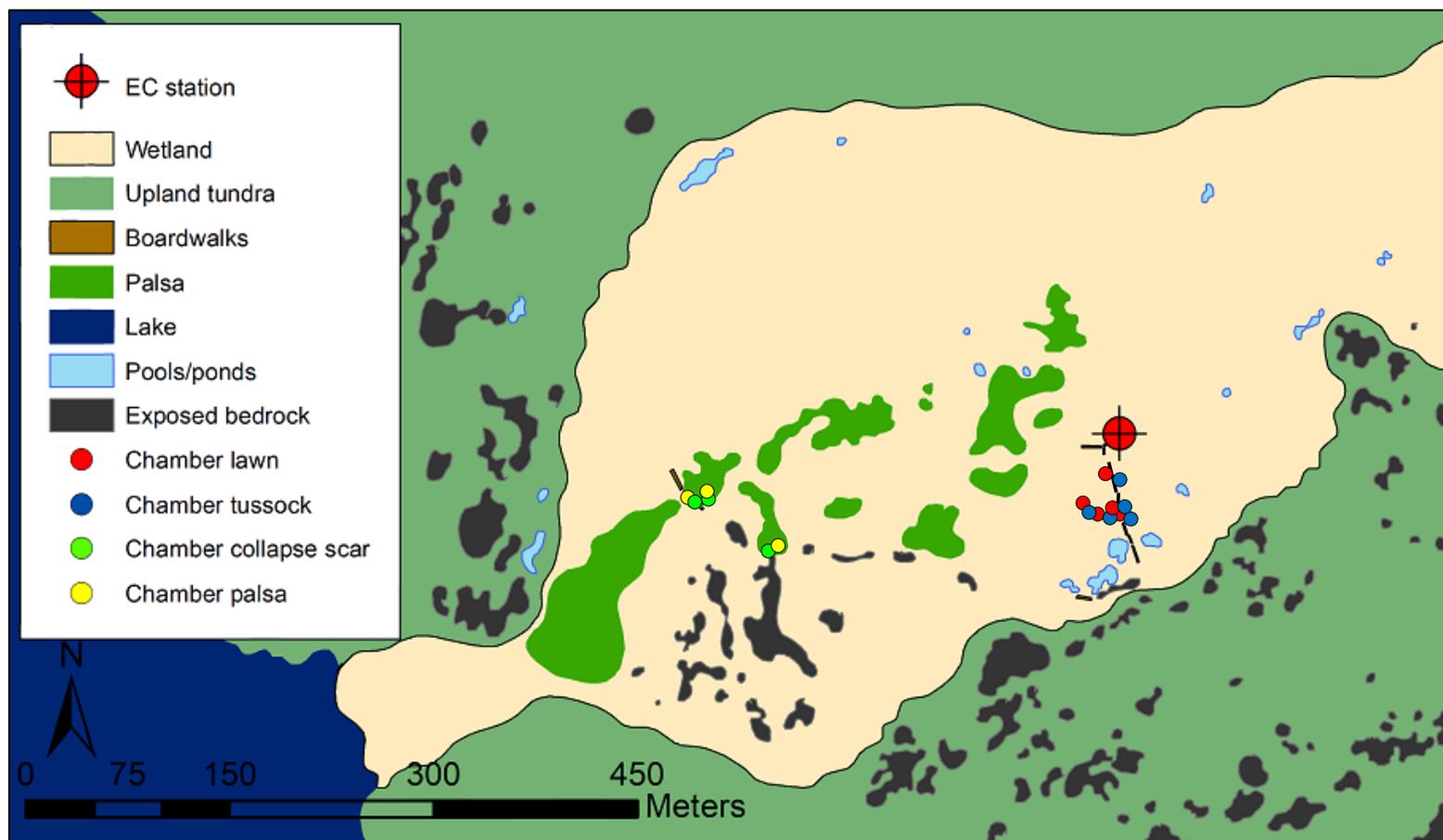


Figure 2. Extent of the wet sedge meadow at Daring Lake with adjacent uplands. The site includes 16 collars for F_{CH_4} measurements; 10 near the EC tower and 6 collars within an area defined by collapse scars and palsas.

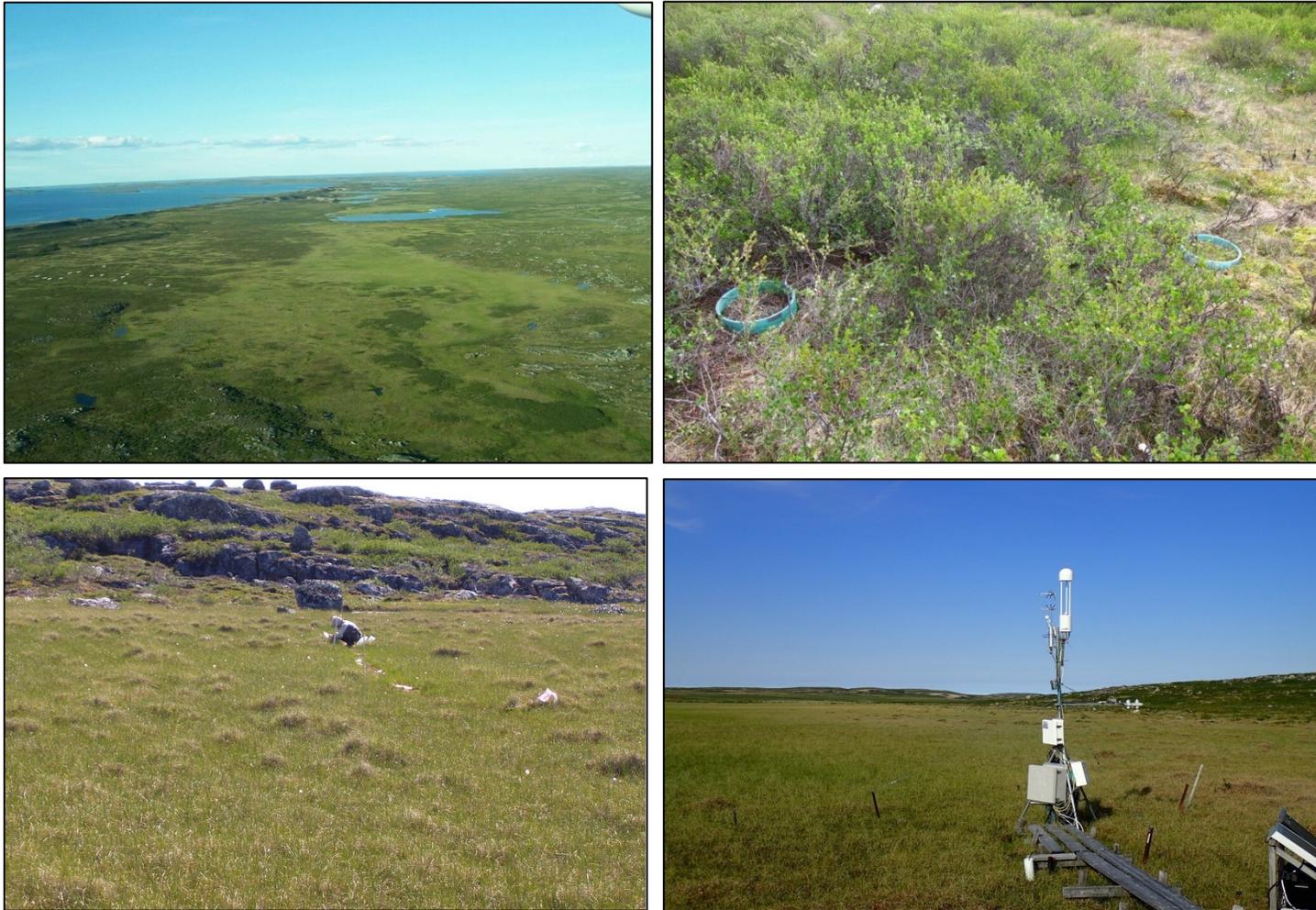


Figure 3. Aerial view of palsas extending across the wet sedge meadow (top left). Palsa and collapse scar features including two collars for F_{CH_4} measurements (top right), EC station looking east (bottom right) and view from the EC tripod looking south toward the lawn and tussock collars (bottom left) (Photos: E. Humphreys).



Figure 4. Peat (0-40 cm) from the area surrounding the EC tower (left) and underlying sediment core from an area defined by palsas and collapse scars (right) with segregated ice lenses (photos: E. Humphreys).

3.2 Chamber measurements

The static non-steady state chamber method was used to measure F_{CH_4} during the growing seasons of 2008-2017. Ten permanent collars were set up at plots characterized by both hummock and lawn microtopography from 2008-2017. Six collars were located to areas characterized by palsas and collapse scar features (2009-2010 and 2015-2017). Although the palsa and collapse scar collars did not all remain at exactly the same locations over all the years, the microform characteristics were relatively consistent within the 4 microform categories. Opaque chambers were sealed to each collar and measured F_{CH_4} over 20-minute periods as described by Wilson and Humphreys (2010). At the beginning of each measurement and every 5 minutes after, air was mixed inside the chamber by pumping an attached 60 mL syringe to ensure a homogenous sample and 24 mL of air was sampled and transferred to an evacuated 12 mL vial. All vials were analyzed on a gas chromatograph equipped with a flame ionization detector (GC-FID) (CP 3800, Varian, CA, USA) at Carleton University's Biometeorology lab. The GC-FID was operated at 300°C with He as the carrier gas at a flow rate of 30 mL min⁻¹. Five standards of increasing CH₄ concentration ranging from 1 to 47 ppm along with He were used to develop the linear relationship between concentration and the integrated area under the chromatogram.



Figure 5. Emma Riley and Caitlyn Proctor perform chamber measurements on lawn and tussock plots (left) and a view of lawn and tussock plots along boardwalks at the main fen area (right).

Chamber F_{CH_4} was calculated using the following equation:

$$F_{CH_4} = \frac{V}{A} \frac{P}{RT} \frac{dx}{dt} \quad [\text{Eq. 2}]$$

where F_{CH_4} in $\text{nmol m}^{-2} \text{s}^{-1}$ is proportional to the rate of change of CH_4 over time (dx/dt). R is the gas constant of $8.314 \text{ J K}^{-1} \text{ mol}^{-1}$, T is the temperature in the chamber in Kelvin approximated using a thermocouple buried 2 cm below the moss surface beside each collar, P is the barometric pressure in Pa measured at the EC station, and V and A are the chamber volume and area of 31.6 cm^3 and 70.2 cm^2 , respectively. The rate of change of CH_4 was determined by the linear regression of five CH_4 concentrations over the 20-minute sampling interval. Up to two anomalous CH_4 concentration were removed from the time series due to sampling or analysis error, precipitation or ebullition events. The rejection of 1 point from a series occurred 32 times and rejection of 2 points from the series occurred twice over 1010 measurements. Regressions with R^2 values of < 0.85 were rejected for quality control purposes except in cases where fluxes were near-zero. Measurements where ebullition or other situations where a single concentration in the time series was inconsistent with a diffusive flux (e.g. non-monotonic relationships), that data point was excluded from the regression analysis. In total 3.4% of the flux measurements were rejected from 1010 measurements. Positive values represent F_{CH_4} losses from the surface whereas negative fluxes represent CH_4 uptake by the ecosystem. To compare results to other studies, F_{CH_4} were converted to $\text{mg CH}_4 \text{ m}^{-2} \text{ d}^{-1}$ or $\text{mg CH}_4 \text{ m}^{-2} \text{ hr}^{-1}$ from $\text{nmol m}^{-2} \text{ s}^{-1}$ using the molecular weight of CH_4 and assuming no diel variation in F_{CH_4} .

For plot-level chamber F_{CH_4} , several environmental variables were measured adjacent to collars, in an area with similar microtopography, vegetation and apparent moisture status.

Soil/peat temperature at 2, 5 and 10 cm depths were read from installed thermocouples using a

digital thermometer (HH91 Portable digital thermocouple, Omega, Laval, QC, Canada). Thaw depth was determined by inserting a 1 cm diameter steel rod vertically into the peat to the depth of resistance. Water table depth (WT) was measured in a well beside each collar using a ‘bubbler’ (a steel tube with plastic tubing in which air was blown until bubbles were heard and the depth to the water surface was noted). The WT measurements were always performed after chamber F_{CH_4} measurements, assuming that the bubbler may introduce CO_2 below the peat surface. Surface volumetric water content (VWC) was measured using a probe (Hydrosense II, Campbell Scientific Inc., Logan, UT, USA) equipped with 20 cm rods inserted vertically into the peat. The default calibration was used and extended linearly on the wet end of the calibration resulting in maximum VWC values of 92%. The Hydrosense II (soil moisture probe) has an accuracy of 3% assuming an electrical conductivity of < 4 dS/m. However, soil moisture measurements are most accurate over space within short time spans. Over multiple years with measurements taken by different people and using an earlier model of the Hydrosense probe, relationships between VWC, period and WT were not consistent. Linear regressions were performed on VWC when greater than 50%, and period readings for each year to gap-fill VWC values when the default calibration range was exceeded. For 2008, VWC and WT did not correlate consistently as VWC values were up to 20% greater than what was possible given the peat bulk density (approximately $0.04 - 0.12$ g cm⁻³) and porosity (approximately 99% - 92%) (calculated using a peat particle density of 1.5 g cm⁻³, measured using a pycnometer by Silins

and Rothwell (1998)). VWC values for 2008 were thus approximated using the linear relationship between WT and VWC from 2009-2017.

3.3 Eddy covariance measurements

The EC instrumentation was mounted on a 2.5 m tripod and consisted of a 3-D sonic anemometer (R3-50, Gill Institute, Lymington, UK), a CO₂/H₂O open-path infrared gas analyzer (LI-7500, LI-COR Inc., Lincoln, NE, USA) and an open-path low-power CH₄ analyzer (LI-7700, LI-COR Inc., Lincoln, NE, USA). The LI-7500 measures CO₂ and H₂O densities using IR spectroscopy, measuring radiation absorbed by CO₂/H₂O molecules and corresponding concentrations. The LI-7700 measures CH₄ densities using Wavelength Modulation Spectroscopy (WMS), where light emitted from the laser is modulated to a frequency of 1.6 μm , corresponding to a methane absorption band (LI-COR, 2011). The resulting signal is demodulated and compared to a reference signal shape to determine CH₄ concentrations (LI-COR Inc., 2011). Wind speed in three dimensions, CH₄, CO₂ and H₂O concentrations were measured at a rate of 10 Hz and stored on a datalogger (CR3000, Campbell Scientific, Logon, UT, USA).

EC-derived F_{CH_4} was measured during the growing seasons of 2015, 2016 and 2017. Mean flux densities of CH₄ were calculated using the EC technique for a 30 min period from the covariance of high frequency vertical velocity and CH₄ density fluctuations (Baldocchi, 2003). Fluctuations were determined as the difference from the 30 min mean after two axis coordinate rotation was applied to account for any sensor tilt. To correct for underestimation of F_{CH_4} due to sensor separation, path averaging and other instrumentation characteristics, high frequency spectral corrections were applied following Massman (2000) and low frequency corrections

following Moncreiff *et al.* (2004)). Corrections to account for thermal expansion and dilution by water vapour were applied to 30-minute means following the equations derived by Webb *et al.* (1980) (LI-COR Inc., 2011). An equivalent pressure was calculated to account for the impact of temperature, pressure and water vapour on spectroscopic measurements (LI-COR Inc., 2011). Friction velocity, a measure of turbulence, was determined using the square root of the covariance of vertical (w) and horizontal (u) wind components as described by Aubinet *et al.* (2012). Fluxes were computed using EddyPro v6.2.1 software package (LI-COR Inc., Lincoln NE).

Measurements of F_{CH_4} were removed from further analyses when the CH_4 open-path sensor windows were obscured (due to rain, dew, dirt, or during manual or automated cleaning intervals indicated when the analyzer's RSSI, relative signal strength indicator, was less than 20), when the CH_4 analyzer or other EC instruments malfunctioned, and during power failures. Friction velocity thresholds of 0.1 m s^{-1} were applied to remove nighttime measurements with insufficient vertical transport of CH_4 . Daily F_{CH_4} values were determined as the mean of all retained F_{CH_4} when there were at least 8 half hour quality measurements available.

3.4 Environmental variables

Environmental variables were measured continuously at a rate of 5 s and stored as 30-minute averages on two dataloggers (CR21X and CR3000, Campbell Scientific) on the fen tripod. Water table depth was recorded continuously using a float and potentiometer apparatus relative to the peat surface until 2014, after which a pressure level sensor (OTT PLS, OTT Hydromet, Kempton, Germany) was used. Soil temperatures at 5, 10, 20 and 40 cm depths were measured using copper-constantan thermocouples and soil moisture was measured using two

probes (CS616, Campbell Scientific, Edmonton, Canada) (Lafleur & Humphreys, 2008). Upwelling and downwelling PAR were measured using quantum sensors (LI-190SA, LI-COR Inc., Lincoln, NB, USA), 4-component net radiation was measured using solarimeters and pyrgeometers (CNR1, Kipp & Zonen, Delft, The Netherlands), while air temperature and humidity was measured using an HMP45C probe (VaisalaOyj, Helsinki, Finland). Atmospheric pressure and wind speed were measured using a barometer (PTB101B, Vaisala Oyj, Helsinki, Finland) and anemometer and vane (Wind Monitor, R.M. Young, Traverse City, IM, USA), respectively at a weather station approximately 560 m to the NW (Lafleur & Humphreys, 2008).

3.5 Porewater sampling

Porewater samples were taken at three depths at four hummock and four lawn plots 3 times throughout the 2017 growing season. A sipper was constructed using a hollow 0.5 cm diameter steel tube with inlet holes at the bottom 5 cm of the rod. The sipper was inserted into the peat at 5-10, 15-20, 30-35 and 40-45 cm below the surface. A 60 mL Luer-Lok syringe and three-way stopcock was used to withdraw 60 mL of pore water, which was discarded before sampling 25 mL of pore water. The syringe was then filled with 35 mL of ambient air and shaken for two minutes to equilibrate the dissolved gases with the headspace air. The air was stored in an evacuated 100 mL Wheaton serum bottle and later analyzed for CH₄ and CH₄ isotopic signatures described below. The pore water was filtered through a 0.45 µm filter and kept cool until later analysis of DOC, SUVA₂₅₄, and TN.

3.5.1 Dissolved Organic Carbon

Porewater samples were analyzed for TN, DOC and specific UV absorbance (SUVA₂₅₄). Porewater samples of approximately 20 mL were filtered using vacuum filtration with a 0.45 µm

filter paper. They were then acidified with 1M HCl to a pH of 2-3. DOC was measured as ‘non-purgeable’ organic carbon (NPOC) on a total organic carbon analyzer (Schimadzu TOC-5000A, Schimadzu, Kyoto, Japan) at McGill University. After purging inorganic carbon fractions, OC was combusted to CO₂ and its concentration determined using IR absorption spectroscopy. The samples were then run individually on a UV-Vis spectrophotometer (Cary 60, Agilent, Santa Clara, CA).

3.5.2 Dissolved CH₄ and δ¹³C

Dissolved CH₄ concentrations were determined using a GC-FID/TCD (GC-2010, Shimadzu, Kyoto, Japan) with a 30 m capillary column (Carboxen PLOT 1010, Supelco, Bellefonte, PA). The GC was calibrated with certified CH₄ standards of 5, 1000, 10000 and 50000 ppm. δ¹³C was determined using a ¹³C-CH₄ analyzer (G2201i, Picarro Inc., CA, USA). Samples were first analyzed for dissolved CH₄ on the GC and then diluted using high purity synthetic air (Air Liquide). Sample aliquots of 20 mL were then injected into the G2201i within 1-3 days. These analyses were carried out at the University of Münster by the Ecohydrology and Biogeochemistry Group.

3.6 Vegetation survey

Vegetation characteristics were monitored during the growing season. Leaf area index (LAI) measurements were made using the point frame method (Wilson, 1959) and a handheld plant canopy analyzer (LAI-2200C, LI-COR Inc., Lincoln, NE, USA) at 5 plots on a transect south of the EC station. LAI measurements were taken weekly over the course of seven weeks from late June to August. The point frame method uses a 50 × 50 cm frame with interlacing fishing line to form 25 equal sized 4 x 4 cm grids. The frame was suspended above the

vegetation surface using four bamboo sticks marking the four corners of each plot. At each grid intersection, a thin wire pin was dropped to the surface. The number of times individual species touched the pin was recorded for each plot. A measure of leaf area for each species was calculated based on the number of hits and the plot area. The LAI-2200C calculates LAI from above and below canopy measurements of incoming radiation detected by a fisheye optical sensor. A light scattering correction was applied to each LAI value based on open sky measurements to account for the proportion of radiation not absorbed by the vegetation, which particularly important under direct sun (LI-COR Inc., 2016).

At each flux collar, percent cover was estimated for each species coverage by eye. The percentages were broken down into three broad categories; vascular, non-vascular and sedges.

3.7 Data Analysis

Statistical analysis was performed using R (R 3.3.2, The R Foundation for Statistical Computing, 2016). Each chamber plot was characterized during the 2017 growing season and was used to investigate factors influencing spatial and temporal variations in chamber F_{CH_4} using linear mixed effect models with categorical variables (microform), vegetation characteristics (% cover *Carex* /*Eriophorum* spp.) and environmental variables (air/peat temperature, VWC, WT and thaw depth). Over all years, spatial and temporal variations in chamber F_{CH_4} were analyzed using multiple linear regressions. Logarithmic transformations to F_{CH_4} were applied when necessary to meet the assumptions of parametric tests. When F_{CH_4} included negative values, F_{CH_4} were translated before transformation based on minimum values. To investigate spatial effects, models were performed using values from all plots and then with plots separated by microform. To isolate the spatial components driving F_{CH_4} variability, a model was run with values averaged

by microform. To investigate the temporal effects on F_{CH_4} variability, data were investigated over multiple years and included year and microform as fixed effects when all data were combined. Repeat measures at a given location were accounted for by setting collar as a random effect.

Regression trees and principle component analysis (PCA) were used to identify the variables associated with spatial and temporal variations in 2017 chamber F_{CH_4} using ‘rpart’ and ‘party’ packages for tree construction and design, respectively (R, R Core Team, 2016). Default settings in rpart [v. 4.1-13] were used. CART is a non-parametric analysis that splits data using recursive partitioning. CART analyzes the divisions in explanatory variables that best reduces variance in the response variable (Lawrence & Wright, 2001). The result is a hierarchical tree where each branch is defined by the conditions that will likely produce certain response variable values based on the dataset. The results of the CART were then compared with a principle components analysis (PCA) and multiple linear regression models.

The EC footprint determines the surface area measured by the gas analyzer and is defined as the contribution of each surficial feature to the vertical flux (Aubinet *et al.*, 2012). The distance of the footprint from the tower depends on atmospheric stability and surface roughness, where unstable conditions and increased turbulence results in shorter distances (Aubinet *et al.*, 2012). An analysis of the EC flux footprint was performed following Kljun *et al.* (2004) in EddyPro v6.2.1. The 70% cumulative flux distance sometimes extended beyond 150 m from the EC tower. These F_{CH_4} data points as well as those when the distance was greater than 115 m in the SE direction were filtered as they extended beyond the wetland. The 70% cumulative flux distance and peak flux distance were plotted using a circular plot frame, so that these values could be visualized relative to the EC tower. They were then compared to a simplified vegetation

map of the wetland and the surrounding area. Using the same plot and map, F_{CH_4} and wind direction were plotted when air temperature was greater than $15^{\circ}C$ to relate source area to F_{CH_4} during relatively warm periods (and to remove the potential bias of early growing season F_{CH_4} when plants were still developing and soil thaw was minimal).

4 Chapter: Results

4.1 Spatial variability in F_{CH_4}

The microforms differed considerably in their vegetation, edaphic and microclimate characteristics and F_{CH_4} (Figure 6, Table 1). The palsas were much drier with no WT above the frost table through the growing season and near-zero F_{CH_4} . There was less soil thaw at the palsa locations despite warmer near surface peat soil temperatures. Collapse scars had comparable VWC, thaw depth and WT values to tussock plots while mean F_{CH_4} were substantially lower for all years. Collapse scars also had the lowest percent cover of both vascular plants and sedges, and highest percent cover of *Sphagnum*. Lawns had the highest WT, VWC and largest mean F_{CH_4} from both the 2017 growing season and all years combined. Temperatures at all depths were relatively consistent between lawns and tussocks, with similar thaw at lawns and tussock plots with differences in depth reflecting the ~5 – 10 cm difference in tussock surface height relative to lawns. Details of F_{CH_4} from each year are given in Appendix A.

At the ecosystem scale, EC F_{CH_4} was roughly half the magnitude of emissions observed at lawns and tussocks and similar at times to collapse scar F_{CH_4} (Figure 6). In 2017, daily mean EC F_{CH_4} (± 1 standard error, SE) on the dates chamber measurements were made was 52 ± 4 $\text{nmol m}^{-2} \text{s}^{-1}$. In all three years on all dates when EC F_{CH_4} were available in July and August, mean daily EC F_{CH_4} was 39 ± 1 $\text{nmol m}^{-2} \text{s}^{-1}$ (54 ± 2 $\text{mg CH}_4 \text{ m}^{-2} \text{ day}^{-1}$). In 2016, average May and June EC F_{CH_4} was 13 ± 2 $\text{nmol m}^{-2} \text{s}^{-1}$ (18 ± 2 $\text{mg CH}_4 \text{ m}^{-2} \text{ day}^{-1}$) and 28 ± 2 $\text{nmol m}^{-2} \text{s}^{-1}$ (39 ± 2 $\text{mg CH}_4 \text{ m}^{-2} \text{ day}^{-1}$), respectively.

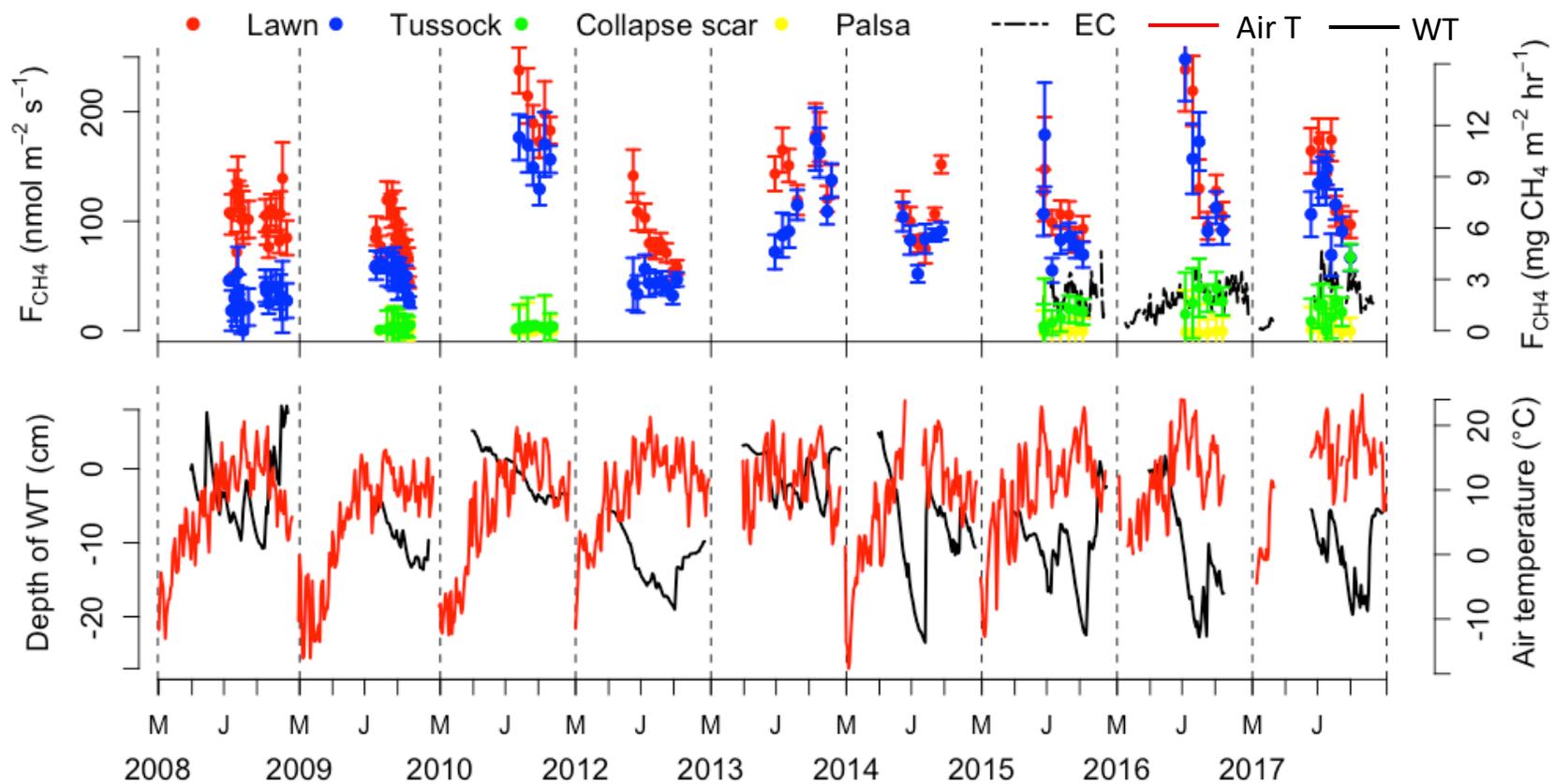


Figure 6. Mean daily F_{CH_4} measured using chamber and eddy covariance techniques (top panel) and WT relative to the lawn surface and air temperature (bottom panel) from May-September, 2008-2017 (excluding 2011). May and July are indicated as ‘M’ and ‘J’ on the x-axis. Each chamber F_{CH_4} point is the mean of 3–5 daytime chamber measurements depending on microform and year. Daily EC F_{CH_4} are averaged on days with at least 8 half hourly measurements that met quality criteria. Short gaps of 5 days or less are linearly interpolated.

Table 2. Chamber F_{CH_4} , vegetation and environmental characteristics classified by lawn, tussock, collapse scar and palsa microform. Median and/or mean ± 1 standard error are from 8 sampling days during the 2017 growing season and 5 collars each for lawn and tussock microforms and 3 collars each for collapse scars and palsas. Over the 9 years, 408, 404, 63, and 63 F_{CH_4} measurements were used to compute means for the lawn, tussock, collapse scar, and palsa microforms, respectively.

	Lawns	Tussocks	Collapse scar	Palsa
Median, mean 2008 – 2017 F_{CH_4} ($nmol\ m^{-2}\ s^{-1}$)	105, 118 \pm 4	64, 77 \pm 5	1, 10 \pm 2	0, 0 \pm 0
Median, mean 2017 F_{CH_4} ($nmol\ m^{-2}\ s^{-1}$)	130, 141 \pm 10	96, 112 \pm 10	2, 20 \pm 7	0, 2 \pm 2
0-20 cm VWC (%)	86 \pm 0	61 \pm 2	63 \pm 2	34 \pm 2
WT (cm)	-7 \pm 1	-19 \pm 1	-14 \pm 2	n/a
thaw depth (cm)	41 \pm 1	47 \pm 1	48 \pm 3	38 \pm 2
T _{2cm} ($^{\circ}C$)	13 \pm 1	13 \pm 1	17 \pm 1	20 \pm 1
T _{5cm} ($^{\circ}C$)	11 \pm 1	11 \pm 0	13 \pm 1	14 \pm 1
T _{10cm} ($^{\circ}C$)	10 \pm 0	10 \pm 0	9 \pm 1	8 \pm 1
Vascular plant cover (%)	34 \pm 4	54 \pm 6	12 \pm 9	49 \pm 14
<i>Carex/Eriophorum</i> spp. cover (%)	30 \pm 9	38 \pm 4	12 \pm 4	20 \pm 10
<i>Andromeda polifolia</i> cover (%)	3 \pm 2	15 \pm 2	n/a	n/a
<i>Sphagnum</i> spp. cover (%)	66 \pm 4	46 \pm 6	88 \pm 9	47 \pm 12
0-10 cm bulk density ($g\ soil\ cm^{-3}$)*	0.04 \pm 0.01	0.04 \pm 0.01	0.08 \pm 0.04	0.08 \pm 0.01
12-40 cm bulk density ($g\ soil\ cm^{-3}$)#	0.19 \pm 0.01	0.19 \pm 0.01	n/a	n/a
pH [^]	5.0 \pm 0.1	4.9 \pm 0.1	4.9 \pm 0.1	4.9 \pm 0.01

The following variables are not from the exact 2017 collar locations: *Bulk density values taken from analyses by Piquette (2009).

#Bulk density values taken from analyses of a 40-cm peat core overlain by lawn and tussock microforms by Okolo (Figure 3 in 2008).

[^]6 samples/microform (A Sarno, personal communication).

Spatial trends in F_{CH_4} were investigated using plot-level measurements (Table 2) and mixed linear models (with collar as a random effect) over the 2017 growing season. With all plots combined, microform, specifically lawns and tussocks, explained 75% of the variance in F_{CH_4} along with VWC (Table 3). Within the lawn plots, 5-cm soil temperature, percent cover of *Carex/Eriophorum* spp. and VWC explained 61% of F_{CH_4} variability (Table 3, Figure 7). For collapse scar plots, although there is an apparent effect of percent cover of *Carex/Eriophorum* spp. (Figure 7), the use of a mixed effect model resulted in significant coefficients for VWC and 10-cm soil temperature only. This model explained 81% of the variance of F_{CH_4} for collapse scar plots (Table 3). For tussock plots, thaw depth alone explained 28% of F_{CH_4} variability. None of the measured variables were significant for palsa plot F_{CH_4} .

PCA was run with four components based on the eigenvalues of each component, where a fifth did not significantly increase the proportion of variance explained. The first principle component (PC1) explained 30% of the variance within the dataset, where the loadings indicated an increase in F_{CH_4} with a simultaneous increase in VWC and PC2 explained 28% of the variance within the dataset and loadings indicated an increase in F_{CH_4} with increasing percent cover of *Carex/Eriophorum* spp. Loadings on PC3 and PC4 explained less than 25% of the variance within the dataset and did not have obvious relationships with any of the variables.

According to the biplot created with PCA loadings, F_{CH_4} correlated most with VWC followed by percent cover of *Carex/Eriophorum* spp. These interpretations were based on the size and direction of the loadings, where arrows of greater length and of similar direction

represent a strong positive correlation. Microform clustered on the biplot due to the strength of these relationships in lawn and tussock plots relative to palsa and collapse scar plots (Figure 8).

The results from the CART were somewhat similar to those of PCA, where microform and VWC were both important in determining differences in chamber F_{CH_4} . Percent cover of *Carex/Eriophorum* spp. was not a resultant variable within the tree, likely as percent cover of *Carex/Eriophorum* spp. was statistically significant as an explanatory variable across lawn plots only (Figure 9). Soil temperature (10 cm) and thaw depth also did not appear within the tree (Figure 9).

For the 9-year record of chamber F_{CH_4} with all plots combined, 78% of the variability in log transformed F_{CH_4} was described using a linear mixed effect model with collar as a random effect and microform, specifically lawn, tussock and palsa, year, 2-cm soil temperature and VWC as fixed effects (Table 3).

Table 3. Linear mixed effect models describing significant spatial and temporal trends in F_{CH_4} both among and between lawn, tussock, collapse scar and palsa plots. T_5 and T_{10} are 5 and 10 cm soil temperatures, VWC is soil moisture, TD is thaw depth, %Carex is the percent cover of *Carex/Eriophorum spp.*, WT is water table, and lawn, tussock and collapse scars are referred to in equations as the fixed effects of each microform. Collar is set as a random effect in each model with the exception of the model for the 2017 seasonal means where microform was not set as a fixed effect in order to highlight abiotic and biotic variable effects.

Year	Plot type	Equation	R^2	p	RMSE
All	All	$\text{Log}(F_{CH_4}) = 1.7(\text{Lawn}) + 1.5(\text{Tussock}) - 0.5(\text{Palsa}) + 0.03(\text{Year}) + 0.01(T_{10}) + 0.01(\text{VWC}) - 69 \text{ nmol m}^{-2} \text{ s}^{-1}$	0.76	<0.001	0.4
2017	All	$F_{CH_4} = 116(\text{Lawn}) + 84(\text{Tussock}) + 0.6(\text{VWC}) - 12 \text{ nmol m}^{-2} \text{ s}^{-1}$	0.75	<0.001	34
	Lawn	$F_{CH_4} = 7.8(T_5) + 3.8(\% \text{Carex}) + 1.7(\text{VWC}) - 178 \text{ nmol m}^{-2} \text{ s}^{-1}$	0.61	<0.001	31
	Tussock	$F_{CH_4} = -2.9(\text{TD}) + 238 \text{ nmol m}^{-2} \text{ s}^{-1}$	0.28	<0.01	32
	Collapse scar	$\text{Log}(F_{CH_4}) = -0.3(T_{10}) - 0.1(\text{VWC}) + 9 \text{ nmol m}^{-2} \text{ s}^{-1}$	0.81	<0.001	0.7
	Mean microform	$F_{CH_4} = 3.4(\text{WT}) + 3.1(\% \text{Carex}) - 4.2(\text{TD}) + 249 \text{ nmol m}^{-2} \text{ s}^{-1}$	0.77	<0.001	23

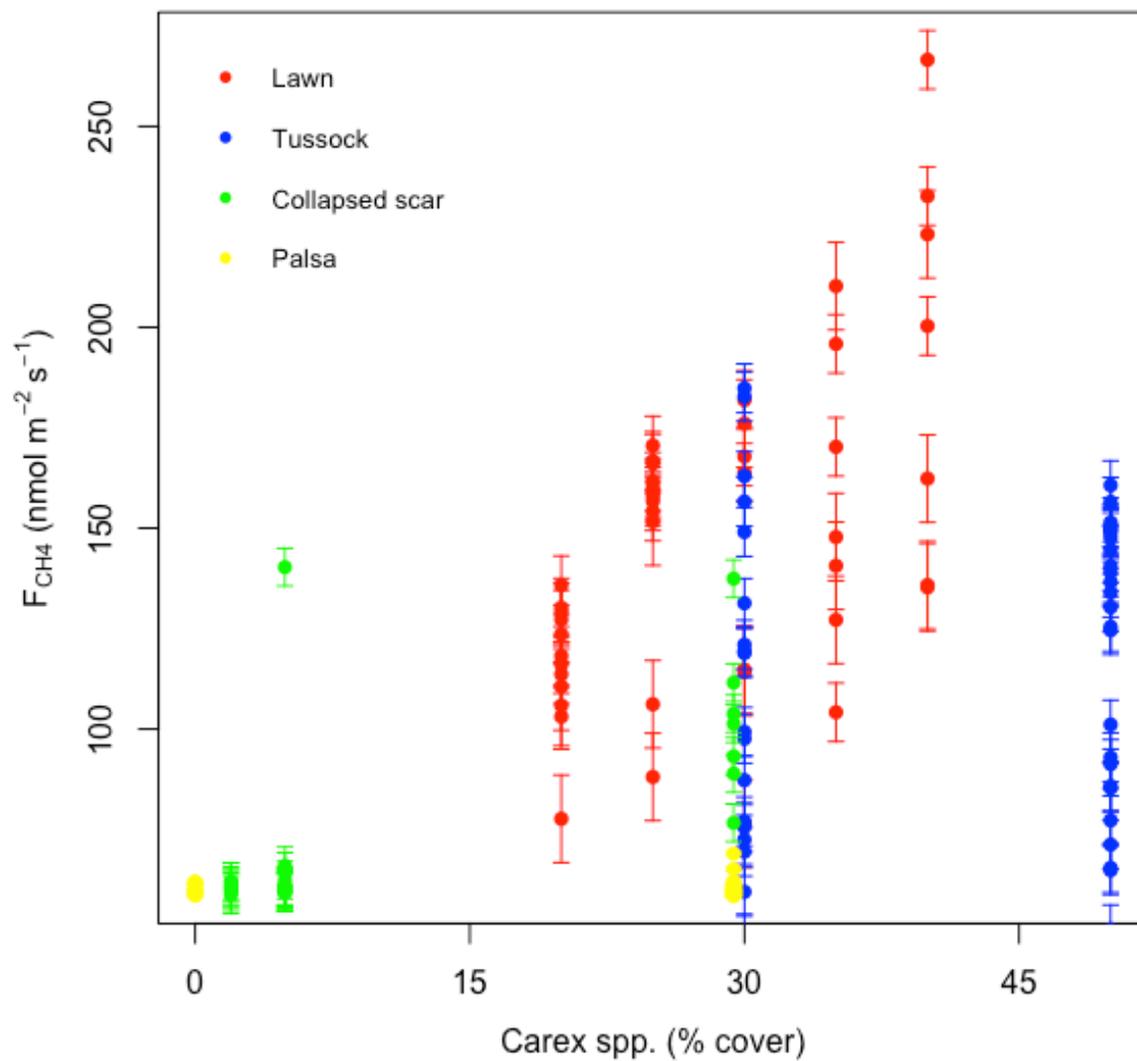


Figure 7. Across lawn plots, 2017 chamber F_{CH₄} increased with increasing peak growing season percent cover of *Carex/Eriophorum* spp.

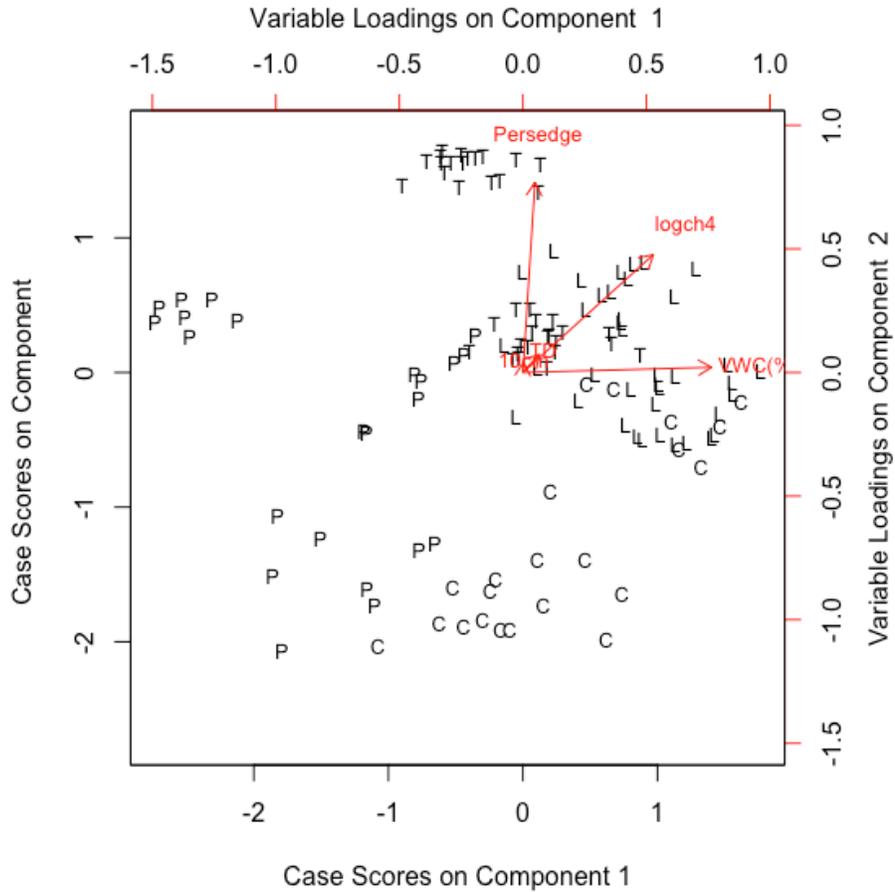


Figure 8. Loadings from PC1 and PC2 from PCA analysis of environmental variables and 2017 chamber F_{CH_4} . (L=Lawn, T=Tussock, C=Collapse scar, P=Palsa). TD=Thaw depth, t_{10cm} =Soil temperature at a depth of 10 cm, Persedge = % cover of *Carex/Eriophorum* spp., logch = chamber F_{CH_4} , VWC = percent volumetric water content.

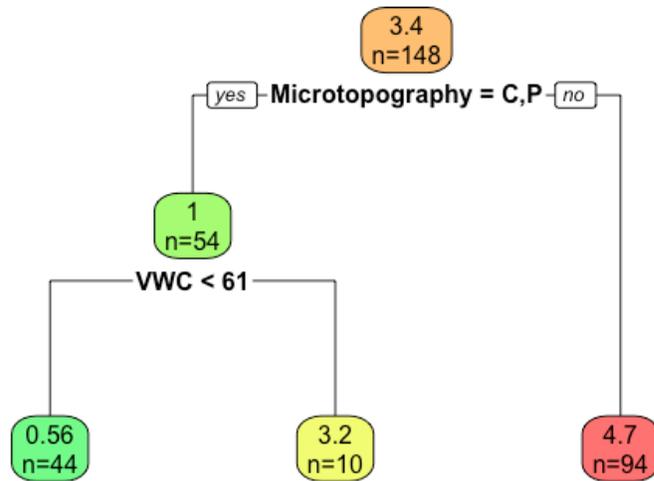


Figure 9. Regression tree where predictor variables for 2017 chamber F_{CH_4} are microform (C = Collapse scar and P = Palsa vs. T = tussock and L = lawn), and VWC. Complexity parameters for the first and second split are 0.70 and 0.08, respectively.

4.2 EC footprint analysis

A footprint analysis was performed for the growing season of 2017 to assess the influence of source area on EC F_{CH_4} . When the nighttime atmosphere was adequately turbulent ($u^* > 0.1$), the 70% cumulative flux distance (the distance from the tower where 70% of the F_{CH_4} originated) was on average 103.4 ± 1.7 m. When the footprint extended beyond the measurement area (> 150 m), EC F_{CH_4} were rejected. The peak flux distance (distance upwind from the EC station at which the greatest proportion of the F_{CH_4} originated) was on average 36.5 ± 0.2 m.

To examine the spatial variation of EC F_{CH_4} , July and August measurements were used when the 70% footprint distances were within 80 m of the flux tower (Figure 10). Lower CH_4 emissions originated from upwind areas between 100° and 290° (approximately SE to NW) which included some of the palsa area. South of the flux tower was an area characterized by lawns and tussocks but also included small ponds at the margins of the fen (pond F_{CH_4} was not surveyed). The largest F_{CH_4} originated from upwind areas between 300° - 60° which largely coincided with an area dominated by lawns and tussocks (Figure 10). The heterogeneity of the surface type surrounding the flux tower resulted in significantly different F_{CH_4} ($F=130$, $p<0.001$) as well as significant differences in air temperature, friction velocity, vapour pressure and net radiation (Table 4).

Based on the map in Figure 10, palsas covered 24% and lawns/tussocks 65% of the area within 80 m of the flux tower. It was roughly estimated that collapse scars made up 3% of the palsa area and tussocks made up 30% of the lawn/tussock areas. Ponds, which were not surveyed for F_{CH_4} , made up 11% of the area but in this case was assumed to have fluxes similar to lawns. Therefore, lawn, tussock, collapse scar, and palsa area was set to 53, 23, 1 and 23 % of the area, respectively. The average daytime July and August 2017 mean (\pm SD) F_{CH_4} was $51 \pm$

$2 \times 10^{-2} \text{ nmol m}^{-2} \text{ s}^{-1}$ when the daytime 70% flux footprint was within 80 m of the tower (87% of the daytime measurements that met quality control criteria). Weighting the chamber F_{CH_4} by the source areas listed above resulted in an average F_{CH_4} of $100 \pm 4 \text{ nmol m}^{-2} \text{ s}^{-1}$.

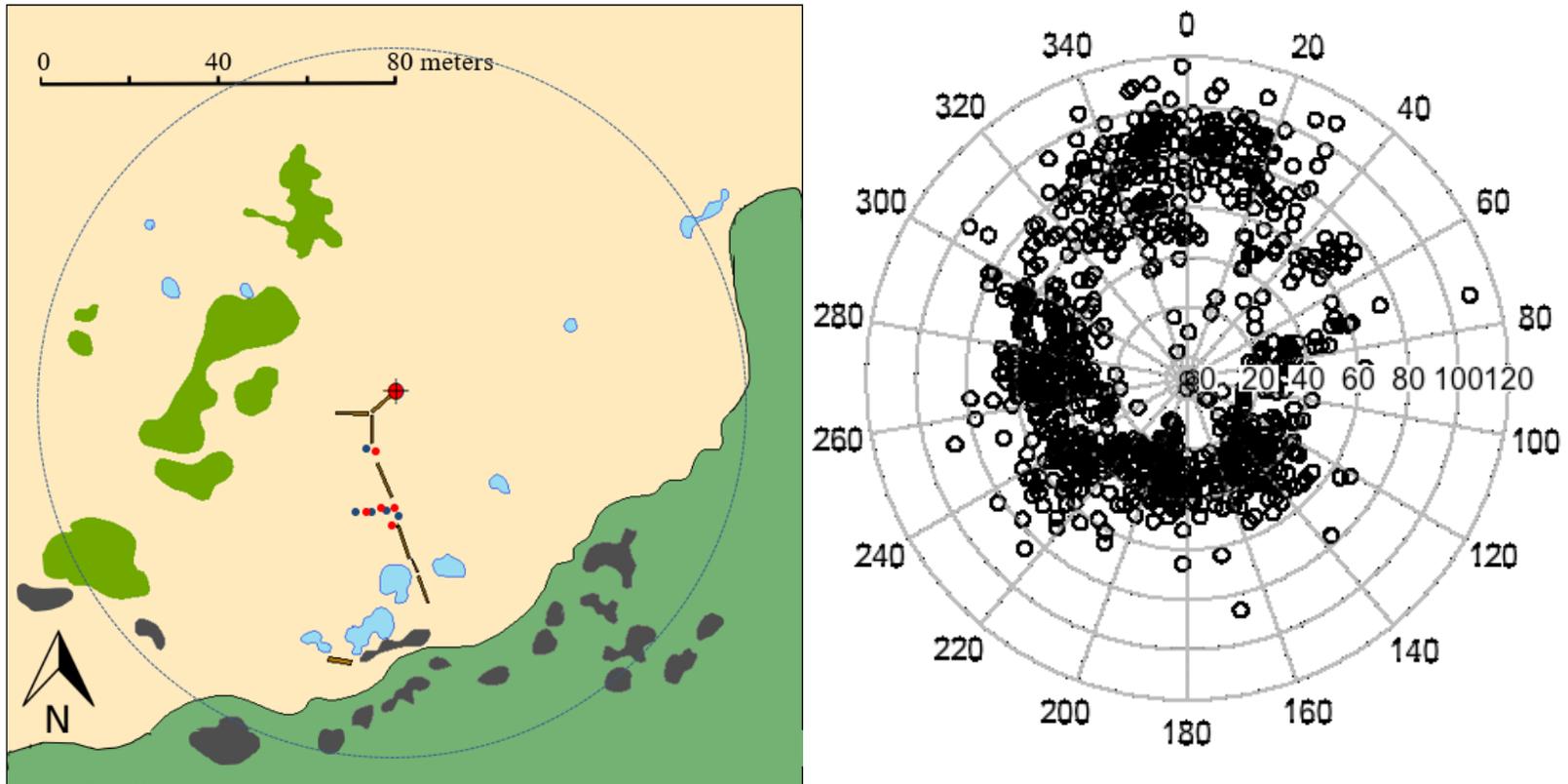


Figure 10. Right: the magnitude of F_{CH_4} (scale across center in $nmol\ m^{-2}\ s^{-1}$) from July and August 2017 plotted with wind direction (angle from N noted around the perimeter) when 70% of the flux footprint was within 80 m of the flux tower. Left: the map of the wet sedge meadow (see Figure 2 for legend) with the area within 80 m of the tower circled.

Table 4. Differences in F_{CH_4} and climatic variables including air temperature, friction velocity (u^*), vapour pressure (VP), net radiation (Q^*) and water table depth (WT) based on source area relative to the EC tower with corresponding standard error. Median F_{CH_4} values are noted before mean values. Significant differences ($p < 0.05$) in variables among source areas were determined using an ANOVA and Tukey HSD post-hoc test and are noted by different subscript letters within a column.

Surface type	F_{CH_4} (nmol m ⁻² s ⁻¹)	Air temp. (°C)	u^* (m s ⁻¹)	VP (kPa)	Q^* (W m ⁻²)	WT (cm)	Wind direction (°)
Lawn/Tussock	61.1, 60.2 ± 1.28x10 ⁻⁴ ^a	15.2 ± 0.2 ^a	0.34 ± 0.01 ^a	1.1 ± 0.0 ^a	254 ± 7 ^a	-12.0 ± 0.2	200-236, 320-120
Lawn/Tussock/ Pond	32.2, 33.0 ± 8.18x10 ⁻⁴ ^b	18.7 ± 0.2 ^b	0.39 ± 0.01 ^b	1.3 ± 0.0 ^b	227 ± 9 ^b	-13.4 ± 0.3	120-200
Palsa	50.0, 50.1 ± 8.8x10 ⁻⁴ ^c	17.3 ± 0.3 ^c	0.36 ± 0.01 ^c	1.0 ± 0.0 ^c	294 ± 9 ^a	-13.1 ± 0.3	236-320

4.3 Temporal variability

4.3.1 Diel patterns

Half hour daytime EC F_{CH_4} varied with radiation driven variables, such as 20-cm soil temperature, air temperature, net radiation and friction velocity, as well as vapour pressure (Figure 11, Table 5). Other variables including wind direction, relative humidity, and other soil temperature depths did not improve the model. The relationship between daytime EC F_{CH_4} and these variables differed based on year, where friction velocity explained a significant proportion of variability across all three years (Table 5). The log transform of EC F_{CH_4} was used in the models for years where data was positively skewed from large yet infrequent F_{CH_4} , which increased both the normality of the data distribution and the R^2 of resultant models.

Nighttime EC F_{CH_4} was typically lower ($22.6 \pm 0.8 \text{ nmol m}^{-2} \text{ s}^{-1}$) than daytime F_{CH_4} ($50.8 \pm 2.9 \text{ nmol m}^{-2} \text{ s}^{-1}$) and was associated with relatively low near-surface soil temperatures and/or low friction velocity and net radiation values. In contrast, chamber F_{CH_4} collected over a 24-hour period showed little diel variation (Figure 12). Both air and 2-cm soil temperature explained a significant proportion of variance of EC F_{CH_4} during this period ($R^2 = 0.45$, $p < 0.001$).

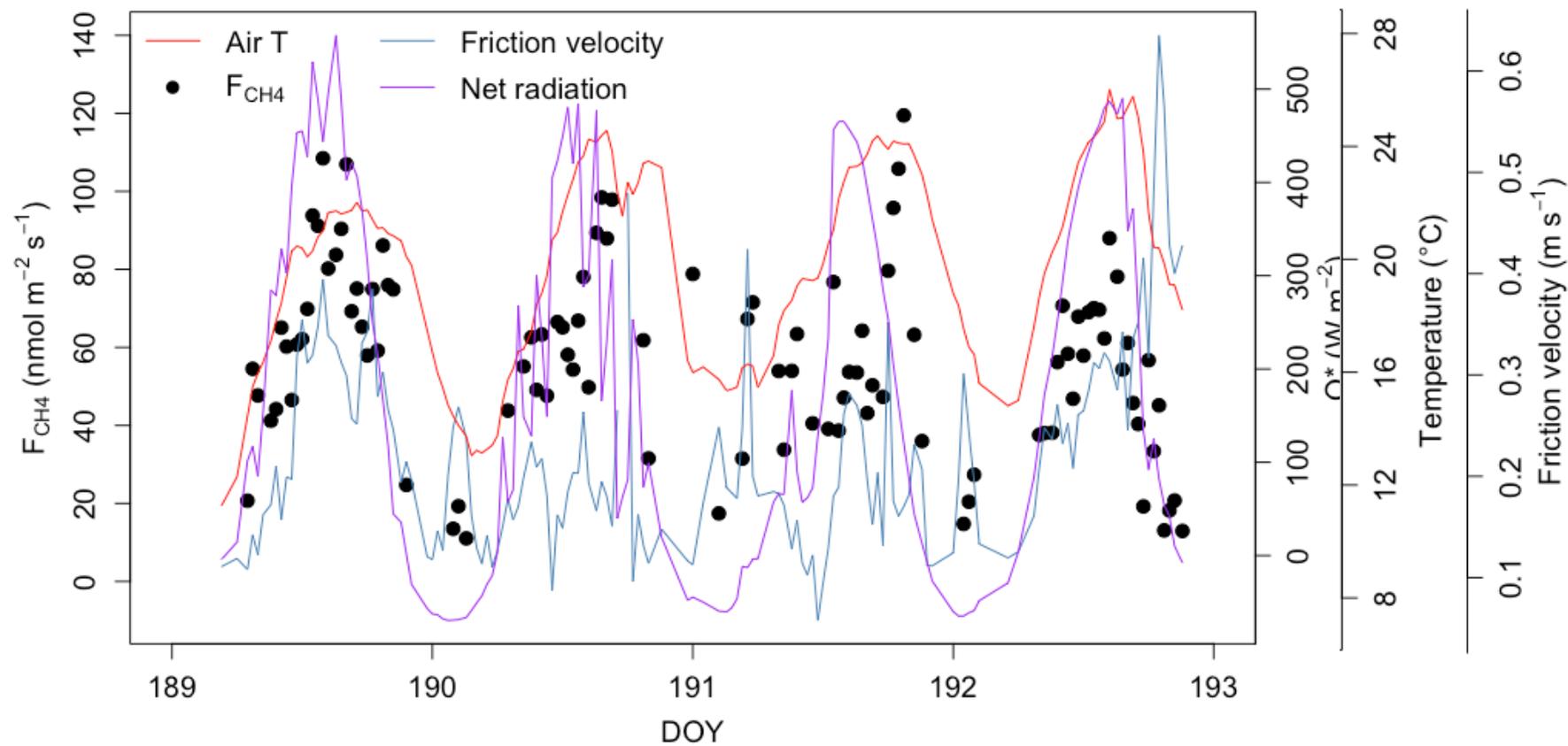


Figure 12. EC F_{CH_4} , friction velocity, air temperature (Air T) and net radiation (Q^*) over 4 days (July 8th – 11th, 2017)

Table 5. Linear regression equations for daytime (8:00-17:00) EC F_{CH_4} and for 24 hr values July 10-11, 2017, coinciding with the dates with 24 hr chamber F_{CH_4} . T_{air} , T_5 , T_{10} , T_{20} are air, 5, 10 and 20-cm soil temperature, respectively, VP is vapour pressure, Q^* is net radiation and u^* is friction velocity.

Year	Equation	R^2	p
2015	$\log(\text{daytime } F_{CH_4}) = 0.0014(Q^*) - 0.9(u^*) - 0.5(VP) + 4.3 \text{ nmol m}^{-2} \text{ s}^{-1}$	0.43	<0.001
2016	$\log(\text{daytime } F_{CH_4}) = 0.13(T_{20}) - 0.1(u^*; T_{20}) + 3.3 \text{ nmol m}^{-2} \text{ s}^{-1}$	0.39	<0.001
2017	$\log(\text{daytime } F_{CH_4}) = 0.5(u^*) + 0.05(T_{air}) + 0.001(Q^*) + 2.6 \text{ nmol m}^{-2} \text{ s}^{-1}$	0.50	<0.001
2017 (July 10-11)	$\log(24\text{hr } F_{CH_4}) = 0.17(T_{air}) - 0.11(T_2) + 1.7 \text{ nmol m}^{-2} \text{ s}^{-1}$	0.45	<0.001

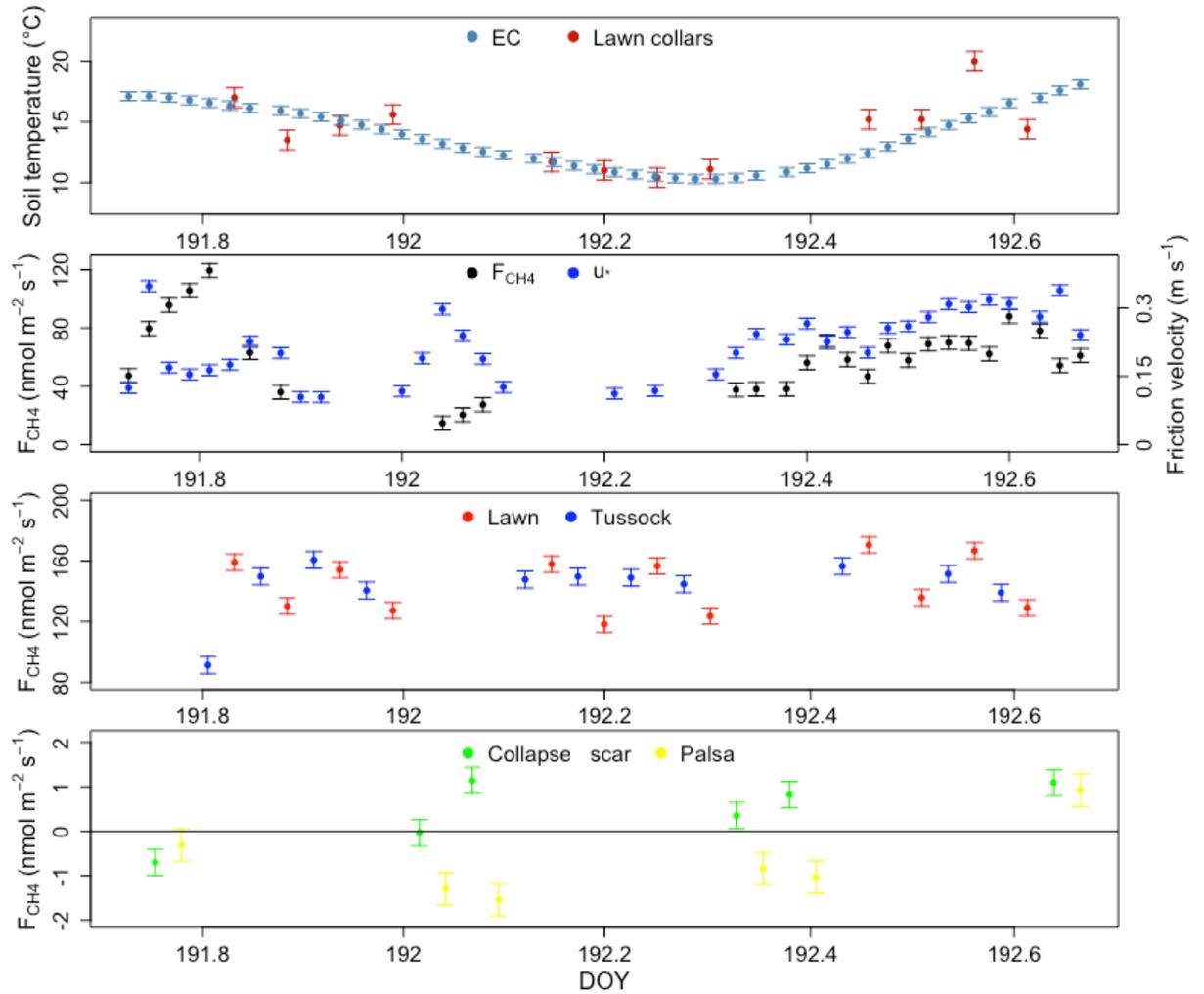


Figure 13. Diel EC F_{CH_4} , soil temperature and friction velocity (u^*) from July 10-11 (DOY 191-192), 2017. Soil temperature measurements are from the EC station (5 cm) and from the lawn collars (2 cm). The bottom two panels display a 24-hour set of F_{CH_4} measurements using non-steady state chambers. Measurements were performed on two lawn plots, two tussock plots, and one collapse scar and palsa plot. The horizontal line marks where values become negative and therefore represent CH_4 uptake.

4.3.2 Seasonal patterns

Both EC and chamber F_{CH_4} varied within a growing season (Figure 6) as well as among years. In most years, EC and chamber F_{CH_4} was greatest in late June/early July (Figure 6). Generally, soil temperatures and WT were negatively correlated for all depths, with the greatest correlations at depths of 40 and 60 cm ($r = 0.50-0.90$). The EC F_{CH_4} record was near continuous from May through September 2016. In that year, the model with the greatest coefficient of determination included 20 cm soil temperature and WT (Table 6, Figure 14). No other variables (e.g. air temperature, vapour pressure, relative humidity, etc.) improved the model. Combining the two variables and adding interaction terms did not improve the models. In 2015 and 2017, only July and August EC F_{CH_4} measurements were available. The models with highest R^2 differed among all three years (Table 6).

All 9 growing seasons between 2008 and 2017 were analyzed to investigate seasonal trends in chamber F_{CH_4} . VWC and 10-cm soil temperature explained a significant proportion of seasonal variance in chamber F_{CH_4} for all growing seasons combined (2008-2017). A linear mixed effect model predicted that a 5 % increase in VWC and a 5 °C increase in air temperature would result in an F_{CH_4} increase of 14 nmol $m^{-2} s^{-1}$ where collar and year were input as random effects. When chamber F_{CH_4} were separated by year, relationships between soil or air temperature, VWC, WT and F_{CH_4} varied (Table 6). Several growing seasons displayed relationships between F_{CH_4} and site-level WT. These relationships were most pronounced in 2009, 2010, 2012 and 2017 (Table 6, Figure 13), where a linear mixed effect model resulted in significant coefficients for WT for the four growing seasons combined. During the 2013 growing

season, variability in F_{CH_4} was explained by soil temperature alone. This year was particularly wet and cold (Figure 6) with mean air temperature and WT of 12.6°C and -2.5 cm, respectively on measurement days. LAI values determined using both the point frame method and the handheld canopy analyzer peaked mid-growing season during all years but did not explain seasonal F_{CH_4} variability from 2008-2017.

Table 6. Linear regressions and mixed effect models for mean daily EC F_{CH_4} and chamber F_{CH_4} , respectively across multiple growing seasons. MEMs were performed using collar as a random effect from 2008-2017 and year when all years were combined. T_{air} , T_5 , T_{10} , T_{20} are air, 5, 10 and 20-cm soil temperature, respectively, VWC is soil moisture, WT is water table depth, VP is vapour pressure, Q^* is net radiation, u^* is friction velocity, TD is thaw depth, %Carex is percent cover of *Carex/Eriophorum* spp. and m is microform.

	Year	Model	R^2	p
EC	2015	$F_{CH_4} = -52.5(u^*) - 22.4(VP) + 0.07(Q^*) + 67.3 \text{ nmol m}^{-2} \text{ s}^{-1}$	0.37	<0.001
	2016	$F_{CH_4} = 1.3(T_{20}) - 0.61(WT) + 18.3 \text{ nmol m}^{-2} \text{ s}^{-1}$	0.41	<0.001
	2017	$\log(F_{CH_4}) = 0.16(T_{20}) - 4.6 \text{ nmol m}^{-2} \text{ s}^{-1}$	0.54	<0.001
	all	$F_{CH_4} = 2.7(T_{20}) + 2.3(\text{year}) + 0.06(Q^*) - 4.7 \text{ nmol m}^{-2} \text{ s}^{-1}$	0.36	<0.001
Chamber	2008	$F_{CH_4} = 1.8(T_{air}) + 1.3(VWC) - 55.3 \text{ nmol m}^{-2} \text{ s}^{-1}$	0.39	<0.001
	2009	$F_{CH_4} = 2.6(WT) + 1.8(T_{10}) + 78.0 \text{ nmol m}^{-2} \text{ s}^{-1}$	0.70	<0.001
	2010	$F_{CH_4} = 11.7(WT) + 214 \text{ nmol m}^{-2} \text{ s}^{-1}$	0.41	<0.05
	2012	$\log(F_{CH_4}) = 0.09(WT) + 5.8 \text{ nmol m}^{-2} \text{ s}^{-1}$	0.45	<0.01
	2013	$F_{CH_4} = 3.6(T_5) + 90.5 \text{ nmol m}^{-2} \text{ s}^{-1}$	0.25	<0.05
	2014	$F_{CH_4} = 4.4(T_5) + 2.8(VWC) - 134 \text{ nmol m}^{-2} \text{ s}^{-1}$	0.38	<0.05
	2015	$F_{CH_4} = 4.6(T_{10}) + 2.1(VWC) - 92.8 \text{ nmol m}^{-2} \text{ s}^{-1}$	0.79	<0.01
	2016	$F_{CH_4} = 3.0(VWC) - 82.4 \text{ nmol m}^{-2} \text{ s}^{-1}$	0.42	<0.01
	2017	$F_{CH_4} = 2.3(\%Carex) - 3.5(TD) + 2.0(WT) + 222 \text{ nmol m}^{-2} \text{ s}^{-1}$	0.64	<0.001
	all	$\log(F_{CH_4}) = 0.01(T_2) + 0.01(VWC) + 0.04(m:\text{year}) + 67 \text{ nmol m}^{-2} \text{ s}^{-1}$	0.76	<0.001
	2009-2012, 2017	$F_{CH_4} = 3.4(WT) + 110.0 \text{ nmol m}^{-2} \text{ s}^{-1}$	0.45	<0.001

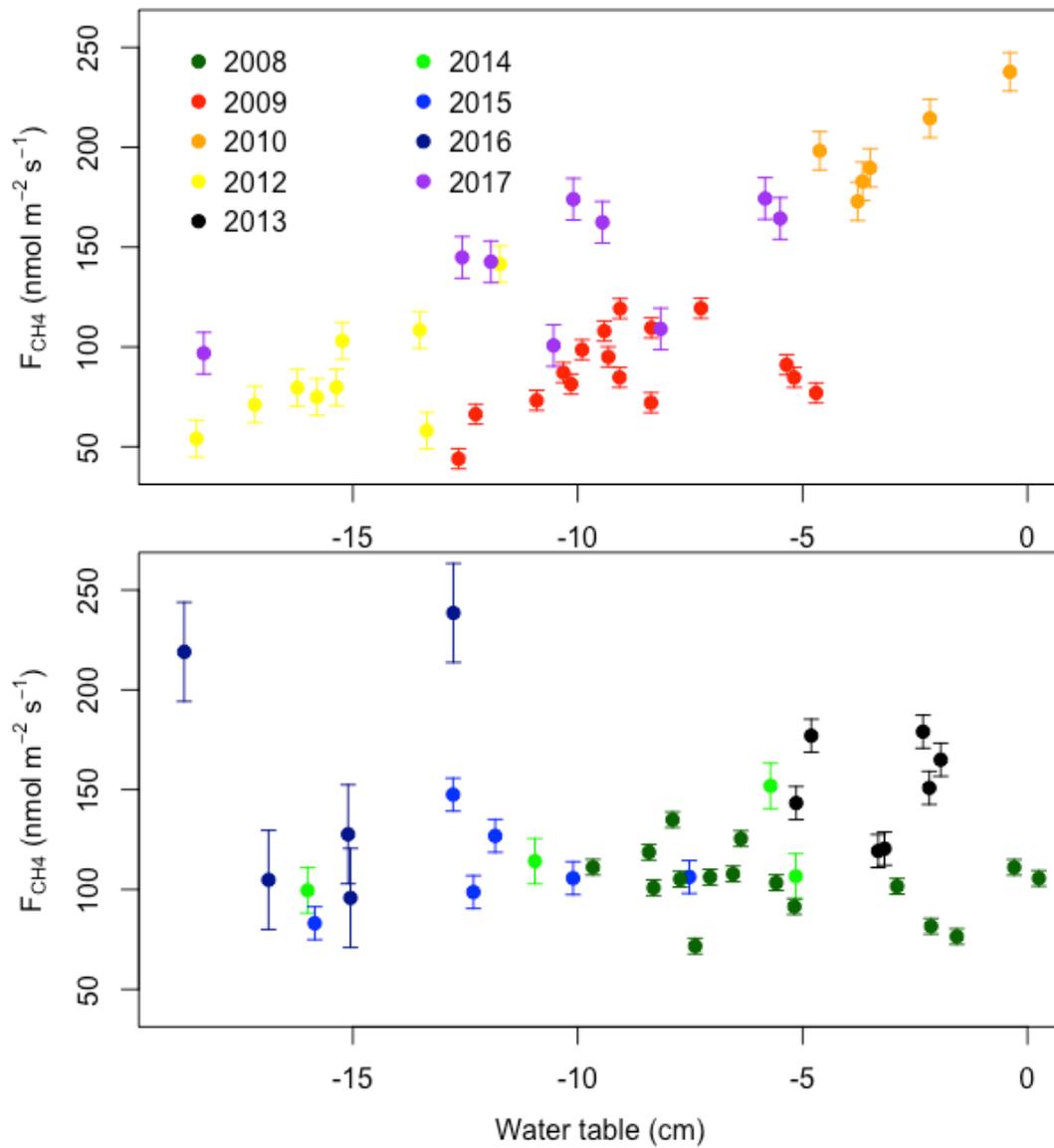


Figure 14. Daily mean lawn chamber F_{CH_4} and site-level WT between 2009-2012 and 2017 (top) and from 2008, 2013-2016 (bottom). Years were separated based on significant coefficients for WT as an explanatory variable for chamber F_{CH_4} with collar as a random effect.

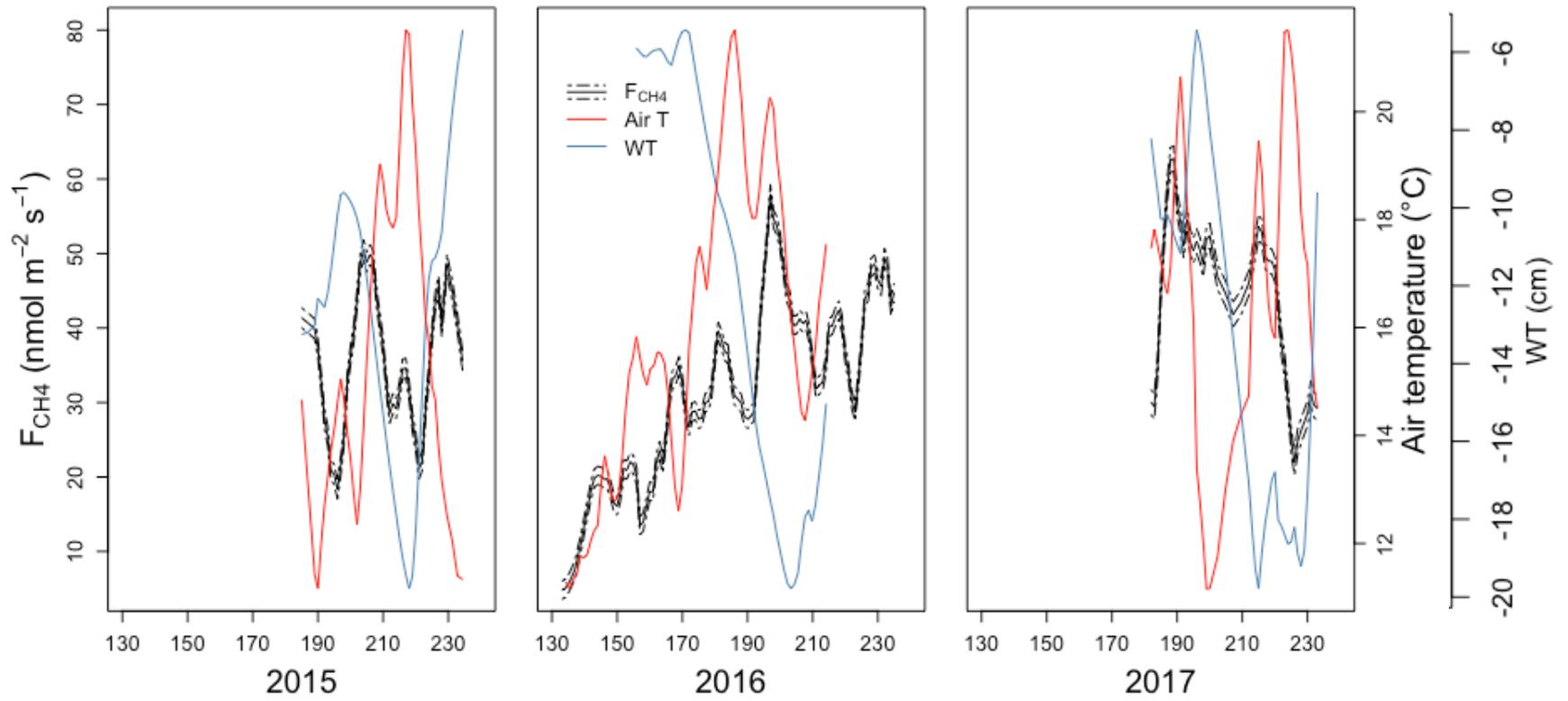


Figure 15. Five-day moving averages using half hour measurements of EC F_{CH_4} , WT and air temperature over the 2015, 2016 and 2017 growing seasons.

4.3.3 Interannual trends

As noted earlier, year was a significant variable in a mixed effects model describing spatial and temporal variations in chamber F_{CH_4} (Table 6). Large year-to-year variations in F_{CH_4} are best highlighted by tussock and lawn chamber F_{CH_4} which varied from $40 \pm 2 \text{ nmol m}^2 \text{ s}^{-1}$ (average in 2008) to $159 \pm 11 \text{ nmol m}^2 \text{ s}^{-1}$ (average in 2010) and $86 \pm 6 \text{ nmol m}^2 \text{ s}^{-1}$ (average in 2012) to $200 \pm 11 \text{ nmol m}^2 \text{ s}^{-1}$ (average in 2010), respectively. Year-to-year variation in F_{CH_4} was smaller for collapse scars ($3 \pm 1 \text{ nmol m}^2 \text{ s}^{-1}$ in 2009 and $29 \pm 10 \text{ nmol m}^2 \text{ s}^{-1}$ in 2016), and negligible for palsas ($-1 \pm 0.3 \text{ nmol m}^2 \text{ s}^{-1}$ in 2016 and $3 \pm 0.3 \text{ nmol m}^2 \text{ s}^{-1}$ in 2010) (Figure 6). Greatest emissions from lawn and tussock microforms were during the 2010 growing season when mean VWC values were $86 \pm 2 \%$ and $92 \pm 1 \%$ for tussocks and lawns, respectively (Figure 6, Appendix 1, Table A-1&A-2) and the water table was on average 0.7 cm below the lawn surface and never dropped below 7 cm of the surface (Figure 6). Lowest emissions from lawn microforms and the second lowest emissions from tussock microforms were both during the 2012 growing season, when mean VWC was the lowest (or second lowest) of all years and the average water table was $12.4 \pm 0.4 \text{ cm}$ below the peat surface. The water table dropped further below the surface in other years (e.g. 2014 through 2017) but did not remain as consistently low (Figure 6).

Mean July and August EC F_{CH_4} varied by only 3 to 9 $\text{nmol m}^{-2} \text{ s}^{-1}$ among the three years. Mean July and August EC F_{CH_4} were largest in 2017, coinciding with the highest July and August soil and air temperatures of the three growing seasons (Appendix 1, Table A-3). As noted above, models describing seasonal variation in EC F_{CH_4} varied

among the three years (Table 6). The only variables that consistently explained temporal variations in EC F_{CH_4} were 20-cm soil temperature and net radiation (Table 6).

4.4 DOC, TN, SUVA

Porewater samples were taken on three days throughout the 2017 growing season; July 6th, 22nd and August 6th. Due to spatial differences in WT depth, porewater was extracted from a minimum depth of 5 cm for lawn plots and 15 cm for tussock plots. Porewater was extracted from only one of the collapse scar plots on one day where the WT was within 5 cm of the peat surface. Otherwise WT levels were too low to obtain samples from respective depths from the peat surface. This collapse scar plot had low DOC, TN, dissolved CH_4 and high $SUVA_{254}$ (mean values from 3 depths between 5 and 40 cm below the surface of $19.1 \pm 1.4 \text{ mg L}^{-1}$, $0.97 \pm 0.23 \text{ mg L}^{-1}$, $1132 \pm 439 \text{ ppm}$ and $6.8 \pm 0.2 \text{ L mgC}^{-1} \text{ m}^{-1}$, respectively) indicative of lower rates of microbial activity and relatively aromatic DOC. At the 15 and 30 cm depths where DOC, TN, and dissolved CH_4 were measured regularly at both depths, there were no significant differences associated with depth, date or microform (Appendix, Table A-6). Only $SUVA_{254}$ was significantly lower in lawns at these two depths (Appendix, Table A-6).

Within the tussock and lawn plots, trends in concentrations of DOC, TN and dissolved CH_4 and $SUVA_{254}$ were not always consistent across the three sampling dates and at various depths. For tussocks, DOC increased with depth ($R^2=0.39$, $p<0.001$), $SUVA_{254}$ decreased ($R^2=0.43$, $p<0.001$) and TN increased ($R^2=0.66$, $p<0.001$). There were no statistically significant changes in dissolved CH_4 with depth at tussock plots. Similar trends were observed for lawns where DOC increased with depth ($R^2=0.23$,

$p < 0.01$), SUVA₂₅₄ decreased ($R^2 = 0.20$, $p < 0.05$), and TN increased ($R^2 = 0.47$, $p < 0.001$) while dissolved CH₄ also increased ($R^2 = 0.19$, $p < 0.05$).

There was a tendency for DOC to decrease (Figure 16) and SUVA₂₅₄ to increase over the growing season 15 cm below tussock surfaces (Figure 15). However, these temporal patterns were not statistically significant ($R^2 = 0.70$, $p = 0.10$; $R^2 = 0.76$, $p = 0.08$, respectively). Similarly, there was no significant change in TN while there was a significant decrease in dissolved CH₄ ($R^2 = 0.29$, $p < 0.01$) at 15 cm for tussock surfaces and for all depths below lawn surfaces ($R^2 = 0.30$, $p < 0.01$). There were no discernable differences over time at the lawns for any of the other porewater variables. Dissolved CH₄ correlated with F_{CH_4} across locations (30-cm CH₄ $r = 0.46$, $p < 0.05$; 40-cm CH₄ $r = 0.81$ $p < 0.05$) while there was no significant correlation for 5 and 15 cm depths.

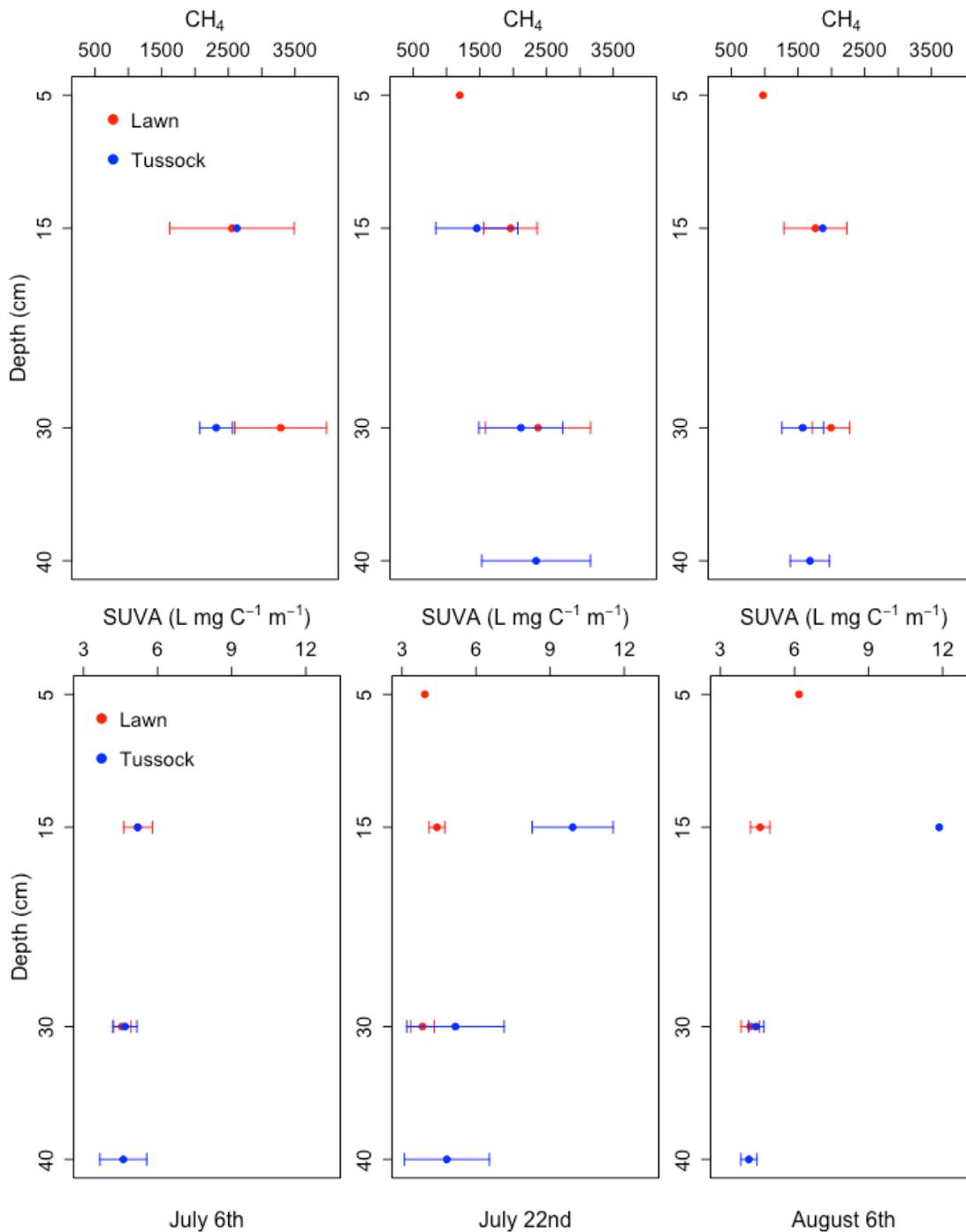


Figure 16. Dissolved CH₄ (ppm) and SUVA (L mg C⁻¹ m⁻¹) for lawn and tussock plots at depths of up to 40 cm on three different dates in 2017.

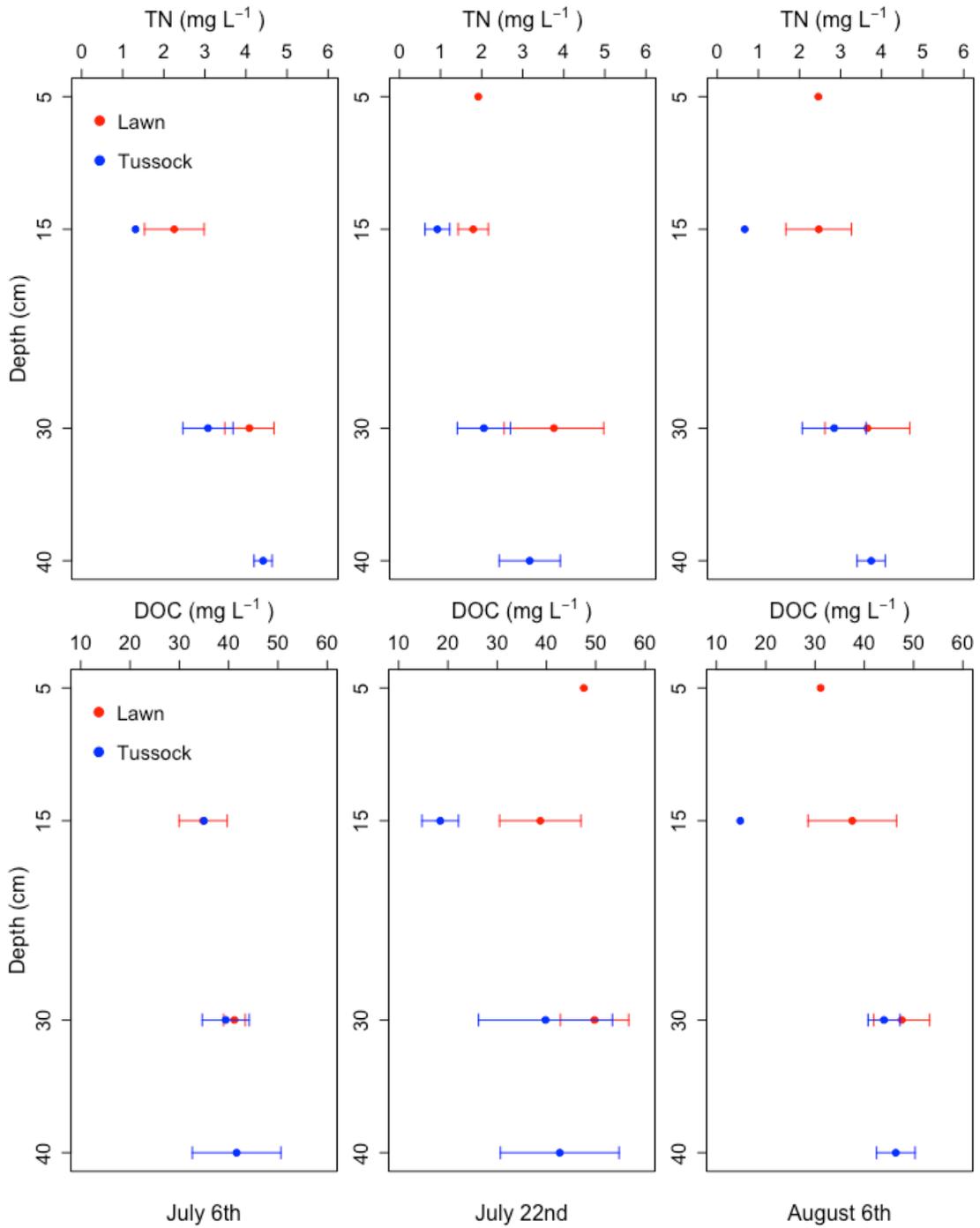


Figure 17. TN (mg L⁻¹) and DOC (mg L⁻¹) for lawn and tussock plots at depths of up to 40 cm on three different dates in 2017.

4.5 CH₄ and CO₂ isotope signatures

Delta ¹³C-CH₄ in the 2017 porewater samples ranged from -53.6 ‰ to -77.2 ‰, with a mean of -64.9 ± 1.0 ‰ for all depths across all sample dates at lawns and -62.6 ± 1.0 ‰, at tussocks. The difference between tussock and lawns was more notable at a depth of 15 cm (Figure 17) where lawn CH₄ signatures were heavier (-57.1 ± 0.9 ‰) than tussocks (-65.7 ± 1.7 ‰), however this difference was not significant nor were the differences at 30 cm significant (Appendix, Table A-6). There was a tendency for depletion in ¹³C-CH₄ with depth (model: $\delta^{13}\text{C-CH}_4 = -0.29 (\text{depth}) - 52.8$ ‰ (RMSE: 3.3, $p < 0.01$)) and a negative relationship between ¹³C-CH₄ and ¹³C-CO₂ at 30-40 cm for tussock plots ($R^2 = 0.30$, $p < 0.01$). There was also a significant depletion of ¹³C-CH₄ with depth at lawns but only on July 6th (model: $\delta^{13}\text{C-CH}_4 = -0.34 (\text{depth}) - 58.3$ ‰ (RMSE=1.16, $p < 0.001$). Porewater on this sampling date also had the highest dissolved CH₄ at 30 cm and the highest F_{CH₄} for both tussock and lawn plots (Table 7). ¹³C-CH₄ values became increasingly depleted over the growing season 15 cm below lawn surfaces (Table 7).

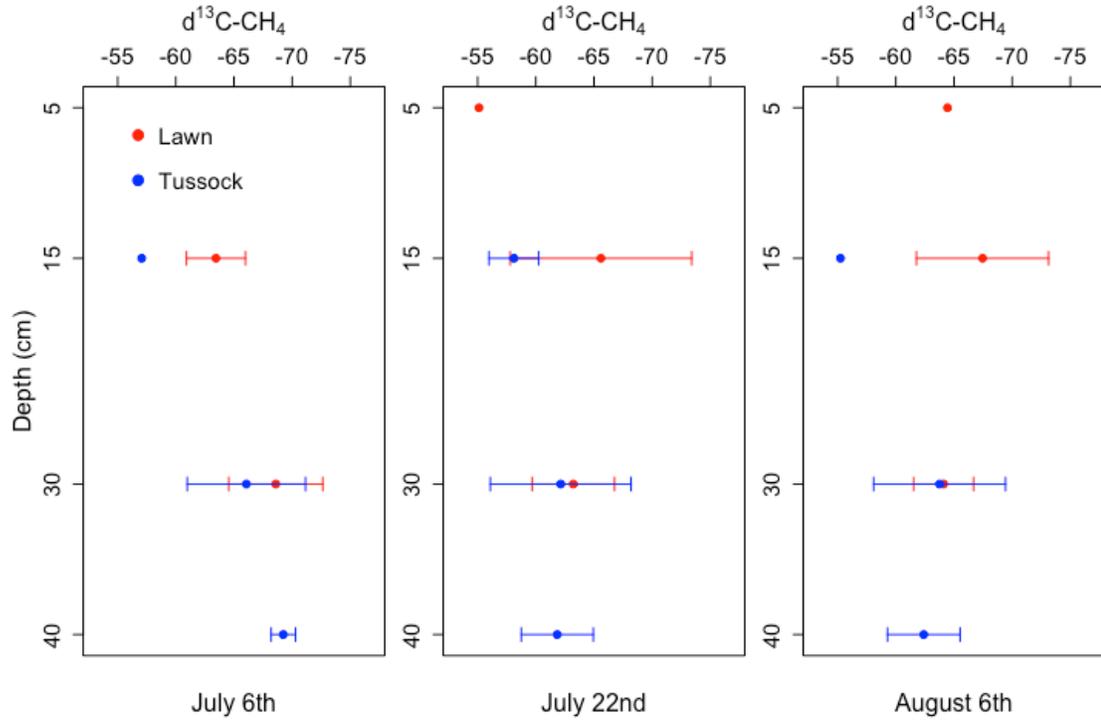


Figure 18. Methane isotope composition from porewater CH_4 with increasing depth for lawn and tussock plots on three different dates in 2017.

Table 7. Dissolved CH₄ concentrations and δ¹³C values for CH₄ and CO₂ from porewater samples from 5 cm to a maximum depth of 40 cm from the peat surface. Standard error (SE) is listed for measurements with more than 1 replicate plot for the corresponding date.

Date	Microform/ Depth (cm)	δ ¹³ C-CH ₄ (‰)				δ ¹³ C-CO ₂ (‰)				[CH ₄] (ppm)				F _{CH₄} (nmol m ⁻² s ⁻¹)	WT (cm)
		5	15	30	40	5	15	30	40	5	15	30	40		
July	Collapse scar	-65.1	-65.5	-71.3		-24	-21.4	-19.1		303.4	1293.4	1798.1		66.3	0.0
	Lawn		-63.5	-68.6			-11.3	-10.3			2552.5	3285.3		162.4	-5.8
			± 1.5	± 2.3			± 0.6	± 0.6			± 539.2	± 396.3		± 14.0	± 0.9
	Tussock		-57.1	-66.1	-69.2		-12.7	-12	-10.9		2627.4	2317.2	3537.0	140.1	-19.4
				± 2.9	± 0.7			± 0.2	± 0.9			± 141.7		± 15.3	± 3.6
July 22 nd	Lawn	-55.1	-65.6	-63.2		-13.1	-12.2	-12.8		1199.1	1959.7	2372.1		100.7	-6.6
			± 3.9	± 1.8			± 0.8	± 1.3			± 200.5	± 393.9		± 19.6	± 1.0
	Tussock		-58.1	-62.1	-61.8		-12.9	-13.2	-12.5		1453.2	2115.2	2343.3	90.9	-15.2
			± 1.5	± 3.0	± 1.5		± 0.7	± 0.9	± 0.5		± 434.6	± 314.5	± 407.5	± 8.9	± 2.1
August 6 th	Lawn	-64.4	-67.5	-64.1		-17.7	-11.8	-13.6		975.2	1758.8	1994.2		96.9	-13.5
			± 2.8	± 1.3			± 0.6	± 1.1			± 235.7	± 140.5		± 17.8	± 1.5
	Tussock		-55.2	-63.8	-62.4		-13.8	-13.7	-15.0		1870.4	1569.6	1678.5	66.6	-20.4
				± 2.8	± 1.6			± 1.0	± 1.0			± 155.9	± 146.4	± 14.8	± 1.3

4.6 Source CO₂ and CH₄ isotope signatures

Source isotopic signatures were roughly approximated using the Keeling plot approach. This method requires the isotope signatures of both emitted and atmospheric CH₄ and CO₂. Isotope signatures of emitted CH₄ were collected from tussock and lawn plots on August 7th and August 21st 2014 by leaving the chamber closed for 20 min and sampling at the end of this period. The source $\delta^{13}\text{C-CH}_4$ values of both lawns and tussocks ranged from -89 ‰ and -69 ‰, while source $\delta^{13}\text{C-CO}_2$ values range from -27 ‰ to -20 ‰. Mean source $\delta^{13}\text{C-CH}_4$ values were -76.5 ± 1.9 ‰ and -71.6 ± 2.0 ‰ and mean source $\delta^{13}\text{C-CO}_2$ values of -23.3 ± 0.7 and -26.1 ± 1.3 ‰ for lawn and tussock plots, respectively (Figure 18). There were no significant differences between lawn and tussock source isotopic signatures using both sampling dates combined. For lawn plots only, source $\delta^{13}\text{C-CO}_2$ was significantly less negative on August 21st relative to August 7th ($t=3.01$, $p<0.01$). The source $\delta^{13}\text{C-CH}_4$ was significantly more negative for lawn plots on August 21st relative to August 7th ($t=-2.8$, $p<0.04$) (Figure 18). The production pathway for both lawn and tussock CH₄ is likely carbonate reduction (e.g. hydrogenotrophic methanogenesis) as characteristic signatures range from 110‰ – 60‰ while acetate fermentation signatures range from 65‰ – 50‰ (Whiticar, 1999).

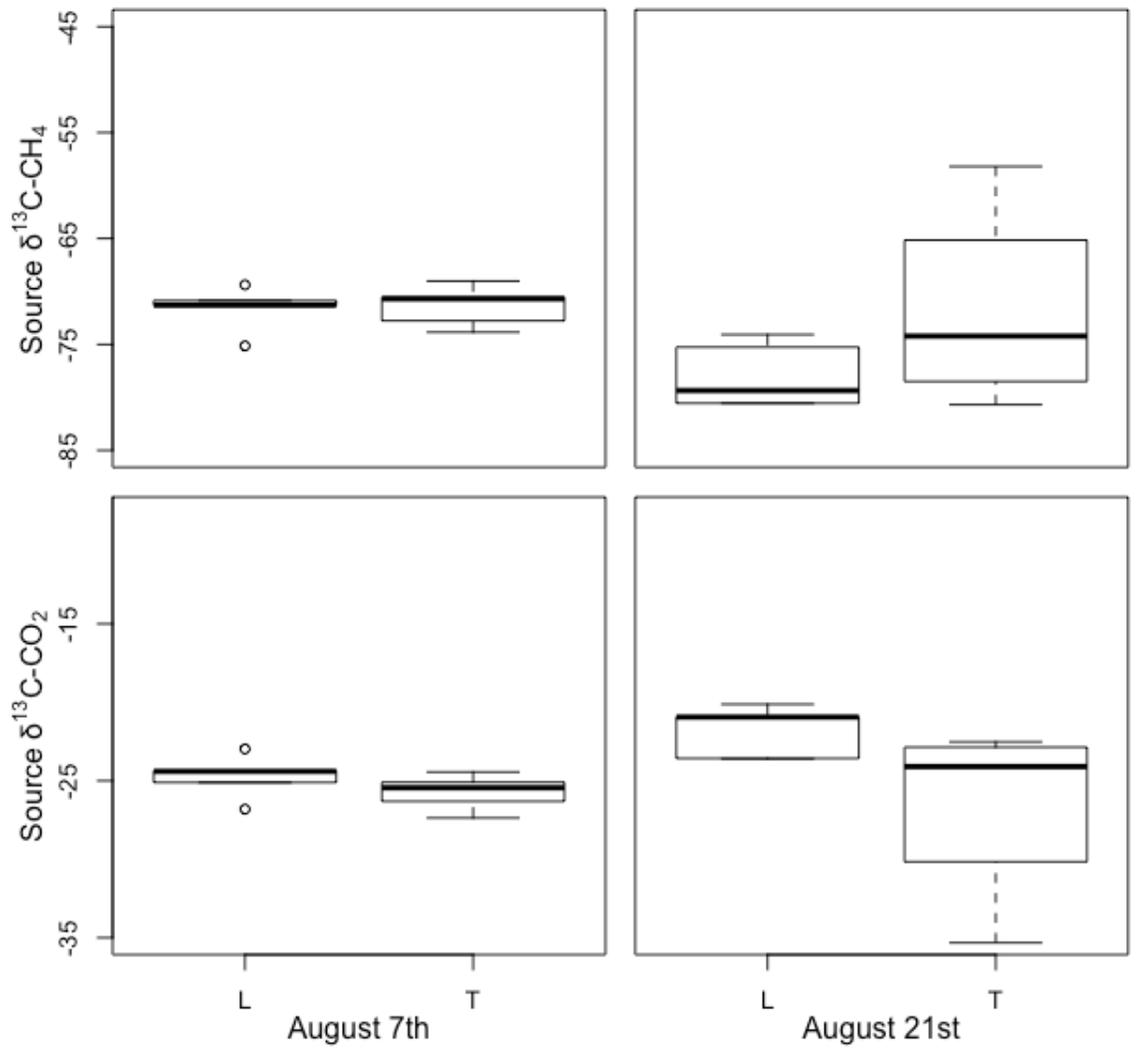


Figure 19. Source isotopic signatures for CH₄ and CO₂ for lawn and tussock plots during the 2014 growing season.

5 Chapter: Discussion

The results of this study highlight the importance of biotic and abiotic drivers of F_{CH_4} , with the importance of different factors varying at several different spatial and temporal scales. This scale-dependence reveals the relative importance of CH_4 production, transportation and consumption processes on the rate of CH_4 released from the Arctic wet sedge meadow at Daring Lake. An understanding of scale-dependent emergent processes is important when predicting future rates of F_{CH_4} . Similarly, the effect of measurement technique on F_{CH_4} assessment is important to consider when monitoring the response of F_{CH_4} to climate and landscape change and can help inform future studies on potential biases in sampling and research design.

5.1 Comparison to other wetland and Arctic sites

Daily mean and median chamber F_{CH_4} from the Daring Lake fen for all years, and when weighted by surface area ($111.6 \pm 2.2 \text{ mg CH}_4 \text{ m}^{-2} \text{ day}^{-1}$ and $97.6 \text{ mg CH}_4 \text{ m}^{-2} \text{ day}^{-1}$, respectively) and when arithmetically combined ($118.5 \pm 2.8 \text{ mg CH}_4 \text{ m}^{-2} \text{ day}^{-1}$ and $108.0 \text{ mg CH}_4 \text{ m}^{-2} \text{ day}^{-1}$, respectively) were comparable to values from a meta-analysis of wetland F_{CH_4} emissions around the world with mean and median fluxes ranging from 45 to 96 and 6 to 51 $\text{mg CH}_4 \text{ m}^{-2} \text{ day}^{-1}$, respectively where the largest mean and median values ($112.2 \pm 6.2 \text{ mg CH}_4 \text{ m}^{-2} \text{ day}^{-1}$ and $68.4 \text{ mg CH}_4 \text{ m}^{-2} \text{ day}^{-1}$, respectively) were from nine wetland sites across Alaska and northern Europe (Turetsky *et al.* 2014). Weighted chamber F_{CH_4} were comparable to those across four sites in the Alaskan Arctic coastal plain near Barrow and Ivotuk (McEwing *et al.*, 2015) but larger than multiple wetland sites, including an Alaskan wet meadow on the north slope of the Brooks

mountain range (Schimel, 1995) and both EC (Friborg *et al.*, 2000) and chamber (Strom *et al.*, 2015) values from fen sites in NE Greenland near the Zackenberg research station. The growing season at Daring Lake is longer and warmer than many of these sites but as noted by Turetsky *et al.* (2014), more southerly locations did not always have greater chamber F_{CH_4} than these Arctic and subarctic sites.

Although mean summer (July & August) EC F_{CH_4} were roughly 50% of the chamber F_{CH_4} at Daring Lake, they were similar to those from a fen in NE Greenland (Friborg *et al.*, 2000) and a subarctic fen in Churchill, Manitoba (Hanis *et al.*, 2013). EC F_{CH_4} were much higher than a sedge/grass moss meadow wetland at Lake Hazen (Emmertson *et al.*, 2014) and an Alaskan wet sedge tundra site (Euskirchen *et al.*, 2017). Compared to non-Arctic sites, the Daring Lake EC F_{CH_4} were slightly lower than a boreal rich treed fen in Northern Alberta (Long *et al.*, 2010), and a temperate restored wetland (Knox *et al.*, 2015) but larger than those from a boreal Finnish fen (Rinne *et al.*, 2007) and a temperate ombrotrophic bog (Brown *et al.*, 2014). As with the chamber F_{CH_4} , EC F_{CH_4} was highly variable among sites and more southerly locations did not always appear to have larger F_{CH_4} .

5.2 Environmental variables influencing spatial and temporal F_{CH_4} variability

Spatial and temporal F_{CH_4} variability derived from both chamber and EC measurements was largely driven by moisture and/or temperature-related variables and microform classifications (Table 8). Moisture-related variables (WT, VWC) were important as drivers of chamber F_{CH_4} variability across different microforms, between multiple lawn and collapse scar plots, and over multiple seasons. Highest values of WT/VWC coincided with the largest yearly mean chamber F_{CH_4} . The importance of

VWC and WT has been identified by many other studies (Christensen *et al.*, 2000; McEwing *et al.*, 2015; Moore *et al.*, 2011; Moore & Knowles 1989; Olefeldt *et al.*, 2012; Strom & Christensen 2007; Torn & Chapin 1993; Waddington *et al.*, 1996), where saturated soils reduce rates of methanotrophy and high WT levels increase the depth of the anaerobic zone which may increase CH₄ production rates by increasing substrate availability and/or by promoting reducing conditions that favour methanogenesis (Kettunen *et al.*, 1999; Seybold *et al.*, 2002). F_{CH₄} and dissolved CH₄ concentrations were correlated at 30 and 40-cm depths which suggests that rates of methanogenesis are important in determining resulting F_{CH₄}.

The importance of microform on F_{CH₄} variability was in part a result of differences in WT/VWC among microforms. Methanotrophy was likely higher at tussock plots, based on negative correlations between $\delta^{13}\text{C}_{\text{CH}_4}$ and $\delta^{13}\text{C}_{\text{CO}_2}$. The enrichment of $\delta^{13}\text{C}_{\text{CH}_4}$ and simultaneous depletion in $\delta^{13}\text{C}_{\text{CO}_2}$ is characteristic of methanotrophy, where methanotrophs preferentially use lighter ¹²C molecules and leave behind the heavier ¹³C (Whiticar, 1999). Using the ¹³C depleted CH₄ as their substrate, CO₂ produced by methanotroph respiration also has a depleted ¹³C_{CO₂} signature relative to that of aerobic SOM decomposition. Although the isotopic signatures were only roughly derived using a two-point Keeling approach, $\delta^{13}\text{C}_{\text{CH}_4}$ values of $-76.5 \pm 1.9 \text{ ‰}$ and $-71.6 \pm 2.0 \text{ ‰}$ for lawns and tussocks, respectively, were within the range observed using chambers in the Fennoscandian Arctic and close to the coherent signature of -71 ‰ observed above these wetlands (Fisher *et al.*, 2017). Carbonate reduction tends to become more important with decreasing availability of fresh OM, with increasing depth in the peat profile (Chasar *et al.*, 2000; Hornibrook *et al.*, 1997; Nakagawa *et al.*, 2002),

and has been linked to latitude, vegetation and pH (Holmes *et al.*, 2015). The dominance of carbonate reduction over acetate fermentation at the Daring Lake meadow is expected given the low pH at this site.

In the current study, neither WT nor VWC consistently explained variation in F_{CH_4} across all temporal and spatial scales. VWC was an important driver when considering spatial variability of the entire wetland (e.g. among microforms), where there was a large range in VWC (coefficient of variation=27%) compared to that of soil temperature (coefficient of variation=16%), demonstrating the idea that variables with large ranges may have greater explanatory power (Moore *et al.*, 2011). At a temperate Canadian bog (Mer Bleue), Moore *et al.* (2011) consistently found an increase in average F_{CH_4} with increasing WT among a) plots and b) among years (peat temperature was the best predictor of F_{CH_4} among months) after averaging all plot F_{CH_4} . The proportion of variation in temporal F_{CH_4} to WT was relatively small in contrast. At Daring Lake, years when VWC or WT values were generally high throughout an entire growing season (e.g. 2013) and temperatures were relatively low, seasonal variations in F_{CH_4} could be more sensitive to temperature-related variables. However, among years, higher WT levels were associated with larger F_{CH_4} during the 2010, 2013, 2016, and 2017 chamber measurement periods. During these periods, WT was generally within 5 cm of the surface. The exceptions included 2008 when high WT occurred at the end of the summer when air was rapidly cooling. Also, in 2016, large F_{CH_4} were observed as the WT dropped and temperatures rose steeply. Similar trends have been reported in several wetland C budget studies as ‘episodic’ fluxes (Bellisario *et al.*, 1990; Strack *et al.*, 2004; Treat *et al.*, 2007). The decrease in WT affects local pressure gradients such that CH_4 is released faster than

it can be consumed by methanotrophs in the overlying oxic peat layers (Windsor *et al.*, 1992). Decreasing WT is also often related to increases in soil and air temperature, enhancing bacterial production and consumption processes. An inverse relationship between EC F_{CH_4} and WT and a positive relationship between EC F_{CH_4} and temperature was observed during periods of both the 2015 and 2017 growing seasons (Figure 14). This was observed by Brown *et al.* (2014) and Goodrich *et al.* (2015) and described in terms of several potential mechanisms such as degassing, enhanced diffusivity and increased production rates as noted above. These studies also noted a lack of ‘recovery’ of F_{CH_4} once WT increased after drawdown due to reduced methanogenesis as a result of a replenishment of alternate electron acceptors and/or reduced substrate availability after longer periods of aerobic decomposition. Moore *et al.* (2011) found that WT drawdown in the late summer had the most profound effect on inter-annual F_{CH_4} as the largest emissions could occur at that time when peat was warmest. At Daring Lake, as at a northern Manitoba wetland (Bubier *et al.*, 2005), WT over the whole growing season had a strong effect on F_{CH_4} and particularly during mid-summer rather than late summer. It is possible that the shorter growing seasons and typically cold weather during late summer at these more northerly peatlands may help explain the smaller importance of late summer (ie. August) WT. The relationship between F_{CH_4} and WT and VWC is therefore dissimilar between spatial and temporal scales in part due to the various mechanisms involving F_{CH_4} production, transport and consumption that are important across space and time.

Table 8. The importance of several abiotic and biotic variables in driving variation in chamber (plot-scale) and EC (ecosystem) F_{CH_4} , represented by the occurrence of significant coefficients in linear mixed effect and regression models and interpretation of CART and PCA analyses.

Variable	Plot-scale	Ecosystem
Moisture-related	Spatial variation (among and within microforms) Seasonal variation, Inter-annual variation**	Seasonal variation*
Temperature-related	Spatial variation (among and within microforms) Seasonal variation	Diel variation, Seasonal variation Inter-annual EC F_{CH_4} **
Vegetation-related	Spatial variation***	
Microform	Spatial variation	Spatial variation
Year	Seasonal variation****	

* inverse relationship with WT **Associations between the variable and the magnitude of yearly mean F_{CH_4} ***Among lawn plots only ****Year:microform interaction drives variability chamber F_{CH_4} (2008-2017)

Temperature-related variables (air temperature, 2, 5, 10 and 20-cm soil temperatures and TD) were important in models describing chamber F_{CH_4} among and within different microforms and over multiple seasons. Temperature was an important driver for over EC-derived F_{CH_4} at the diel scale, over multiple seasons and within seasons where increases in summer mean air and soil temperatures corresponded to increasingly large mean summer F_{CH_4} . The temperature dependence of CH_4 production is well known through effects on microbial activity and on substrate production (through vegetation production), and even on dissolved CH_4 solubility. Although methanotrophy is also a temperature dependent process, this is likely not as important at this site as soil temperature and F_{CH_4} were consistently positively correlated. Although temperature-related variables helped explain overall chamber F_{CH_4} variability, its impact was more important temporally than spatially. For example, higher F_{CH_4} from lawn compared to tussock plots was likely unrelated to increased CH_4 production with temperature as soil temperatures were significantly less at lawn plots. Similarly, negligible emissions from the palsa plots was more readily attributed to unsaturated soils rather than shallower thaw.

Using EC methods, we observed significant diel variation in F_{CH_4} , where daytime F_{CH_4} were associated net radiation and variables driven by radiation such as air temperature, friction velocity and soil temperature. In accordance to conclusions drawn by Moore et al. (2011), where the nature of the relationship between CH_4 and explanatory variables is related to the range of observations, diel variations are linked to radiation, the variable with the greatest possible range given the diel scale. Nighttime F_{CH_4} were on

average 54% lower than daytime F_{CH_4} . Diel variation in F_{CH_4} is reported in several northern (Hanis *et al.*, 2013; Long *et al.*, 2010; Mikkela *et al.*, 1995) and Arctic wetlands (Nakano *et al.* 2000), and is usually associated with temperature (Hanis *et al.*, 2013; Hendriks *et al.*, 2007; Long *et al.*, 2010), friction velocity (Kim *et al.*, 1998) or solar radiation (Kim & Verma, 1998; Kim *et al.*, 1998; Long *et al.*, 2010; Whiting & Chanton, 1996). EC measurements are only possible due to turbulent gas transfer, where lack thereof causes small or negligible F_{CH_4} to be observed. This is unlikely the sole mechanism driving diel variation as the trend persisted when data points were filtered based on low u^* values. A possible mechanism driving diel variation in EC F_{CH_4} is the plant mediated transport of CH_4 driven by convective flow. Soil/air temperature and solar radiation enhance the temperature and humidity gradients responsible for convective flow. Plant-mediated transport, as a mechanism likely contributing to F_{CH_4} variability between multiple lawn plots, could be contributing to F_{CH_4} over time through diel changes in convective flow and has been suggested for other studies (Kim *et al.*, 1998; Whiting & Chanton, 1996). The lack of comparable diel variation in chamber F_{CH_4} is likely due to differences in methodology, as the chamber technique used in this study effectively eliminates turbulent air flow. The changes in microclimate created by the enclosing chamber can also affect temperature gradients related to plant-mediated convective flow. In an alpine wetland in the Tibetan Plateau, diel variations in F_{CH_4} also differed based on the measurement technique (Yu *et al.* 2013). Diel variation existed for both chamber and EC values, but Yu *et al.* (2013) suggested that inhibition of plant-

mediated transport due to ‘chamber effects’, where turbulence and gradient-driven transport are diminished was responsible for differences in F_{CH_4} patterns.

Vegetation characteristics, specifically the presence of vascular plants, can influence wetland F_{CH_4} through increased organic substrate supply and increased transport through aerenchymatous tissues. At Daring Lake, the percent cover of sedges explained significant variation in F_{CH_4} among lawn plots only. However, comparison of SUVA_{254} between lawn and tussock plots indicate SOM quality differences (more readily decomposable organic matter at lawn plots) that could be in part a function of vegetation production and play a role in driving larger F_{CH_4} from lawns. Relationships between vascular plant cover and F_{CH_4} has been shown in many Arctic wetlands (Joabsson *et al.*, 1999; McEwing *et al.*, 2015; Schimel, 1995; Ström *et al.*, 2003). Contrary to the current study, CH_4 emissions from Alaskan wet sedge meadows were less dependent on vascular plant cover at wet sites compared to dry sites, and dry sites with substantial vascular plant cover had comparable F_{CH_4} to wet sites (McEwing *et al.*, 2015). McEwing *et al.* (2015) defined their wet sites as those with WT levels at or above the surface during the measurement period. Lawn plots in the current study are likely more dependent on vascular plant transport of F_{CH_4} due to WT levels that are consistently lower than 5 cm from the peat surface. Although this mechanism was only investigated in 2017, it likely introduces temporal F_{CH_4} variability across the whole period (2008-2017) as it interacts with microform WT and soil moisture.

5.3 Microform as an integrated set of explanatory environmental variables

Microform emerged as an important driver of spatial variability of F_{CH_4} at both the plot and ecosystem level as these pre-determined classifications have characteristic

differences in soil temperature, moisture, nutrient availability, plant composition and productivity and OM decomposition (Bubier *et al.*, 1993) which can be linked to small but important differences in elevation either driven by frost heave (palsas), ice lens degradation (collapse scars), or vegetation habit (tussocks). Such differences in climatic and ecological properties influence F_{CH_4} through CH_4 productivity, transport and/or consumption. The emergence of microform as a variable driving F_{CH_4} over space suggests that these plot classifications can characterize more F_{CH_4} variability than multiple environmental variables combined. Microform has been linked to spatial variability in F_{CH_4} in Canadian boreal peatlands (Bubier *et al.*, 1993), Alaskan wet sedge meadows (Whalen & Reeburgh, 1992) and Minnesota peatlands (Crill *et al.*, 1988), and is important for determining how peatland CH_4 cycling will respond to future climatic changes (Strack & Waddington, 2007). For example, F_{CH_4} differ based on varying responses of microform to changes in WT, vegetation composition and air/soil temperature (Strack & Waddington, 2007), controlling the response of the wetland as a whole to climatic change. Following this idea, changes in percent cover of sedges will likely affect future F_{CH_4} from the Daring Lake meadow due to the high spatial coverage of lawns.

EC F_{CH_4} differed slightly based on upwind source area and the proportion of fen characterized by lawns tussocks and/or ponds or palsas. Despite negligible emissions/small uptake from plot-level palsas, upwind areas with palsas had similar EC CH_4 emissions than to areas dominated by lawns and tussocks and greater emissions than the areas with lawn and tussocks and pond areas. The similarity in F_{CH_4} with direction, despite large microform F_{CH_4} differences observed using chambers, may be due to the

contributions from further upwind. The flux footprint represented 70% of the flux source area such that an additional 30% of the flux may have included more upland terrain where F_{CH_4} are negligible or even reflect small rates of CH_4 uptake (Hayne, 2009). Fluxes from areas with open water surfaces have been investigated by Spott (2003), where during calm conditions the water bodies emitted 2-10 $\text{mg CH}_4 \text{ m}^{-2} \text{ d}^{-1}$ compared to 89 $\text{mg CH}_4 \text{ m}^{-2} \text{ day}^{-1}$ from vegetated surfaces, where differences are largely related to available substrates for methanogenic activity. However, emissions from subarctic wetland ponds may also be much greater (1830 $\text{mg CH}_4 \text{ m}^{-2} \text{ day}^{-1}$; Laurion *et al.* 2010). In the current study, fluxes from ponds were not measured but are likely small in comparison to peatlands dating from pre-Holocene periods (Jones & Yu, 2010), where long term C accumulation results in larger reservoirs of stored CH_4 .

In addition to distinct VWC, WT and vegetation differences, below-ground indices provided further explanation for microform-driven F_{CH_4} variability. As previously stated, differences between lawn and tussock plots were related to SOM quality and rates of methanotrophy. With similar VWC, WT and vegetation characteristics, differences between collapse scar and lawn plots were greatest in their SOM quality, where collapse scars had much higher SUVA_{254} values. The collapse scar plot also had lower dissolved CH_4 than any other plot throughout the 2017 growing season at 5, 15 and 30 cm depths. SOM quality differences at collapse scars could be due to their mechanism of formation, as subsided areas from former peat mounds with segregated layers of ice and mineral soil. Bubier *et al.* (1995) observed large and variable F_{CH_4} from collapse scar sites, ranging from 19-108 $\text{mg CH}_4 \text{ m}^{-2} \text{ d}^{-1}$ and higher than fen sites dominated by hummocks and hollows. Bubier *et al.* (1995) also point out that increased air temperatures and

subsequent peat plateau or palsa degradation can lead to increased F_{CH_4} in discontinuous permafrost zones. Although the Daring Lake meadow is underlain by continuous permafrost, and collapse scar F_{CH_4} were not as large, the dynamics of palsa degradation will likely play a role in long-term CH_4 cycling at the meadow.

Inter-annual variability of chamber F_{CH_4} was large and dominated by changes in lawn and tussock F_{CH_4} related to WT and VWC. As variability among years was highest for tussock plots, it is likely that rates of methanotrophy as affected by WT position was largely responsible for inter-annual variability in chamber F_{CH_4} . Variability in EC F_{CH_4} was comparatively small, although the measurement period represented fewer growing seasons. Mean EC F_{CH_4} increased with increasing mean air and soil temperatures, suggesting that CH_4 productivity is driving inter-annual variation in EC F_{CH_4} . This mechanism does not emerge for chamber F_{CH_4} as both spatial and temporal components of variation are integrated over the multi-year period (2008-2017). This is shown by the significant interaction between year and microform driving variability in chamber F_{CH_4} over all growing seasons.

5.4 Differences between and limitations of plot and ecosystem-scale F_{CH_4} measurement methods

The results of this study indicate a substantial difference between F_{CH_4} measured by EC and manual chamber methods. Weighting chamber F_{CH_4} by area type did not greatly improve the comparison. Chamber fluxes also had much greater variability over space and time relative to those measured using EC, which is expected due to the spatial heterogeneity that is sampled using plot measurements. Relationships between F_{CH_4} and climatic and abiotic variables differed based on methodology although seasonal variation

in both EC and chamber F_{CH_4} was driven by a moisture and/or temperature-related variable, depending on the range and rate of change of both variables given the growing season. Differences between the two techniques are also partially due to the temporal representativeness of the half-hourly EC values compared to chamber measurements that are performed 1-2 times per week. Although Yu *et al.* (2013) showed no significant differences between F_{CH_4} measured by either EC, manual or closed chamber techniques with similar seasonal variation in F_{CH_4} , Sachs *et al.* (2010) found different seasonal variation, peak F_{CH_4} and F_{CH_4} controls using simultaneous EC and closed chamber techniques in Siberian Arctic tundra. EC F_{CH_4} showed no clear seasonal variation while chamber F_{CH_4} decreased towards the end of the growing season. Controls of EC F_{CH_4} included near-surface turbulence, low atmospheric pressure and precipitation while chamber F_{CH_4} were related to air temperature. At a high Arctic wetland meadow at Lake Hazen (Emmertson *et al.*, 2014), both F_{CH_4} magnitudes and seasonal dynamics differed between EC and chamber measurements. The authors in that study suggested the differences were due to the EC measurements representing a much wetter surface compared to chambers which were situated at drier margins of the wetland.

Large uncertainties are introduced when up/down scaling F_{CH_4} between plot and ecosystem levels. This is further aggravated by the difficulty in characterizing episodic flux (e.g. ebullition), which is an important method of CH_4 transport (Windsor *et al.*, 1992) but is not typically captured by chamber measurements. Ebullition measurements, the quantification of CH_4 -containing bubbles from porewater and within the peat profile, were not performed as part of this study.

Another limitation of this study relates to the measurement methods. The EC

method requires steady-state atmospheric conditions, homogeneous surface characteristics and flat terrain for accurate measurements that allow for the comparison of turbulent exchange of an entity to biological consumption/production rates (Baldocchi, 2003). The underestimation of nighttime flux was addressed by filtering data with friction velocities less than 0.1 m s^{-1} , but anomalies related to the heterogeneous wetland surface and surrounding upland terrain remain an issue. Limitations of the chamber method include repeated measurements and soil/peat disturbances that may cause an over-estimation of fluxes which may help explain differences between EC and chamber values. Chamber measurements also represent a distinct moment in time throughout the daytime only. However, the lack of temporal variation in chamber F_{CH_4} over a 24-hour period suggested that these discrete measurements could approximate daily average values. When comparing F_{CH_4} between chamber and EC-derived values, challenges arose when representing the EC footprint with plot measurements. Much of the area of the footprint was not measured using the chamber technique and provides a potential explanation for the inconsistencies between EC and chamber F_{CH_4} . Although F_{CH_4} values were not comparable between methods, the use of both EC and chamber methods allowed for the identification of many important mechanisms driving F_{CH_4} over both time and space.

Finally, the current study focused on growing season fluxes only. Although F_{CH_4} is expected to be low throughout winter, there may be CH_4 bursts associated with active layer thaw and freeze in the spring and fall, respectively that are important to year-round estimates of CH_4 emissions (Mastepanov *et al.*, 2008; Pirk *et al.*, 2015).

6 Chapter: Conclusion

There was large F_{CH_4} variability over time and space at the Daring Lake Arctic wet sedge meadow over the growing seasons of 2008 to 2017 attributed to differences in microform, VWC, WT, temperature, vegetation composition, radiation and year. Seasonal averages varied between 118-277 $\text{mg CH}_4 \text{ m}^{-2} \text{ d}^{-1}$ and 40-52 $\text{mg CH}_4 \text{ m}^{-2} \text{ d}^{-1}$ for chamber and EC values, respectively. Relationships between EC and chamber F_{CH_4} and climatic and abiotic variables included some similar drivers over time and space. Both EC and chamber F_{CH_4} variability was driven by microform over space, which could be linked to differences in vegetation (ie. presence of sedges) and moisture status. Over time, both EC and chamber F_{CH_4} variability was driven by moisture and/or temperature-related variables. Chamber F_{CH_4} variability was linked to variations in SOM quality and percent cover of sedges, through varying rates of methanotrophy, CH_4 production and plant-mediated transport, respectively.

The importance of moisture and/or temperature related variables in driving F_{CH_4} variability was dependent on the range and rate of change of each variable given the scale, where varying rates of change can introduce confounding effects of multiple competing mechanisms. Variables with large ranges of values (VWC over space, radiation over 24 hours) explained larger proportions of variability in F_{CH_4} than others. Inter-annual variability in F_{CH_4} was related to VWC/WT and soil temperature for chamber and EC methods, respectively. Both moisture and temperature-related variables are important for driving F_{CH_4} over large time scales, yet significant relationships vary based on methodology and the spatial and temporal representativeness of the method. The combination of chamber and EC methods allowed for an investigation of a variety of

mechanisms acting over time and space that would be difficult to assess with either method alone. Although chamber and EC measurements are integrating different sized areas, it is unclear if comparing these values is a true comparison of scale. Changes to the sampling design would improve the spatial representativeness of chamber measurements, potentially helping to identify if the discrepancies between chamber and EC F_{CH_4} are related to scale or the method itself.

Temporal dynamics in microform across the wetland will likely play a role in long-term C cycling and CH_4 emissions, where larger F_{CH_4} can be expected from continued peat degradation at the Daring Lake wet sedge meadow once collapse scars develop into lawns. When predicting future F_{CH_4} from Arctic wetlands, we can generally expect higher F_{CH_4} with warmer and wetter conditions. Predictions of future F_{CH_4} require accurate representation and integration of multiple, sometimes competing, processes that contribute to the spatial and temporal variability of wetland CH_4 emissions.

Appendices

Appendix A

Table A-1. Yearly mean Tussock F_{CH_4} , volumetric water content (VWC) and peat temperature (2 cm depth) with corresponding standard error. Median F_{CH_4} values are noted before mean values.

Year	F_{CH_4} (nmol m ² s ⁻¹)	VWC (%)	T _{2cm} (°C)
2008	38.5, 39.4 ± 2.5	63.3 ± 2.3	14.7 ± 0.6
2009	52.0, 46.0 ± 3.1	41.4 ± 1.8	14.1 ± 0.4
2010	161.0, 158.6 ± 11.2	85.9 ± 2.4	18.4 ± 1.0
2012	33.5, 42.6 ± 4.7	39.6 ± 2.9	19.1 ± 0.7
2013	107.2, 122.6 ± 10.5	85.3 ± 0.7	14.6 ± 0.9
2014	85.0, 85.1 ± 8.0	84.6 ± 0.9	15.5 ± 0.8
2015	75.3, 82.1 ± 7.3	84.8 ± 0.9	12.3 ± 0.5
2016	114.6, 132.1 ± 13.5	81.4 ± 0.7	12.6 ± 0.6
2017	119.2, 109.7 ± 6.1	55.2 ± 1.0	13.2 ± 0.4

Table A-2. Yearly mean lawn F_{CH_4} , volumetric water content (VWC) and peat temperature (2 cm depth) with corresponding standard error. Median F_{CH_4} values are noted before mean values.

Year	F_{CH_4} (nmol m² s⁻¹)	VWC (%)	T_{2cm} (°C)
2008	104.0, 104.3 ± 4.2	89.5 ± 1.3	14.7 ± 0.6
2009	83.6, 91.9 ± 4.6	88.6 ± 0.8	13.1 ± 0.4
2010	202.3, 199.3 ± 11.3	91.5 ± 1.3	18.3 ± 1.0
2012	82.1, 85.6 ± 5.8	75.9 ± 2.1	17.7 ± 0.5
2013	142.5, 152.0 ± 8.3	87.5 ± 0.5	13.3 ± 0.7
2014	97.6, 104.7 ± 6.0	86.9 ± 0.4	14.1 ± 0.6
2015	102.2, 103.0 ± 6.2	87.1 ± 0.5	11.8 ± 0.4
2016	120.8, 152.6 ± 21.0	81.6 ± 0.9	11.0 ± 0.4
2017	140.6, 142.8 ± 6.6	71.1 ± 1.5	12.5 ± 0.4

Table A-3. Yearly mean collapse scar F_{CH_4} , volumetric water content (VWC) and peat temperature (2 cm depth) with corresponding standard error. Median F_{CH_4} values are noted before mean values.

Year	F_{CH_4} (nmol m ² s ⁻¹)	VWC (%)	T _{2cm} (°C)
2009	2.8, 2.8 ± 0.8	73.2 ± 2.3	13.9 ± 0.5
2010	3.4, 3.3 ± 0.3	81.3 ± 1.1	19.6 ± 0.8
2015	11.9, 12.9 ± 4.8	62.3 ± 4.9	17.0 ± 1.1
2016	28.2, 29.1 ± 9.8	62.9 ± 4.2	15.2 ± 1.2
2017	17.2, 18.6 ± 6.0	63.5 ± 3.5	17.4 ± 0.8

Table A-4. Yearly mean palsa F_{CH_4} , volumetric water content (VWC) and peat temperature (2 cm depth) with corresponding standard error. Median F_{CH_4} values are noted before mean values.

Year	F_{CH_4} (nmol m ² s ⁻¹)	VWC (%)	T _{2cm} (°C)
2009	0.1, 0.8 ± 0.4	31.2 ± 1.4	13.5 ± 0.4
2010	0.2, 3.3 ± 0.3	27.7 ± 1.1	18.9 ± 1.1
2015	-0.3, -0.4 ± 0.2	32.4 ± 2.2	20.5 ± 1.5
2016	-1.2, -1.3 ± 0.3	37.8 ± 3.4	20.1 ± 1.3
2017	-0.3, 0.6 ± 0.6	32.7 ± 3.8	20.0 ± 1.0

Table A-5. July and August mean EC F_{CH_4} , net radiation, WT, air and peat temperature (20-cm depth) with corresponding standard deviation for 2015-2017 growing seasons. Median F_{CH_4} values are noted before mean values.

Year	F_{CH_4} (nmol m ² s ⁻¹)	T _{air} (°C)	T _{20cm} (°C)	Q*	WT (cm)
2015	28.4, 33.4 ± 2.4x10 ⁻²	12.6 ± 7.1	7.1 ± 4.5	125 ± 177	-12.1 ± 6.0
2016	37.7, 39.1 ± 2.1x10 ⁻²	13.9 ± 7.0	7.5 ± 3.6	154 ± 177	-15.9 ± 7.8
2017	37.6, 42.0 ± 2.6x10 ⁻²	15.2 ± 6.9	7.6 ± 4.0	138 ± 174	-12.3 ± 4.5

Table A-6. Linear mixed model results testing for differences in porewater samples between microform, depth and time where plot was treated as a random effect.

Variable	Fixed effects	DF	t-value	p
TN	microform	6	1.9	>0.05
	depth	6	-1.7	>0.05
	date	5	-0.7	>0.05
	microform:date	5	2.2	>0.05
	microform:depth	5	-1.9	>0.05
	depth:date	5	1.7	>0.05
	[CH ₄]	microform	6	0.8
depth		6	-0.6	>0.05
date		5	-0.2	>0.05
microform:date		5	2.3	>0.05
microform:depth		5	-0.8	>0.05
depth:date		5	0.6	>0.05
DOC		microform	6	-0.4
	depth	6	-0.1	>0.05
	date	5	-0.5	>0.05
	microform:date	5	1.6	>0.05
	microform:depth	5	0.4	>0.05
	depth:date	5	0.1	>0.05
	SUVA ₂₅₄	microform	6	0.6
depth		6	-1.1	>0.05
date		5	-1.4	>0.05
microform:date		5	-8.7	<0.001
microform:depth		5	-0.6	>0.05
depth:date		5	1.1	>0.05
$\delta^{13}\text{C}_{\text{CH}_4}$		microform	6	-0.1
	depth	6	0.2	>0.05
	date	5	-0.1	>0.05
	microform:date	5	-1.3	>0.05
	microform:depth	5	0.1	>0.05
	depth:date	5	-0.2	>0.05
	$\delta^{13}\text{C}_{\text{CO}_2}$	microform	6	-0.9
depth		6	0.8	>0.05
date		5	-0.2	>0.05
microform:date		5	1.7	>0.05
microform:depth		5	0.9	>0.05
depth:date		5	-0.8	>0.05

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