

Carbon fluxes from high-centred polygonal terrain in the Northwest Territories

by

Abra Frances Martin  
BAS., University of Guelph, 2012

A Thesis Submitted in Partial Fulfillment  
of the Requirements for the Degree of

MASTER OF SCIENCE

in the School of Environmental Studies

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**Supervisory Committee**

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**Supervisor**

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**Departmental Member**

Dr. Elyn R. Humphreys, Carleton University  
**Outside Member**

## Abstract

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Northern regions account for approximately 30% (1035 Pg) of the world's soil organic carbon (SOC). Much of this carbon is currently stored in permafrost soils, which are vulnerable to increasing air and ground temperatures. Permafrost landscapes rich in ground ice, such as high-centred polygonal terrain, are likely to be highly vulnerable to thaw. Degradation of ice wedges in high-centred polygonal terrain causes increased moisture and ground temperatures. These environmental controls are likely to have a large impact on carbon cycling in this terrain type. My M.Sc. research combined both lab and field-based analyses to investigate current and potential carbon emissions from high-centred polygonal terrain in the Tuktoyaktuk Coastlands.

To estimate the magnitude of future emissions from this terrain type I incubated six permafrost cores collected at two sites. Peat cores from four depths were each incubated under four conditions (cold anaerobic, warm anaerobic, cold aerobic, warm aerobic). The observation that carbon mineralization rates do not vary with depth demonstrates that the soil carbon liberated from permafrost in high-centred polygonal terrain will not be limited by SOC quality. This experiment also shows that emission rates will be moderated by temperature and moisture levels, and will be primarily in the

form of CO<sub>2</sub>. To examine the impact of ice-wedge thaw on carbon emissions in high-centred polygonal terrain, we combined opaque chamber measurements of flux and estimates made from water samples using a gas diffusion model. Field sampling at two sites contrasted carbon emissions from polygon centres (n=18), wet troughs (n=18) and ponds (n=20). We also measured ground temperature and soil moisture using thermistors and a moisture sensor. Our field results demonstrate that ice-wedge degradation results in increased ground temperature, deeper active layers, and increased CO<sub>2</sub> and CH<sub>4</sub> emissions. Contrary to our expectations, CO<sub>2</sub> emissions were not limited by waterlogged conditions, demonstrating the importance of anaerobic CO<sub>2</sub> production. Our field measurements demonstrate that increasing temperatures are correlated with rising CO<sub>2</sub> emissions in aerobic environments, and rising CO<sub>2</sub> and CH<sub>4</sub> emissions in anaerobic environments. Taken together, these two studies demonstrate that as ground temperatures increase in high-centred polygonal terrain, carbon emissions from ecosystem respiration are likely to increase.

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## **Dedication**

This thesis is dedicated to H. Stuart Innes who valued education “in the widest sense”.

## Chapter 1 - Introduction

Northern regions hold approximately 30% of the world's belowground organic soil carbon (Hugelius et al. 2014). Currently, much of this carbon is stored in permafrost soils, which are sensitive to warming temperatures (Schuur et al. 2008). Climate change is projected to increase the average global surface temperature by up to 5.5°C by 2100, with temperature changes being most pronounced at northern latitudes (scenario RCP8.5, IPCC 2013). Global surface temperatures have already increased 0.89°C over the 1901-2012 period (Stocker et al. 2013), with these increases being amplified across the Arctic (Serreze et al. 2000). In Alaska and Siberia increases in average temperature between 1954 to 2003 have been in the range of 2 to 3°C (Hassol 2005). In the Mackenzie Delta region rising temperatures have resulted in more than a 3°C increase in annual mean air temperature, and an increase of 1.5-2.5°C in permafrost temperature since 1970 (Burn and Kokelj 2009). Increasing permafrost temperatures are expected to have major implications for the global climate system. Warming permafrost could release as much as 174 Pg of carbon to the atmosphere by 2100 and could result in an additional 0.42°C of warming by 2300 (Schuur et al. 2015).

Much of the soil carbon stored in permafrost is located in peatland ecosystems (Hugelius et al. 2014), which are common across much of the Arctic and subarctic. In these ecosystems, low temperatures and acidic soils result in primary productivity rates exceeding those of decomposition. This leads to carbon storage in partially decomposed organic matter known as peat. Historically, peatland ecosystems have acted as significant carbon 'sinks' (Callaghan et al. 2004). However, as environmental conditions are altered due to climate change the balance between productivity and decomposition rates may

change, shifting peatlands from carbon sinks to sources (Hobbie et al. 2002; Schuur et al. 2008).

High-centred polygonal terrain is a form of patterned ground common across the low Arctic landscape that hosts deep peat deposits. These peatlands have high ground ice content in the form of ice wedges, which makes them sensitive to increases in ground temperature (Jorgenson et al. 2006). Ice wedges form when cold winter conditions cause the ground to crack and in the spring snow melt water enters these cracks and refreezes. Over multiple years, this phenomenon creates large ice wedges in the ground that can have a width of several metres (Mackay 1989; Mackay 1984). The presence of ice wedges in the landscape creates a network of depressions (known as troughs), which divide the landscape into polygons. Based on the micro-position of the polygon centre in relation to the trough, polygons can be classified as either low-centred or high-centred (MacKay 2000). Our research focuses on high-centred polygons (Fig. 3-1).

Recent evidence, from remote sensing of sites in Alaska, shows that temperature increases are leading to ice wedge degradation and thermokarst (ground subsidence due to permafrost thaw). According to Jorgenson et al. (2006), thermokarst due to ice wedge degradation has the potential to affect 10-30% of the lowland Arctic landscape. Ice-wedge degradation results in increases in surface moisture, active layer depth, mean annual ground temperature and ground subsidence (Jorgenson et al. 2006). High moisture levels and the accompanying latent heat effects cause longer freeze-back durations in high-centred polygonal terrain, which has resulted in some highly degraded ice wedges not refreezing over winter (Kokelj et al. 2014). Melt ponds from degraded ice wedges

could also affect the surrounding polygonal peat through lateral heat flow (Jorgenson et al. 2010).

These changes are likely to have significant impacts on the environmental controls of carbon cycling (Schuur et al. 2008; Lee et al. 2010; Kokelj and Jorgenson 2013). As the effects of increasing temperature and moisture are not independent (Hobbie et al. 2000), they need to be considered in tandem to achieve a comprehensive understanding of how changing environmental controls will affect carbon cycling.

Higher temperatures may result in higher decomposition rates, exceeding any gains due to increased primary productivity (Mack et al. 2004). However, high moisture levels may lead to a switch from aerobic to anaerobic decomposition, resulting in lower overall emission rates but higher methane (CH<sub>4</sub>) emissions (Schlesinger and Bernhardt 2013b; Davidson and Janssens 2006; Funk et al. 1994; Elberling et al. 2013).

Understanding the nature of these changes is critical because CH<sub>4</sub> has 25 times greater warming potential than carbon dioxide (CO<sub>2</sub>) over a 100 year time period (IPCC 2013).

To date, the impact of ice wedge degradation on carbon flux has not been well quantified in polygonal terrain, with the majority of studies examining low-centre polygonal terrain in Alaska (Billings et al. 1982; Zona et al. 2011) and Siberia (Wagner et al. 2003; Corradi et al. 2005). The overall goal of my MSc research is to increase our understanding of the effects of ice wedge degradation on carbon emissions in high-centred polygonal terrain in the Tuktoyaktuk Coastlands.

To examine the effects of both temperature and moisture on CO<sub>2</sub> and CH<sub>4</sub> emissions in high-centred polygonal terrain we conducted a 1) field study and 2) a laboratory experiment. In this thesis these two studies are presented in stand-alone

chapters (Chapters 2 and 3). This research is particularly significant because high-centred polygonal terrain is abundant in the study region, covering up to 37% of the landscape in some regions (Steedman 2014) and continued increases in ground temperatures are expected to drive additional thermokarst (Stocker et al. 2013).

In Chapter 2 of this thesis, we examine the research question: **What is the potential contribution of currently frozen peat in polygonal terrain to future carbon emissions?** This chapter examines the decomposability of soil carbon currently frozen in high-centred polygonal terrain near Tuktoyaktuk. To explore this question, we incubated soil from various depths at two different temperature and moisture conditions in a lab at the University of Victoria.

In Chapter 3 of this thesis, we examine the research question: **What is the effect of ice wedge degradation in high-centred polygonal terrain on carbon (CO<sub>2</sub> and CH<sub>4</sub>) emissions in the Tuktoyaktuk Coastlands?** To explore this question we quantified CO<sub>2</sub> and CH<sub>4</sub> emissions using in-situ chamber measurements over different degradation classes at two high-centred polygons sites in the subarctic and Arctic. An automated CO<sub>2</sub> exchange (ACE) system was also used to characterize hourly flux from a polygonal centre at the Arctic site. These carbon flux measurements were linked to temperature and moisture measurements to characterize the effect of temperature and moisture on carbon flux.

In Chapter 4 of this thesis, I examine how the two components of my research complement each other and discuss the overall significance of this research. In this chapter I also present several avenues for future research such as the need to better

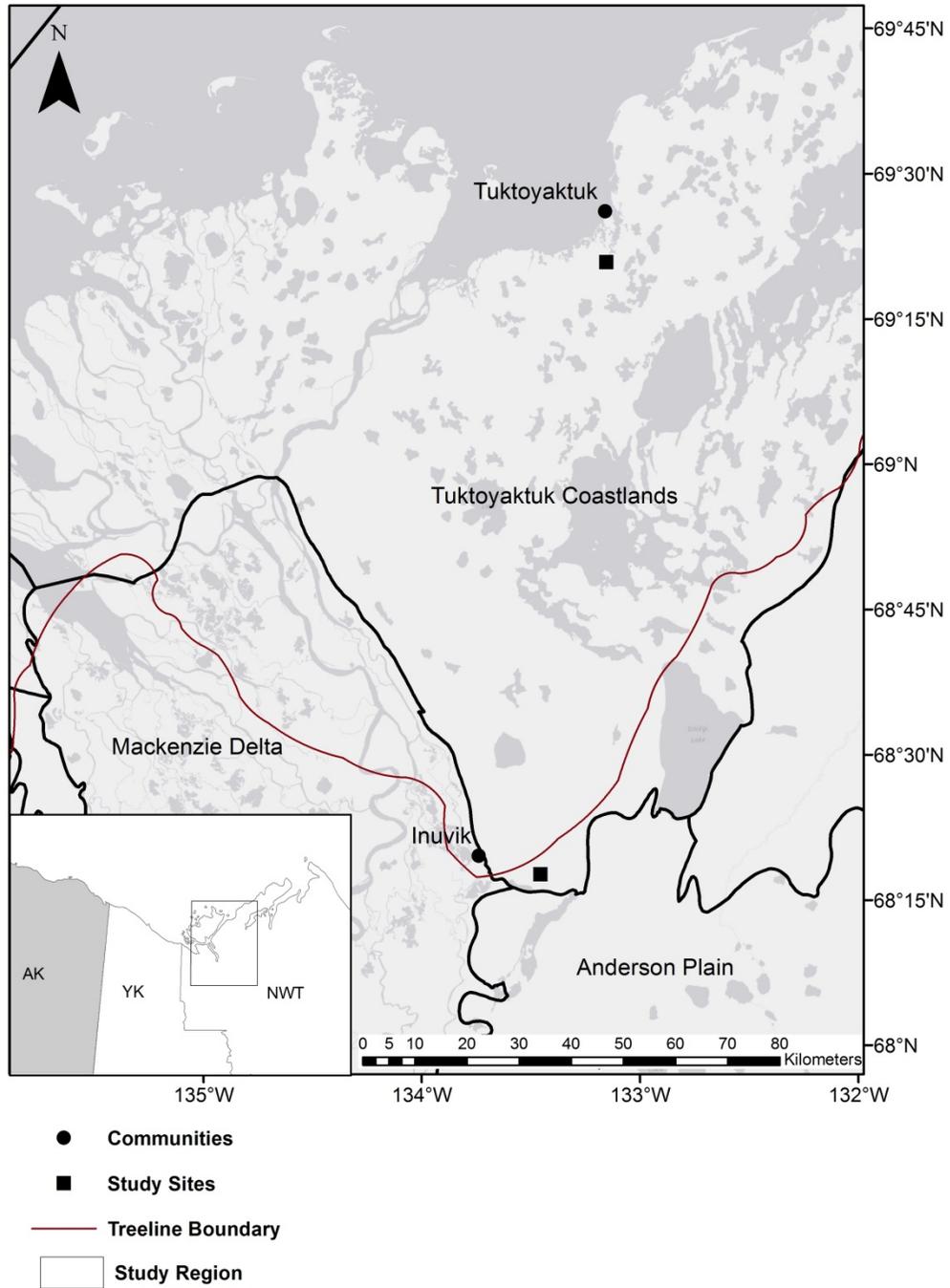
characterize carbon quality within sites among degradation classes, and across more sites in the region.

The remainder of this introduction provides key background of permafrost dynamics and the environment and glacial history of the study area.

## **I. The Mackenzie Delta – An overview**

### **i. Physiography**

Our study sites are located in the Tuktoyaktuk Coastlands (see Fig.1-1). This low-lying area rarely exceeds 60 m above sea level. It stretches from the eastern edge of the Mackenzie Delta to the Amundsen Gulf. The area is characterized by rolling hills comprised of glacial deposits and areas of lacustrine plain (Rampton 1988). The terrain is underlain by ice-rich permafrost and characterized by periglacial landforms such as pingos and ice wedge polygons (Burn 2010).



**Figure 1-1.** Map of the study area showing study sites, nearby communities, and ecoregion boundaries. The red line shows the limit the 1:1 tree: upland tundra cover ratio as mapped by (Timoney et al. 1992).

## **ii. Climate**

The climate of the Mackenzie Delta region is typical of the southern end of the continental continuous permafrost zone (Burn and Kokelj 2009). The climate shows a gradient between Fort McPherson (mean annual air temperature:  $-7.3^{\circ}\text{C}$ , mean total precipitation: 310 mm) and Tuktoyaktuk (mean annual air temperature:  $-9.8^{\circ}\text{C}$ , mean annual precipitation: 151 mm) (Burn 2010). This climatic gradient also strongly influences regional vegetation, which is characterized by two transitions. In the southern part of the study area open spruce woodlands with thick organic deposits transition to low shrub tundra in the north. In the northern part of the study area low shrub communities transition to tundra dominated by dwarf shrubs (Fraser et al. 2014; Lantz et al. 2013; Lantz et al. 2010). Rising temperatures in addition to disturbances such as fire are resulting in the northwards advance of shrubs. The presence of shrubs creates a positive feedback loop, as shrub-dominated sites demonstrate lower albedo and deeper snow packs, which increase ground temperatures and contribute to proliferation of shrubs (Lantz et al. 2013).

## **iii. Surficial Geology**

Clastic and carbonate sedimentary rock from the Pleistocene epoch form the bedrock of the Mackenzie Delta region (Dixon, Dietrich, and McNeil 1992; Rampton 1988). However, the Wisconsinan glaciation period had a significant impact on the

surficial geology of the region. At its maximum extent thirty thousand years ago (ca. 30 ka BP), the Laurentide Ice Sheet extended westward to the lowlands beside the Mackenzie river (Evans 2005) and was bordered by the Mackenzie and Richardson mountains (Duk-Rodkin and Lemmen 2000). By twenty two thousand years ago (22 ka BP) the ice sheet had begun to retreat (Duk-Rodkin and Lemmen 2000), with the area around Inuvik becoming ice-free around 14 500 years ago (Ritchie 1985). As the glacier retreated, it left till deposits that cover much of the region (Duk-Rodkin and Lemmen 2000). Till is a composite of different sizes of material (from clay-size to boulder-size). The study area is within the zone of continuous permafrost that is composed of fine grained soils, which generally contain ground ice. At the 1:1 000 000 scale, the majority of the areas between Inuvik and Tuktoyaktuk is mapped as having thick morainal deposits while areas around Tuktoyaktuk have alluvial, lacustrine and glaciofluvial deposits as well (Aylsworth et al. 2000).

## **II. The development of polygonal peatlands**

Permafrost thaw during the Holocene warm interval resulted in the development of thermokarst lakes. The subsequent drainage of these lakes has produced thousands of lacustrine basins which host organic deposits (Murton 1996). Due to warmer temperatures, thermokarst activity was particularly intense between 10 000 and 9 000 years ago (Rampton 1988), with numerous thermokarst basins being created in the Tuktoyaktuk Coastlands between 13-8 ka, which now host polygonal peatlands (Murton 1996). Polygonal peatlands begin to form in winter, when cold temperatures result in

thermal contraction originating at the top of the permafrost (Mackay 1989). In the spring, melt-water flows into these cracks and refreezes. While ice wedge growth begins immediately, multiple years of this contraction cracking can produce large ice wedges (Mackay 1974).

Organic deposits, such as in the lacustrine basins in the Tuktoyaktuk Coastlands, are more susceptible to continued ice-wedge growth due to two main factors. First, organic soils have shallower active layers than mineral soils. This is due to the low thermal conductivity of thawed peat, the high latent heat in saturated frozen peat, and partitioning of available energy to evaporation from the surface mosses (Kokelj et al. 2014). As the permafrost in peatlands is located closer to the surface than in mineral soils, it is subject to lower temperatures during the winter. Second, saturated organic soils when frozen promote ground heat loss and a more rapid decline in ground temperature compared to fine grained soils where the latent heat effects are distributed over a range of temperatures below 0°C due to their high unfrozen water content (Kokelj et al. 2014). Furthermore, frozen organic soils are also more susceptible to thermal cracking due to their higher volumetric water content caused by their low bulk density and high porosity. Ice has a high thermal-contraction coefficient and thus the high-ice content in organic soils makes them more likely to experience thermal cracking (Andersland and Ladanyi 2004).

Ice wedge polygons can be classified in multiple ways. The main distinctions are between low-centre and high-centre polygons and direction of ice wedge growth. Low-centre polygons have low centres, which generally host ponds and have raised rims. High-centred polygons have raised centres that are relatively well-drained (Zoltai and

Tarnocai 1975). Low-centred polygons contain less peat than high-centred polygons (Zoltai and Tarnocai 1975) and are considered to be younger features that can evolve into high-centred polygons as peat accumulates in the centre (MacKay 2000) or as troughs subside (Peterson and Billings 1980). Ice-wedge growth is classified based on the direction of growth into three categories: 1) epigenetic; 2) syngenetic; and, 3) anti-syngenetic. Epigenetic ice wedges grow wider, occur where the ground is stable, and has little or no removal or addition of material (i.e. erosion, or peat formation). Syngenetic ice wedges grow wider and upwards and occur when there is permafrost aggradation, for example from fluvial sedimentation. Anti-syngenetic wedges grow downwards and are found on hillsides where the tops of the wedges are degraded by erosion. In the case of anti-syngenetic wedges, these wedges grow downwards at approximately the same rate as the top of the ice wedge is degraded (Mackay 1990; Mackay 1995; MacKay 2000). This thesis will focus on high-centre polygons with syngenetic ice wedges.

Remote sensing has demonstrated that high-centred polygonal terrain is not uniformly distributed throughout the Mackenzie Delta area. While ice wedges may exceed 50% of the earth materials in the top 1-2 m of soil (Pollard and French 1980), Kokelj et al. (2014) found that in the Tuktoyaktuk Coastlands, polygonal peatlands constituted up to 40% of the landscape and ice wedges usually exceeded 3 m-width. However, further south, there are fewer ice wedges and they seldom exceed 2 m in width. In the southern subarctic forest, relict ice wedges are only found in peatlands. Steedman (2014) confirmed this pattern of variation in the region of the Tuktoyaktuk Coastlands where high-centred polygonal terrain covered up to 10% of the landscape but with high-density areas in the north exhibiting densities up to 37%. This higher abundance of ice-

wedge polygons is correlated with a higher abundance of lacustrine sediments, a colder climate, and a thinner snow cover.

### **III. Permafrost Dynamics**

#### **i. Definition of permafrost**

Permafrost is defined by thermal and temporal criteria rather than soil type. It is characterized as ground (soil or rock) that maintains a continuous temperature at or below freezing ( $0^{\circ}\text{C}$ ) for at least two years. Permafrost can be categorized into zones by coverage of landscape by frozen ground: continuous ( $>90\%$ ), discontinuous (50-90%), sporadic (10-50%), and isolated (0-10%). Permafrost represents 23.9% of the total exposed land area in the Northern hemisphere (Zhang et al. 1999). The depth of zero annual amplitude (10 to 200 m) is the depth at which permafrost temperature does not show seasonal variation. Ground temperatures from this depth can be used as an indicator of the climate regime. Inter-annual temperature variation decreases with depth, which allows decadal trends to be interpreted from deep permafrost temperature data (Romanovsky et al. 2002).

#### **ii. Factors that influence permafrost temperature**

Ground temperature is a result of the balance of heat flux between the air and the ground. In its most basic form, this is the net exchange of radiation between the surface

and the atmosphere. This exchange is the sum of latent heat flux (condensation, evaporation), sensible heat flux (flux of heat by convection and wind, from the ground to the air), and ground heat flux (through conduction, from soil or rock to the surface). The magnitudes of these fluxes vary by location and over time. Local conditions such as type of vegetation, moisture levels, organic deposits, and depth of snow have a large impact on this energy exchange. Climate change impacts on moisture levels, snow depth, and vegetation, for example, will alter these heat fluxes and this energy exchange and thus result in changes to ground temperatures (Williams and Smith 1989).

Due to increasing air temperatures, permafrost temperatures at the depth of zero annual amplitude are warming (Osterkamp and Romanovsky 1999; Romanovsky et al. 2010). Lachenbruch and Marshall (1986) found that surface permafrost temperature increased by 2-4°C during the early to mid-20<sup>th</sup> century. However, warming permafrost is not a uniform process and is not solely influenced by rising temperature. Topography, hydrology, vegetation, geology and disturbance contribute to the distribution and characteristics of permafrost (Osterkamp 2007). These factors allow permafrost to persist at mean annual air temperatures (MAAT) as high as 2°C and to degrade at MAAT as low as -20°C (Jorgenson et al. 2010). A recent synthesis found that colder permafrost is warming at a faster rates than warmer permafrost (with temperatures closer to 0°C), which was attributed to latent heat effects (Romanovsky et al. 2010).

Latent heat is the energy absorbed or released by a substrate when it undergoes a phase change. For ice to thaw, latent heat is absorbed by the substrate from the surroundings. The effects of latent heat are much more prominent in permafrost soils closer to 0°C, as warming permafrost soils near 0°C result in a phase shift (and the

absorption of latent heat), whereas the lack of a phase shift in colder soils, means latent heat effects are less significant. Thus, latent heat effects allow permafrost to persist at temperatures near zero while colder permafrost shows greater changes in temperature with the same increases in heat (Smith et al. 2010).

Topography can also contribute to permafrost warming as it allows for water and snow to pool in depressions on the landscape (Mackay 1993). Surface water, including water from ice wedge degradation, provides an important positive feedback. Due to its low (~5%) albedo, surface water can absorb heat and increase temperatures to approximately 10°C above MAAT (Jorgenson et al. 2010). Furthermore, organic soils are generally poorly drained and have higher thermal heat capacities than well-drained, gravelly soils. This means that organic soils take longer to cool down in winter and to heat up in summer, creating a “thermal offset” (Burn and Smith 1988; Jorgenson et al. 2010b). In the context of changing climatic conditions, thermal offset may result in the persistence of permafrost at ground surface temperatures greater than 0°C (Osterkamp and Romanovsky 1999).

Snow depth significantly influences ground thermal regimes as it acts as a barrier to convective heat loss during the winter and thus insulates the ground (Nobrega and Grogan 2007; Osterkamp 2007). Snow has the opposite effect in the spring, as it slows the warming of the ground in spring. However, overall snow increases the mean annual ground temperature by as much as 2 to 7°C (Zhang et al. 1997). Other factors that influence winter ground temperatures are thaw season length, the interactions of snow with wind, and the density of the snow (Zhang et al. 1997).

Vegetation composition also plays a role in permafrost ground temperatures. In the winter, the presence of shrubs allows snow to accumulate and insulate the ground. Snow collects in shrubs, increasing snow depth by an estimated 10-20%, resulting in increased spring runoff and acting as a better insulator per unit thickness than non-shrub patches (Sturm et al. 2001; Sturm et al. 2005). In the summer, shrubs may shade the ground resulting in lower ground temperatures (Williams and Smith 1989), however, shrub presence has also been shown to experimentally reduce summer permafrost thaw (Blok et al. 2010).

As ice-rich permafrost thaws, ground subsidence can create disturbances, which have a large effect on ground thermal regimes (Williams and Smith 1989). Thermokarst disturbance can also result in major changes to surface topography and ecosystems dynamics due to changes in moisture (Jorgenson et al. 2001; Fortier et al. 2007; Grosse et al. 2011). Ice-rich permafrost, such as ice-wedge terrain, may transform into thermokarst even under moderate climate warming scenarios (Jorgenson et al. 2006).

### **iii. Permafrost active layer**

The top-layer of soil in permafrost regions, which thaws and refreezes every year, is called the “active layer.” The active layer plays a critical role in the carbon cycling function of the landscape as it influences plant-rooting depth and hydrological processes (Schuur et al. 2008). The thickness of the active layer, which varies in the continuous permafrost zone from tens of centimetres to 2 m, influences the amount of soil organic matter exposed to above zero temperatures.

The active layer has been shown to respond to short-term fluctuations in temperature (i.e. summer air temperature) (Smith et al. 2010) and has been deepening with warmer summer temperatures. Burn and Kokelj (2009) found that active layer depths increased by an average of 8 cm at Illisarvik on Richards Island from 1983 to 2008. Another factor that has been found to influence active layer depth is increased soil moisture, which favours vegetation growth (Mackay 1995; Zona et al. 2012). This vegetation results in the shading of the ground surface, which decreases active layer depths (Mackay 1995). Thus, active layer levels are not solely controlled by increasing air temperature.

Increasing permafrost temperatures are not always correlated with deepening active layers. For example, if temperature increases occur during the winter season, active layer depth may not change (Osterkamp 2007). However, changing snow depths could be responsible for offsetting increasing winter temperatures (Mackay 1995).

#### **iv. Linking permafrost thaw to the carbon cycle**

Permafrost thaw will result in changing environmental conditions, such as moisture levels and ground temperatures. These environmental conditions have a direct impact on carbon cycling as both temperature and moisture are primary controls on carbon cycling (Hobbie et al. 2000). Historically, northern peatland ecosystems have acted as carbon 'sinks' due to productivity rates exceeding those of decomposition (Callaghan et al. 2004). However, changes to environmental conditions due to permafrost thaw, and the thawing of previously frozen soil organic carbon (SOC), means that these ecosystems

could become net sources of carbon to the atmosphere (Hobbie et al. 2002). Due to the large amount of soil carbon stored in permafrost, the ways that carbon cycling dynamics respond to permafrost thaw may have an important impact on concentrations of CO<sub>2</sub> and CH<sub>4</sub> in the global atmosphere (Schuur et al. 2008). Thus, understanding the effects of permafrost thaw on carbon cycling will contribute to our understanding of future climate warming.

## **Chapter 2 – Potential CO<sub>2</sub> and CH<sub>4</sub> emissions from high-centred polygonal terrain in the Tuktoyaktuk Coastlands, NT**

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## Introduction

Northern soils hold 1305 Pg (uncertainty range: 1140-1476 Pg) of the world's soil organic carbon (SOC) (Hugelius et al. 2014). Currently, much of this SOC (147 Pg) is frozen in the permafrost of northern peatlands (Tarnocai et al. 2009; Hugelius et al. 2014). However, this SOC may be vulnerable to mineralization if thawed (Schuur et al. 2015). Rising air temperatures at high latitudes have coincided with significant increases in permafrost temperature over the past several decades (Smith et al. 2010; Serreze et al. 2000). It is widely anticipated that increasing ground temperature will result in active layer deepening and thermokarst development (ground subsidence due to permafrost thaw) (Kokelj and Jorgenson 2013).

Active layer deepening and more widespread thermokarst will have significant implications for the global climate system, because they could release 37-174 Pg of carbon to the atmosphere by 2100, resulting in an additional 0.42 °C of warming by 2300 (Schuur et al. 2015). At present it is unclear if all the carbon currently frozen in permafrost will be easily decomposed when thawed. Permafrost soils may include more recalcitrant carbon, which has been previously exposed to microbial activity and is resistant to decomposition (Grosse et al. 2011). However, northern peatlands with organic matter that was quickly integrated into the permafrost may contain large quantities of labile carbon (Zoltai and Tarnocai 1975; Zoltai 1993; Dutta et al. 2006; Zimov et al. 2006; Schuur et al. 2008). Recent studies using isotopic analysis in Alaska and Sweden have demonstrated increased carbon emissions from recently thawed permafrost in subarctic blanket bogs and moist acidic Arctic tundra (Dorrepaal et al. 2009; Schuur et al. 2009; Pries et al. 2013). While the chemical composition of SOC contained in the permafrost is a large determinant of whether the SOC currently frozen in the permafrost will be mineralized upon

thaw, other factors that may influence carbon emissions include chemical and physical protection within the soil matrix (Oades 1988; Six et al. 2002; Sollins et al. 1996), microbial activity and communities (Waldrop et al. 2010), and nutrient availability (Hobbie et al. 2002) and other edaphic factors (Davidson and Janssens 2006). Since SOC varies from region to region, more case studies are needed to determine whether newly unfrozen peat will be recalcitrant or labile (Davidson and Janssens 2006; Schuur et al. 2008).

Ice-rich terrain is more sensitive to increasing temperatures than other landscapes, because it is more vulnerable to the development of thermokarst with permafrost thaw (Jorgenson et al. 2006; Schuur et al. 2008). For example, polygonal terrain is a common feature of the landscape in the western Canadian Arctic and is characterized by the presence of large ice wedges, which are sensitive to increasing temperatures and anthropogenic disturbance (Steedman 2014; Kokelj et al. 2014; Raynolds et al. 2014). Recent temperature increases in Alaska and the Northwest Territories have been associated with increased thermokarst in high-centred polygonal terrain (Jorgenson et al. 2006; Steedman 2014). Ice-wedge degradation is expected to have a large impact on carbon cycling because degradation results in increased soil moisture, increased ground temperature, and deepens the active layer (Jorgenson et al. 2006). Changes to surface hydrology accompanying subsidence in high-centred polygonal terrain will create anoxic conditions in some areas (Steedman 2014) that may result in lower overall carbon emissions (Elberling et al. 2013), but an increase in methane (CH<sub>4</sub>) production (Schlesinger and Bernhardt 2013b). Alternatively, increased temperature associated with increased moisture in polygonal terrain may result in an overall increase in carbon emissions (Chapter 3). Due to the fact that polygonal terrain occupies 10-30% of the landscape in the western Arctic (Jorgenson et al. 2006; Steedman 2014) assessing the potential decomposability of the SOC in these soils

under various environmental conditions is important to consider when evaluating the potential loss of SOC as active layers deepen with warming. Since changing environmental conditions (soil moisture, oxygen availability, temperature) are all likely to have an impact on gaseous carbon emission rates, they need to be analyzed in tandem.

In this study we used an incubation approach to assess potential decomposability of peat currently frozen in high-centred polygonal terrain in the Tuktoyaktuk Coastlands. Incubation studies are an experimental approach that can be used to reduce ecosystem complexity and simulate environmental conditions to help understand the impacts of anticipated changes (Grosse et al. 2011). By controlling temperature and moisture as variables of interest, in this study we explore the vulnerability of deep and shallow SOC in high-centred polygonal terrain undergoing ice wedge degradation. Specifically, lab incubations were used to test the hypothesis that the peat in this study area had comparable potential decomposability that did not depend on depth below the frost table. We hypothesize that rapid peat accumulation and integration into the permafrost table during the Holocene in this region resulted in a similar chemical structure of the peat throughout the permafrost such that the SOC in these samples would readily mineralize once thawed.

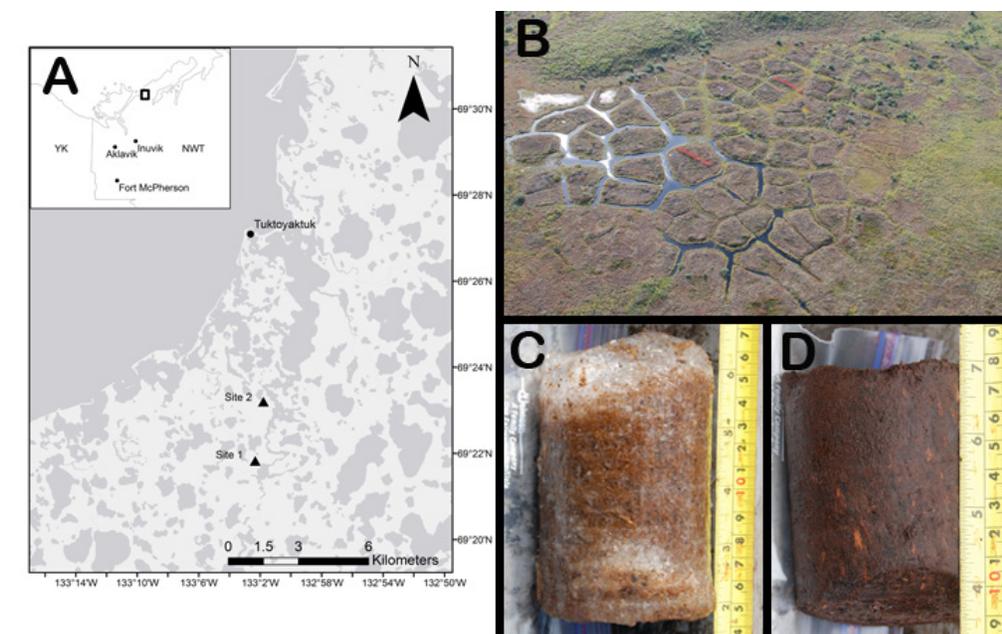
## **Methods**

### **Site description**

The cores used for incubations in this study were collected from two areas of high-centred polygonal terrain in the Tuktoyaktuk Coastlands (Fig. 2-1). The Tuktoyaktuk Coastlands is a low-lying area in the Western Canadian Arctic with an elevation that rarely exceeds 60 m above sea level. This landscape was covered by the Laurentide ice sheet during the Wisconsinan

glaciation between 20 and 25 ka B.P. (Duk-Rodkin and Lemmen 2000). As the temperature began to warm around 15 000 B.P. (Murton 2001), numerous thermokarst lakes formed and subsequently drained during the mid-Holocene (Murton 1996). These small lacustrine basins typically host high-centred polygonal terrain with peat deposits between 1 and 3 meters (Vardy et al. 1997). Today, high-centred polygonal terrain covers approximately 10% of the Tuktoyaktuk Coastlands (Steedman 2014).

The climate of the Tuktoyaktuk Coastlands is cold with temperatures below freezing from October to April (Lantz et al. 2010). The mean annual air temperature at Tuktoyaktuk is -10.2°C (Kokelj et al. 2014) and the total annual precipitation is 166.1 mm (Environment Canada 2015). The vegetation at the study area is dominated by dwarf shrubs (*Betula glandulosa* Michx., *Rhododendron subarcticum* Harmaja (G.D. Wallace), *Vaccinium vitis-idaea* L., *Vaccinium uliginosum* L., *Empetrum nigrum* L.) and lichen within polygon centres, and sedges (*Carex* spp., *Eriophorum* spp.) and other hydrophilic vegetation in ice wedge troughs.



**Figure 2-1.** (A) Map showing the study sites in the Tuktoyaktuk Coastlands. Inset map at the upper left shows the location of our two study sites; (B) Photo of Site 1 showing high centre polygons surrounded by melt ponds. The orange snow fences visible in the centre and upper right of the photo are approximately 12 m long; (C) Pool ice and fibrous peat (80-90 cm) from Site 2; and, (D) Fibrous peat (70-80 cm) from Site 2.

### Soil Core Collection

On August 11 and 13, 2014, a total of six cores were collected from two polygonal peatlands approximately 2.6 km apart (Site 1: 133°02'05 W, 69°21'58 N where cores 1 – 3 were collected from the centre of three separate polygons within 13 m of each other; Site 2: 133°01'25 W, 69°23'20 N where cores 4 -6 were also collected from the centre of three separate polygons within 8 m of each other). Cores were collected using a 7.5-cm diameter Cold Regions Research and Engineering Laboratory (CRREL) coring kit. Each core was extracted in 20 cm sections, which were divided into 10 cm subsections in the field. The unfrozen active layer was discarded. The depth to frozen peat (25-40 cm) and the depth of core were recorded for each core. At Site 1,

cores were shorter (119-139 cm) because the peat deposit was shallower than Site 2 (268-333 cm) (Table 2-1). Coring was stopped when either ice (>20 cm) or mineral soil was reached. Descriptions and photos (Figure 2-1, Tables 2-1 and 2-2) were taken for each section of core and cores were kept frozen and transported to the University of Victoria where they were thawed and prepared for incubations.

**Table 2-1.** Physical description of the six cores collected at the two sites. Active layer was measured while coring and ice content was estimated visually. Bulk density was calculated as the grams of dry soil divided by the volume of the core. NA is noted for the 210+ cm depth at Site 1 as all cores were shorter than 210 cm.

<b>Site</b>	<b>Site 1</b>				<b>Site 2</b>			
<b>Core Number</b>	1	2	3	Mean $\pm$ SD	1	2	3	Mean $\pm$ SD
<b>Depth of Active Layer (cm)</b>	25	37	40	34 $\pm$ 7.9	30	36	35	33.7 $\pm$ 3.2
<b>Depth of Core (cm)</b>	121	119	139	126.3 $\pm$ 11.0	333	268	233	278 $\pm$ 50.7
<b><u>Estimated Ice Content of Cores</u></b>								
40-70cm	0%	0%	0%	0%	0%	20%	40%	20%
70-100cm	10-30%	5%	0%	8.3%	0-5%	30%	80%	37.5%
100-130cm	70-80%	~80%	70%	75%	~10%	10%	80%	33%
210cm+	NA	NA	NA	NA	~90%	5%	10%	35%
<b><u>Bulk Density (g dry soil cm<sup>-3</sup>)</u></b>								
40-70cm	0.137	0.155	0.123	0.14 $\pm$ 0.02	0.109	0.092	0.148	0.12 $\pm$ 0.03
70-100cm	0.267	0.138	0.132	0.18 $\pm$ 0.08	0.104	0.152	0.080	0.11 $\pm$ 0.04
100-130cm	0.177	0.076	0.085	0.11 $\pm$ 0.06	0.148	0.092	0.038	0.09 $\pm$ 0.06
210cm+	NA	NA	NA	NA	0.103	0.160	0.098	0.12 $\pm$ 0.03

**Table 2-2.** Physical descriptions of cores collected from different depths.

<b>Site 1</b>	Core 1	Core 2	Core 3
<u>Depth of Peat</u>			
40-70cm	Icy, fibrous peat with some occlusions of mineral soil	Fibrous peat	Fibrous peat with some woody fragments
70-100cm	Icy, fibrous peat transitioning to pool ice at the base of the core	Fibrous peat with ice lenses at base of core	Saturated fibrous peat
100-130cm	Pool ice with suspended organics	Pool ice with suspended organics and mineral soil	Fibrous peat with pool ice at bottom
<b>Site 2</b>	Core 1	Core 2	Core 3
<u>Depth of Peat</u>			
40-70cm	Fibrous peat	Icy peat with pool ice	Ice with organic matter
70-100cm	Fibrous peat with some ice chunks	Icy peat with pool ice	Icy peat with pond ice
100-130cm	Fibrous peat with ice increasing with depth	Icy peat	Ice with organic matter
210cm+	Icy peat transitioning to ice at 245cm, then to mineral soil at 310cm	Icy peat	Icy dark peat

### Incubations

To explore the effects of peat depth on potential decomposability of SOC, sections of core from below the depth of thaw when the soil was collected were organized into four depth categories (40-70 cm, 70-100 cm, 100-130 cm, and 210 cm+). Cores from Site 1, had representative samples from depths of 40-70 cm, 70-100 cm, and 100-130 cm, and cores from Site 2, had samples taken from depths of 40-70 cm, 70-100 cm, 100-130 cm and 210 cm+.

Each sample as described above ( $n = 21$  from six cores) was thawed and drained overnight to remove excess water as all samples were saturated or contained ground ice. These samples were then divided into four sections. From each drained core,  $30 \text{ cm}^3$  of soil was removed, weighed, and placed in a 500 mL mason jar equipped with a septum. These jars were randomly assigned to one of four treatments: 1) cold anaerobic ( $\sim 1^\circ\text{C}$  and anoxic); 2) warm anaerobic (room temperature and anoxic); 3) cold aerobic ( $\sim 1^\circ\text{C}$  and oxic); 4) warm aerobic (room temperature and oxic). Cold treatments were placed in a dark fridge, which was approximately  $1^\circ\text{C}$ . Room temperature treatments were placed inside a dark cooler with a temperature of  $18\text{-}20^\circ\text{C}$ . In anaerobic treatments oxygen-free conditions were created by adding 120 mL of  $\text{O}_2$ -free water to each jar and then flushing the jar with  $\text{N}_2$  gas at a rate of 20 L/min for one minute. All aerobic samples were flushed with  $\text{CO}_2$ -free air (Air Ultra Zero T, Praxair,  $<5 \text{ ppm CO}_2$ ) for one minute. A blank jar was included with each treatment, for a total of four blank jars. At the end of the experiment all soil samples were reweighed and then dried at  $60^\circ\text{C}$  and weighed again to provide a bulk density estimate.

Gas samples were taken from all treatments after 0 hours, 24 hours, 48 hours, and then weekly for 9 weeks for a total of 12 gas samples per jar. At the time of sampling,  $28 \text{ cm}^3$  of gas ( $\text{N}_2$  for anaerobic treatments,  $\text{CO}_2$ -free air for aerobic treatment) was injected into the jar followed by the removal of  $28 \text{ cm}^3$  of air from the jar so as to not create a vacuum. All gas samples were stored in pre-evacuated vials (Exetainer 739B, Labco Ltd, Buckinghamshire, UK) sealed with silicon and a rubber septum and were analyzed using a gas chromatograph (CP 3800, Varian, CA) equipped with a flame-ionizer detector (FID) and methanizer. Helium was used as a carrier gas at  $30 \text{ mL min}^{-1}$ . Gas was separated in a column oven with a temperature of  $50^\circ\text{C}$  using a Haysep N 80/100 pre-column (0.32 cm diameter x 50 cm length), and Poropak QS

80/100 mesh analytical columns (0.32 cm diameter x 200 cm length). A minimum of three replicates of five standards were analyzed in each run for quality control and to establish the linear relationship between chromatogram area and gas concentration. The CO<sub>2</sub> and CH<sub>4</sub> standards ranged from ambient to 2.5%.

### **Chemical analysis**

To characterize the organic deposits at each site, four representative samples from the following two depth classes: 40-70cm (cores 1, 2, 4, and 6), 100-130cm (cores 1, 3, 4, and 5), and three representative samples from the 210+ cm depth class (cores 4, 5, and 6) (n=11) were chosen from the pool of all core samples and were sent to the University of Guelph. Total carbon content was determined using a LECO SC-444 carbon analyzer (LECO Corporation, St. Joseph, MI). To determine inorganic carbon content, a subsample of soil was ashed at 475°C for three hours, and then analyzed with the same instrument. Organic carbon content was estimated as the difference between total and inorganic carbon content. To determine the nitrogen content of the soil, subsamples of soil were dried, ground and then combusted in a sealed system. The nitrogen compounds released were reduced, and the N<sub>2</sub> gas released was measured using a LECO LP-428 nitrogen analyzer (LECO Corporation, St. Joseph, MI).

Chemical fractionation was performed using the method outlined in Ryan et al. (1990). First soil samples were dried between 34-38°C, and ground fine enough to pass through a 0.85 mm mesh. To determine ash content, a subsample of this soil was ashed for 1 hour at 250°C, 3 hours at 425°C, and then weighed. To extract the soluble fats, 2-4 g of the dried soil was placed in Foss FiberCap capsules (23 µm pore size) and extracted in 250 mL dichloromethane using a

classical soxhlet apparatus. Samples were then refluxed for 2.5 hours then extracted through Whatman 934-AH glass microfiber filters to remove any particulates. To remove the solvent, a rotary evaporator was used and the residue was dried for 24 hours at 45°C. The insoluble residue was dried at room temperature in a fume-hood to remove any residual solvent, and then extracted with 35 mL of nanopure water for 3 hours at 98°C. The soluble filtrate from this extraction was used to estimate the overall content of simple sugars using a glucose standard (Masuko et al. 2005). Finally, to separate the remaining residue into hydrolysed carbohydrates and ash-free lignin, the insoluble residue from the hot water extraction was extracted with 20 mL of 72% H<sub>2</sub>SO<sub>4</sub> for 1 hour at 30°C. This solution was then diluted to a 2.5% H<sub>2</sub>SO<sub>4</sub> and extracted for another hour at boiling temperature and then filtered through a Whatman 934-AH glass microfiber filter. The resulting soluble filtrate was further analyzed for hydrolyzed carbohydrates using a glucose standard (Masuko et al. 2005) and then dried (34-38°C). To determine lignin content, the dried residue was then ashed and the difference between the weight of the dried residual and the ashed weight was reported as lignin content.

### Data Analysis

Rates of CO<sub>2</sub> and CH<sub>4</sub> production were calculated following the methods by Robertson et al. (1999) using the following equation:

$$F_{\text{CO}_2} = cV \left( \frac{P}{RT} \right) \times m_c \times \frac{m_s}{d}$$

where  $c$  is the CO<sub>2</sub> or CH<sub>4</sub> of the sample (ppm),  $V$  is the volume of the jar headspace (L),  $P$  is the pressure (kPa),  $R$  is the ideal gas constant (J mol<sup>-1</sup> K<sup>-1</sup>),  $T$  is the incubation temperature (K),  $m_c$  is

the molecular weight of the gas ( $\text{g mol}^{-1}$ ),  $m_s$  is the dry soil weight (g), and  $d$  is the time since last sampling (days). Concentrations were corrected for dilution during sampling.

$Q_{10}$  rates were calculated using the following equation:

$$Q_{10} = \left( \frac{F_2}{F_1} \right)^{\frac{10}{T_2 - T_1}}$$

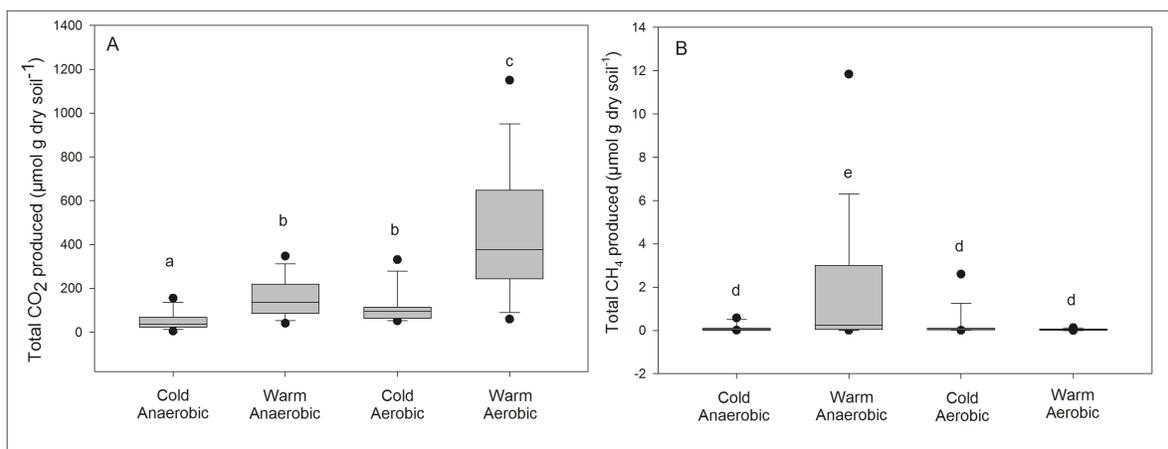
where  $F_2$  is the rate of  $\text{CO}_2$  or  $\text{CH}_4$  flux at room temperature ( $T_2$ ), and  $F_1$  is the rate of  $\text{CO}_2$  or  $\text{CH}_4$  flux in our cold temperature treatment, which was approximately  $1^\circ\text{C}$  ( $T_1$ ) (Kirkham 2011).

To determine if there were differences in  $\text{CO}_2$  and  $\text{CH}_4$  emissions among incubation treatments and core depths we constructed mixed effects models (Littell 2006). Specifically, we used the GLIMMIX procedure in SAS (version 9.3) and modelled incubation treatment, depth, and their interaction as fixed effects. Site (i.e. Site 1 or 2) was included in the model as a random effect. Since the distribution of  $\text{CH}_4$  and  $\text{CO}_2$  flux values and model residuals indicated that neither  $\text{CO}_2$  or  $\text{CH}_4$  flux were normally distributed, a lognormal distribution (DIST=LOGN) was used in these models. To test for differences among treatments, we used the LSMEANS procedure to perform Tukey-Kramer adjusted multiple comparisons (Littell 2006).

To determine if carbon quality varied with core depth or between sites, we used a generalized linear model (GLM procedure) to test for significant differences in each soil fraction. In these models depth, site, and the interaction between the two terms were included as the independent variables. Our sample size ( $n=11$ ) was too small to use mixed models to examine the potential contribution of measured soil fractions to  $\text{CO}_2$  and  $\text{CH}_4$  emissions. Pearson correlations using the CORR procedure in SAS were used to examine correlations between chemical fractions and carbon flux, which were normalized per gram of carbon. These correlations showed that chemical fractions were highly collinear (Table 2-4)

## Results

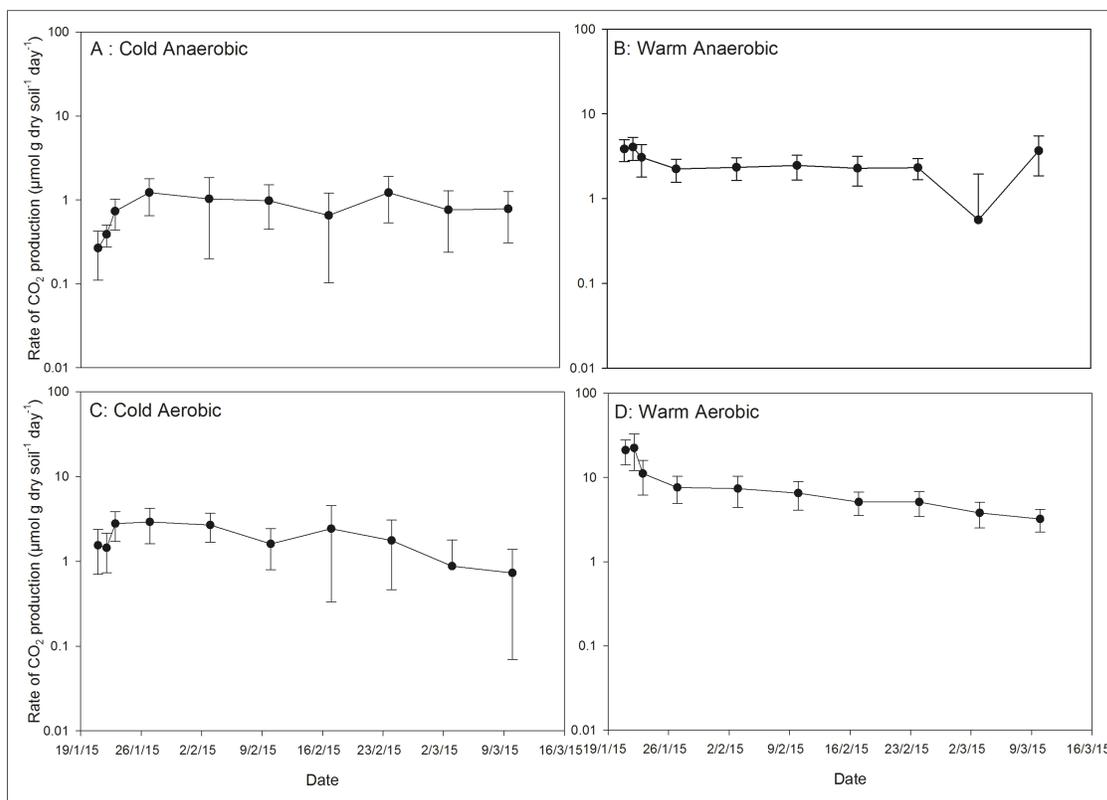
Total CO<sub>2</sub> and CH<sub>4</sub> produced during the incubations (Figs 2-3 & 2-4) varied significantly among treatments ( $p < 0.0001$ , Fig. 2-2, Table 2-3). The highest CO<sub>2</sub> production was in the warm aerobic treatment (Fig 2-2a). Intermediate amounts of CO<sub>2</sub> were produced from the warm anaerobic treatment and the cold aerobic treatment. The lowest amount of CO<sub>2</sub> evolved was in the cold anaerobic treatment (Fig 2-2a). CH<sub>4</sub> production was significantly higher in the warm anaerobic treatment compared to all other treatments where negligible CH<sub>4</sub> was produced (Fig. 2-2b). The CO<sub>2</sub> and CH<sub>4</sub> evolved did not vary among depth classes (Table 3,  $p = 0.64$  and  $0.42$  for CO<sub>2</sub> and CH<sub>4</sub>, respectively).



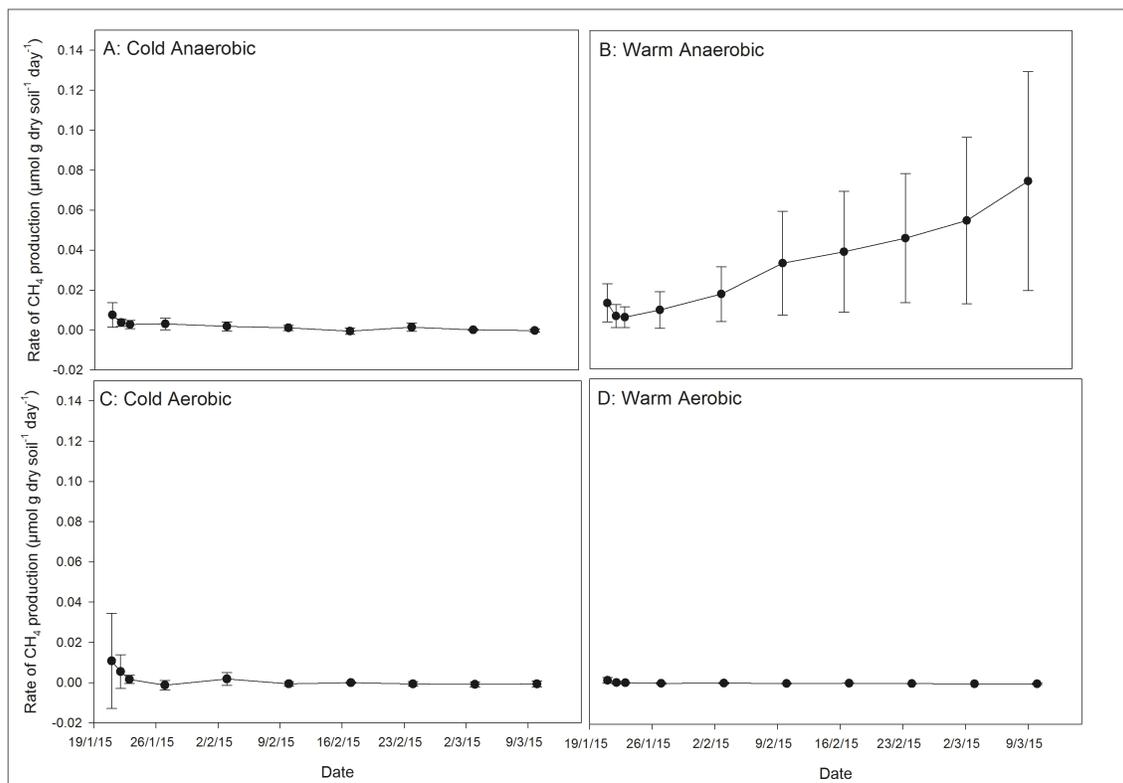
**Figure 2-2.** Boxplot of total: (A) CO<sub>2</sub> emissions, and; (B) CH<sub>4</sub> emissions from different incubation treatments. Cold treatments were kept in a dark fridge around 1°C, and warm treatments (18-22°C) were kept in a cooler at room temperature. The solid black line inside the box shows the median, the ends of the box represent the 25<sup>th</sup> to 75<sup>th</sup> percentiles, the whiskers show the 10<sup>th</sup> and 90<sup>th</sup> percentiles, and the dots denote 5<sup>th</sup> and 95<sup>th</sup> percentiles. Bars showing the same letter are not significantly different. Statistical differences were determined using general linear models and the LSMEANS function (GLIMMIX, SAS).

**Table 2-3.** ANOVA table from mixed effects models of cumulative CO<sub>2</sub> and CH<sub>4</sub> emissions (GLIMMIX, SAS). Dependent variables were CO<sub>2</sub> and CH<sub>4</sub>. Fixed effects were depth and treatment, and site was included as a random factor. A lognormal distribution was used for both CO<sub>2</sub> and CH<sub>4</sub>.

CO <sub>2</sub>	numDF	denDF	F-value	p-value
<b>Treatment</b>	<b>3</b>	73	<b>29.85</b>	<b>&lt;0.0001*</b>
Depth	3	73	0.56	0.6433
Treatment x Depth	9	73	0.28	0.9790
CH <sub>4</sub>	numDF	denDF	F-value	p-value
<b>Treatment</b>	<b>3</b>	<b>68.01</b>	<b>8.01</b>	<b>0.0001*</b>
Depth	3	68.21	0.95	0.4213
Treatment x Depth	9	68	0.62	0.7792



**Figure 2-3.** Rates of CO<sub>2</sub> production over the 63-day incubation period. Experimental treatments included: (A) Cold anaerobic; (B) Warm anaerobic; (C) Cold aerobic, and; (D) Warm aerobic. Solid circles show the mean emission rate and the bars represent the 95% confidence interval of the mean. The y axis is on a log scale.



**Figure 2-4.** Rates of CH<sub>4</sub> production (µmol g of soil<sup>-1</sup> day<sup>-1</sup>) over the 63-day incubation period. Experimental treatments included: (A) Cold anaerobic; (B) Warm anaerobic; (C) Cold aerobic; and, (D) Warm aerobic. Solid circles show the mean emission rate and the bars represent the 95% confidence interval of the mean.

CH<sub>4</sub> production was significantly more sensitive to temperature than CO<sub>2</sub> emissions, with Q<sub>10</sub> values of 4.3 and 1.2, respectively, for anaerobic treatments. Significant quantities of CH<sub>4</sub> were not produced under aerobic conditions. CO<sub>2</sub> production under aerobic conditions was more sensitive to temperature (Q<sub>10</sub> = 2.4) than under anaerobic conditions (Q<sub>10</sub> = 1.2).

There were no differences in soil chemical properties with depth or between the two sites sampled (Appendix 1, p=0.12-0.94). However, it is likely that the small sample size (n=4) and in some cases, large variation within depth classes (Appendix 2), may have limited our ability to

detect differences. Pooling samples from all depths, total carbon ranged from 9.4% to 48.8%, and organic carbon ranged from 9.2 to 48.6%. There was also considerable variation in inorganic carbon (0.14 to 2.02%); nitrogen (0.66 to 2.99%); lignin (9.8 to 63.3%), and; C:N (14.2 to 24.3) among samples.

Neither CO<sub>2</sub> nor CH<sub>4</sub> flux was significantly correlated with organic carbon content (not shown), likely because most (9 out of 12) samples had similar organic carbon content (32.8-48.6%). When production rates of CO<sub>2</sub> were normalized on a per C basis there were no significant correlations with any of the chemical fractions measured (Table 2-4). CH<sub>4</sub> production on a per C basis had a positive correlation with C:N ratio ( $r=0.61533$ ,  $p=0.0439$ , Table 2-4). Many of the chemical fractions were highly correlated with each other (Table 2-4)

The ice content and bulk density of permafrost varied between the two peatlands sampled. At Site 1, ice increased with depth, and all sections from depths between 100-130 cm had > 70% of ice content. Cores from Site 1 demonstrated transitions from fibrous peat to pure ice at approximately 100 cm, and thus did not include the deeper depth class (+210 cm) (Table 2-2). Cores from Site 2 showed more variability in ice content between replicates, with the 100-130 cm depth range having ice content between 10 and 80%, and the 210 cm+ depth category having an even greater range of ice content (5-90%) (Table 2-1). Cores from Site 2 had limited pool ice content in the 70-100 cm depth class and did not show the same transition from fibrous peat to pool ice as seen in cores from Site 1, but instead transitioned to dark icy peat then mineral soil (Table 2-2).



## Discussion

Like previous studies (Zona et al. 2012; Turetsky 2004; Kane et al. 2013), our incubations show that when warmed SOC under aerobic and anaerobic conditions will be mostly mineralized to CO<sub>2</sub> as opposed to CH<sub>4</sub>. On average, CO<sub>2</sub> production was 79 times that of CH<sub>4</sub> emissions. Since polygon centres are aerobic environments and constitute over 95% of the polygonal landscape (Steedman 2014) these are applicable to the majority of SOC stocks in this terrain type. Waterlogged conditions created by ice wedge degradation and subsidence will increase the area that is conducive to CH<sub>4</sub> production. However, since potential increases will only affect a small proportion (roughly 5%) of this terrain type, current CH<sub>4</sub> emissions (Chapter 3) and future emissions are likely to be relatively small contribution to flux on a landscape scale. However, given that our incubations were conducted under ideal conditions at artificially high temperatures, our observed results are subject to limitations. Actual in-situ carbon release is likely to be influenced by field conditions such as the mineralization of different carbon pools at different temperatures (Biasi et al. 2005) and the structure of the soil matrix (Oades 1988; Six et al. 2002; Sollins et al. 1996).

This study demonstrates that both temperature and oxygen availability control rates of SOC mineralization. These findings are consistent with numerous incubation studies showing that increasing temperatures result in higher emissions (Treat et al. 2014; Dutta et al. 2006; Hobbie et al. 2002; Mikan et al. 2002; Lupascu et al. 2012) and that anaerobic conditions result in the increased production of CH<sub>4</sub> and decreased CO<sub>2</sub> emissions (Elberling et al. 2013; Lee et al. 2012). Observed Q<sub>10</sub> values were comparable

to others studies for both CO<sub>2</sub> and CH<sub>4</sub> which ranged from 1.9 to 5.8 and 0.5 to 300 (Lupascu et al. 2012; Hamdi et al. 2013, respectively).

The rapid decline in CO<sub>2</sub> emissions that we observed in the warm aerobic treatment suggests that it is possible that when polygonal terrain thaws, there will be a pulse of carbon mineralization that will decrease over time. This is consistent with the three-pool decomposition model, which divides carbon into fast, slow and passive fractions, based on turnover times, with the fast fraction decomposing within a few days to a month, the slow fraction turning over within a few years, and the passive fraction turning over within a few years to thousands of years (Schädel et al. 2014). CH<sub>4</sub> produced in the first few days in the warm anaerobic treatment may also be the mobilization of this ‘fast’ fraction. However, it could also have been due to more suitable conditions for methanogenesis being created over time as alternative electron acceptors were depleted and the very negative redox conditions associated with methanogenesis were reached, or the methanogen community grew (Schlesinger and Bernhardt 2013b).

The potential decomposability of peat from high-centred polygonal terrain did not differ with depth. This may be a result of the majority of the peat currently frozen in the permafrost having been produced in a specific time period during the development of our sites. Multiple analysis of cores from the Tuktoyaktuk Coastlands demonstrates that between 8000 to 4000 B.P. was a time of high peat accumulation when current high-centre polygons were graminoid fens (Vardy et al. 1997; Vardy et al. 2000). As permafrost aggradation was also occurring during this time period ( Zoltai 1995; Murton 1996; Vardy et al. 2000), it is likely that peat from our site once produced was integrated relatively quickly into the permafrost, thus protecting it from future decomposition. Since

then, peat production has been relatively slow, with Vardy et al. (1997) concluding that the upper 25 cm of peat represents the last 4000 years of peat accumulation at a polygonal peatland located near our study site.

Our findings are supported by research in Alaska and Siberia showing that permafrost carbon from different depths is equally labile (Waldrop et al. 2010; Dutta et al. 2006) and that the magnitude of our carbon production rates in a laboratory setting are within the huge range of rates obtained for other organic deposits from other Arctic terrain types (Table 2-5). As a result, we conclude that emissions of CO<sub>2</sub> and CH<sub>4</sub> to the atmosphere with active layer deepening in high-centred polygonal terrain will not be constrained by the nature of the organic matter in these peat deposits.

The consistent C:N ratios found at all core depths indicates that the organic matter in high-centred polygonal terrain may be similarly degraded. C:N ratios have been posited as an indicator of the degradation state of soil carbon (Kuhry and Vitt 1996; Wickland and Neff 2008) with C:N ratios decreasing as decomposition occurs (Malmer and Holm 1984). In a meta-analysis, Schädel et al. (2014) found that higher C:N ratios were associated with a large slow carbon pool (with a turnover time of a couple years), and a small passive carbon pool (with a turnover time of thousands of years). However, the use of C:N ratios in peat as an indicator of decomposition state may be only applicable during the very early stages of decomposition, as C:N ratios remain consistent after decomposition passes the 4<sup>th</sup> stage of the von Post humification index (Wang et al. 2015). Sedge peat tends to have lower C:N ratios than *Sphagnum* peat (Kokfelt et al. 2010; Hodgkins et al. 2014), which may result in the lower C:N ratios observed in our study than others such as Wang et al. (2015). The C:N ratios of our cores were similar

with those presented in Diochon et al. (2013) (10.1-25.3) and to those in Vardy et al. (2000) (13.7-21.1).

**Table 2-5.** Comparison of CO<sub>2</sub> and CH<sub>4</sub> flux from this study (bold) to other incubation studies. Table is organized by length of incubation. Results from this study are in bold.

Authors	Depth of peat (cm)	Type	Location	Length of incubation (days)	Temperature (°C)	Anaerobic CH <sub>4</sub> Production (μmol g soil <sup>-1</sup> d <sup>-1</sup> )	Aerobic CH <sub>4</sub> Production (μmol g soil <sup>-1</sup> d <sup>-1</sup> )	Anaerobic CO <sub>2</sub> Production (μmol g soil <sup>-1</sup> d <sup>-1</sup> )	Aerobic CO <sub>2</sub> Production (μmol g soil <sup>-1</sup> d <sup>-1</sup> )
Turetsky et al. (2005)	5-10	Rich fens	Alberta	2	18-20	1.80x10 <sup>-1</sup> to 6.0x10 <sup>-1</sup>	-4.0x10 <sup>-1</sup> to 2.0x10 <sup>-1</sup>	4.06x10 <sup>1</sup> ±1.3	5.57x10 <sup>1</sup> ±2.3
Lupascu et al. (2012)	22-50	Peatland in discontinuous permafrost	Sweden	3	4 to 24	1.68±1.37	NA	NA	NA
Moore et al. (1994)	0-20	Wetland ecosystem on the James Bay coast	Northern Ontario	5	15	6.23x10 <sup>-4</sup> to 1.87	NA	NA	NA
Mikan et al. (2002)	0-25	Wet meadow tundra, moist tussock tundra and moist shrub tundra	Alaska	27	-12 to +14	NA	NA	NA	1.59x10 <sup>1</sup> to 3.64x10 <sup>1</sup>
Treat et al. (2014)	29-100	Black spruce and tundra peatlands	Alaska	30	-5 to +20	NA	NA	1.36	2.87
Kane et al. (2012)	10	Rich fen	Alaska	38	22	7.8x10 <sup>-3</sup> ±1.5x10 <sup>-3</sup>	NA	1.41x10 <sup>1</sup> ±0.9	1.06x10 <sup>1</sup> ±1.5
Turetsky (2004)	5-75	Peatland in discontinuous permafrost	Northern Saskatchewan	48	18 to 20	NA	NA	2.29x10 <sup>1</sup> ±1.4	2.81x10 <sup>1</sup> ±1.4
Zona et al. (2012)	0-50	Vegetated drained lake basin	Alaska	56	4	1.27x10 <sup>-1</sup> to 1.272	NA	9.27x10 <sup>-1</sup> to 8.81	NA
<b>This study</b>	<b>40-210</b>	<b>High-centred polygonal terrain</b>	<b>Northwest Territories</b>	<b>63</b>	<b>1 and 18-20</b>	<b>1.58x10<sup>-2</sup> ±3.77 x10<sup>-2</sup></b>	<b>2.0x10<sup>-3</sup> ±8.0x10<sup>-3</sup></b>	<b>1.61±1.36</b>	<b>4.40 ±4.50</b>
Waldrop et al. (2009)	100	Black spruce forest in continuous and discontinuous permafrost	Alaska	98	-5 and 5	5.0x10 <sup>-3</sup> to 1.0x10 <sup>-1</sup>	NA	NA	2.55 to 1.86x10 <sup>1</sup>
Hobbie et al. (2002)	10	Moist acidic and non- acidic tundra	Alaska	216	4 to 15	NA	NA	NA	4.2 to 2.31x10 <sup>1</sup>
Dutta et al. (2006)	10-13 000	Yedoma soils	Siberia	400	5 to 15	NA	NA	NA	4.54x10 <sup>-2</sup> to 6.82x10 <sup>-2</sup>
Lee et al. (2012)	4-10 000	Moist acidic tussock tundra, non-acidic tundra, and yedoma sites (mineral soil)	Alaska and Siberia	500	15	7.48x10 <sup>-6</sup> ±3.74x10 <sup>-5</sup> to 1.45x10 <sup>-2</sup> ±7.34x10 <sup>-3</sup>	NA	7.27x10 <sup>-3</sup> ±1.36x10 <sup>-3</sup> to 2.27x10 <sup>-2</sup> ±9.09x10 <sup>-4</sup>	4.86x10 <sup>-2</sup> ±7.72x10 <sup>-3</sup> to 1.31x10 <sup>-1</sup> ±3.31x10 <sup>-2</sup>
Lee et al. (2012)	5-15	Moist acidic tundra (organic soil)	Alaska	500	15	2.12x10 <sup>-2</sup> ±1.14x10 <sup>-2</sup> to 3.38x10 <sup>-2</sup> ±4.34x10 <sup>-2</sup>	NA	2.7x10 <sup>-1</sup> ±4.0x10 <sup>-2</sup> to 3.20x10 <sup>-1</sup> ±4.0x10 <sup>-2</sup>	1.80±4.30x10 <sup>-1</sup> to 3.27±4.10x10 <sup>-1</sup>

## **Implications**

Our research demonstrates that emissions from thawing permafrost will not be constrained by SOC quality in the permafrost and that any future emissions will likely be at least partially mediated by temperature and moisture. Given that the majority of polygonal terrain consists of mesic polygon centres, and not wet troughs and melt ponds, it is likely that most of the carbon release will occur under aerobic conditions. This indicates that temperature will likely be an important control of future carbon emissions from this terrain type, and that the majority of emissions will be in the form of CO<sub>2</sub>. These findings are supported by our field observations (see Chapter 3). If active layer deepening continues at a rate of 0.32 cm year<sup>-1</sup> (Burn and Kokelj 2009) over the next several decades, it is likely that carbon emissions will also increase as previously frozen SOC becomes unthawed and available to be decomposed. However, the low (<5 °C) ground temperatures (Figure 3-4, Table 3-3, Chapter 3) will likely act as a constraint on future carbon emissions.

## **Key Findings**

- i. CO<sub>2</sub> emissions constituted the majority of emissions from thawed permafrost in both anaerobic and aerobic incubations.
- ii. Both temperature and anaerobic conditions constrained carbon emissions in laboratory conditions.

- iii. SOC characteristics did not vary with permafrost depth, suggesting that if unthawed, SOC quality will not limit future decomposition rates.

## **Chapter 3 – Ice wedge degradation and CO<sub>2</sub> and CH<sub>4</sub> emissions in the Tuktoyaktuk Coastlands, NT.**

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## **Introduction**

Rapid temperature increases in the Arctic are likely to have serious implications for Arctic ecosystems and global carbon cycling (Schuur et al. 2008; Hinzman et al. 2005). Mean annual global surface temperature has increased 0.85 °C since 1901, with warming being most pronounced at northern latitudes (Alexander 2013). Warming has been observed across the entire Arctic (Serreze et al. 2000), with increases in average annual air temperature (from 1950-2003) in Alaska, Siberia and the western Canadian Arctic between 2-3°C (Hassel 2005). Global circulation models project that the global average surface temperature will increase by up to 5.5°C by 2100, with temperature changes being most pronounced at northern latitudes (scenario RCP8.5, IPCC, 2013).

Permafrost soils hold an immense amount of soil organic carbon (SOC) (1307Pg; uncertainty range: 1140-1476Pg) (Hugelius et al. 2014). Much of this carbon is present in the organic soils of peatland ecosystems. Organic soils (Histosols and Histels) contribute disproportionately to total carbon storage in northern regions as they store 14% of SOC while only representing 5% and 7% of permafrost affected soils, respectively (Hugelius et al. 2014). This is due to low rates of net primary productivity, which have exceeded decomposition over long periods of time, and resulted in carbon accumulation as partially decomposed organic matter (peat). These peatland ecosystems represent significant carbon sinks that play a critical role in the global carbon cycle (Callaghan et al. 2004).

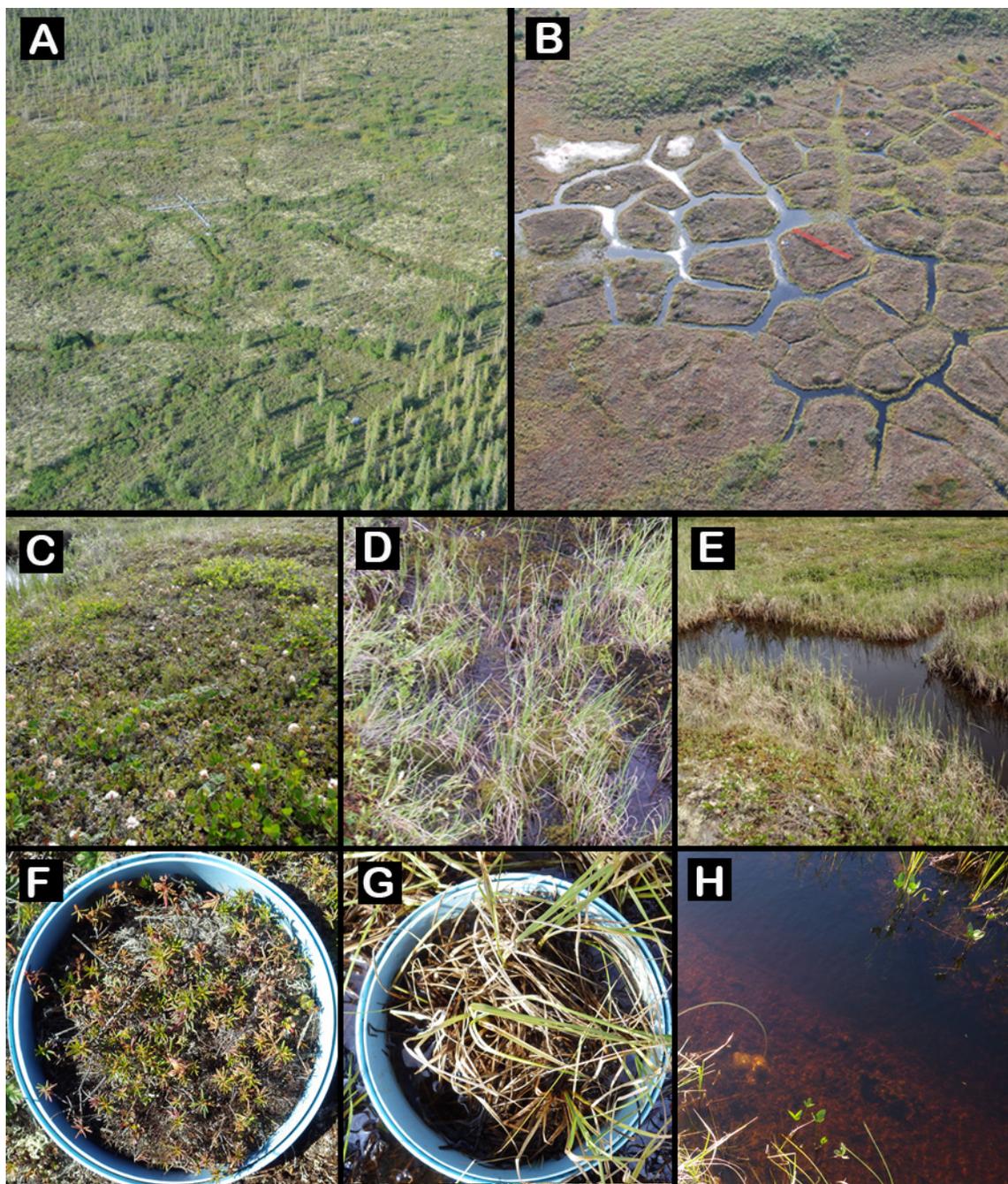
Ongoing changes in temperature and precipitation are likely to modify the balance between productivity and decomposition rates in Arctic and subarctic peatlands, transforming them from sinks to sources of carbon that add to the atmospheric load of

greenhouse gases including carbon dioxide (CO<sub>2</sub>) and methane (CH<sub>4</sub>) (Oechel et al. 1993; Schuur et al. 2008; Grosse et al. 2011). It is estimated that thawing permafrost could release 37-174 Pg of carbon to the atmosphere by 2100, and permafrost carbon feedbacks alone could result in an additional 0.42 °C of warming by 2300 (Schuur et al. 2015).

Polygonal peatlands are a form of patterned ground that hosts thick organic deposits and large ice wedges (Zoltai and Tarnocai 1975; Vardy et al. 1997). Ice wedges form when winter thermal contraction cracks are in-filled with melt-water, which freezes. Continued cracking and infilling can result in large ice wedges being formed over many years (Mackay 1989). These ice wedges interconnect and form a polygonal pattern across the landscape, which is characterized by depressed troughs underlain by ice wedges, and polygons (Fig. 3-1). Polygons have a mean diameter of 30 m across (MacKay 1972) and can be classified as either high-centred or low-centred (MacKay 2000). High-centred polygons have raised dry centres (Fig 3-1) whereas low-centred polygons have depressed centres generally characterized by standing water (Pielou 1994). This paper focuses on high-centred polygonal terrain.

Common in low-lying lacustrine basins across the Arctic, polygonal peatlands are likely to be particularly sensitive to increasing air temperature because they have high ground ice content in the form of ice wedges (Kokelj et al. 2014). Recent evidence from remote sensing suggests that temperature increases can lead to widespread ice wedge degradation and thermokarst (ground subsidence due to permafrost thaw) (Jorgenson et al. 2006). This form of thermokarst has the potential to affect 10-30% of the Arctic lowland landscape (Jorgenson et al. 2006) and will likely have significant impacts on carbon cycling (Schuur et al. 2008; Lee et al. 2010; Kokelj and Jorgenson 2013).

As ice-wedges degrade, troughs show increased soil moisture, active layer thickness, mean annual ground temperature and ground subsidence (Jorgenson et al. 2006). Moderate trough degradation may be characterized by some subsidence, increased moisture and the presence of sedge species such as *Carex* spp. (Fig. 3-1). Severe degradation in troughs causes the formation of melt ponds that do not support rooted plants (Fig. 3-1). The volume and depth of water in these ponds may extend the duration of freeze-back and in some locations the underlying soil may not freeze fully over winter (Kokelj et al. 2014).



**Figure 3-1.** Photographs showing study sites and degradation classes: A) Abarctic field site near Inuvik, boardwalks are to the left of where chamber measurements occurred; B) Arctic field site near Tuktoyaktuk, the two orange lines are snow fences for another research project; C) Polygon centre with no ice wedge and no degradation with gas sampling collar (F); D) Shallow trough as a result of moderate ice wedge degradation with gas sampling collar (G); E) Melt pond due to severe ice wedge degradation and close-up view (H).

Warmer soils and deeper thaw throughout high-centred polygonal terrain features may result in increased CO<sub>2</sub> emissions as decomposition rates are enhanced. Emissions may even exceed carbon gains brought about by increased net primary productivity from nutrient mineralization and a longer growing season (Mack et al. 2004). However, the formation of saturated soils or pools with standing water as a result of ice wedge degradation is likely to limit aerobic decomposition processes (Funk et al. 1994; Davidson and Janssens 2006; Schlesinger and Bernhardt 2013b) and decrease CO<sub>2</sub> emissions (Oberbauer et al. 2007; Elberling et al. 2013). The switch to anaerobic conditions may increase methane (CH<sub>4</sub>) production and emission to the atmosphere (Schlesinger and Bernhardt 2013b).

In this research we explored the effects of ice wedge degradation on CO<sub>2</sub> and CH<sub>4</sub> emissions along a gradient of ice wedge degradation in high-centred polygonal terrain at an Arctic and subarctic site. Chamber flux measurements were used to test the following hypotheses: 1) increased soil temperature in degraded troughs drives increased carbon emissions (both CO<sub>2</sub> and CH<sub>4</sub>) and 2) advanced degradation and ponding will create anoxic conditions that lead to a decrease in CO<sub>2</sub> production and an increase in CH<sub>4</sub> production.

## **Methods**

### **Study Area**

This study was carried out in the Tuktoyaktuk Coastlands in the Western Canadian Arctic (Fig. 1-1). This area is characterized by gentle topography and thousands

of small lakes (Rampton 1988). Between 30 and 25 ka B.P., the Tuktoyaktuk Coastlands were covered by the Laurentide ice sheet (Duk-Rodkin and Lemmen 2000). As this ice sheet receded, numerous thermokarst lakes formed and then subsequently drained during the Holocene (Murton 1996). Today approximately 10 % of the Tuktoyaktuk Coastlands are occupied by small lacustrine basins that host high-centred polygon terrain underlain by thick peat deposits (Steedman 2014; Zoltai and Tarnocai 1975; Vardy et al. 1997).

The contemporary climate of this region is characterized by mean annual air temperatures of  $-9.0^{\circ}\text{C}$  at Inuvik and  $-10.2^{\circ}\text{C}$  at Tuktoyaktuk and conditions typically below freezing from October to April (Environment Canada 2015). In the summer there is a strong latitudinal temperature gradient with average growing season air temperatures (1970-2005) being  $3.3^{\circ}\text{C}$  warmer in Inuvik than Tuktoyaktuk (Lantz et al. 2010). There is also a precipitation gradient with Tuktoyaktuk receiving a mean total annual precipitation (1970-2006) of 166.1 mm, and Inuvik receiving 254.8 mm (Environment Canada 2015). Over the period of record (1970-2006), mean annual air temperatures at Inuvik have increased by more than  $2.5^{\circ}\text{C}$ . This increase in air temperature has been mirrored by an increase of  $1.5\text{-}2.5^{\circ}\text{C}$  in permafrost temperature since 1970 (Burn and Kokelj 2009).

The regional climate gradient is accompanied by two transitions in the dominant vegetation. In the southern part of the study, open spruce woodlands transition into tundra dominated by upright shrubs (*Salix* spp., *Alnus viridis* Chaix. and *Betula glandulosa* Michx.) (Lantz et al. 2010). Towards the northern end of our study area, upright shrub tundra is replaced by dwarf shrub tundra dominated by ericaceous shrubs and sedges (*Rhododendron subarcticum* Harmaja (G.D. Wallace), *Vaccinium vitis-idaea* L., *Carex* spp. and *Eriophorum* spp.) (Lantz et al. 2010).

## Field Measurements

The effect of ice wedge degradation on soil respiration was measured at a subarctic site near the community of Inuvik, NT (68°18'55.67"N, 133°25'53.51"W) and 119 km north at an arctic site near Tuktoyaktuk, NT (69°21'58.08"N, 133°2'6.29"W). Each site is located in an area of high-centred polygonal terrain dominated by dwarf shrubs (*Betula glandulosa* Michx., *Rhododendron subarcticum* Harmaja (G.D. Wallace), *Vaccinium vitis-idaea* L., *Vaccinium uliginosum* L., *Empetrum nigrum* L.), sedges (*Eriophorum* spp., *Carex aquatilis* Wahlenb.) and lichen. Both sites had areas differentially affected by degradation. We classified these areas as: 1) non-degraded areas without ice wedges (polygon centres), 2) moderately degraded ice wedges (wet troughs), and 3) highly degraded ice wedges (melt ponds) (Fig 3-1). Polygon centres were characterized by terricolous lichen, *Rubus chamaemorus* L., *Rhododendron subarcticum* Harmaja (G.D. Wallace) and *Vaccinium vitis-idaea* L.. Average visual community composition estimates for these species were 45%, 10%, 30%, and 10%, respectively. The polygon units are separated by troughs over intersecting ice wedges. Wet troughs had standing water and were typically dominated by *Carex aquatilis* Wahlenb., which had an average cover of 65%. Melt ponds were deeper and characterized by standing water and an absence of rooted vegetation. All melt ponds at our subarctic site had moss mats present, whereas moss was absent in all our Arctic melt ponds.

To measure CH<sub>4</sub> and CO<sub>2</sub> flux at each site we used manual, static, non-steady state chambers (see Bubier et al. (1995)). At each of the two study sites, nine replicate

polygon centres, nine replicate wet troughs and 10 replicate melt ponds were measured. For the polygon centres and wet troughs, PVC collars 24.3 cm in diameter and 30 cm tall were installed to a depth of 25 cm (Fig 3-1). The top of the collars were grooved and filled with water during sampling to create an air-tight seal with the sampling chamber. Chambers were 34 cm tall and constructed of polycarbonate, made opaque using black duct tape to limit photosynthesis, and fitted with a vent consisting of a 10 cm coiled 1/8" diameter copper pipe to maintain constant pressure during sampling. During the growing season, CO<sub>2</sub> and CH<sub>4</sub> fluxes were measured between 11:00 and 16:00 at the subarctic site on: June 27, July 17, July 31<sup>st</sup>, and August 21<sup>st</sup>, and at the arctic site on: July 3<sup>rd</sup>, July 12<sup>th</sup>, July 29<sup>th</sup>, and August 15<sup>th</sup> 2013. Average air temperature on those four dates was 14.06 ±5.29 °C at the subarctic site and 12.14 ±5.23 °C at the arctic site.

Sampling involved sealing the chamber into the water filled collar groove and drawing a 24 mL sample from the chamber through a line fitted with a septum attached to a three way luer-stopcock at 0, 10, 20 and 30 minutes. Before drawing the air from the chamber, air in the chamber volume was mixed by pumping the syringe attached to the gas sampling line five times. Air samples were transferred into pre-evacuated vials with a small amount of magnesium perchlorate as a dessicant (Exetainer 739B Labco Ltd., Buckinghamshire, UK). Ambient air samples were also taken to provide a measure of sample integrity. Four measurements of soil temperature at 5 cm from the surface (either ground or water) and soil moisture integrated between 0 and 6.8 cm from the surface were also taken during sampling at each collar. The moisture measurements were taken using a soil moisture probe (W.E.T. sensor, type WET-2, Delta-T, Cambridge, UK) calibrated using the organic soils at each site. Water table depth was determined for each

collar in a wet trough by measuring the height from the top of the soil to the surface of any standing water. Thaw measurements were also collected in 2012 and are used in this paper to generally characterize differences among plots. In late August 2012, thaw depth measurements at both the Arctic and subarctic sites were taken by setting up a 10 by 10 m grid, with 110 evenly spaced sampling points and using an active layer probe, which was pushed into the ground to the depth of refusal. In the case of melt ponds where standing water was present, thaw depth was measured as the distance between when the probe encountered some resistance (i.e. hit soil) to the depth of refusal (i.e. hit permafrost). Using this grid design total active layer measurements were collected for polygon centres (each site  $n=27$ ), wet troughs (subarctic,  $n=15$ ; Arctic,  $n=19$ ), and melt ponds (subarctic,  $n = 3$ ; Arctic,  $n= 10$ ).

We used two approaches to estimate gas flux from melt ponds. At each site we installed ten 15.24 cm diameter funnels to collect gas produced at the bottom of the ice wedge ponds. Each funnel was equipped with a sampling line ending in a 3-way luer-lock stopcock and was secured in pond sediments using a weight on the top of the funnel (Huttunen et al. 2001), however these funnels never collected sufficient gas for analysis (from one or two bubbles to up to  $6 \text{ cm}^3$ ) suggesting ebullition was a minor transport process for  $\text{CO}_2$  and  $\text{CH}_4$  emissions at these small melt ponds. We also estimated gas flux from ponds using the diffusion method (Laurion et al. 2010) by sampling surface water. At each pond, 30 mL of surface water was collected using a 60 mL syringe, and then 30 mL of ambient air was then pulled into the syringe and the contents of the water-filled syringe were then shaken for 1 minute to equilibrate the gas stored in the water with the air. Then, 24 mL of the air was then transferred to a pre-evacuated vial for analysis. An

ambient air sample for each pond measurement was also taken to calculate ambient CO<sub>2</sub> and CH<sub>4</sub> concentrations. Water temperature and water depth was measured at the time of sampling. Ambient air temperature, pressure and wind speed at the time of sampling was obtained from an Environment Canada weather station 2.45 km from the subarctic site and 7.17 km from the arctic site (Environment Canada 2015).

Gas samples were analysed for CO<sub>2</sub> and CH<sub>4</sub> on a gas chromatograph (CP 3800, Varian, CA) with a methanizer and flame-ionization detector which were operated at 350°C and 300°C, respectively. Helium was used as a carrier gas at 30 mL min<sup>-1</sup>. Gas was separated using a Haysep N 80/100 pre-column (0.32 cm diameter x 50 cm length), and Poropak QS 80/100 mesh analytical columns (0.32 cm diameter x 200 cm length) in a column oven with a temperature of 50°C. A minimum of three replicates of five standards were used to maintain quality control and establish the linear relationship between chromatogram area and gas concentration. The CO<sub>2</sub> standards ranged from ambient to 2.5% and the CH<sub>4</sub> standards ranged from slightly below ambient to 2.5%.

### **Gas Flux Estimates**

The flux of CH<sub>4</sub> or CO<sub>2</sub> in the chambers was estimated from the change in gas concentration over the 30 minute sampling interval,

$$\text{Flux} = \left( \frac{p_a V}{A} \right) \left( \frac{dx}{dt} \right)$$

where  $p_a$  is the density of dry air (kg m<sup>-3</sup>, determined using ambient air temperature and pressure from the Environment Canada weather station), V is the volume of the chamber (0.0159 m<sup>3</sup> plus 0.002 m<sup>3</sup> for the volume within the collars to the surface of the soil or

water),  $A$  is the area of the chamber ( $0.0464 \text{ m}^2$ ) and  $dx/dt$  is the rate of change of the mixing ratio of either  $\text{CH}_4$  or  $\text{CO}_2$  ( $\mu\text{mol mol}^{-1} \text{ s}^{-1}$ ) (Wilson and Humphreys 2010).

To calculate  $\text{CO}_2$  and  $\text{CH}_4$  flux from the surface water samples, first the initial ( $P_i$ ) and final headspace ( $P_f$ ) partial pressures of  $\text{CO}_2$  and  $\text{CH}_4$  were calculated from the gas chromatograph readings (in  $\mu\text{mol mol}^{-1}$ ) and the atmospheric pressure at sampling (in atm). Then, dissolved gas ( $C_{[\text{pw}]}$ ) in the surface water samples ( $\mu\text{mol L}^{-1}$ ) was determined using the following,

$$C_{[\text{pw}]} = P_f \left( \frac{V_h T}{V_w R} \right) - P_i \left( \frac{V_h T}{V_w R} \right) + K_H (P_f - P_i)$$

where  $K_H$  is Henry's constant for  $\text{CO}_2$  or  $\text{CH}_4$  ( $\text{mol L}^{-1} \text{ atm}^{-1}$ ) calculated for freshwater using water temperature following Weiss (1974) and Wanninkhof (1992), respectively,  $R$  is the ideal gas constant ( $\text{L atm mol}^{-1} \text{ K}^{-1}$ ), and  $V_h$  and  $V_w$  are the volumes of the headspace and water after equilibration (L) (Dinsmore et al. 2009). Median (minimum and maximum) readings for headspace  $\text{CO}_2$  was 4331 (440, 14278)  $\mu\text{mol mol}^{-1}$  and 103 (1.7, 14496)  $\mu\text{mol mol}^{-1}$  for  $\text{CH}_4$ .

Flux across the water-air interface ( $\mu\text{mol m}^{-2} \text{ s}^{-1}$ ) was calculated using the thin boundary layer model using measurements of wind speed and gas concentrations in the air and water (Laurion et al. 2010),

$$\text{Flux} = k (C_{[\text{pw}]} - C_{[\text{amb}]})$$

where  $C_{[\text{pw}]}$  total pore water concentration in the surface water ( $\mu\text{mol L}^{-1}$ ) and  $C_{\text{amb}}$  is the equilibrium ambient concentration of  $\text{CO}_2$  or  $\text{CH}_4$  in the atmosphere ( $\mu\text{mol L}^{-1}$ ). The gas transfer coefficient,  $k$  ( $\text{cm h}^{-1}$ ), was empirically derived using the Schmidt number ( $Sc$ ) and  $k$  measured for  $\text{SF}_6$  flux normalized to a Schmidt number of 600 ( $k_{600}$ ) following (Wanninkhof 1992) and Cole and Caraco (1998),

$$k = k_{600} \left( \frac{Sc}{600} \right)^{-0.5}$$

$$k_{600} = 2.07 + 0.215 \times U_{10}^{1.7}$$

where  $U_{10}$  is wind speed ( $\text{m s}^{-1}$ ) 10 m above the ground.  $U_{10}$  was obtained as hourly averages from the nearby Environment Canada stations.

### Hourly Flux, Temperature and Moisture Measurements

To explore the effects of soil moisture and ground temperature on variation in  $\text{CO}_2$  flux, an automated soil  $\text{CO}_2$  exchange (ACE) station (ADC BioScientific) with a transparent lid was used at a single polygon centre to measure  $\text{CO}_2$  fluxes, PAR and soil temperature at 5 cm at hourly intervals. An on-board infrared gas analyser recorded changes in  $\text{CO}_2$ , and a venting system ensured that pressure did not rise above ambient levels. Once the hourly measurement started, ambient air was pumped in to the chamber at a controlled rate ( $280 \mu\text{mol s}^{-1}$ ) and successive  $\text{CO}_2$  readings took place every 10 seconds until either one of two criteria were met: 1) equilibrium was reached, and the rate of change was less than  $0.1 (\Delta \text{CO}_2 (\mu\text{mol m}^{-3}) / \Delta \text{time (s}^{-1}))$ ; or, 2) 8 minutes elapsed. The following calculation was used to determine  $\text{CO}_2$  flux ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ):

$$\text{Flux} = u_s(\Delta c)$$

where  $u_s$  is the molar flow of air per area of soil ( $\text{mol m}^{-2} \text{s}^{-1}$ ) and  $\Delta c$  is the difference in  $\text{CO}_2$  concentration in the soil chamber between successive samplings (ADC BioScientific 2009). To complement the static chamber analyses, we only used the hourly measurements when PAR was low ( $< 100 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) such that the measured fluxes

would more likely be dominated by respiration process with only small or negligible rates of photosynthesis. As a result, there were 1 to 12 hourly measurements per day.

To demonstrate the effect of temperature on CO<sub>2</sub> emissions, Q<sub>10</sub> was calculated based on the method used by Xu and Qi (2001), who modelled flux by fitting an exponential model to the following equation:

$$\text{Flux} = ae^{bT}$$

where F is CO<sub>2</sub> flux (μmol m<sup>-2</sup> s<sup>-1</sup>), a and b are fitted parameters using the NLIN procedure in SAS version 9.3 (Littell 2006), and T is the soil temperature at 5cm (°C). Q<sub>10</sub> was then estimated using the following equation:

$$Q_{10} = e^{10b}$$

This data was paired with data from thermistors and moisture sensors that were installed in 2012 at the Arctic field site at two polygon centres, three wet troughs and two melt ponds. Temperature measurements (5, 50, 100 cm) were made every 2 hours using temperature sensors (Onset Computing, HOBO™, TMC20-HD, accuracy: ± 0.25°C) and moisture probes (at the soil surface) (Onset Computing, HOBO™, S-SMC-M005, accuracy: ±3.1%) attached to data loggers (Onset Computing, HOBO™, U12-008 and H21-002). Thermistors were installed using water jet drilling and moisture probes were installed by hand.

### **Statistical Analysis**

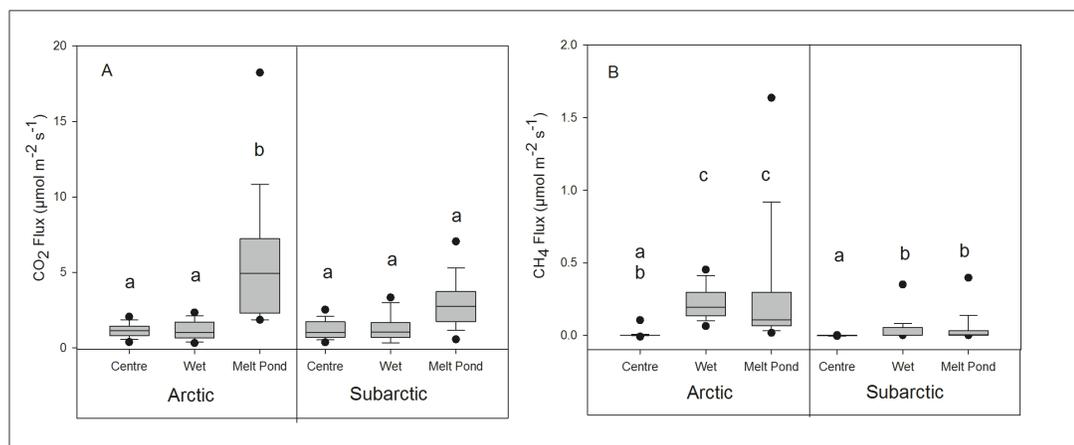
To determine if there were differences in CO<sub>2</sub> and CH<sub>4</sub> among degradation classes we used SAS 9.3 to construct mixed effects models. Specifically, we used the GLIMMIX procedure and modelled site (arctic and subarctic) and treatment (degradation class) and

their interaction as fixed effects and individual plots as a random effect. Since, the distribution of CH<sub>4</sub> flux values and model residuals indicated that CH<sub>4</sub> flux was not normally distributed, a lognormal distribution (DIST=LOGN) was used in these models. To test for differences among degradation classes and sites when there were interactions between fixed effects we used the LSMEANS procedure to perform Tukey-Kramer adjusted multiple comparisons (Littell 2006). To examine correlations between active layer, temperature and precipitation and CO<sub>2</sub> and CH<sub>4</sub> fluxes we calculated the Spearman rank correlation coefficient using SAS version 9.3.

## **Results**

### **Manual Chamber Flux Measurements**

CO<sub>2</sub> emissions from melt ponds at our arctic site were significantly higher than both polygon centres and wet troughs at both the arctic and subarctic site and from melt ponds at our subarctic site (Table 3-1, Fig. 3-2a). The pattern of CH<sub>4</sub> emissions was similar at both sites with highest emissions in melt ponds and wet troughs, followed by polygon centres (Fig. 3-2b,  $p < 0.0001$ ). However, the arctic site had larger CH<sub>4</sub> emissions than the subarctic site (Fig. 3-2b). Dissolved concentrations of CO<sub>2</sub> and CH<sub>4</sub> at the melt ponds were high with median concentrations of 452 and 0.8  $\mu\text{mol L}^{-1}$ , respectively at the subarctic site and 327 and 9.3  $\mu\text{mol L}^{-1}$ , respectively at the arctic site.



**Figure 3-2.** Boxplots of (A) CO<sub>2</sub>, and; (B) CH<sub>4</sub> emissions from polygon centres (no degradation), wet troughs (moderate degradation) and melt ponds (severe degradation) in high-centred polygonal terrain at a subarctic and arctic site. The solid black line inside the box shows the median, the ends of the box represent the 25<sup>th</sup> to 75<sup>th</sup> percentiles, the whiskers show the 10<sup>th</sup> and 90<sup>th</sup> percentiles, and the dots denote 5<sup>th</sup> and 95<sup>th</sup> percentiles with n=36. Boxes with the same letter are not statistically different (GLIMMIX, SAS).

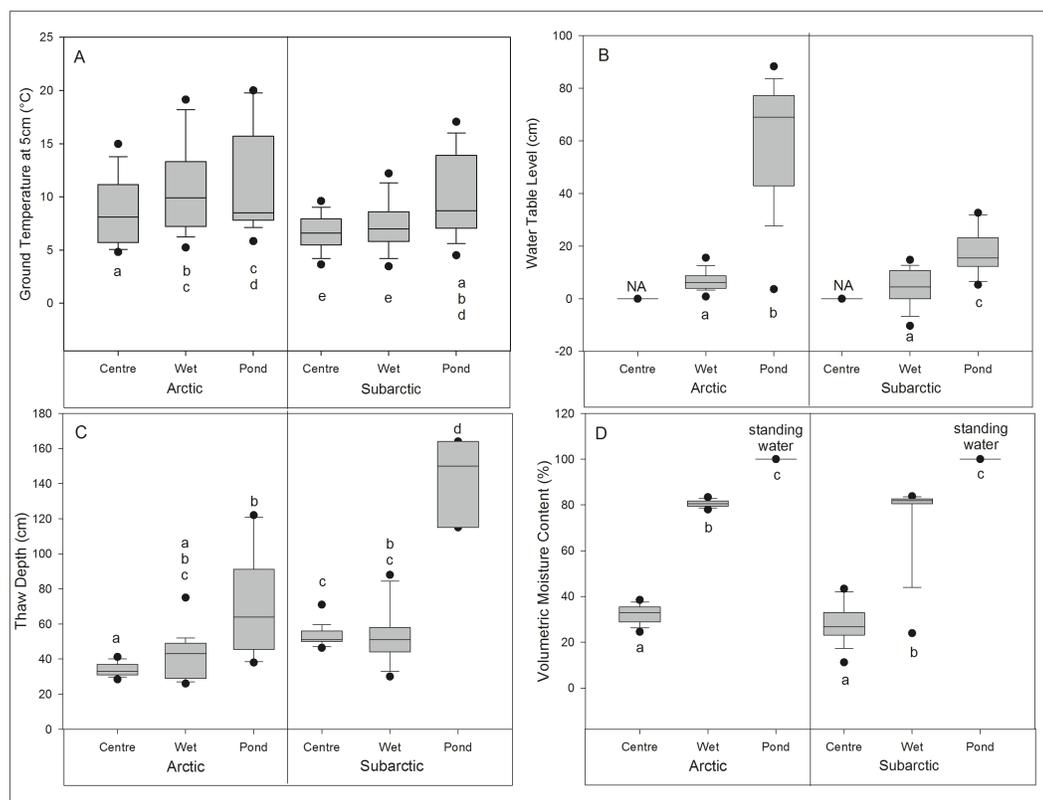
**Table 3-1.** ANOVA table from mixed effects models of CO<sub>2</sub> and CH<sub>4</sub> (GLIMMIX, SAS). Dependent variables were CO<sub>2</sub> and CH<sub>4</sub>. Fixed effects were site and treatment (degradation class). The plot sampled was included as a random effect. Significant effects are shown in bold text.

CO <sub>2</sub>	numDF	denDF	F-value	p-value
Site	1	51.5	3.8	0.0558
<b>Treatment</b>	<b>2</b>	<b>51.5</b>	<b>23.6</b>	<b>&lt;0.0001</b>
<b>Site x Treatment</b>	<b>2</b>	<b>51.5</b>	<b>4.6</b>	<b>0.0143</b>
CH <sub>4</sub>	numDF	denDF	F-value	p-value
Site	1	64.1	43.2	<0.0001
<b>Treatment</b>	<b>2</b>	<b>53.7</b>	<b>24.2</b>	<b>&lt;0.0001</b>
Site x Treatment	2	53.7	1.1	0.3329

Thaw depth (from two years prior), and soil moisture, water depth and temperature measurements collected during flux measurements all varied among the degradation classes at each research site and between research sites (Fig. 3-3). Standing water was not present in polygon centres and as expected, water table was much higher in melt ponds than in wet troughs (Fig 3-3b). The depth of water in wet troughs was similar ( $5.8 \pm 5.8$

cm) at the arctic and subarctic sites, while the arctic site had much deeper melt ponds ( $61.2 \pm 23.2$  cm) than the subarctic site ( $17.3 \pm 8.1$  cm) (Fig. 3-3b). Volumetric moisture content varied among degradation classes with consistent differences between the two sites (Figure 3-3d, Table 3-2). Moisture levels were lower in polygon centres, typically less than 40% while wet troughs were fully or nearly fully saturated ( $> 70\%$ ) at all the arctic site plots and all but one plot in the subarctic site.

At both sites, thaw depth increased with increasing degradation, although differences among degradation classes were not always significant (Fig 3-3c, Table 3-2). Note that thaw depth at the ponds was determined relative to the surface water level. Overall, there was more thaw at the subarctic ( $59.3 \pm 25.5$  cm) than arctic site ( $43.0 \pm 18.8$  cm). Similarly, water temperature at 5 cm below the top of the water in ponds was greater than 5 cm soil temperature in polygon centres at both arctic and subarctic sites. There was no difference in the pond water temperature between the two research sites while the centres and wet troughs were cooler at the arctic site (Fig 3-3a).



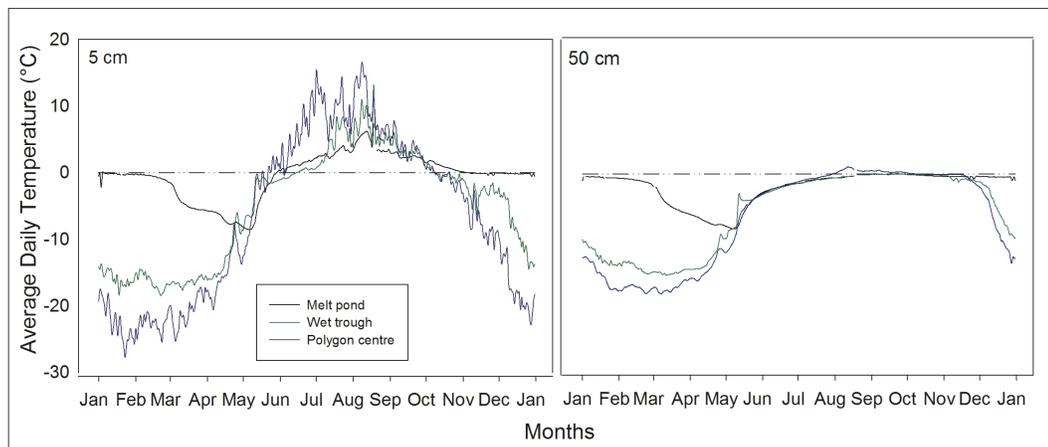
**Figure 3-3.** Active layer and soil moisture in high-centred polygonal terrain in the arctic and subarctic measured in 3 degradation classes (polygon centres, wet troughs and melt ponds): A) ground temperature during sampling from 5 cm from the top of the soil or the top of the standing water (°C); B) water table level (cm), NA indicates that no water table level was present in the active layer in polygon centres; C) thaw depth (cm); and, D) volumetric water content (%) measured using a handheld moisture probe in 2013. Box plots are as described in Fig 3 with sample sizes ranging from 3 to 165. Boxes with the same letters are not statistically different (GLM, SAS).

**Table 3-2.** ANOVA tables for general linear models of ground temperature during chamber measurements, water table levels, active layer thickness and volumetric soil moisture (GLM, SAS). Independent variables were treatment (degradation class), site and the interaction between the two. Significant effects are shown in bold.

	Source	DF	Type 1 SS	Mean Square	F Value	Pr>f
<b>Ground Temperature</b>	<b>Treatment</b>	<b>2</b>	<b>671.5</b>	<b>335.8</b>	<b>29.9</b>	<b>&lt;0.0001</b>
	<b>Site</b>	<b>1</b>	<b>1161.5</b>	<b>1161.5</b>	<b>103.5</b>	<b>&lt;0.0001</b>
	<b>Site*Treatment</b>	<b>2</b>	<b>86.4</b>	<b>43.2</b>	<b>3.9</b>	<b>0.0218</b>
<b>Water Table Height</b>	<b>Treatment</b>	<b>1</b>	<b>38448.6</b>	<b>38448.6</b>	<b>242.8</b>	<b>&lt;0.0001</b>
	<b>Site</b>	<b>1</b>	<b>13475.3</b>	<b>13475.3</b>	<b>85.1</b>	<b>&lt;0.0001</b>
	<b>Site*Treatment</b>	<b>1</b>	<b>13377.9</b>	<b>13377.9</b>	<b>84.5</b>	<b>&lt;0.0001</b>
<b>Active Layer Thickness</b>	<b>Treatment</b>	<b>2</b>	<b>19659.3</b>	<b>9829.7</b>	<b>57.1</b>	<b>&lt;0.0001</b>
	<b>Site</b>	<b>1</b>	<b>11488.3</b>	<b>11488.3</b>	<b>66.7</b>	<b>&lt;0.0001</b>
	<b>Site*Treatment</b>	<b>2</b>	<b>7141.1</b>	<b>3570.5</b>	<b>20.7</b>	<b>&lt;0.0001</b>
<b>Soil Moisture</b>	<b>Treatment</b>	<b>2</b>	<b>102872.3</b>	<b>51436.2</b>	<b>592.0</b>	<b>&lt;0.0001</b>
	<b>Site</b>	<b>1</b>	<b>757.1</b>	<b>757.1</b>	<b>8.7</b>	<b>0.0037</b>
	<b>Site*Treatment</b>	<b>2</b>	<b>42.8</b>	<b>21.4</b>	<b>0.3</b>	<b>0.7821</b>

Daily average soil temperature was the most variable (at 5 and 50 cm depths) in the polygon centre at the arctic site, which had the warmest average growing season (June 1<sup>st</sup>-August 31<sup>st</sup>) temperature at 5 cm (7.8 °C) and the coldest average winter temperatures (December 1<sup>st</sup>-March 31<sup>st</sup>) at 5 cm (-19.4 °C) of the three degradation classes (Fig. 3-4, Table 3-3). Melt ponds had the least temperature variation at 5 cm below the ground surface (below 39 cm ± 28 cm of water) over the year with coolest soils in the growing season (2.8 °C) and the warmest in the winter (-1.3 °C). Polygon centres had the coldest annual temperatures followed by wet troughs then melt ponds (Table 3-3). This difference in annual temperature was mirrored in the length of thaw season. Polygon centres were unthawed for 23 fewer days in 2013 compared to the melt ponds although

the melt ponds thawed latest in the summer (Table 3-3). Wet troughs were unthawed for 12 days longer than polygon centres (Table 3-3).



**Figure 3-4.** Average daily temperature (2013) at 5 cm (left) and 50 cm (right) in the soil of a polygon centre, wet trough and melt pond at our arctic site, near Tuktoyaktuk, NT. The dashed reference line shows 0°C.

**Table 3-3.** Freeze and thaw dates estimated using thermistor data (August 2012-August 2014) collected from the arctic field site at 5 cm depth. Thaw dates were defined as the day when the temperature rose above 0°C for three consecutive days. Thaw season was calculated as the number of days between 5 cm thaw and freeze dates. Average temperatures were calculated using 5 cm depth and the summer and winter seasons were defined as June 1<sup>st</sup> to August 31<sup>st</sup> and December 1<sup>st</sup> to March 31<sup>st</sup>.

<b>Degradation class</b>	<b>Thaw date 2013 (5 cm)</b>	<b>Freeze-date 2013 (5 cm)</b>	<b>Thaw season length (days)</b>	<b>Average Annual Temp. (°C)</b>	<b>Average Growing Season Temp. (°C)</b>	<b>Average Winter Temp. (°C)</b>
Polygon Centre	24/05/2013	08/10/2013	137	-6.28	7.80	-19.37
Wet Trough	28/05/2013	27/10/2013	149	-4.00	4.47	-11.79
Melt Pond	01/06/2013	08/11/2013	160	-0.40	2.80	-1.34

CO<sub>2</sub> fluxes in polygon centres and wet troughs at both sites were positively correlated with daily and 48 h integrated air temperatures (as measured at local weather stations) and 5 cm soil temperature regardless of the difference in moisture levels between these two degradation classes (Table 4). CO<sub>2</sub> emissions from melt ponds were not correlated with ground temperature or air temperature. CH<sub>4</sub> emissions were only positively correlated with temperature in wet troughs.

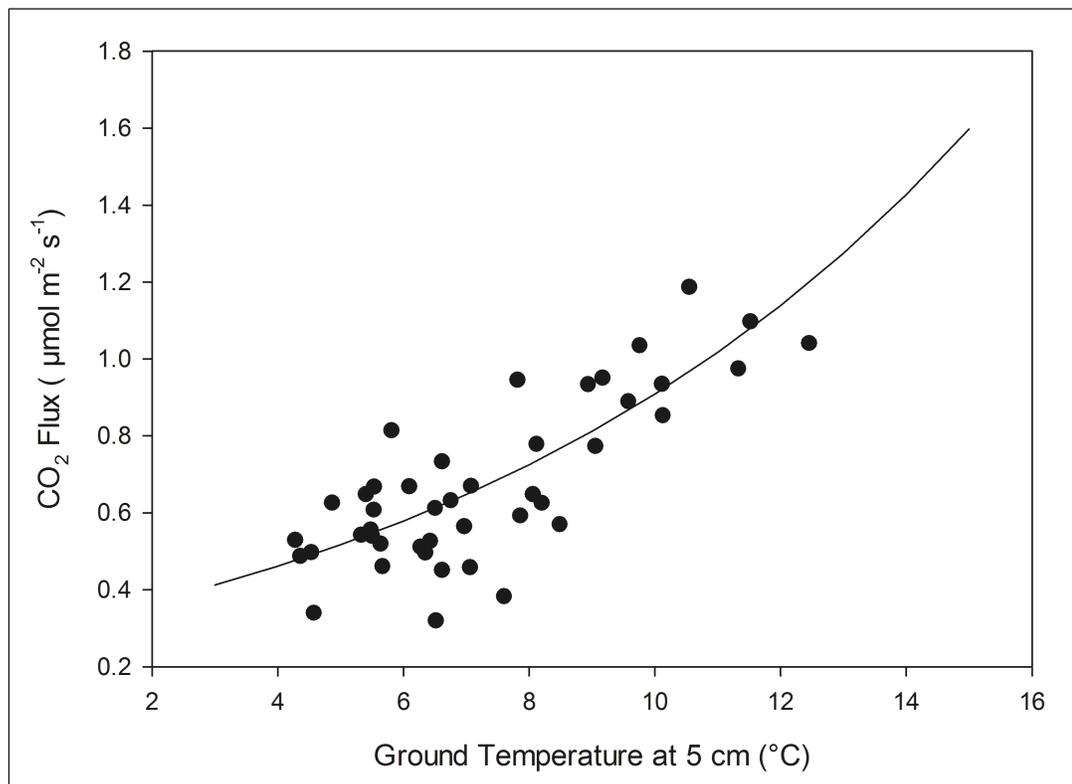
Rain occurred on one and two out of the four sampling days at the Arctic and subarctic sites, respectively. CO<sub>2</sub> flux was only positively correlated with precipitation in the two days preceding sampling at polygon centres and negatively correlated with VWC at wet troughs (Table 4). CH<sub>4</sub> emissions were not correlated with precipitation on the day of sampling, though the total amount of precipitation in the two days preceding sampling was negatively correlated with CH<sub>4</sub> flux at polygon centres, wet troughs and melt ponds (Table 4).

**Table 3-4.** Spearman rank correlations for comparisons of gas flux at polygon centres, wet troughs and melt ponds with the following environmental data: 1) volumetric water content (VWC); 2) soil temperature (5cm); 3) average air temperature on the day of sampling; 4) the average air temperature 0-48 hours before gas sampling; and 5) the total precipitation on the sampling day. Significant correlations are noted with \* and those with r values > 0.3 are shown in bold. The p-value associated with the correlation is shown in brackets.

<b>Gas and degradation class</b>	<b>Volumetric Water Content (%)</b>	<b>Temperature 5 cm (°C)</b>	<b>Temperature Day of (°C)</b>	<b>Temperature 2 days (°C)</b>	<b>Precipitation Day of (mm)</b>	<b>Precipitation 2 days (mm)</b>
<b>CO<sub>2</sub></b>						
Centre	0.07 (0.5114)	<b>0.50</b> ( <b>&lt;0.0001*</b> )	<b>0.67</b> ( <b>&lt;0.0001*</b> )	<b>0.63</b> ( <b>&lt;0.0001*</b> )	0.15 (0.21)	0.26 (0.0220*)
Wet trough	-0.24 (0.0413*)	<b>0.42</b> ( <b>0.0002*</b> )	<b>0.48</b> ( <b>&lt;0.0001*</b> )	<b>0.39</b> ( <b>0.0007*</b> )	-0.15 (0.2189)	-0.08 (0.5276)
Melt Pond	NA	-0.13 (0.2629)	0.01 (0.9023)	0.05 (0.6772)	-0.02 (0.8436)	-0.22 (0.0623)
<b>CH<sub>4</sub></b>						
Centre	0.11 (0.3533)	0.04 (0.7447)	-0.09 (0.4103)	-0.09 (0.4370)	-0.04 (0.7426)	-0.27 (0.0169)
Wet trough	-0.15 (0.2115)	<b>0.31</b> ( <b>0.0072*</b> )	-0.14 (0.2388)	-0.12 (0.2882)	0.00 (1.0000)	<b>-0.36</b> ( <b>0.0020*</b> )
Melt Pond	NA	-0.04 (0.7308)	-0.13 (0.2615)	-0.12 (0.3021)	-0.05 (0.6992)	<b>-0.37</b> ( <b>0.0011*</b> )

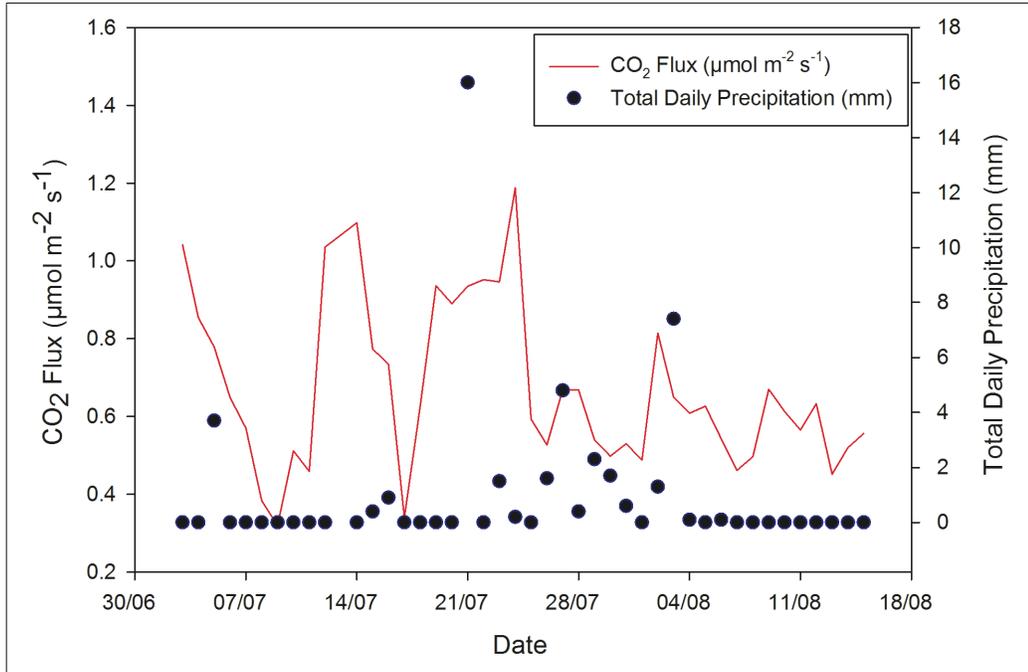
### Hourly CO<sub>2</sub> Exchange

Hourly CO<sub>2</sub> flux measurements on a polygon centre at the arctic site with the ACE station demonstrated a strong relationship with soil temperature at 5 cm ( $Q_{10} = 3.09$ , Fig. 3-5). Emissions from the ACE station were approximately half that of manual chamber measurements and showed less variation (ACE Station:  $0.69 \pm 0.26 \mu\text{mol m}^{-2} \text{s}^{-1}$ ,  $n = 369$ ; chamber measurement:  $1.20 \pm 0.73 \mu\text{mol m}^{-2} \text{s}^{-1}$   $n = 36$ ). While net CO<sub>2</sub> flux demonstrated strong correlation with temperature, it was not related to soil moisture and precipitation. This may have been due to the low variability in both moisture (0.1553 to 0.1741  $\text{m}^3 \text{m}^{-3}$ ) and precipitation (0 to 16mm, Fig. 3-6) over the summer.



**Figure 3-5.** Daily average net CO<sub>2</sub> fluxes (Net Carbon Dioxide Exchange Rate) ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) in high-centred polygonal centre near Tuktoyaktuk, NT plotted against soil temperatures at 5 cm.

The average  $Q_{10}$  value was 3.09. The equation plotted is  $R = R_{10}Q_{10}^{\left(\frac{T-10}{10}\right)}$  where R is the net CO<sub>2</sub> exchange rate,  $R_{10}$  is the net CO<sub>2</sub> exchange rate at 10°C, and T is the ground temperature at 5 cm ( $r_{\text{pseudo}}=0.64$ ,  $p<0.0001$ ).



**Figure 3-6.** Daily Average CO<sub>2</sub> Flux ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ), and total daily precipitation (mm) in high-centred polygon centre near Tuktoyaktuk, NT from July 2<sup>nd</sup>, 2014 to August 15<sup>th</sup>, 2014.

## **Discussion**

### **Impact of ice wedge thermokarst on carbon flux**

This research demonstrates that more widespread ice wedge thermokarst will increase the magnitude of CO<sub>2</sub> and CH<sub>4</sub> fluxes, particularly in the Arctic. At our Arctic site, CO<sub>2</sub> emissions were 4.6 times greater in melt ponds compared with centres and wet troughs. CH<sub>4</sub> emissions were 11.8 times greater in wet troughs and melt ponds than polygon centres. While our subarctic site showed the same emission trends among degradation classes, the magnitude of difference between degradation classes was smaller with no significant differences among degradation classes for CO<sub>2</sub> emissions. This was in keeping with results from other studies, which have examined degraded and flooded landscapes in the Lena Delta (Wagner et al. 2003; Kutzbach et al. 2004) and Alaska (Zona et al. 2012; Zona et al. 2009; Oechel et al. 1995).

Ice wedge thaw deepens the active layer, which potentially liberates previously frozen carbon allowing it to be released to the atmosphere. Our field study shows that the magnitude of this release will be moderated by site differences. Variation in CO<sub>2</sub> and CH<sub>4</sub> emissions between sites was likely caused by differences in trough depth and the age of thermokarst. The arctic site had deeper melt ponds, which resulted in deeper thaw at the bottom and on the sides of troughs. This additional thawed peat likely represents an added source of allochthonous carbon to deeper melt ponds (Laurion and Mladenov 2013), and thus provides additional carbon substrate for mineralization. The difference in melt pond depths between our two sites is due to different ice wedge degradation

histories. The subarctic site has relict ice wedges, which are truncated well below the current depth of thaw suggesting that melt occurred during a warm episode in the mid-Holocene (Kokelj et al. 2014; Burn 1997). Given the much older state of degradation, it is likely that much of the easily decomposable SOC has already been mineralized at our subarctic site leaving only less decomposable SOC (Grosse et al. 2011; Schmidt et al. 2011; Schädel et al. 2014). This would result in lower CO<sub>2</sub> and CH<sub>4</sub> emissions (Updegraff et al. 1995; Ström et al. 2012). Given that benthic respiration is an important source of CO<sub>2</sub> in thaw ponds (Breton et al. 2009), the lability of the SOC at the bottom of the melt pond is likely an important contributor to carbon mineralization rates.

#### **The importance of CO<sub>2</sub> and CH<sub>4</sub> emissions in waterlogged environments**

The production of notable amounts of CO<sub>2</sub> and negligible amounts of CH<sub>4</sub> from polygon centres is in keeping with the aerated status of those locations (Schlesinger and Bernhardt 2013a). Ice wedge thaw resulting in wet troughs and melt ponds had greater CH<sub>4</sub> emissions because saturated anoxic soils provided favourable conditions for net methanogenesis and limited opportunity for methanotrophy (Funk et al. 1994; Davidson and Janssens 2006; Schlesinger and Bernhardt 2013b).

Contrary to our hypothesis, waterlogged soils did not limit CO<sub>2</sub> emissions. It is a possible that surface conditions remained aerated to allow for aerobic respiration, particularly in subarctic melt ponds, which had floating moss mats that would have consumed CO<sub>2</sub> and produced O<sub>2</sub> through photosynthesis. There was no moss in the Arctic melt ponds, and this lack of photosynthesis may have contributed to the higher CO<sub>2</sub>

fluxes we observed from these ponds. However, we believe it is likely that the bottom of wet troughs and melt ponds provided conditions favourable for anaerobic respiration. (Negandhi et al. 2014) found that ponds over ice wedges were hypoxic at the bottom due to thermal stratification, and the presence of purple non-sulfur bacteria, which do not produce oxygen. Furthermore, anaerobic respiration has been shown to be a significant source of CO<sub>2</sub> emissions in a flooded drained lake basin with ice wedge polygons near Barrow, Alaska, as Zona et al. (2012) observed high CO<sub>2</sub> emissions, which they attributed to Fe-reduction by *Rhodoferrax ferrireducens*. The reduction of Fe(III) and humic substances is a major metabolic pathway for CO<sub>2</sub> emissions in Arctic environments (Lipson et al. 2010; Lipson et al. 2012) and the analysis of pore water at Barrow showed high concentrations of ferric ions (Zona et al. 2012).

#### **Carbon fluxes: comparisons to other studies**

The melt ponds in high-centred polygonal terrain in our area are a comparable or greater source of CO<sub>2</sub> and CH<sub>4</sub> than other forms of thermokarst or other anaerobic environments (Table 3-5). Our fluxes were slightly greater than carbon fluxes from permafrost thaw ponds in the Canadian subarctic and Arctic (Laurion et al. 2010), polygonal ponds and runnel ponds in the Canadian Eastern Arctic (Negandhi et al. 2013), and non-thermokarst water bodies in Alaska (Kling et al. 1991). However, our fluxes were orders of magnitude smaller than wetland ponds in the Hudson Bay Coastlands (Hamilton et al. 1994). Taken together, this suggests that carbon emissions from most

small water bodies (thermokarst and non-thermokarst) may be fairly constrained across the Canadian Arctic.

The high-centre polygons in the Tuktoyatuk Coastlands produce similar amounts of CO<sub>2</sub> (Table 5, Olivas et al. 2011; Olivas et al. 2010; Zona et al. 2011) to other sites in continuous and discontinuous permafrost zones. In terms of CH<sub>4</sub> emissions, our sites were comparable, but near the lower range of CH<sub>4</sub> emission values observed in other Arctic and subarctic ecosystems (Corradi et al. 2005; Nakano et al. 2000; Christensen et al. 2000; Christensen 2004; Turetsky et al. 2002).

**Table 3-5.** Comparison of CO<sub>2</sub> and CH<sub>4</sub> flux from this study (bold) to other studies using the dissolved gas and/or chambers. Studies are arranged by latitude (north-south).

Authors	Location	Landscape	Method	CO <sub>2</sub> (μmol m <sup>-2</sup> s <sup>-1</sup> )	CH <sub>4</sub> (μmol m <sup>-2</sup> s <sup>-1</sup> )
<b>This study</b>	<b>Western Arctic (68° 21'N, 133° 43' W and 69°26'N, 133°1' W)</b>	<b>High-centred polygonal terrain</b>	<b>dissolved gas</b>	<b>2.0 x 10<sup>-2</sup> to 1.9 x 10<sup>1</sup></b>	<b>-1.0 x 10<sup>-4</sup> to 1.1x 10<sup>1</sup></b>
Kling et al. (1991)	Alaska (68°19'-70°13'N, 148°10'- 149°23'W)	Rivers and lakes	dissolved gas and chambers	-6.37 x 10 <sup>-2</sup> to 6.92 x 10 <sup>-1</sup>	NA
Negandhi et al. (2014)	Canadian Eastern Arctic (73°09'N, 79°58'W)	Low-centred polygonal ponds	dissolved gas	-9.38 x 10 <sup>-2</sup> to 8.90 x 10 <sup>-1</sup>	2.32 x 10 <sup>-4</sup> to 7.29 x 10 <sup>-2</sup>
Laurion et al. (2010)	Canadian Subarctic and Arctic (55°16'N, 79°58'W and 73°09'N, 79°58'W)	Thermokarst ponds	dissolved gas	-2.37 x 10 <sup>-1</sup> to 1.32	3.47 x 10 <sup>-4</sup> to 6.51 x 10 <sup>-2</sup>
Hamilton et al. (1994)	Hudson Bay lowlands (51°28' – 51°33'N, 80°52'- 81°49'W)	Wetland ponds	dissolved gas	9.73 x 10 <sup>5</sup> to 2.89 x 10 <sup>6</sup>	7.94 x 10 <sup>4</sup> to 1.30 x 10 <sup>5</sup>

**Table 3-6.** Comparison of CO<sub>2</sub> and CH<sub>4</sub> flux from this study (bold) to other studies using the static chamber method. Studies are arranged by latitude (north-south).

Authors	Location	Landscape	Permafrost	CO <sub>2</sub> (μmol m <sup>-2</sup> s <sup>-1</sup> )	CH <sub>4</sub> (μmol m <sup>-2</sup> s <sup>-1</sup> )
Christensen et al. (2000)	NE Greenland (74°30' N, 21°00' W)	<i>Cassiope</i> heath, hummocky fen, continuous fen, grassland and <i>Salix</i> <i>arctica</i> snowbed	Continuous	1.69 x 10 <sup>6</sup> ± 1.07 x 10 <sup>3</sup>	7.62 x 10 <sup>4</sup> ± 1.73 x 10 <sup>4</sup>
Sommerkorn (2008)	Siberia (72°23' N, 99°43' E)	Low-centred polygonal terrain	Continuous	2.63 x 10 <sup>-2</sup> to 1.03	NA
Nakano et al. (2000)	Siberia (71°30' N, 130°0' E and 68°30' N, 161°24' E)	Wetlands and grasslands	Continuous	NA	3.34 x 10 <sup>4</sup> to 2.03 x 10 <sup>5</sup>
Olivas et al. (2010)	Alaskan Coastal Plain (71°19' N, 156° 37' W)	Drained lake basin	Continuous	-3.93 x 10 <sup>-1</sup> (±6.0 x 10 <sup>-2</sup> ) to -8.42 x 10 <sup>-1</sup> (±6.0 x 10 <sup>-2</sup> )	NA
Zona et al. (2011)	Alaskan Coastal Plain (71° 17' N, 156° 35' W)	Drained lake basin	Continuous	6.0 x 10 <sup>-1</sup> to 1	NA
<b><i>This study</i></b>	<b><i>Western Arctic (69°26' N 133°1' W and 68° 21' N 133° 43' W)</i></b>	<b><i>High-centred polygonal terrain</i></b>	<b><i>Continuous</i></b>	<b><i>-1.10 to 4.10</i></b>	<b><i>-4.14 x 10<sup>-1</sup> to 2.02</i></b>
Corradi et al. (2005)	NE Siberia (68°36' N, 161°20' E)	Tussock tundra	Continuous	NA	1.41 x 10 <sup>5</sup> ± 5.82 x 10 <sup>4</sup>
Christensen et al. (2004)	Subarctic Sweden (68°22' N, 19°03' E)	Peatland	Continuous	NA	4.68 x 10 <sup>4</sup> to 5.20 x 10 <sup>4</sup>
Vogel et al. (2009)	Alaskan Coastal Plain (63°52' N, 149°15' W)	Tundra	Continuous	-1.98 (± 2.9 x 10 <sup>-2</sup> ) to -2.68 (±3.8 x 10 <sup>-2</sup> )	NA
Bubier et al. (1995)	Northern Manitoba (55°54' N 98°25' W)	Peatland complex	Discontinuous	NA	-2.89 x 10 <sup>3</sup> to 7.37 x 10 <sup>4</sup>
Turetsky et al. (2002)	North-Central Saskatchewan (55°51' N, 107°41' W)	Boreal peatland	Discontinuous	2.32 x 10 <sup>-3</sup> to 1.69 x 10 <sup>-1</sup>	-2.78 x 10 <sup>-4</sup> to 3.98 x 10 <sup>-3</sup>

## **Environmental drivers of flux**

Our observations suggest that short-term CO<sub>2</sub> and CH<sub>4</sub> emissions are controlled by air and ground temperatures. Both polygon centres and wet troughs showed strong correlations with ground and air temperatures. The relationship between carbon flux and temperatures may reflect a direct effect of temperature on reaction kinetics (Davidson and Janssens 2006). These conclusions are consistent with previous studies showing that temperature is significantly correlated with CO<sub>2</sub> emissions (Oberbauer et al. 2007; Elberling et al. 2008; Mikan et al. 2002; Zona et al. 2012) and with CH<sub>4</sub> emissions in wet environments (Bubier et al. 1995; Christensen et al. 1995). A meta-analysis by Rustad et al. (2001) also found that warming increased soil respiration rates by 20%. It is likely that melt ponds did not show short-term correlations with air temperatures because water insulated soils below from short-term variations in temperature. However, the fact that melt ponds had the warmest annual temperatures, the longest thaw seasons and the highest carbon emissions indicate that longer-term warming will lead to increased carbon emissions.

Some research has shown that large amounts of rain can limit carbon flux (Wilson and Humphreys 2010; Wille et al. 2008). The lack of any correlation between precipitation on sampling days and CO<sub>2</sub> and CH<sub>4</sub> emissions at our sites may have been due to our small sample size or the low precipitation during the summer of 2014 (Environment Canada 2015). Negative correlations between precipitation in the two days preceding sampling and CH<sub>4</sub> emissions were likely caused by increases in gas transfer following rainfall induced mixing (Guérin et al. 2007; Ho et al. 1997).

## Implications

Our results suggest that increasing ice wedge thermokarst will lead to an increase in both CO<sub>2</sub> and CH<sub>4</sub> emissions from ecosystem respiration. Rising temperatures will drive more widespread ice wedge thermokarst (Jorgenson et al. 2006), deepening the active layer and increasing the magnitude of CO<sub>2</sub> and CH<sub>4</sub> emissions. The magnitude of this increase will be moderated by site differences, with more recent thermokarst in the northern area of our study likely showing greater carbon emissions. The northern part of our study area is of particular importance, as it has the highest abundance of polygonal terrain in the Tuktoyaktuk Coastlands, and has shown the greatest increase in ice wedge thermokarst (Steedman 2014). A recent analysis of airphotos from 1972 and 2004 shows that the areal coverage of melt ponds in the northern Tuktoyaktuk Coastlands has increased by 0.38%. Across the entire study area this represents an area of approximately 200 000 m<sup>2</sup> (Steedman 2014). This demonstrates that northern sites in the Tuktoyaktuk Coastlands are more susceptible to ice wedge thermokarst disturbance and once degraded, will produce more CO<sub>2</sub> and CH<sub>4</sub> emissions than subarctic thermokarst.

The strong correlation between temperature and carbon flux suggest that increasing temperatures will also result in higher overall emissions from non-thermokarst terrain at these sites. The results from incubation analyses (Chapter 2) demonstrate that carbon currently frozen in the permafrost is vulnerable to release when active layers deepen and permafrost thaws. Longer thaw seasons will also increase the amount of time available for carbon mineralization to occur, increasing emissions. This is consistent with a large body of literature showing a positive correlation between temperature and carbon emissions (Davidson and Janssens 2006; Dutta et al. 2006; Mack et al. 2004; Hobbie et

al. 2000; Davidson et al. 2000; Fang et al. 2005; Knorr et al. 2005; Trumbore et al. 1996) and the prediction of Schuur et al. (2015) that permafrost thaw will result in ~5% to 15% of the terrestrial carbon pool being vulnerable to release by the end of this century. In conclusion, our field study shows that increasing ground and air temperatures will result in increasing carbon flux from polygonal terrain and that the projected increase of thermokarst disturbance is likely to increase the magnitude of this flux.

### **Key Findings**

1. Ice wedge thermokarst results in increased CO<sub>2</sub> and CH<sub>4</sub> emissions relative to non-degraded polygonal terrain.
2. Waterlogged conditions do not limit CO<sub>2</sub> flux.
3. Carbon emissions from ice wedge thermokarst are similar to other forms of thermokarst or anaerobic environments in the Arctic.
4. Temperature is an important driver of both CO<sub>2</sub> and CH<sub>4</sub> flux.

## Chapter 4 – Synthesis and Future Directions

Northern regions hold 1035 Pg of the world's soil organic carbon (Hugelius et al. 2014). Much of this soil carbon is currently frozen in permafrost soils. However, increasing air and ground temperatures will result in active layer deepening and thermokarst development (ground subsidence due to permafrost thaw) (Kokelj and Jorgenson 2013), that will make previously frozen soil organic carbon (SOC) increasingly vulnerable to release to the atmosphere (Schuur et al. 2015). High-centred polygonal terrain is a terrain type common in the low Arctic that is likely to be very vulnerable to thermokarst because of high ground ice content in the form of ice wedges (Jorgenson et al. 2006). Ice-wedge degradation results in terrain subsidence and increased soil moisture and ground temperatures (Jorgenson et al. 2006), which are likely to have a significant impact on carbon cycling (Hobbie et al. 2000). Research on the effect of ice wedge degradation on carbon (CO<sub>2</sub> and CH<sub>4</sub>) emissions is required to better understand the role these landscapes will play in the global carbon cycle. The overall goal of my MSc research was to quantify carbon emissions from high-centred polygonal terrain in the Tuktoyaktuk Coastlands.

In Chapters 2 and 3 of this thesis we explored two separate, but complementary, research questions. Chapter 2 examined the following question: What is the potential contribution of peat currently frozen in high-centred polygonal terrain to future carbon emissions? We tested the hypothesis that peat at different depths was equally decomposable. To do this we incubated six cores from two different sites for 63 days using four different treatments: cold anaerobic, warm anaerobic, cold aerobic and warm aerobic. Chemical analyses were also performed on soil samples. In accordance with our

hypothesis, we found that there was no difference in emission rates or SOC quality among depths. The warm aerobic treatment emitted the most CO<sub>2</sub>, and the warm anaerobic treatment emitted the most CH<sub>4</sub>. However, even in the anaerobic incubation, CO<sub>2</sub> emissions were greater than CH<sub>4</sub>. Our results demonstrate that when thawed, peat in high-centred polygonal terrain will not be limited due to SOC quality. Our results also highlight that environmental controls (levels of oxygenation, temperature) will partially moderate how fast SOC is released to the atmosphere and whether any CH<sub>4</sub> is produced. Overall, this research suggests that active layer deepening and ice wedge degradation in high-centred polygonal terrain will result in increased carbon emissions, with CO<sub>2</sub> representing the bulk of these emissions.

In Chapter 3, we posed the question: What is the effect of ice wedge degradation in high-centred polygonal terrain on current carbon (CO<sub>2</sub> and CH<sub>4</sub>) emissions in the Tuktoyaktuk Coastlands? We proposed two hypotheses: 1) increased soil temperatures in degraded troughs would result in increased carbon emissions (both CO<sub>2</sub> and CH<sub>4</sub>); and, 2) advanced degradation and ponding would create anoxic conditions that would lead to a decrease in CO<sub>2</sub> production, and an increase in CH<sub>4</sub> production. To test these hypotheses we sampled gas flux in the field at two sites. At each site we installed nine gas sampling collars in both polygon centres and wet troughs and used closed sampling chambers to measure CO<sub>2</sub> and CH<sub>4</sub> flux four times during the summer of 2014. At each site we also measured ground temperature and soil moisture using thermistors and a moisture sensor, respectively. To estimate gas flux from melt ponds, we used a wind diffusion model. To quantify daily flux variation, we installed an automatic CO<sub>2</sub> exchange (ACE) station at a polygon centre at our arctic field site. Our results demonstrate that ice wedge degradation

results in increased ground temperature, deeper active layers, and increased CO<sub>2</sub> and CH<sub>4</sub> emissions. Contrary to our expectations, CO<sub>2</sub> emissions were not limited by waterlogged conditions, demonstrating the importance of anaerobic CO<sub>2</sub> production. Both air and ground temperatures were highly correlated with carbon flux in polygon centres and wet troughs. Our study shows that CO<sub>2</sub> and CH<sub>4</sub> emissions associated with ice wedge degradation are similar to other forms of thermokarst or anaerobic environments in the Arctic, and that emissions from these landscapes are likely to increase with rising temperatures.

Schuur and Abbott (2011) outlined three key questions regarding the future of carbon cycling in permafrost: 1) How much permafrost carbon is vulnerable to release? 2) How fast will this release occur? and; 3) What will the form of this release be? Chapters 2 and 3 contribute to these questions by providing an improved understanding of the current and potential contribution of carbon emissions from high-centred polygonal terrain in the Tuktoyaktuk Coastlands.

Chapter 2 illustrates that carbon currently stored in the permafrost of the Tuktoyaktuk Coastlands is vulnerable to release when thawed and that the majority of this release will be in the form of CO<sub>2</sub>, even in anaerobic conditions. Our research demonstrates that when all other variables are held constant, the speed of this release will largely depend on environmental controls, namely temperature and moisture. The in-situ characterization of carbon flux in the field presented in Chapter 3 contributes to a more comprehensive understanding how these controls operate in high-centred polygonal terrain at two sites, one in the subarctic and the other in the Arctic.

Chapter 3 builds on Chapter 2, by demonstrating that, while both temperature and moisture have an effect on carbon mineralization rates, at our field sites ground temperatures act as the primary control of carbon mineralization rates. In addition to providing a good characterization of the current emissions from polygonal peatlands, Chapter 3 also provides a glimpse into future potential emissions by contrasting 3 degradation classes (non-degraded polygon centres, moderately degraded wet troughs and severely degraded melt ponds). Coupled with rates of ice wedge pond formation, our estimates could be used to estimate carbon flux associated with this form of thermokarst.

Overall our research demonstrates that as ground temperatures increase in high-centred polygonal terrain, carbon emissions are likely to increase. Our field measurements demonstrate that increasing temperatures are correlated with rising CO<sub>2</sub> emissions in aerobic environments and rising CO<sub>2</sub> and CH<sub>4</sub> emissions in anaerobic environments. Rising temperatures have also been associated with increased ice wedge ponding (Jorgenson et al. 2006; Raynolds et al. 2014; Steedman 2014), which is likely to further contribute to increases in CO<sub>2</sub> and CH<sub>4</sub> emissions. Our incubation results show that the decomposition of SOC exposed by active layer deepening will not be limited by SOC quality. Taken together, our research demonstrates that rising temperatures will result in more CO<sub>2</sub> and CH<sub>4</sub> being released to the atmosphere from this terrain type.

While our research provides a valuable contribution to our understanding of the dynamics of carbon flux in the Tuktoyaktuk Coastlands, it also identifies several areas where future research is needed. More research is needed to better characterize both SOC quality and microbial populations among sites. Characterizing carbon quality at each site is needed to test the hypothesis that there are differences in substrate quality among the

active layer, permafrost, and different sites. This could be accomplished using the chemical fractionation analyses performed in Chapter 2 on a larger number of samples from multiple sites across the region. Characterizing the microbial population at each site is needed to test our hypothesis that Fe-reducing bacteria were responsible for anaerobic CO<sub>2</sub> production in wet troughs. Microbial characterization could be accomplished by analyzing soil pore water samples using the methods described in Lipson et al. (2010).

Our field studies showed that CO<sub>2</sub> and CH<sub>4</sub> emissions differed between an arctic and subarctic site. To verify that these differences were caused by trough depth and age of thermokarst, and potentially differences in SOC lability between sites, additional research is required to characterize variations in flux among polygonal peatlands in both the south and northern regions of our study area. A more robust sample size of subarctic and Arctic polygonal peatlands would help to verify if there is a consistent difference in the magnitude of emissions between subarctic and Arctic polygonal peatlands. Furthermore, chemical analyses could confirm whether our hypothesis regarding differences in carbon lability between sites is correct.

More research on the impact of primary productivity on CO<sub>2</sub> and CH<sub>4</sub> flux would also contribute to a better understanding of the future emissions from this terrain type. Net primary production is an important process in all ecosystems resulting in impacts on energy, nutrient and carbon flows through the soil-plant-atmosphere continuum. Recent observations show that upright shrubs can rapidly proliferate in the low Arctic (Lantz et al. 2013, Fraser et al. 2014, Myers-Smith et al. 2011). There is some research that suggests that increases in primary productivity resulting from warming temperatures and increased woody plants may overshadow rising rates of decomposition in tundra

ecosystems (Shaver et al. 2000; Sistla et al. 2013). Future research in polygonal peatlands should include measurements of both primary productivity and net carbon flux to better characterize whether these landscapes are a net carbon source to the atmosphere.

Additional research could also attempt to scale up the findings of our plot-based sampling. This could be accomplished by mapping of the Tuktoyaktuk peninsula using Landsat images and classifying terrain types (polygon centres, melt ponds, etc.) using a similar method to Lara et al. (2015). Pairing the areal coverage of high centre polygons, wet troughs and melt ponds with the more comprehensive characterization of carbon flux suggested above to determine the variation between individual polygonal peatlands, would allow for a landscape-level estimate of carbon flux from these landscapes.

Future research could also focus on integrating terrain specific case studies like the research in this thesis into carbon cycling models. Currently, abrupt permafrost thaw, which describes processes such as thermokarst formation, is not included in large-scale carbon cycling models (Schuur et al. 2015). To include abrupt permafrost thaw in large-scale carbon cycling model, a synthesis of case studies in multiple forms of thermokarst would need to be combined with regional or global scale maps of these disturbances to provide broad-scale estimates of the carbon flux associated with thermokarst disturbance. This approach would improve the accuracy of these models.

As temperatures continue to increase, the impact of permafrost thaw on carbon flux and the global climate forcing will become critically important. Polygonal terrain is a significant component of the landscape in the western Canadian Arctic. My thesis provides a significant contribution our understanding of the current and potential contribution of this landscape to carbon flux from permafrost environments.

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## Appendices

**Appendix 1.** ANOVA tables for general linear models of total carbon, inorganic carbon, organic carbon, nitrogen, ash, soluble fats, simple sugars, hydrolyzed carbohydrates and lignin (GLM, SAS). Independent variables were depth, site and the interaction between the two.

	Source	DF	Type 1 SS	Mean Square	F Value	Pr>f
Total Carbon	Depth	2	196.69	98.35	0.64	0.5558
	Site	1	70.86	70.86	0.46	0.5190
	Depth x Site	1	106.65	106.65	0.69	0.4324
Inorganic Carbon	Depth	2	0.81	0.40	0.99	0.4185
	Site	1	0.36	0.36	0.89	0.3771
	Depth x Site	1	0.33	0.33	0.81	0.3987
Organic Carbon	Depth	2	210.87	105.43	0.65	0.5506
	Site	1	60.39	60.39	0.37	0.5609
	Depth x Site	1	95.08	95.08	0.59	0.4687
Nitrogen	Depth	2	1.19	0.60	2.69	0.1359
	Site	1	0.0015	0.0015	0.01	0.9365
	Depth x Site	1	0.71	0.71	3.22	0.1159
C:N	Depth	2	4.99	2.49	0.18	0.8363
	Site	1	17.30	17.30	1.27	0.2964
	Depth x Site	1	1.03	1.03	0.08	0.7912
Ash	Depth	2	844.64	422.32	0.77	0.4978
	Site	1	516.33	516.33	0.94	0.3636
	Depth x Site	1	185.00	184.99	0.34	0.5791
Soluble fats	Depth	2	0.86	0.43	0.23	0.7986
	Site	1	0.14	0.14	0.08	0.7908
	Depth x Site	1	0.0098	0.0098	0.01	0.9440
Simple Sugars	Depth	2	2614.43	1307.22	1.09	0.3873
	Site	1	2337.23	2337.23	1.95	0.2055
	Depth x Site	1	1887.44	1887.44	1.57	0.2500
Hydrolyzed Carbohydrates	Depth	2	24.68	12.34	0.32	0.7490
	Site	1	105.22	105.22	2.72	0.1978
	Depth x Site	1	29.25	29.25	0.76	0.4487
Lignin	Depth	2	455.60	227.80	0.43	0.6665
	Site	1	90.25	90.25	0.17	0.6921
	Depth x Site	1	311.13	311.13	0.59	0.4684

**Appendix 2.** Results from chemical fractionation of soil using the method of Ryan et al. (1990). Comparing chemical fractions by depth using a general linear model in SAS (GLM, SAS) found no significant differences ( $>0.05$ ) among depths and soil fractions (Table 2-4). Averages with standard deviations are presented for all samples by depth class. Range of raw values are included in brackets.

<b>Depth</b>	<b>40-70cm</b>	<b>100-130cm</b>	<b>210cm+</b>
Total carbon (% dry)	44.08±4.51 (38.0-48.8)	34.37±17.64 (9.4-47.5)	41.00±9.29 (28.2-48.3)
Inorganic carbon (% dry)	0.18±0.02 (0.1-0.2)	0.59±0.72 (0.2-1.7)	0.80±0.82 (0.3-2.0)
Organic carbon (% dry)	43.90±4.52 (37.8-48.6)	33.76±17.59 (9.2-47.1)	40.2±10.00 (26.2-47.8)
Nitrogen (% dry)	2.45±0.39 (2.1-3.0)	1.67±0.68 (0.7-2.1)	2.06±0.36 (1.6-2.4)
C:N ratio (% dry)	18.35±3.45 (15.2-23.2)	19.42±3.88 (14.2-22.4)	19.89±3.30 (16.9-24.3)
Ash (% dry)	12.17±4.92 (5.1-16.2)	32.47±34.98 (6.8-81.9)	19.54±16.19 (8.4-18.0)
Soluble fats, waxes, oils, etc. (% dry)	1.67±1.39 (0.2-3.5)	1.21±1.23 (0.1-2.4)	1.04±0.97 (0.2-1.9)
Simple sugars (mg/g)	34.81±64.80 (1.6-132)	2.76±2.25 (0.6-5.7)	4.29±2.06 (2.7-7.3)
Ash-free lignin (% dry)	50.64±16.13 (27.0-63.3)	35.62±24.09 (9.8-56.6)	41.82±23.00 (16.2-61.0)
Hydrolyzed carbohydrates (mg/g)	15.10±7.90 (11.6-24.1)	11.15±7.93 (2.2-17.3)	12.18±0.20 (12.0-12.3)