SENSITIVITY OF ARCTIC PERMAFROST CARBON IN MACKENZIE RIVER BASIN PEATLANDS: AN INCUBATION EXPERIMENT TO OBSERVE THE PRIMING EFFECT

A THESIS SUBMITTED TO THE GRADUATE DIVISION OF THE UNIVERSITY OF HAWAIʻI AT MĀNOA IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF

MASTER OF ARTS

IN

GEOGRAPHY

DECEMBER 2015

By

Alexandra L. Hedgpeth

Thesis Committee:
Dave Beilman, Chairperson
Susan Crow
Nicole Hynson
Camilo Mora

Keywords: Permafrost, Carbon, Peatland, Peat, Arctic, Priming Effect

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Acknowledgments

This thesis would not have been possible without the continuous support and tolerance from my supervisor, Dave Beilman. He encouraged me to be both a data driven lab nerd and a theory driven field scientist, while teaching the importance of remembering the overall big picture that drives everything. The combination of guidance from an encouraging supervisor and unwavering group of fellow Geographers and colleagues is the reason why this document exists. The reason I exist, and am the person I am, is due to my family- a group of very important people, who accepted all the distance and missed family events over the years. To all of these people mentioned here, thank you.

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Chapter 1: General Introduction

Permafrost Soil Organic Matter

Great quantities of organic carbon are preserved in frozen permafrost soils in the Arctic. Contemporary Arctic carbon stocks formed from surface biotic activity are primarily stored in two reservoirs, living biomass and soil organic matter. These large stocks are what make northern high latitude terrestrial ecosystems important to the global carbon cycle. In general, soils in northern high latitudes have been storing large quantities of carbon in unglaciated and recently deglaciated areas since the Last Glacial Maximum (Zimov et al., 2006; Harden et al., 1992). This large amount of carbon accumulation is due to the cold and wet conditions that inhibit decomposition of plant detritus that enter the soil organic matter pool. Permafrost, defined as soil materials, sediments, or rocks that have remained frozen (below 0°C) for two consecutive years or longer, creates positive conditions for carbon storage due to these decomposition-limiting environments (French, 2007). Permafrost covers 25% of the northern hemisphere (Schuur et al., 2008), and is separated into zones defined by the extent of permafrost in each zone; continuous, discontinuous, sporadic, and isolated. Soil organic matter mainly accumulates in the upper soil horizons, and includes carbon in mineral soils (<1% - 20% carbon), and carbon stored in frozen histels in peatlands (soils with 20-60% carbon) (USDA soil survey, 2014; Knoblauch et al., 2013).

Although Arctic permafrost carbon storage is large, considerable uncertainty remains in describing Arctic carbon stocks due mainly to issues associated with the inaccessibility of permafrost regions as well as lack of data on soil depth. With each new assessment that includes more sites and considers deeper soil depths, the estimated amount of soil carbon in the Arctic carbon pool has increased (Batjes, 1996; Ping et al., 2008; Schuur et al., 2015). Northern high latitude terrestrial ecosystems hold 1672Pg of soil carbon in the top 3m (Tarnocai et al., 2009; Schuur et al., 2008; Hugelius et al., 2013). This value, almost 1700 billion tons of organic carbon stored in the northern permafrost zone (IPCC, 2013), reflects the large amount of carbon stored at depths below one meter and is significant in that the permafrost carbon pool weighs in at nearly two times that of carbon in the atmosphere (Zimov et al., 2006; Tarnocai, 2009; Ping et al., 2008). In addition to recent soil carbon synthesis reporting large quantities of deep permafrost carbon, other studies show that these stores of permafrost carbon are susceptible to future thaw (Schadel et al., 2014).

The large carbon pools in Arctic permafrost regions represent a reservoir in the global carbon cycle that is inherently vulnerable to climate warming (Gorham, 1991; Schuur et al., 2008; Schuur et al., 2015). Temperatures in high latitude regions have risen 0.6°C per decade (0.2-3.5 °C) over the past 30 years, which is twice as fast as the global average (IPCC, 2013). This temperature change is triggering some of these areas of extensive, normally frozen soil to thaw; exposing previously protected carbon (Romanovsky et al., 2013), and increasing soil organic matter decomposition rates (Hartley et al., 2008). New syntheses continue to report large quantities of carbon preserved deep within permafrost that are possibly susceptible to thaw (Harden et al., 2012), while highlighting the still remaining gaps in our understanding of this vulnerable carbon pool (Mishra et al., 2013). Due to the complexity of permafrost carbon dynamics, there is a danger of oversimplifying permafrost carbon cycling in earth system models by not fully incorporating necessary carbon cycling processes.

The resilience and vulnerability of permafrost to changing climate is linked to complex interactions between surface topography, hydrology, soil characteristics, vegetation and precipitation (snow and rain) (Jorgenson et al., 2010). The consequences of permafrost thaw range from microsite changes in vegetation, hydrology, and soil decomposition to potential global scale contributions of greenhouse gases (Schuur et al., 2009; Jorgenson et al., 2010). Yet, there is an imperfect understanding of the complex factors and interactions that allow permafrost to persist at mean annual air temperatures as high as +2°C and degrade at temperatures as low as -20°C (Grom and Pollard, 2008). This large range of resilience and vulnerability shows the importance in better identifying and quantifying negative and positive feedbacks. These feedbacks can contribute to the ability of permafrost affected ecosystems to make adjustments and recover from perturbations and thus be resilient to change; or make permafrost more vulnerable, causing shifts in long-term carbon stabilization.

The Permafrost Carbon Feedback

While there are some carbon pools that persist in soils and sediments over long periods of time, evidence shows that there is a large carbon reservoir in the Arctic permafrost region that is vulnerable to change in a warming climate (Schuur et al., 2015). Due to the large carbon stocks in Arctic permafrost, there are increasing concerns about the potential release of significant amounts of this currently protected carbon as greenhouse gases (Schuur et al., 2008; Tarnocai, 2009; Whiteman et al., 2013; Harden et al., 2012). The decomposability of permafrost soil organic matter depends in part on the soil environment, the plant inputs, and also depth in the soil profile (Schuur et al., 2015). Land surface subsidence, or thermokarst, often follows permafrost thaw and can affect surface hydrology (Lee et al., 2012). As a result of thaw effects, soil organic matter can be exposed to either aerobic (above the water table) or anaerobic conditions (Jorgenson et al., 2006). In aerobic soils, carbon dioxide (CO_2) is released by microbial decomposition of soil organic matter in the active layer and near surface permafrost (Harden et al., 2012). In contrast, areas where waterlogging promotes anoxic soils, there is slower decomposition and potentially significant methane (CH_4) production (Lee et al., 2013).

In addition to different release rates, the decomposition of permafrost soil organic matter under different environmental conditions will determine the type of greenhouse gas released. Quantifying the relative amount of CO_2 or CH_4 released from thawing permafrost is essential for determining biological feedbacks, because CH_4 has a 28–34 times larger global warming potential on a 100-year time scale (Treat et al., 2015). Continued warming is not only expected to alter the physical soil environment, but may increase plant productivity and change the composition of plant communities (Hobbie et al., 2000; Hartley et al., 2010). Changes in surface vegetation are likely to alter rates of labile carbon inputs, which may further modify soil organic matter decomposition and long-term carbon storage in permafrost soils (Fontaine et al., 2004; Bradford et al., 2008).

Different approaches to understanding permafrost carbon susceptibility, including laboratory incubations and soil process modeling, estimate that 5-15% of terrestrial permafrost carbon could be vulnerable to release in the form of greenhouse gases during this century under the current warming trajectory, with CO_2 making up the majority of gas released (Schuur et al., 2015). This would mean 130-160Pg of carbon could be released in the form of CO_2 over the next century. This is similar in magnitude to other sources of carbon such as global land use change (average rate of increase 0.12 ppm yr^{-1}) (Le Quere et al., 2014); however, in addition to the direct temperature effects on permafrost thaw and carbon release by decomposition, warming might

trigger indirect alterations to the carbon cycle in permafrost-affected ecosystems (Wild et al., 2014). Higher plant productivity seen with increased temperature can cause an increase in plant inputs to soils from leaf and root litter. Counter-intuitively, this increase in carbon inputs does not always mean increased carbon storage. In one study, a reduction in total carbon stocks were seen with additions of plant-derived material below ground in a sub-arctic system, leading to a net loss of carbon from the soil (Hartley et al., 2012).

There are mainly three ways to study the permafrost carbon pool and its response and influence on the global carbon cycle: field measurements, projective models, and controlled laboratory incubations (Huissteden and Dolman, 2012; Schuur et al., 2008). Laboratory work is useful to pinpoint key mechanisms controlling green house gas release from permafrost soils (Schuur et al., 2015) that are currently not incorporated in ecosystem and Earth System Models (Koven et al., 2013). While the inclusion of environmental controls, soil freeze-thaw dynamics in particular, and a representation of permafrost soil thermodynamics have improved the representation in models of organic carbon turnover (Lawrence et al., 2008; Koven et al., 2013) these models may still be over simplifying permafrost carbon dynamics and inadequately estimating the future fate of permafrost carbon. For example, many current models forecasting long term permafrost carbon dynamics apply a two pool degradation approach solely based on carbon mineralization measurements of "fast" and "slow" carbon (Andren and Katterer, 1997). Specific soil organic matter characteristics and microbial processes that govern decomposition are not well represented (Knoblauch et al., 2013). There are acknowledged uncertainties associated with modeling permafrost carbon, and the small number of studies focusing specifically on permafrost carbon dynamics makes accurate incorporation of carbon regulating parameters difficult (Slater & Lawrence, 2013). Incorporation of laboratory incubation data focused on specific processes of greenhouse gas release, such as this thesis and many other studies included, and could improve these models and their resulting projections and forecasts of permafrost carbon.

Permafrost is a unique system in which there exists a depth beyond which summertime temperatures can reach to thaw the soil; this demarcation between seasonally thawed and frozen horizons is highly variable in space and time and makes modeling soil organic matter difficult. Several climate-scale land models have attempted to include a depth-dependent dimension to better describe soil biogeochemical cycles within permafrost (Rapalee et al., 1998). Including these processes has, in some cases, lead to a sign change in the overall response of permafrost carbon release to warming; i.e. from net gains via increase surface vegetation and storage to net losses via enhanced soil organic matter decomposition (Schaefer et al., 2011). Many simplified permafrost carbon models support this net sign change prediction where permafrost soils loose carbon through enhanced decomposition (Harden et al., 2012; Burke et al., 2012). However, lesser-known carbon cycling and release mechanisms associated with thawing permafrost to date have not been accounted for in many Earth System Models (Ciais et al., 2013). Reducing these uncertainties will require experimental designs to better understand the complex carbon cycling processes associated with environmental change affecting permafrost soil organic matter.

The Priming Effect

In addition to increasing decomposition rates, Arctic warming might also indirectly affect soil organic matter decomposition with the increase of plant net primary productivity and associated plant detritus at the surface and root inputs to the subsurface (Hartley et al. 2008). One of the most poorly understood, yet potentially important, processes that may affect soil carbon

balance under warming-induced net primary productivity increases is soil priming (Bingeman et al., 1953). Soil priming, or the priming effect, is the concept that fresh organic matter inputs (in the form of root exudates, decomposed litter fall, or fine roots) can stimulate increased soil organic matter decomposition (Kuzyakov et al., 2000; Fontaine et al., 2007; Blagodatskaya and Kuzyakov et al., 2008; Wild et al., 2014; Cardinael et al., 2015). Plants supply the soil microbial community with a range of organic compounds of varying decomposability; compounds that can be immediately taken up and used directly for metabolic processes (such as sugars, amino acids, and organic compounds from root exudates) or those that can be easily broken down by extracellular enzymes (cellulose and root litter protein). Soil priming occurs when fresh, easily degradable compound either promotes microbial groups that target complex less degradable soil organic matter, provides energy specifically needed to break down these already present compounds, or provides the needed carbon for microbial growth and stimulates the nitrogen demand facilitating nitrogen mining (Fontaine et al., 2003; Blagodatskaya & Kuzyakov, 2008; Craine et al., 2007; Dijkstra et al., 2013). In a permafrost context, if carbon inputs stimulate soil organic matter decomposition, easily degradable carbon compounds delivered below ground with increased net primary productivity could push permafrost soils to become a source of carbon greater than currently projected by models that do not currently take soil priming into consideration (Cardinael et al., 2015).

When considering the priming effect occurring in nature, there is some doubt as to the existence of priming effects in a "natural soil" setting, with the main argument being that priming effects are artifacts arising from the addition of easily degradable material (Kuzyakov, 2010). However, in natural soils, polymer decomposition produces monomeric sugars, so using a substance such as glucose – the decomposition product of cellulose, the most common polysaccharide in plant litter – in experiments is one approach to simulate this easily degradable substrate (Kogel-Knabner, 2002; Derrien et al., 2004). An increase in soil-derived CO_2 efflux in either a lab or field setting could be due to either increased microbial metabolism of soil carbon (real priming effect) or increased turnover of microbial carbon (apparent priming effect) (Kuzyakov et al., 2000; Nottingham et al., 2009). While there is still debate over whether all detected priming effects are real, apparent, or a combination of both, an apparent priming effect can be seen using a soil carbon mass balance to show that losses of soil carbon in soils amended with substrate are higher than unamended soils after taking the added labile carbon inputs into account. Specifically when examining Arctic regions, where soils are considered nitrogen and energy limited, new nutrients from sources such as root exudates could play an important role in microbial degradation of previously protected soil organic matter (Sistla et al., 2012; Fontaine et al., 2007). Surprisingly little is known about the microbial communities that utilize the immensely large Arctic carbon pool (Campbell et al., 2010). How the alteration of nutrient availability will effect high latitude microbial populations and the ecosystem processes they mediate is even less clear.

The permafrost zone boundaries are arguably going to be areas experiencing the greatest amount of change in carbon dynamics as conditions change in the Arctic. Areas where thawing events would lead to a transition from permanently frozen to permanently unfrozen would drastically change the soil environment and potentially enhance the permafrost carbon feedback (Koven et al., 2015). As soils thaw and new vegetation regimes move north with increased temperatures, deeper permafrost soils along the southern boundary of the permafrost zones could be regions where the priming effect would promote more carbon released to the atmosphere.

Potential Priming Effects in the Mackenzie River Basin

The Mackenzie River Basin is located between 52° and 69° N latitude in the northwest of Canada, covering portions of the Northwest Territories, Alberta, British Columbia, Saskatchewan, and the Yukon Territory (Figure 1.1; Nicholson et al., 1996), draining an area of approximately 1,805,200 km^2 and with a discharge of 12,200 m^3/s to the Arctic Ocean's Beaufort Shelf and Canada Basin (Raymond et al., 2007). The Mackenzie River Basin spans the continuous and discontinuous permafrost zone and is the largest Arctic watershed in North America (Raymond et al., 2007) as well as one of the world's largest wetland regions (Nicholson et al., 1996; Beilman et al., 2008; Vitt et al., 2005). The Mackenzie River Delta is a direct connection between the immense Mackenzie River Basin and the Arctic Ocean (Hilton et al., 2015) making this large ecosystem very unique (Beilman et al., 2008; Cohen, 1997; Morrow et al., 2011; Burn and Kokelj, 2009). Recent estimates suggest over 277Pg of soil organic carbon are locked away in Arctic peatlands, which represents one third of the total atmospheric CO_2 carbon (Tarnocai et al., 2009). Since the end of the last glacial period, these peat soils have been a major atmospheric carbon sink (Harden et al., 1992).

The carbon storage of the Mackenzie River Basin makes this region an important component of the possible Arctic Carbon Feedback response to climate change. Data from Mackenzie River Basin peatlands suggests that this terrestrial carbon stock contains more than 16 Gt of carbon (Vitt et al., 2005). This thesis focused on carbon rich soils from the Mackenzie River Basin to explore the response of active layer and permafrost material to the addition of a labile carbon source. The following research questions guided our hypotheses: 1) is there a priming effect possible for active layer and near-surface permafrost peatland soils of the Mackenzie River Basin? 2) Is the priming effect consistent across latitude? 3) Is the potential priming effect observable and of equal magnitude in still-frozen near-surface permafrost soils as it is in current active layer soils?

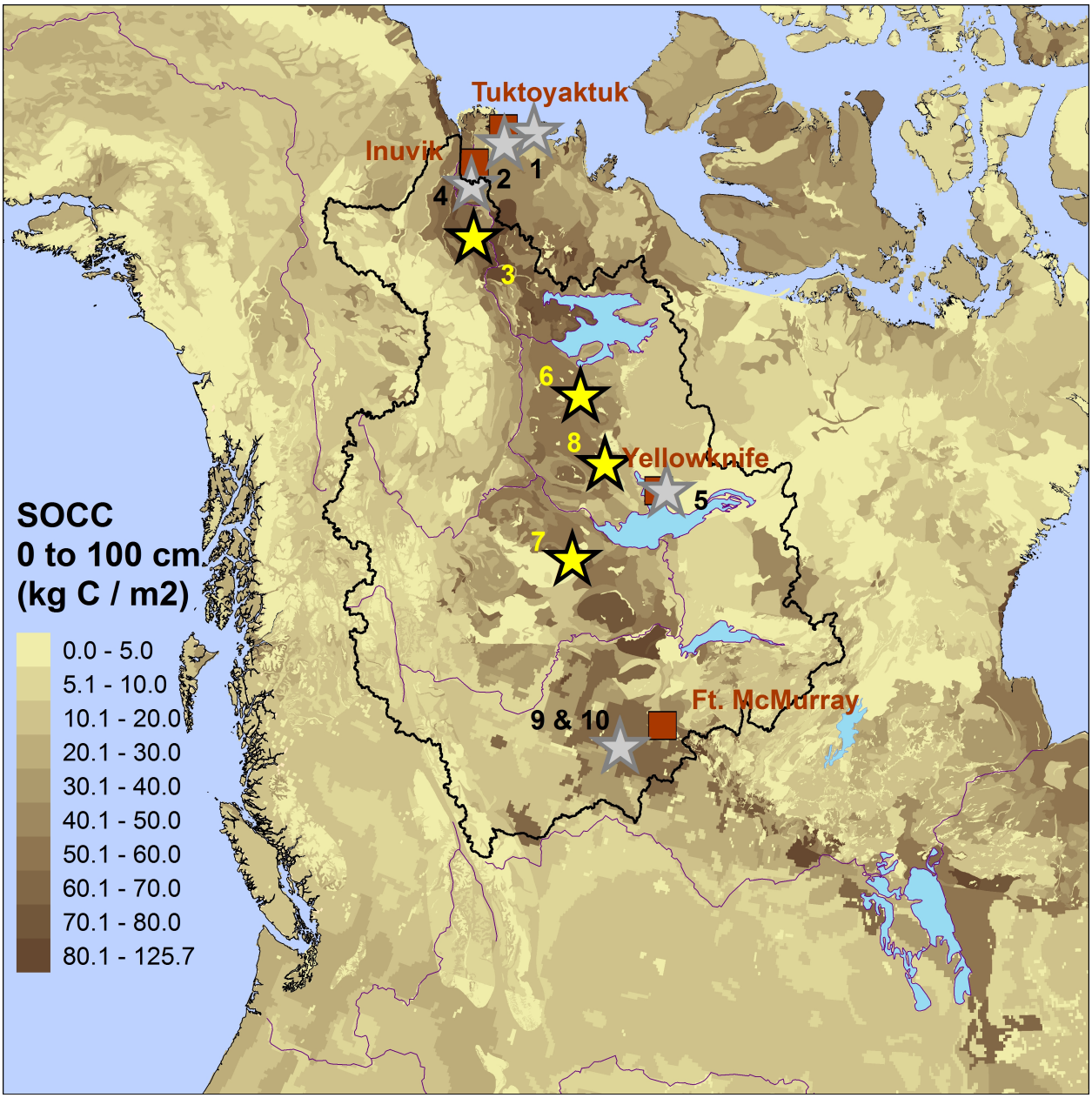

Figure 1.1: Map of study sites and soil carbon density in western North America. Soil organic carbon content (SOCC) in the top 1m is estimated using the Northern Circumpolar Soil Carbon Database (http://bolin.su.se/data/ncscd/?n=ncscd) for permafrost regions and from the IGBP (IGBP-DIS; http://daac.ornl.gov/SOILS/guides/igbp-surfaces.html) for non-permafrost regions. Outline of the Mackenzie River Basin (MRB) is from Beilman et al., 2008. Stars shows sites within the carbon-rich central MRB sampled in July 2013 where yellow stars show sites used in this study, and other gray stars show sites from the same field season conducted for National Science Foundation project NSF 1107981.

Chapter 2: Exploring potential decomposition and the priming effect in Peatland Permafrost Carbon Soils in the Mackenzie River Basin

Introduction

Soils within the northern permafrost zone are estimated to hold 1670Pg of carbon (Tarnocai et al., 2009). Arctic permafrost landscapes are vulnerable to global climate change; any deviation from the characteristically low temperatures and slow decomposition rates would lift the environmental constraints that allow these soils to accumulate and store carbon (Coolen et al., 2011; Dorfer et al., 2013). Arctic temperatures are increasing at a rate of 0.6°C per decade, which is twice as fast as the global average, and will affect soil processes that dictate carbon storage in these regions (IPCC, 2013). Soils and climate are interconnected in that soil processes directly affect greenhouse climate through the sourcing and sinking of atmospheric CO_2, CH_4, and N_2O (Mosier, 1998Lal, 2008). Effects of current and future Arctic temperature rise, and increases in atmospheric CO_2 concentrations will result in an uncertain decrease in the total area under permafrost conditions and a thickening of the active layer (Quinton and Baltzer, 2013). Some previously permafrost-protected soil organic carbon will become available to decomposer communities, and may produce a positive feedback to climate via increased greenhouse gas emissions (Coolen et al., 2011; Knoblauch et al., 2013). This process has been termed the Permafrost Carbon Feedback (Schuur et al., 2015) and considering the amount of carbon stored in permafrost soils (1670Pg), this climatic feedback could be substantial (Huissteden and Dolman, 2012). Biogeochemical processes involved in soil organic matter decomposition under permafrost and thawed conditions are complex and still not fully understood; this is part of the reason that permafrost feedbacks were excluded from the simulations of future climate in the IPCC 4^{th} and 5^{th} Assessment Reports (Vonk et al., 2013).

Climate and Earth System Model projections show both climate and land use change will influence soil carbon dynamics (Cardinael et al., 2015). NOAA reported six Arctic monitoring stations in their air-sampling network (Alaska, Canada, Iceland, Finland, Norway and the North Pacific; Team E, 2015) reading CO_2 concentrations of 400 ppm in the spring of 2012. This elevated atmospheric concentration of CO_2 paired with increasing temperatures can stimulate both surface plant inputs and soil carbon mineralization (Hobbie et al., 2002; Hartly et al., 2010). Uncertainty in the Permafrost Carbon Feedback lies in the timing and exact magnitude of future soil organic carbon changes. To reduce this uncertainty biogeochemical processes that influence long-term soil carbon dynamics need to be addressed and included in current projections and models (Koven et al., 2013; Cardinael et al., 2015).

Indirect effects of climate warming on soil carbon mineralization processes that control carbon release and storage in permafrost have the potential to be overlooked and not represented in earth system models. Studies in both temperate and permafrost soils have shown that new organic matter input can stimulate native soil organic carbon mineralization. This concept is known as the priming effect (Kuzyakov et al., 2000; Fontaine et al., 2007; Blagodatskaya and Kuzyakov et al., 2008; Wild et al., 2014; Cardinael et al., 2015). If carbon inputs stimulate soil organic matter decomposition, easily degradable carbon compounds delivered below ground

could turn these permafrost regions into an even greater source of carbon, exacerbating the Permafrost Carbon Feedback (Cardinael et al., 2015). As it is currently understood, there are two components to the priming effect: new carbon inputs and soil decomposition processes. These components have been identified as a range of inputs from root exudates (Basiliko et al., 2007) to vascular plant litter (, and a range of degradation processes from microbial decomposition of native soil organic matter to nitrogen mining. Specifically, there is interdependence between plant processes that generate inputs and the microbial decomposition processes that generate outputs (Rousk et al., 2015). Plants supply the soil microbial community with a range of organic compounds with varying decomposability. Compounds that can be immediately taken up and used directly as substrate for microbial metabolism (such as sugars, amino acids, and organic compounds from root exudates and above ground leaf litter) or those that can be easily broken down by microbial-mediated enzymes (cellulose and root or leaf litter protein) can stimulate the microbial decomposing community and produce the priming effect (Fontaine et al., 2003; Blagodatskaya & Kuzyakov, 2008; Basiliko et al., 2008). This stimulation of microbial activity occurs when the new easily degradable compound either promotes the growth microbial groups that target complex less degradable soil organic matter, provides energy specifically needed to break down these already present compounds, or provides the needed carbon for microbial growth and stimulates the nitrogen demand facilitating nitrogen mining (Fontaine et al., 2003; Blagodatskaya & Kuzyakov, 2008; Craine et al., 2007; Dijkstra et al., 2013).

Specifically when examining Arctic regions, where soils are considered nitrogen- and energy-limited, new nutrients from easily degradable carbon inputs could play an important role in microbial degradation of previously protected soil organic matter (Fontaine et al., 2007; Sistla et al., 2012). Surprisingly little is known about the microbial communities that utilize the immensely large Arctic carbon pool (Campbell et al., 2010). How the alteration of nutrient availability will affect high latitude microbial populations and the ecosystem processes they mediate is even less clear. Given the observed sensitivity of permafrost regions to climate, as well as the important physical and ecological changes that will occur with a changing climate, an exploration of the potential influence of the priming effect on these soils would improve our understanding of the response of permafrost carbon to global change.

Objectives and Hypothesis

The goal of this laboratory incubation experiment was to better understand the potential for priming effects to occur and alter carbon balance in carbon-rich peatland permafrost soils within the Mackenzie River Basin, Canada along a north-south transect. Geographical effects on soil processes can potentially be seen in the specific responses and vulnerabilities of these soils across latitude. Temperature, precipitation, and permafrost SOM quality are some examples of ecosystem characteristics that are in part determined by location; all influence microbial activity driving carbon cycling processes (Treat et al., 2014). Assuming that characteristics of organic matter affect the magnitude of the priming effect, expected differences in carbon quality between the northern and southern sites may exhibit different potential for the priming effect. Hartley et al. (2010) found that low nutrient availability, especially nitrogen, produces the most pronounced priming effect when labile compounds were added to the soil. Regions with poor nutrient availability will exhibit more of a priming effect due to microbial mining for necessary nutrients to support new microbial growth (Hartley et al., 2010; Kuzyakov et al., 2000; Kuzyakov, 2010). Assuming the microbial communities are similar in structure between the permafrost peatland sites used in this experiment, microbial decomposition will not be controlled by community

composition, but instead by limiting factors specific to the soil ecosystem of each site. The geographic factors directing priming potentials of permafrost soils in the Mackenzie River Basin will consist of site specific variations caused by latitudinal effects.

Permafrost-affected earth materials has two components, the seasonally-thawing active layer and consistently-frozen permafrost below. The active layer is a dynamic surface layer that thaws to varying depths each year and, where vegetated, is typically characterized by fresh plant litter and younger organic matter. The upper part of the permafrost, or 'near-surface' permafrost, is often made up of more decomposed organic matter and can be a mixture of organic and inorganic/clastic materials. The preservation of material in permafrost soils is greater than in non-permafrost counterparts owing to the influence of sub-freezing conditions on free water and microbial activity. If soil organic matter is similar between these two layers, the active layer and upper permafrost may exhibit similar potential for the priming effect. Conversely, if the difference in decomposition state or other factors of the material between the two layers is sufficient, vulnerability to priming may be different. The near surface permafrost contains soil organic carbon of particular interest in terms of current and future environmental change because it is this carbon that will be come newly available if thawing of permafrost removes the pre-exiting thermal protection. This near-surface permafrost carbon will be incorporated into the active layer as the thaw front moves deeper into the soil profile and new carbon becomes exposed. This research will use a laboratory soil incubation and substrate addition experiment to specifically explore the following questions:

1) *What is the potential for a priming effect induced by an easily degradable substrate to affect the balance of soil carbon in active and near-surface permafrost peat of the Mackenzie River Basin?*

2) *Is the potential for soil carbon losses induced by a priming effect in response to an easily degradable substrate the same along a latitudinal gradient?*

The priming effect is defined by an increase in native soil organic matter mineralization in the presence of a fresh, labile substrate, which may be experimentally observed by applying a mass balance equation to measure extra respired carbon following substrate addition. I hypothesize this will be seen in Mackenzie River Basin permafrost peat soils if the original soil environment is either low in energy or nutrients for decomposing microbial communities. Microbes within permafrost peat soils will use the substrate addition carbon as a preferred source of energy, or as energy to generate necessary enzymes to mineralize otherwise unavailable nutrients in these soils. An increase in soil-derived CO_2 efflux in either a lab or field setting could be due to either increased microbial metabolism of soil carbon (real priming effect) or increased turnover of microbial carbon (apparent priming effect) (Kuzyakov et al., 2000; Nottingham et al., 2009). Observing the priming effect in these soils would provide evidence that soil respiration in Mackenzie River Basin peatlands can be influenced by an interaction between new labile inputs and the decomposition of bulk native soil organic matter. Climate induced changes in these permafrost peat environments and the surface plant communities may induce greater respiration from previously protected material than what is currently being seen.

To my knowledge, this is the first priming experiment to compare priming potentials along a latitudinal gradient in the Mackenzie River Basin. By selecting similar *Sphagnum fuscum*

peat plateaus along a N-S transect, this thesis aims to observe the changes in priming potentials seen with latitude. Permafrost Zones and surface vegetation are closely related to latitudinal trends that govern climate and surface temperature regimes. Summer air temperature has been increasing in northern high latitudes, and trends from three stations in the Mackenzie River Basin (Figure 2.1) show this increasing pattern across the transect used in this experiment. Arctic temperatures, including those in the Mackenzie River Basin, are predicted to continue to increase at a rate faster than the global average (IPCC AR5) that may promote a longer more productive growing season within this region (Nicholson et al., 1996) and deepen active layer depths. This could shift permafrost and vegetation biome boundaries northward, causing changes in the soil environment due to thaw effects and changing the types of litter inputs to soil ecosystems.

Methods

Field Sampling

In July 2013, eight permafrost peatland sites along a north-south transect spanning 52° to 69° N latitude in the central lowlands of the Mackenzie River Basin were sampled (Figure 1.1). Monoliths of the active layer were obtained using a 5x5x100cm box corer and serrated stainless steel knife. Permafrost cores were extracted using a power head (Stihl BT121) driving a 9-cm diameter, 30cm-long core barrel fixed with a diamond drill bit (Professional® B680 Hard (541 06 01-51)) based on a modified version of Calmels et al. (2005). Coring was conducted to the base of the soil profile. Profile sections were wrapped in plastic film and aluminum foil and kept frozen following collection. Soils were maintained at -23°C prior to analysis. Coring locations were selected using visual observation of vegetation to best represent the conditions at each site. A total of 10 sites were visited in 2013; for the purpose of this laboratory study, four sites were chosen from the latitudinal transect. The four chosen sites are all *Sphagnum fuscum* dominated peat plateaus and are within the continuous (MRB3) and discontinuous (MRB6, MRB7, MRB8) permafrost zones (Figure 1.1). Soil from the active layer (10-20cm) and the near-surface permafrost layers (35-65 cm; depending on active layer depth at each site) from these sites were used in the incubation experiment.

Carbon Content and Age

At each of the selected sites, material from each core was measured for carbon and nitrogen content, bulk density, organic matter content, stable carbon isotope ratios ($\delta^{13}C$). A series of radiocarbon (^{14}C) ages of organic matter was obtained. Measurements of bulk density and organic matter content were taken from bulk soil at one or two-centimeter increments following protocol from Chambers et al (2010). Bulk soil carbon and nitrogen were measured using elemental analysis (ECS 4010 CHNSO Analyzer) following grinding sample to 250µm fineness on a Retsch MM220. Measurements for $\delta^{13}C$ were made by CRDS on a Picarro G2201-i Analyzer. Carbon stocks for the top 30-cm, 100-cm, and total core lengths were calculated using measured bulk density (g cm^{-3}) and carbon content (%C). All BP (before present) ages were calibrated with the Calib 7.1 calibration program (Stuiver and Reimer, 1993) and IntCal13 calibration curve (Reimer et al., 2013). Although peat is regarded generally as a reliable material for ^{14}C dating, Kilian (1995) found that bulk material can be affected by vertical movement of dissolved organic carbon in the peat column, and may result in inaccurate 14C ages. The same

appears to be true when the samples are not completely cleaned of rootlets (e.g. of Ericaceae) that contain contemporary carbon. Therefore, when accurate ^{14}C dating of peat is desired, the use of only aboveground plant material is recommended (Porazinska et al., 2003; Nilsson et al. 2001). Isolated *Sphagnum* plant parts were preferably used because it formed the bulk of most peat deposits, it is a moss and therefore does not have roots, and growth is upward from the apex only.

Potential decomposability and priming effect

Soils were incubated in 700ml 'snap-seal' containers and lids with silicone sealing rings and locking tabs ('Lock & Locks') fitted with septa in the lid for gas sampling. The incubations were carried out on four laboratory replicates of active layer and permafrost soil (average 2g dry soil material) from each site. Soils were at field moisture content when placed into the containers aiming for comparable carbon content between similar depths within the same site. There was a 30-day equilibrium period at 10°C prior to the start of experimental treatments to allow for stabilization following disturbance. Soil-only controls were incubated with lids off until the first sampling period. Substrate addition samples were treated with D-glucose additions added at a rate of 0.5mg glucose carbon per gram soil carbon. Each site therefore contained active layer and near surface permafrost control and substrate addition replicates, making up the depth and substrate addition treatments. The four sites included in the incubation experiment span a latitudinal transect (Figure 1.1) and as a whole, describe the latitudinal treatment.

The incubations took place in a controlled growth chamber (Model 6021-1, Caron Products & Services Inc., Marietta, OH), at 10°C. Soils were maintained at field moisture conditions by rewetting with deionized water to sustain constant weight; rewetting took place every other day following data collection. Respiration rates were determined on days 0, 1, 2, 3, 4, 5, 7, 9, 11, 14, 17, 20, 23 following the start of the incubation, with the first sampling occurring immediately after substrate addition. Between sampling days, containers remained in the incubation chamber with the lids off. During sampling, lids were placed and headspace samples were collected every four hours over the course of 12 hours (ex. t_0 = 6am and t_3 = 10pm). Ten milliliters of headspace air was pulled from each container using an airtight syringe. Six milliliters from the syringe was immediately injected into an evacuated glass exetainer (< 1 torr), and CO_2 concentration was quantified on a Perkin Elmer Clarus® 580 Gas Chromatograph.

Based on measured respiration from both amended and control containers, apparent priming was calculated using a mass balance approach (Kuzyakov, 2000). Extra mineralization of soil carbon following glucose addition can be detected when the amount of CO_2-C respired from the amended soils is larger than that measured in the corresponding controls, after accounting for the added glucose carbon. This detection of the apparent priming effect is described by the following mass balance equation:

$$\text{Extra mineralized carbon} = \left(\text{Amended soil respired carbon} - \text{Control respired carbon}\right) - \text{Glucose carbon}$$

Each site and depth priming effect was calculated using control and treatment averages. As well as subtracting control averages from treatment averages, the amount of glucose carbon added was also subtracted as an average for the specific site and depth.

Experimental Assumptions

Due to the circumstances surrounding this experiment there are several caveats to address before assessing the results. The material used in this incubation experiment was collected from four Artic peatlands with each site being represented by a single core. This arguably provides enough information for a latitudinal comparison. Although within-site heterogeneity was not addressed in this study, permafrost peat plateaus are dominated by similar species, making a single core a possible representation of the peat at the individual site. The samples incubated were not standardized to moisture content to allow this difference to potentially be seen as a factor adding to latitudinal differences across the sites. The cores were taken and immediately wrapped in plastic and aluminum for transport to minimize the possibility of contamination that could effect microbial respiration seen in the incubation containers.

Statistical Analysis

All statistics were performed with R Studio Version 0.99.447 © 2009-2015 RStudio, Inc. (R Development Core Team, 2015). Parametric methods were used and data was transformed to meet assumptions of normal distribution and homoscedasticity. It was identified that no outliers existed in the cumulative CO_2 data by using `outlierTest` function in R, where Bonferonni p-value is used to identify the most extreme observations. There were significant deviations from normality for the total (all sites and depths) cumulative CO_2 data seen in normal QQ-plots. The Fligner-Killeen median test is a test for homogeneity of variances that is robust against departures from normality (Conover et al., 1981). It can be argued that the variances in total cumulative respiration are homogeneous (p-value > 0.05).

Using the `spreadlevelplot` function to compute a Tukey spread-level plot of log(hinge-spread) vs. log(median) for the observations it was identified that the data violated assumptions of homoscedasticity; the function fits a line to the Tukey spread-level plot and calculates a spread-stabilizing transformation from the slope of the line. The power transformation suggested by the spread level plot output (-0.253) was used and corrected violations of normality and homoscedasticity assumptions.

Three-Way ANOVA was performed on cumulative CO_2 respiration following the 23-day experiment to see statistical differences between substrate-added and control cumulative respiration across site and depth treatments. The three-way ANOVA analysis was chosen to identify interactions between the three between-subject factors (substrate addition, site, and depth) on respiration. Two-Way ANOVAs were performed to test for differences across all control sites and depths. This analysis identifies interaction only between site and depth effects on control respiration. Results for all analysis were considered significant at the $p = 0.05$ level.

Results

Site and Soil Characteristics

The total organic soil depth at four permafrost peatland sites along the MRB transect (Figure 1.1) ranged from 142 to 259 cm (Table 2.1). The average bulk density measurements

show a lack of trend with latitude (Table 2.1). MRB6 has the lowest bulk density ($\rho = 0.099 \pm 0.05$) and is almost two times less than the highest bulk density seen at MRB7 ($\rho = 0.184 \pm 0.22$). Differences in carbon content between the four cores were small, and using averages from entire core lengths the mean carbon content value from all four sites was 44.2% (± 4.1%). The mean nitrogen content of soil at the four sites varied from 0.4 (± 0.2) to 1.5 (± 0.8) with the highest values seen in MRB6 and MRB7. The difference in nitrogen had a very large effect on the C/N ratio between each site. The mean C/N ratio of soil at the four sites ranged from 48.2 (± 39.9) to 110.1 (± 34.1), with the lowest values at MRB6 and MRB7.

Radiocarbon ages for basal samples from the base of each permafrost peat core ranged from 4489 ± 54 calBP (MRB8) to 9641 ± 63 calBP (MRB7), which is consistent with peatland ecosystem age patterns in the MRB (Yu et al. 2009). The estimated ages for the active layer material across the four sites ranged from 42 calBP at MRB7 to 588 calBP at MRB8 (Table 2.1). Near-surface permafrost soil was consistently older than active layer soils and ranged from 510 calBP at MRB3 to 1972 calBP at MRB7 (Table 2.1). For organic soil included in the incubation experiment, MRB7 had a large difference in age between the active layer (42-143 calBP) and near-surface permafrost soil (852-1972 calBP). However, the soil characteristics between the layers are similar regardless of this age difference (active layer %C = 43.8±3.8, near surface permafrost %C= 43.5±2.2; active layer %N = 0.5±0.1, near surface permafrost %N = 0.8±0.3). This similarity between active layer and near surface permafrost characteristics is seen in the other three cores (MRB3, MRB6, and MRB8), however the C/N ratio has a larger range between depths in the two sites MRB7 and MRB6. The carbon stocks for the upper 30 cm were also calculated and compared at the sites and ranged between 40.36 and 147.71 kg C m^{-2} (Table 2.1). The carbon storage for the top 100 cm at the sites ranged from 246.24 to 449.99 kg C m^{-2} (Table 2.1).

Basal Respiration

The cumulative CO_2 efflux is shown in Figure 2.1 from calculated respiration rates from each sample day. Cumulative respiration over the course of the 23-day incubation period shows a very similar pattern between active layer and near surface permafrost (figure 2). In all four sites, there is a divergence between the two layers at day 6, with final μgCO_2-C values from the sites being typically higher in active layer soils (average difference between final active layer and near surface permafrost 2265.80 μgCO_2-C g^{-1} Soil-C). This difference in respiration in the two layers was found to be significant ($p<0.05$; table 4). Even with this significantly higher amount of respiration seen overall in the active layer, there are some sites where the near-surface permafrost respiration is higher than the active layer at other sites. For example, MRB6 near surface permafrost cumulative respiration (12,510 μgCO_2-C g^{-1} Soil-C) is more than two times greater than the second largest active layer respiration generated at MRB8 (12,510 μgCO_2-C g^{-1} Soil-C).

However, the difference across the sites had even more of an effect on CO_2 production ($p<0.05$; table 4). Compared to the respiration at the other three sites included in this experiment, respiration in MRB6 soils was very high even after the 30-day stabilization period (Figure 2.2). The variability between sites is apparent when comparing the large respiration seen at MRB6 with the other sites (active layer total = 17746.58 μgCO_2-C g^{-1} Soil-C, near surface permafrost total = 12510.28 μgCO_2-C g^{-1} Soil-C), when the second largest baseline respiration is almost three times less at MRB8 (active layer total = 4592 μgCO_2-C g^{-1} Soil-C, near surface permafrost total = 3571 μgCO_2-C g^{-1} Soil-C).

Evidence for Priming Effect

Figure 2.3 shows the respiration patterns for substrate addition and control samples of the active layer and near-surface permafrost soils of the four sites. The overall behavior of CO_2 production is similar between control and substrate addition soils at each site excluding MRB6, where there is observable separation in the respiration totals (Figure 2.3). There is slight difference between substrate addition and control cumulative respiration (Table 2.3) with the average difference between final values being ~80 $\mu gCO_2\text{-}C\ g^{-1}$ Soil-C (Figure 2.4). However, not surprisingly, this relatively small difference in respiration was not significantly different from controls (Figure 2.4; Table 2.4). Looking at the results between depths and sites (Figure 2.4), the most difference was seen in carbon production between site and depth treatments, and glucose addition was found to have little significant effect on total CO_2 production ($p>0.05$; Table 2.4). However, despite the result from the three-way ANOVA, the amount of $\mu gCO_2\text{-}C\ g^{-1}$ Soil-C respired at two sites was enough to observe an apparent priming effect (Figure 2.5). Comparing the amount of total respired carbon from controls and glucose addition, after subtracting the amount of added glucose-carbon from each value, an apparent priming effect was seen both MRB7 and MRB6 (Figure 6) but it should be noted that a priming effect was not detected in two out of four experimental cases.

Discussion

Soil properties and organic carbon stocks

Compared to permafrost soils generally, including both organic and mineral soils, the MRB permafrost peatlands studied here have very high carbon storage. Previous studies report that peat soils in the continuous and discontinuous permafrost zones of western North America have an average maximum summer active layer thaw depth of 25 cm (range of 35-70 cm), suggesting these study sites are typical in active layer depth and are comparable to most permafrost peatland soils regionally (Treat et al., 2014; Tveit et al., 2013; Basiliko et al., 2012). We found that soil carbon was high and relatively consistent across the sites (%C average 44.2 ± 4.1), with slightly larger values in near surface permafrost in the two northernmost sites, and larger active layer values in the two southern sites (Table 2.2). Treat et al. (2014) report that three peat sites in Alaska (located at 63.571°N, 157.730°W) also had higher carbon content in the active layer (42%) than the underlying permafrost below 50 cm (31%). The environmental characteristics at the higher latitudes could inhibit decomposition and promote the preservation of carbon at depth. These values of carbon content both for the active layer and near surface permafrost are high compared to publications focused on permafrost soils (Uhlirova et al., 2007 (34.8% ± 3.57); Wild et al., 2014 (9.4%)). However, when compared to studies focused on peatland soils, the carbon content seen here is very similar (Basiliko et al., 2008; Loisel et al. 2014; Treat et al., 2015). The mean carbon content of these peatlands are in line with values reported by two northern peatland synthesis; both Loisel et al. 2014 and Treat et al., 2015 describe *Sphagnum* dominated peatlands as having values in the 42 - 49 % range. Nitrogen content found in *Sphagnum*-dominated peatlands is lower than other peat types and the values seen here (average N = 0.98 ± 0.5) is within the range seen by previous studies (0.9 ± 0.4 %;

Treat et al., 2014). The C/N ratios of the peat material used in the experiment averaged to 72.77±29.6, which is higher than other reported values (Loisel et al. 2014 (C/N = 55); Treat et al., 2015 (C/N = 37.5); Treat et al., 2015 (C/N = 62.0)). This could be representative of a higher abundance of *Sphagnum* peat, which can cause C/N ratios to be three times higher than other mosses (Treat et al., 2015).

The active layer and near-surface permafrost soil used in the incubations were from similar depths, however the ^{14}C-derived age of organic matter was variable between sites (Table 2.2). The active layer material, not surprisingly, was consistently younger than the near surface permafrost eliminating cryoturbation as a process influencing soil carbon cycling, and this is consistent with the accumulation process and other radiocarbon measurements at these sites (Beilman et al., 2015). The youngest material is found in MRB3 and MRB7, the northernmost and southernmost sites, suggesting the age of active layer material at similar depth (10-20 cm) across the sites is more strongly affected by local site factors and does not follow a latitudinal pattern.

The carbon stocks for the upper 30cm were also calculated and compared at the sites and ranged between 4 and 14 kg C m^{-2} (Table 2.1). The carbon storage for the top 100 cm at the sites ranged from 25 to 45 kg C m^{-2} (Table 2.1), which is higher the range of circumpolar stocks of permafrost carbon reported by Hugelius et al., 2014 for both depths in this region (15 - 30 kg C m^{-2} for top 30-cm, 30 - >70 kg C m^{-2} in the top 100-cm). These measurements in this study have been made on a local scale compared to the NCSCDv2 polygon-based digital database, which could explain the differences in carbon stocks seen here (Hugelius et al., 2014).

Control Respiration

Soils are the most heterogeneous part of the biosphere, and this is evident in the differences between depths and sites in the soil characteristics as well as the respiration rates observed in this incubation experiment. The four sites included in this experiment were all chosen for their visible similarities in that they are all peat plateaus in the Mackenzie River Basin with similar dominant plant species. Regardless of this similarity, when soils from different sites and similar depths are examined, the cumulative baseline respiration seen between these four sites is significantly different ($p<0.05$; Table 2.3), and there is even evidence of within site variability between CO_2 production at different depths ($p<0.05$; Table 2.3). However, there are some similarities seen in the respiration data that can be considered generalities at these sites over this incubation period. At all sites, active layer material is more easily decomposed than the near surface permafrost following the 30-day stabilization period. This is indicated by the larger cumulative CO_2 generated from active layer material, which is on average ~54% higher than the underlying permafrost (figure 2). However, it should be noted that these samples have not been inoculated so differences in microbe community composition may be an important driver of these differences in respiration. Evidence suggests however, that soil respiration is controlled by something other than present microbial community structure (See Chapter 3). Other studies focusing on permafrost soils also found a similar trend where organic matter at depth was slower to decompose than the overlying active layer material (Wild et al., 2014). The active layer soils at each site is also consistently younger than the near surface permafrost, suggesting they are less decomposed and have more easily decomposable organic matter. Soil nitrogen increases with depth; however, this nutrient presence has no affect on the respiration activity seen in the near surface permafrost when compared to the active layer; i.e. regardless of the increased nitrogen content at depth, the active layer still produced more CO_2. This could suggest that below ground

soils contain nitrogen made unavailable to microbes by being tied up in aggregates, or soil microbes do not have the necessary energy to generate enzymes to metabolize the nitrogen present. This lack of respiration response to higher nitrogen in below surface horizons was seen in a recent study where tundra soils, whose C/N ratio and nitrogen content was similar to the overlaying topsoil, demonstrated lower nitrogen transformation rates (Wild et al., 2013; Wild et al., 2014; Treat et al., 2014). However, the decreased nitrogen in MRB6 soils (0.3-0.5% nitrogen) does not prevent an increased production in CO_2 compared to MRB7 (0.5-0.8% nitrogen). This suggests that nitrogen bound in organic materials is could be less available to microorganisms or there is another limiting nutrient that is affecting respiration in these soils (Kaiser et al., 2007).

Site MRB6, in the middle latitudes of the Mackenzie Basin, has the lowest %N of all active layers (0.3 ± 0.03) and lowest %N of all near-surface permafrost (0.5 ± 0.2), as well as the lowest bulk density of all near-surface permafrost (Bulk Density= 0.097 ± 0.02 g cm^{-3}) and among lowest $\delta^{13}C$ (-26.3‰). This is evidence could suggst a soil ecosystem at this site that allows a different set of microbial dynamics not present at the other three sites. *Sphagnum* tends to have higher C/N ratios than vascular plants (Kuhry and Vitt, 1996; Wang et al., 2015), which is seen in the high C/N ratios in site MRB6. However, bulk peat contains variable contributions from a range of plant sources and is very rarely exclusively one moss species (Loader et al., 2007). The variability seen at MRB6 could indicate a lack of isotopic enriched (less negative compounds) that are present in the other sites. This could be due to the bulk $\delta^{13}C$ being influenced by contributions of different plant litter inputs. Different organic compounds found in peat soils have different isotopic signatures – for example soluble carbohydrates from vascular plants are more enriched in $\delta^{13}C$ compared to lipids or lignins found in mosses (Benner et al. 1987, Wedin et al. 1995, Adams & Grierson 2001). However, another explanation for the enrichment seen in MRB6 is microbial discrimination against heavier carbon during decomposition. Differences in microbial populations or communities at MRB6 could result cause variations in metabolism causing in a difference in $\delta^{13}C$ in the remaining substrate and could contribute to the difference seen in respiration. Krab et al.(2013) showed that vascular litter inputs altered the diets of soil invertebrates, and changed the source of CO_2 efflux from *Sphagnum* to birch residues (*Betula pubescens*). As the soil organisms preferentially metabolized the vascular inputs, this created a strong difference in the isotopic signatures of the litter. MRB6 could have more vascular plant inputs that cause a strong dietary preference and build up of low $\delta^{13}C$ Sphagnum litter, and this shows the heterogeneity across the sites with respect to possible controls and context dependency of the priming effect seen in these soils.

Experimental results and evidence for priming

When more CO_2-C evolves from substrate-amended soil than control soils, after the addition of glucose carbon is taken into consideration, evidence for the priming of decomposition of original soil organic matter has been observed. The priming effect is a carbon cycling process that promotes the loss of native soil carbon fueled by an increased availability of plant-derived organic compounds. The response to glucose addition was variable across the four sites (Figures 2.4 and 2.5). In soils where substrate addition produced more cumulative respiration than control soils, there was an average 141% increase in production of CO_2 with the highest seen in near-surface permafrost soils of MRB7 (Figure 2.4). Even with the increase in cumulative respiration

seen with substrate addition, this was not a constant response across all the sites and the effect of glucose addition on total cumulative respiration was not significant ($p>0.05$; Figure 2.4). This is similar to the finding of Basiliko et al. (2012) where the maximum carbon addition (1.0 mg C) in the form of synthetic root exudates (solution of glucose, acetic acid, and an amino acid solution) to peatland soils produced 4.7 mg of carbon (expressed as a sum of both CO_2 and dissolved organic carbon) compared to the 4.1 mg produced by the controls. This difference was statistically insignificant despite the increase in carbon production seen in the treated peat samples. Another study, specifically in permafrost soils, found the addition of glucose did not significantly affect respiration in organic topsoils (9.4%C) but did increase respiration two- to threefold the mineral subsoil (0.6%C) (Wild et al., 2014).

An apparent priming effect was seen at the end of the incubation in two sites (Figure 2.5). MRB7, the southernmost site, showed extra respiration of CO_2 in both the active layer (~171.8 μg extra CO_2 - C) and near surface permafrost (~236.6 μg extra CO_2 - C), and MRB6 showed evidence for priming only in the near-surface permafrost, but a large amount of extra CO_2-C (~ 2770.0 μg extra CO_2 – C). Apparent priming effects were seen at these sites despite the insignificant effect of substrate addition on respiration overall ($p=0.4808$), except at MRB7 where there was a significant difference between near surface permafrost addition and baseline respiration (Figure 2.4). This result is perhaps not surprising, given the small magnitude of the observed priming effect against the large variable baseline respiration values and the fact that the priming effects were calculated using these averages (four replicates).

The between-site differences in total cumulative respiration were the most striking, and the site effect was highly significant ($p<0.05$; Table 2.4). This was somewhat unexpected, as these sites were chosen specifically for their similarity in dominant vegetation (*Sphagnum fuscum* and *Cladina*/*Cladonia* lichens) and landform type. There was a significant interaction term between site and substrate addition, giving further evidence that the response of these permafrost peatlands is very dependent on location specific environmental conditions (Table 2.4). Of the few priming studies in permafrost soils (Wild et al., 2014; Hartley et al., 2010) and peatlands (Basiliko et al., 2007; Fan et al., 2013; Ye et al., 2015), none have examined the response of different locations along a transect with similar soil characteristics. Here the response of four peatlands sites with similar soil characteristics and similar origin of litter inputs had different responses to the addition of a labile substrate.

Conclusion

Arctic permafrost peatlands hold over 1600Pg of soil carbon that could be vulnerable to environmental change and upon release could impact global climate. The Mackenzie River Basin is an Arctic carbon hotspot with much of the region containing more than 50 kg m^{-2} soil organic carbon (Figure 1.1) with some areas with more than 100 kg m^{-2} (Hugelius et al., 2013) including our study sites that were as high as 44.9 kg m^{-2} in the top 100-cm (Table 2.1). The sites included in this experiment from the Mackenzie River Basin were chosen for their similarity and this is reflected in similar soil characteristics seen at each site (Table 2.1). All four sites had similar carbon content, a similarity that extended into the near surface permafrost, while percent nitrogen increased as you moved down the soil profile (Table 2.2). The difference in quality between soil layers narrowed as you moved further south, suggesting more separation between active layer and near surface permafrost dynamics at the northern sites.

Here, it was demonstrated that the addition of a labile substrate might enhance carbon mineralization in some Arctic peatland soils, but the occurrence of an apparent priming effect

was difficult to stimulate experimentally. The apparent priming effects seen in 2 out of 4 soils in this study suggest that carbon mineralization rates in arctic permafrost peatland soils may be relatively insensitive to the addition of easily degradable single compounds such as glucose, and suggest that the priming effect may be of limited importance for the role of permafrost peatlands in the Permafrost Carbon Feedback. The peatland soils in this study show resilience against the priming effect and suggest that it may not represent an important additional carbon cycling linkage between surface plants and soil in these peatland ecosystems. This lack of detectable priming response is notable given that the substrate used, glucose, is an extremely labile compound, that the incubation was carried out at 10°C, and that soil conditions were well aerated and controlled. Soil carbon priming may not be a significant carbon cycling phenomenon for permafrost peatland soils in the Arctic, at least in peatland soils common to the continental northwest North American Arctic.

Table 2.1: Soil Characteristics from the four sites used in the experiment. Percent carbon (%C) and nitrogen (%N) are calculated using the whole length of the core taken at each corresponding site. Delta 13 C values are calculated here using an average bulk sample.

Site	%C	%N	C/N	BD (g/cm3)	δ13C (‰)	Age (calBP)**	Carbon Stocks (kgC/m-2)			Core Length
							Top 30cm	Top 100cm	Total Core	
MRB3	45.6±6.6	0.9±0.7	83.4±45.0	0.103±0.04	-26.2 ± 0.7	9061 ± 52	7.3	31.4	47.2	163cm
MRB6	43.8±5.7	1.5±0.8	48.2±39.9	0.099±0.05	-27.3 ± 0.7	7519 ± 42	5.7	24.8	42.5	243cm
MRB7	44.6±1.9	1.1±0.7	49.4±35.3	0.184±0.22	-24.5 ± 2.0	9641 ± 63	4.0	24.6	22.7	142cm
MRB8	42.7±2.1	0.4±0.2	110.1±34.1	0.118±0.02	-26.2 ± 1.5	4489 ± 54	14.7	44.9	70.4	239cm

**Calculated ^{14}C values using median probability

Table 2.2 Description of incubated soil depths. Shaded rows are active layer (10-20 cm) and open rows are near surface permafrost soil values (35-45 or 55-65cm). ^{14}C ages are expressed in years BP and have been calculated for the specific depth range incubated using measured dates (shown in supplementary materials; Table 2.4) and the 1950 reference point.

Site	Incubated Depth	%C	%N	C/N	BD (g/cm3)	$\delta^{13}C$ (‰)	Age (calBP)**
3	10-20cm	42.9±1.8	0.3±0.1	143.4±21.6	0.057±0.003	-26.46±0.6	93-293
	35-45cm	44.6±3.7	0.7±0.1	70.9±18.7	0.115±0.039	-25.87±0.4	510-594
6	10-20cm	43.7±0.2	0.3±0.03	129.5±11.2	0.036±0.003	-28.3±0.6	153-309
	55-65cm	44.1±10.5	0.5±0.2	53.0±14.2	0.097±0.02	-26.25±0.4	777-958
7	10-20cm	43.8±3.8	0.5±0.1	129.5±11.2	0.021±0.005	-22.4±0.6	42-143
	35-45cm	43.5±2.2	0.8±0.3	60.8±18.0	0.175±0.041	-22.64±1.2	852-1972
8	10-20cm	45.0±2.5	0.6±0.1	76.6±22.3	0.11±0.015	-27.01±1.5	303-588
	35-45cm	42.2±0.8	0.6±0.2	75.2±15.9	0.126±0.033	-26.34±0.5	952-1222

**Calculated ^{14}C values using median probability

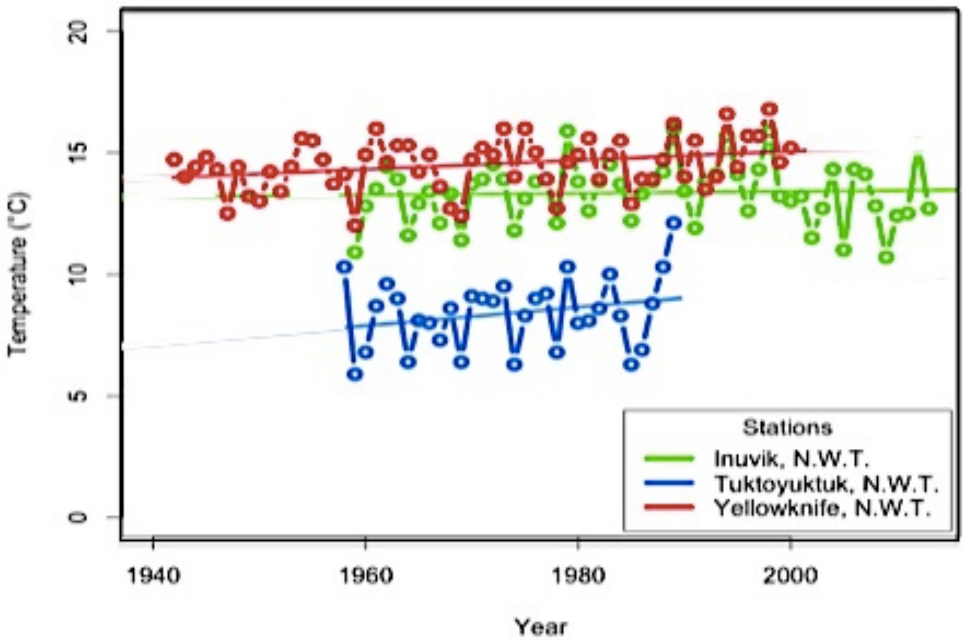

Figure 2.1: Mean summer surface air temperatures for three stations in MRB (Station Data from: Yellowknife,N (62.5 N,114.5 W, Tuktoyaktuk,Nw (69.5 N,133.0 W), Inuvik,N.W.T. (68.3 N,133.5 W)). A positive trend over 30 years is evident at three stations spanning the study area. These stations are spread across a large range of latitude (69.5-62.5 °N) and exhibit different rates of temperature change, 0.05 – 0.07°C (express as rate per decade relative to the zonal rate per decade) respectively. Data used are from Goddard Institude for Space Studies database available to the public: http://data.giss.nasa.gov/cgi-bin/gistemp/find_station.cgi?dt=1&ds=14&name=&world_map.x=122&world_map.y=51. (Accessed October 30, 2014)

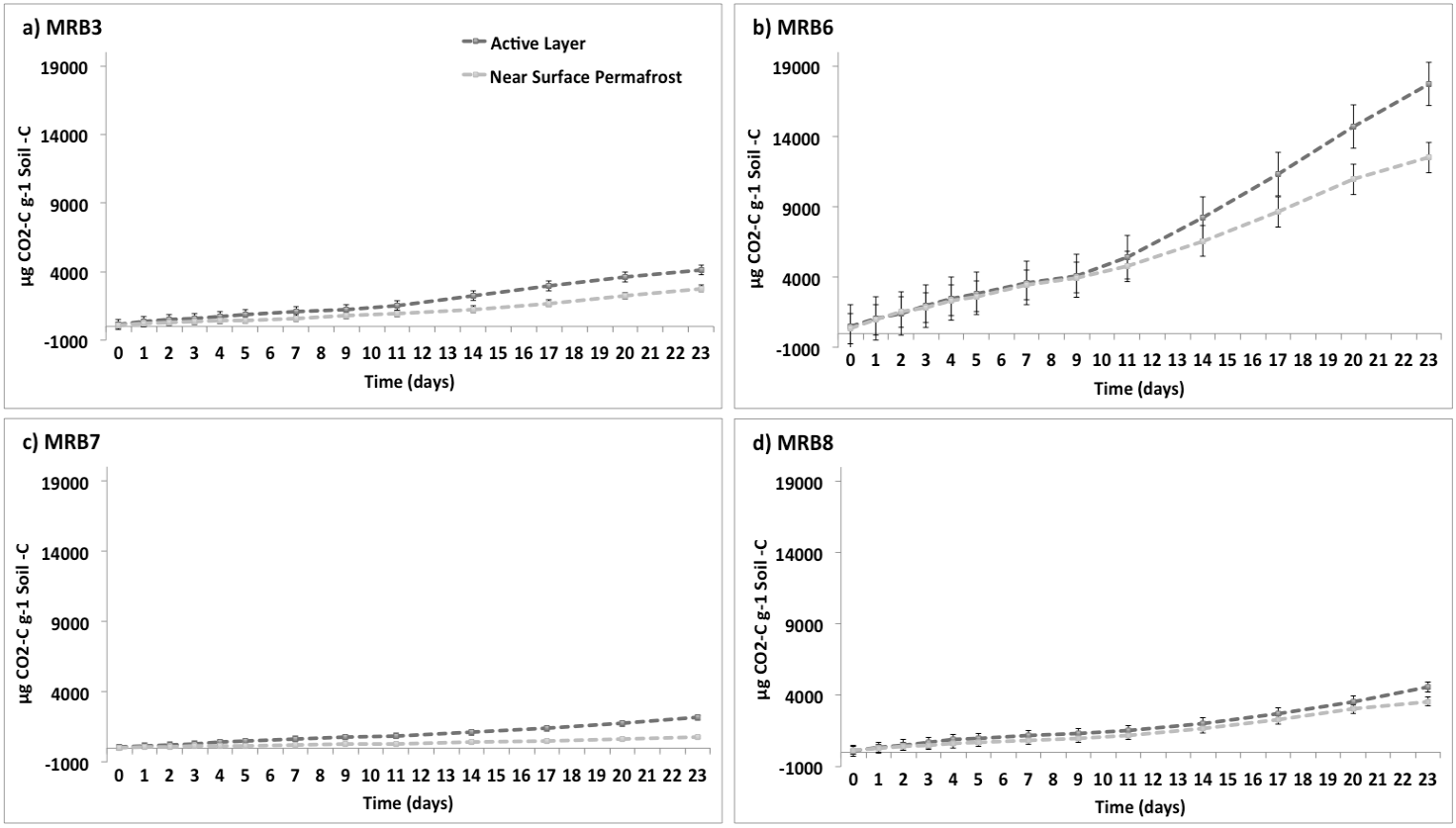

Figure 2.2: Baseline Cumulative Respiration respired CO_2 as µg CO_2-C from the four incubated sites from the Mackenzie River Basin. These are results from incubated control samples only. Points represent averages from four replicates +/- standard errors.

Table 2.3: Results from two-way ANOVA showing the effects of site and depth on final respiration. The following significance code is used to show * 0.05 probability level, ** 0.01 probability level, *** 0.001 probability level.

	Df	SumSq	MeanSq	Fvalue	Pvalue
Site	3	0.0013606	0.0004535	112.887	2.75E-14 ***
Depth	1	0.0001263	0.0001263	31.44	9.02E-06 ***
Site:Depth	3	0.0000433	0.0000144	3.594	0.0282 *
Residuals	24	0.0000964	0.000004		

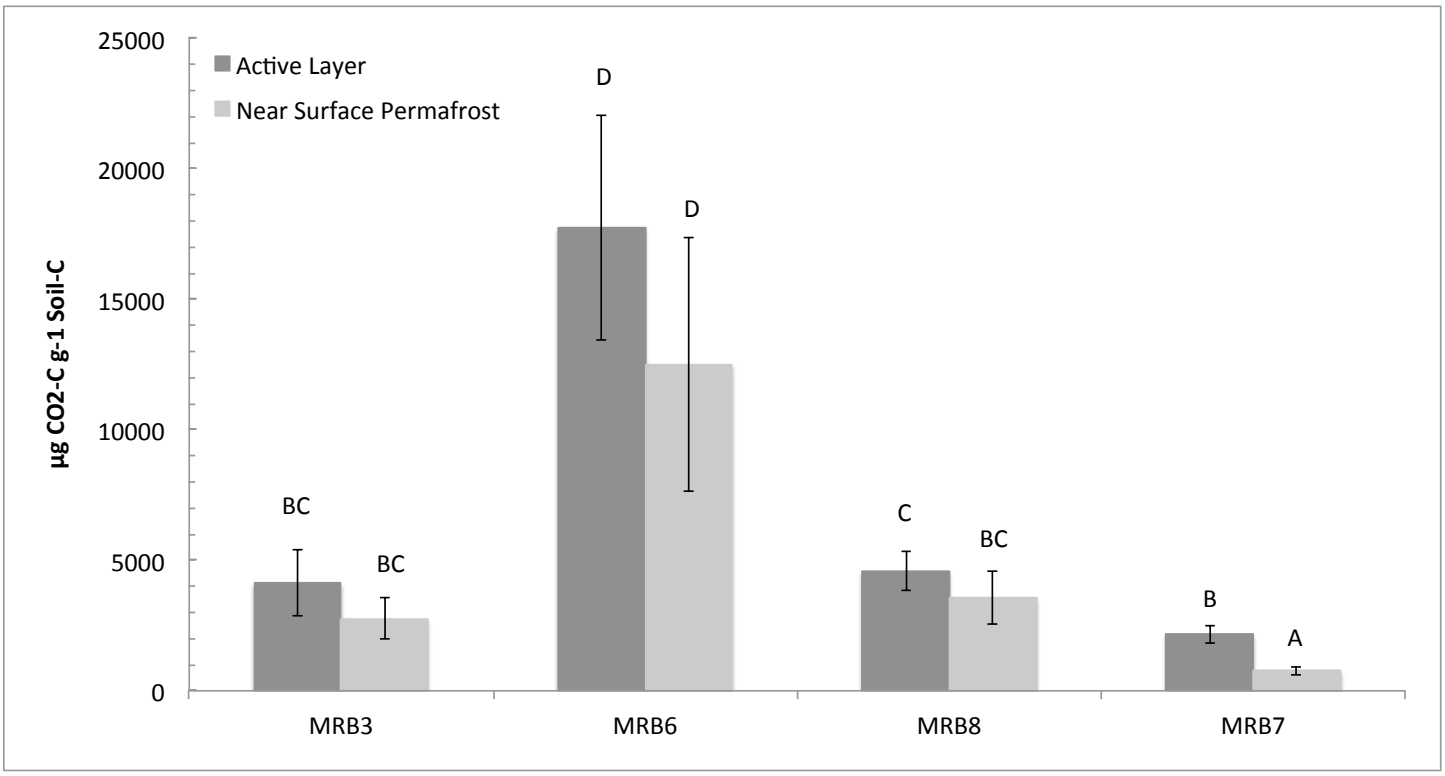

Figure 2.3: Baseline Final Cumulative Respiration Final respiration at the end of the 23 days in µg CO_2-C across all sites and depths included in the incubation experiment. Bars represent averages from four replicates (±SE). Statistical differences calculated using a two-way ANOVA with similar letters showing sites and depths that are not significantly different ($p<0.05$).

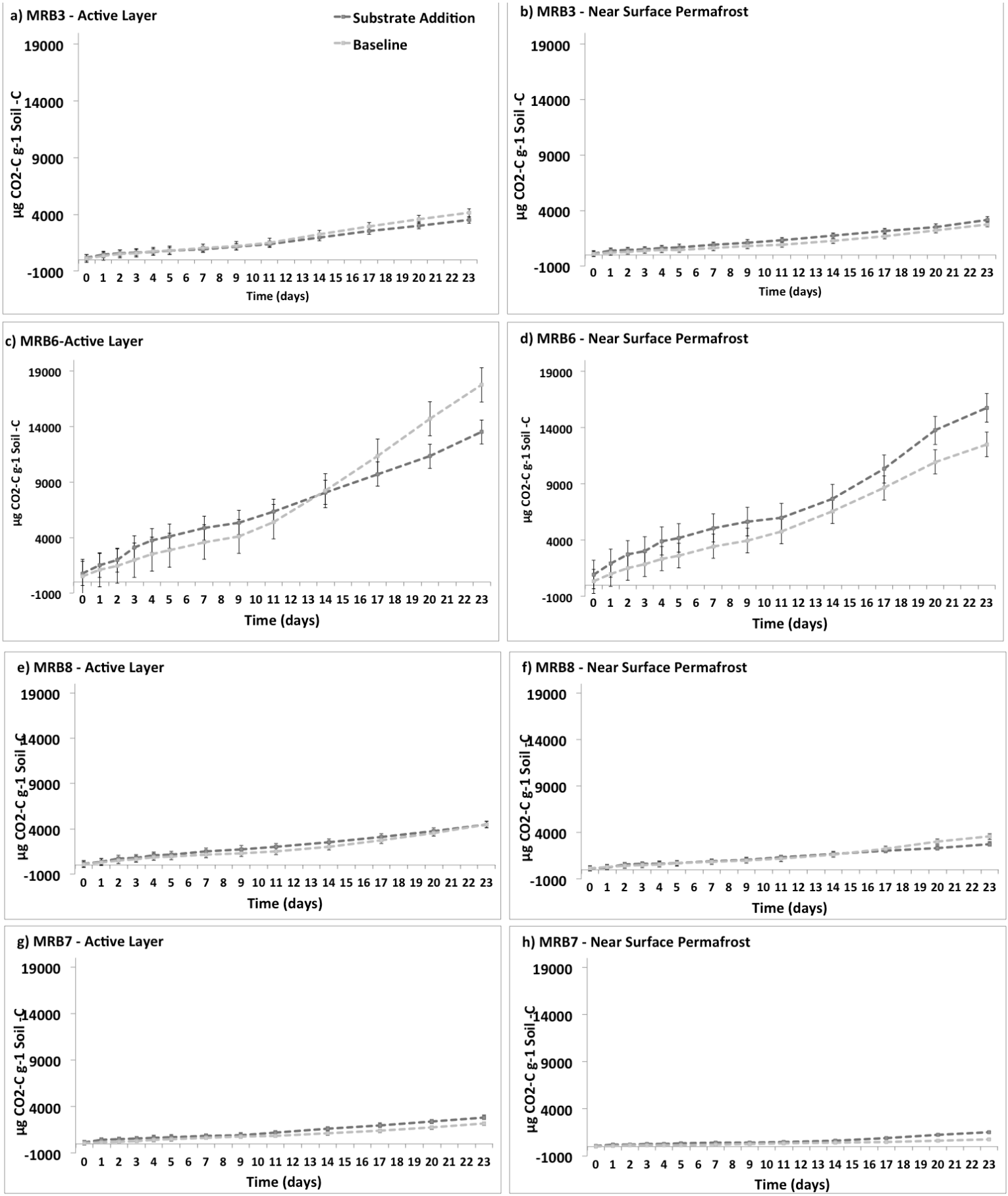

Figure 2.4: Substrate addition and Baseline Respiration Cumulative respired CO_2 as µg CO_2-C g-1 Soil-C from the four incubated sites from the Mackenzie River Basin. These are results from both glucose addition and control samples over the 23 day incubation period. Points represent averages from four replicates (±SE).

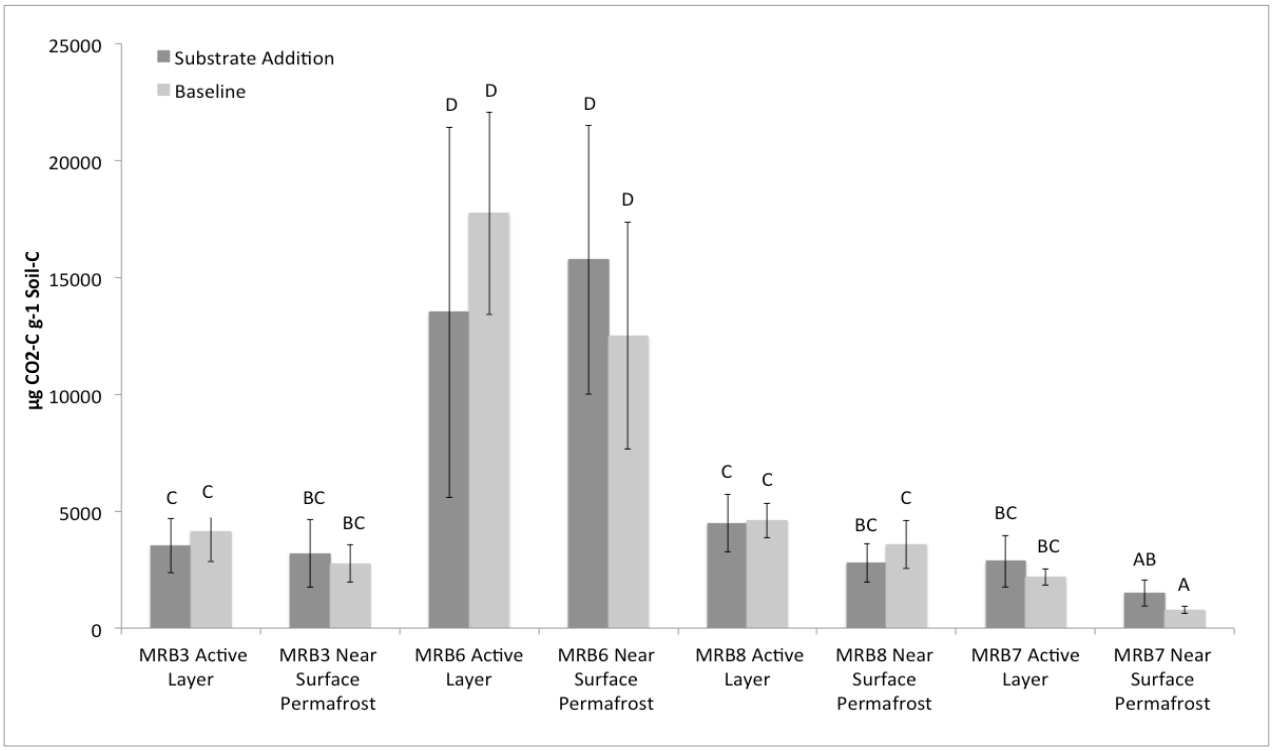

Figure 2.5: Comparison between total cumulative substrate addition and baseline respiration from all sites and depths from the Mackenzie River Basin (MRB) used in the 23 days incubation experiment. Bars represent means calculated from four replicates (±SE). Bars are labeled with simlar letters were not found to be significantly different in the three-way ANOVA ($p<0.05$).

Table 2.4: Results from three-way and reduced two-way ANOVA showing the effects of substrate addition, site and depth on final respiration. Three way interaction was found to be insignificant ($p>0.05$), and was removed from the final two way ANOVA. The following significance code is used to show * 0.05 probability level, ** 0.01 probability level, *** 0.001 probability level.

Reduced Two-Way ANOVA	Df	SumSq	MeanSq	Fvalue	Pvalue
addition	1	0.00011	0.00011	0.504	0.4808
site	3	0.07406	0.024688	113.054	<2.00E-16***
depth	1	0.00556	0.005555	25.441	5.91E-06***
addition:site	3	0.002	0.000667	3.055	0.03637*
site:depth	3	0.00318	0.001058	4.847	0.00477**
Residuals	52	0.01136	0.000218		

Three-Way ANOVA	Df	SumSq	MeanSq	Fvalue	Pvalue
addition	1	0.00011	0.00011	0.521	0.47381
site	3	0.07406	0.024688	116.859	<2.00E-16***
depth	1	0.00556	0.005555	26.297	5.21E-06***
addition:site	3	0.002	0.000667	3.158	0.03303*
addition:depth	1	0.00054	0.000537	2.541	0.11751
site:depth	3	0.00318	0.001058	5.01	0.00421**
addition:site:depth	3	0.00068	0.000226	1.07	0.37077
Residuals	48	0.01014	0.000211		

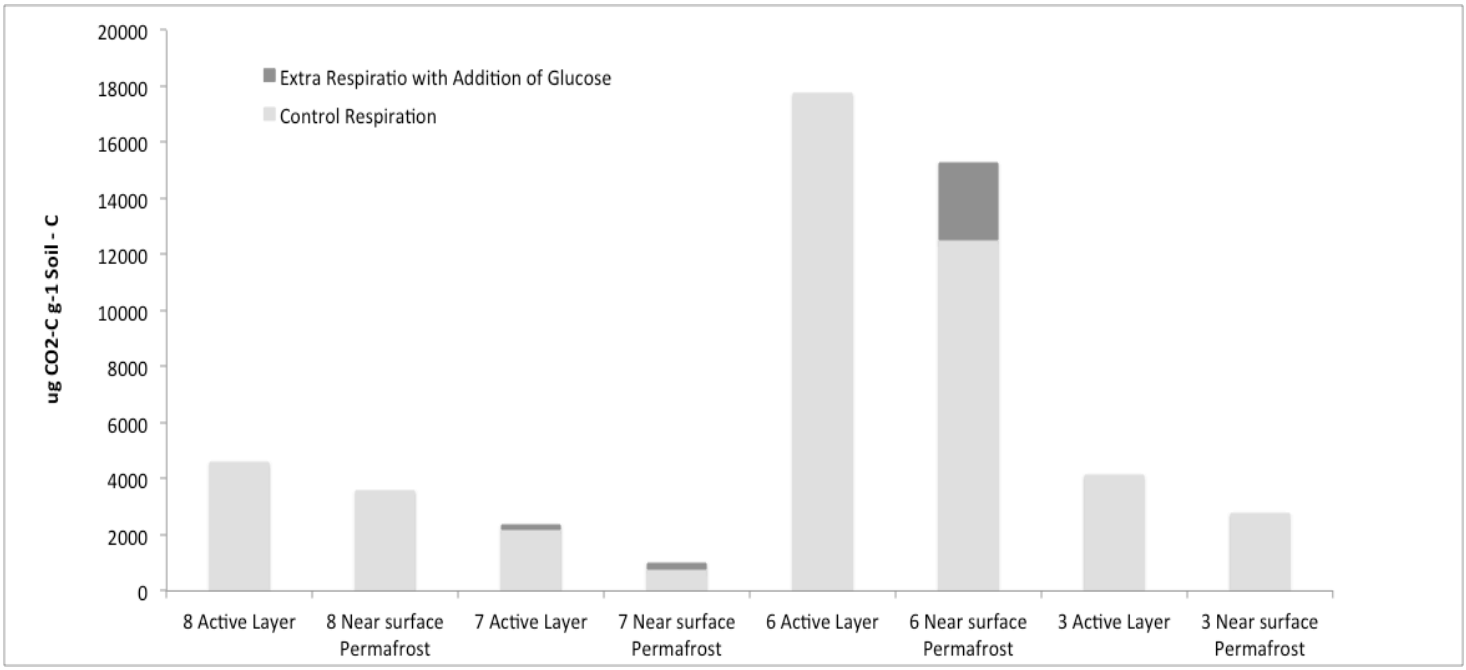

Figure 2.6: Graphical representation of the apparent priming effect Total control sample respiration with dark bars showing additional extra respiration that cannot be attributed to the additional D-glucose carbon. This extra respired carbon as CO_2 represents the apparent priming effect. These values were calculated with the mass balance equation using averages from four replicates.

Chapter 3: Biodegradability of permafrost peatland soil in the Mackenzie River Basin

Introduction

The arctic permafrost region is as an important player in the global carbon cycle because of its immense carbon storage and vulnerability to climate change. Arctic Permafrost Zones cover 25% of the northern hemisphere, contain ~1600Pg of soil carbon or 25% of the worlds organic carbon (Tarnocai et al., 2008; Pare and Bedard-Haughn, 2013). Twenty percent of this carbon resides in the surface layers where the majority of biological processes occur, and where the greatest climate change affects are predicted.. The stability of the carbon stored within permafrost has recently become a focus of Earth system carbon research owing to the poleward amplification of climate warming (IPCC, 2013; Uhlirova et al., 2007). There have already been direct observations of climate change impacts, including increases in soil and surface temperature, permafrost thaw, extended growing season, and changes in surface vegetation, which are likely to cause shifts in ecosystem structure and function of permafrost soils (Chudinova et al., 2006; Sazonova et al., 2004; Euskirchen et al., 2006; Uhlirova et al., 2007). Changes in soil ecosystem dynamics may result in exposure of previously-protected (permafrost) soil organic matter to decomposing microbial communities. These arctic changes may influence the net annual carbon exchange with the atmosphere both in magnitude and even possibly direction Currently, there are seasonal controls on Arctic ecosystems that determine whether a soil is a source or a sink of green house gases to the atmosphere. Euskirchen et al. (2012) found that the timing of a switch from CO_2 sink to source occurs when net CO_2 accumulation during the growing season is generally lost through respiration during the snow-covered months (September–May). The magnitude of the direction of carbon cycling will be effected if seasonal characteristics are altered via climate change.

Arctic peatlands are an important sink globally for atmospheric CO_2 and store 277Pg, making up ~ 30% of the soil organic carbon contained in the permafrost zones (Tarnocai et al., 2009). These Arctic peat soils have acted predominantly as a carbon sink during the Holocene, even though they produce characteristically high release of methane (35Tg / year) making up 6% of the global methane emissions (Cao et al., 1996; Harden et al., 1992; Tveit et al., 2013). The decomposition of organic matter in Arctic peatlands is strongly affected by temperature and water availability. However, soil properties such as soil microbial dynamics, soil organic matter quality, and changes in above ground carbon inputs may also play a big role in the fate of carbon with predicted environmental change. There is debate regarding the fate of permafrost carbon storage and release with climate change. Many studies have stated that alterations in temperature will cause a significant release of constraints preserving carbon in these currently frozen soils by means of thermal erosion, increased microbial decomposition, or permafrost thaw (Schadel et al., 2014; Schuur et al., 2008). In contrast, other studies have suggested that climate change would eventually result in an increase in ecosystem carbon storage (Sistla et al., 2013; Treat et al., 2014). Recent estimates of carbon release to the atmosphere following permafrost thaw by 2100 have varied from 33 to 288 Pg (Treat et al., 2014; Schuur et al., 2013). The uncertainty ultimately lies in a lack of understanding of the controls over decomposition of high latitude soil organic matter, including variability in its biodegradability.

Permafrost conditions include an overlying active layer that thaws seasonally to a depth determined by many factors including current climate. Soil organic matter in the active layer and

near-surface permafrost has been characterized by many studies and physio-chemical analyses (Uhlirova et al., 2007; Waldrop et al., 2010; Diochon et al., 2013). These studies indicate that a large component of carbon in the near-surface permafrost is a labile pool of high biodegradability that is preserved due to lower rates of decomposition. Laboratory incubations have shown that active layer soil organic matter is potentially mineralizable and is not stabilized, suggesting high susceptibility to warming (Treat et al., 2014; Uhlirova et al., 2007; Diochon et al., 2013; Fouche et al., 2014; Schimel et al., 2006). It is expected that climate warming will promote permafrost to thaw and active layers to increase in depth by 0.5-2m in many areas of the arctic by 2099; therefore, not only the soil carbon in the contemporary active layer, but also the near-surface permafrost will be exposed to microbial degradation (Sazonova et al., 2004). While the active layer has been studied extensively, comparable for near surface permafrost soils is limited.

In Arctic soils, soil organic matter affects cycling processes related to soils nutrients. More specifically, the most labile compounds of soil organic matter are considered principal controls on soil nutrient processes such as GHG release and nitrogen mineralization (Pare and Bedard-Haughn, 2013). For example, Grogan et al. (2001) found when adding fresh litter to soil the main source of CO_2 was derived from the fresh inputs, and Buckeridge et al., (2010) higher nitrogen cycling in soils with the highest liability of soil organic matter. The bioavailability of soil organic matter in permafrost soils describes the microbial ability to decompose and utilize a substance, while biodegradability addresses the quality of the substance itself. Biodegradability is a key concept when understanding soil organic matter dynamics and nutrient cycling in circumpolar regions, and can potentially provide important information beyond estimates of a region's carbon storage alone. Interpretation of soil C/N ratio as a simple indicator of organic matter decomposability has been employed in many studies, however examining the behavior of carbon released as CO_2 from degradation would be a better indicator of biodegradability of a soil.

The magnitude of permafrost carbon response to thaw will be dependent on site-specific conditions and the quantity and quality of the soil carbon currently frozen within the permafrost. Rising temperatures associated with climate change are expected to affect the Arctic subsurface, increasing permafrost thaw, and expose previously protected soil organic matter to decomposition (Hugelius et al., 2012; Schuur et al., 2013; Treat et al., 2014; Wild et al., 2014). However, the indirect response of permafrost soil carbon to increased arctic temperatures is less understood. For example, increases in air temperature will also promote net primary productivity and inputs of plant litter, potentially triggering a phenomenon known as the priming effect. This is the concept that fresh organic matter input to soil (in the form of leached aboveground leaf litter, root exudates, decomposed fine roots etc.) can stimulate soil organic matter decomposition (Bingeman et al., 1953; Kuzyakov et al., 2000; Fontaine et al., 2007; Blagodatskaya and Kuzyakov et al., 2008; Wild et al., 2014; Cardinael et al., 2015). If new labile carbon inputs stimulate permafrost soil organic matter decomposition, future permafrost carbon storage and release could deviate from predictions (Cardinael et al., 2015; Fontaine et al., 2007; Wild et al., 2014; Basiliko et al., 2012).

The priming effect has been seen in many soils, although the response of each soil has been somewhat different (Hartley et al., 2012; Fontaine et al., 2007; Basiliko et al., 2012; Wild et al., 2014). Priming in permafrost soil has been shown n only one study (Wild et al., 2014) likewise with priming in temperate peatlands (Basiliko et al., 2007), and to my knowledge the results reported in Chapter 2 are the first to examine the priming effect in permafrost peatlands.

The mechanisms of the priming effect are poorly understood in temperate soils and are likely also convoluted in permafrost peats, however there are several hypotheses that have been specified by priming studies. One in particular states that inputs of labile substrate eliminate energy limitations of microbial communities allowing them to produce energy demanding enzymes capable of degrading soil organic matter for nutrient acquisition (Hamer and Marschner, 2005). The biodegradability, or the extent to which soil microorganisms use organic compounds, will therefore play a big role in the outcome of a priming effect scenario in a specific soil. Bioavailability, in the context of soil carbon cycling, describes the potential of microbes to interact with soil substances; it is not a measure of the utilization of a substance (Marchner and Kalbitz, 2003). Therefore, the uptake of a compound (i.e. bioavailability) does not necessarily result in the breakdown or complete mineralization of that compound. For the purpose of this study, I focus on biodegradability or the utilization of organic carbon compounds by soil microorganisms quantified by the evolution of CO_2.

The objective of this experiment was to better understand the differences in biodegradability in arctic peatland soils and identify whether soil biodegradability controls priming effects in these soils. The following hypotheses were tested:

1) Surface soils demonstrate higher lability and degradability than near surface permafrost soils. Organic matter found in permafrost peatlands is accumulated vertically allowing the accumulation of decomposed and chemically complex organic material at depth. Carbon loss in this organic material at depth may be limited due to its less biodegradable state.
2) Northernmost Arctic soils will have more labile soil organic matter than more southern arctic soils due to low temperature controls on decomposition. Rates of soil organic matter decomposition are generally physically protected at lower temperatures. Physically unprotected organic matter is more accessible to soil microorganisms that can degrade and decompose carbon compounds. Physically unprotected soil organic matter includes fresh or partially decomposed residues, which may be more labile in more northern sites due temperature differences.

3) The observed apparent priming effects of these soils suggest soil properties other than age, carbon and nitrogen content, soil depth, or latitudinal location are related to permafrost peatland priming susceptibility (Chapter 2). The patterns seen in the priming experiment results will be reflected in the biodegradability of these permafrost peats; linking natural microbial utilization of carbon to the priming effect potentials of these soils. This experiment will observe the degradability of these soils without substrate addition, with the use of an inoculation, and a 24hr stabilization period. The priming theory put forward by Kuzyakov et al., 2000 suggests that soils with less biodegradability will be more susceptible to the priming effect, and this will be seen if MRB6 and MRB7 have low respiration rates in the biodegradability experiment.

Methods

Soils

In July 2013, eight permafrost peatland sites along a north-south transect in the central lowlands of the Mackenzie River Basin were sampled. Monoliths of the active layer were

obtained using a 5x5x100cm box corer and serrated stainless steel knife. Permafrost cores were extracted using a power head (Stihl BT121) driving a 10-cm diameter, 30cm-long core barrel fixed with a diamond drill bit (Professional® B680 Hard (541 06 01-51)) based on a modified version of Calmels et al. (2005). Coring was conducted to the base of the soil profile (soils at these sites reached depths between 130 to 259 m), and each profile section was wrapped in plastic film and aluminum foil and permafrost sections were kept frozen in a cooler in the field following collection. Permafrost soils have been maintained at -23°C prior to analysis. Coring locations were selected to best represent the environment at each site. For the purpose of this study, four sites were chosen to best represent the latitudinal transect and match those used in Chapter 2. That is, MRB3, MRB6, MRB7, MRB8 active layer material (10-20cm) and near surface permafrost (35-45 or 55-65 cm depending on upper permafrost depth; Table 2.2) was included in the incubation experiment.

Laboratory Incubation Experiment

In this study 700ml 'snap-seal' containers and lids with silicone sealing rings and locking tabs ('Lock & Locks') were fitted with a septa in the lid for gas sampling. The incubations were carried out on three replicates of active layer and permafrost soil at 10°C. Five to ten grams of wet sample were broken up and placed into labeled containers. Each sample was at field moisture content when placed into the containers aiming for comparable carbon content between similar depths from the same site.

To generate a microbial inoculum, 0.5g of fresh soil from each incubated depth was added to a Falcon tube resulting in ~4g of soil mixture. The tube was filled with 20ml deionized water and put on a rotary shaker for 45min to move microbes from soil pore space into suspension. The suspended solution was then filtered and 1.25ml g-1 soil was added to each incubation container in a way to ensure even application over the sample.

Experimental Assumptions

Due to the circumstances surrounding this experiment there are several caveats that need to be addressed before assessing the results. The material used in this incubation experiment was collected from 4 Artic peatlands with each site being represented by a single core. This arguably provides enough information for a latitudinal comparison, however there is no measurement of within site heterogeneity. The cores were taken and immediately wrapped in plastic and aluminum for transport, however there is the possibility of contamination that could effect microbial respiration seen in the incubation containers. The samples incubated were not standardized to moisture content to allow this difference to potentially be seen as a factor adding to latitudinal differences across the sites.

The inoculation application was specifically used to allow all four soils included in the experiment to be introduced to all types of microbes present in the soil. There was no cell count, species ratio, or species identification analysis conducted. However, here the assumption is that the microbial inoculation allows all microbes exposure to all substrate; soils with better quality will promote more microbial growth and therefore show a greater amount of respiration, where poorer quality soils will only support organisms with necessary abilities to survive and show less amounts of respiration.

Respiration

Cumulative respiration was calculated by taking daily point measurements of headspace CO_2 buildup over ten daysfollowing the start of the incubation with the first sampling occurring immediately following inoculation, 24 hours after soils acclimatized to incubation temperature. Containers were incubated with the lids sealed, and daily sampling of 10mL headspace was pulled from each container using an airtight syringe. Of the 10mL sample, 6mL from the syringe was injected into a glass Exetainer, and CO_2 was quantified on a Perkin Elmer Clarus® 580 Gas Chromatograph. By sampling 10ml of headspace from the 700ml incubation container, and allowing a 24hrs before the following sample, effects from sampling were considered negligible and there was no need to counter sampled volumes with CO_2 free gas.

Statistics

All statistics were performed with R Studio Version 0.99.447 © 2009-2015 RStudio, Inc. (R Development Core Team, 2015). Parametric methods were used and data was transformed to meet assumptions of normal distribution and homoscedasticity. It was identified that no outliers existed in the cumulative CO_2 data by using `outlierTest` function in R, where Bonferonni p-value is used to identify the most extreme observations. There were significant deviations from normality for the total (all sites and depths) cumulative CO_2 data seen in normal QQ-plots. The Fligner-Killeen median test is a test for homogeneity of variances that is robust against departures from normality (Conover et al., 1981). It can be argued that the variances in total cumulative respiration are homogeneous (p-value > 0.05). Two-Way ANOVAs were performed to test for differences across all sites and depths. This analysis identifies an interaction only between site and depth effects on respiration. Results for all analysis were considered significant at the p=0.05 level.

Results

Near-surface soil profiles show a range of bulk density, organic matter content, total carbon and nitrogen elemental concentrations, and $\delta^{13}C$ values (Table 2.2). Radiocarbon measurements of near surface organic matter show that the organic matter in the soils used for the incubation experiment is between 42 and 1972 calBP (Table 2.2). However there is evidence that age of material has no effect on the biodegradability of the soil. It might be expected that older material would be less degradable due to undergoing previous stabilization processes, or be of equal biodegradability by being more preserved due to being frozen at depth. However, the material with the largest amount of CO_2 evolution is neither the youngest or oldest soil (MRB6 near-surface permafrost = 968.4 ± 329.7 μCO_2-C g^{-1} Soil-C; 777-958 calBP). This is evidence for something else besides age and preservation mechanisms controlling the decomposition potentials of MRB6 upon thaw.

There are visible differences in the cumulative respired CO_2 between active layer and near surface permafrost CO_2-C production in all four sites (Figure 3.1), however these differences are not significant (p>0.05; Table 3.1). Despite this statistical insignificance, there is a latitudinal pattern between active layer and near surface permafrost cumulative respiration. At the northernmost sites (MRB3 and MRB6) cumulative respiration from near-surface permafrost soils was an average 12% higher than that of active layer soils. The opposite was seen in the

southern sites where the active layer produced on average 13.1% more CO_2 in MRB8 and 171.0% more CO_2 in MRB7 compared to near-surface permafrost material (Figure 3.2).

Cumulative respiration during incubation significantly differed among the four sites ($p<0.05$). This can be seen specifically in both depths of MRB6 that had larger cumulative respiration compared to the other three sites (active layer = 823.6 ± 126.4 μCO_2-C g^{-1} Soil-C; near-surface permafrost = 968.4 ± 329.7 μCO_2-C g^{-1} Soil-C). Cumulative respiration from active layer soil in MRB7 was also much greater than the active layer respiration seen in MRB3 and MRB8 (active layer = 793.7 ± 266.8 μCO_2-C g^{-1} Soil-C). Both MRB6 and MRB7 active layer material produced the highest cumulative values of CO_2 at the end of the 17 days (Table 3.2), however MRB7 biodegradability was not uniform across the depths, with near-surface permafrost respiring 292.6 ± 33.7 μCO_2-C g^{-1} Soil-C.

Discussion

Treat et al. (2014) found similar responses in cumulative CO_2, with reduced CO_2 production in laboratory soil incubations in active layer samples from the arctic climate zone, where active layer production in boreal climate zones produced 77% larger CO_2 when compared to permafrost samples. Similar to results from this study, even with the higher active layer respiration in southern soils, Treat et al. (2014) found this difference in respiration to be insignificant (Table 3.1; $p>0.05$). A single-site permafrost study by Uhlirova et al. (2007) found the same relationship between depths where the difference between active layer and near surface permafrost respiration as not significantly different. Although soil respiration was similar at both depths in the experiment, there is evidence of a site effect across the transect. This difference across latitude most likely reflects the preservation processes occurring in high latitude sites. The material incubated here was collected from similar depths with different ages. The active layer 20-cm material from the northern sites is similar in age (293 calBP at MRB3, 309 calBP at MRB6) and shows a similar accumulation pattern. In these sites, as material moves through the active layer to be incorporated into the near surface permafrost temperature controls on microbial decomposition could allow relatively undecomposed organic matter to be incorporated into the near-surface permafrost. In contrast the southern sites (MRB7 and MRB8) have a more varied pattern in age at the 20-cm depth (143 calBP at MRB7 and 588 calBP at MRB8), and this could suggest that incorporation of surface material follows a different pattern compared to northern sites. Fresh material found in the northern active layers is less biodegradable compared to the near surface permafrost due to the preservation mechanisms that are not as present in the southern sites.

Despite the similarities in properties between all four sites (Table 2.1) MRB6 seems to be significantly more biodegradable in both active layer and near surface permafrost soils (Figure 3.2). Age can be ruled out as a reason for the difference in degradability seen at this site, as it is neither the youngest nor oldest (active layer = 153-309 calBP, near surface permafrost = 777-958 calBP; Table 2.1). MRB6 has similar soil characteristics (Table 2.1) compared to the other samples used in this experiment; therefore a difference in carbon and nitrogen content can be ruled out as a factor controlling biodegradability. These samples were inoculated to ensure each site initially had similar microbial groups present; this minimizes differences in microorganisms at the beginning of the experiment. However there is evidence that the initial soil environment is different at MRB6 compared to the other sites. The bulk $\delta^{13}C$ of MRB6 active layer soil is 3‰ less than the overall active layer average across the sites, and 2‰ less in the near surface permafrost. This depletion in $\delta^{13}C$ suggests a difference in the initial soil ecosystem at MRB6

prior to incubation and inoculation. The processes that form soil organic matter can determine soil ecosystem characteristics; mainly microbial dynamics or the type of litter inputs that become soil organic matter (Asada et al., 2005). Soil microbes tend to discriminate the lighter ^{12}C as CO_2; causing the remaining soil to become enriched in the heavier isotope (Asada et al., 2005). Microbial degradation controls the quality and state of soil carbon, and the specific types of microbes present will determine the state of the soil environment. Different organic compounds found in peat soils have different isotopic signatures that could also explain the difference seen at MRB6. Soluble carbohydrates are more enriched in $\delta^{13}C$ compared to lipids or lignin (Benner et al. 1987, Wedin et al. 1995, Adams & Grierson 2001), and following their decomposition and release via microbial respiration, the remaining bulk soil could be depleted (more negative) in $\delta^{13}C$. This depletion in $\delta^{13}C$ seen at MRB6, combined with the increased respiration seen in this experiment, along with priming effect results from Chapter 2, suggest that there is a difference in the initial microbial communities or soil carbon compounds that creates an native soil environment that is more degradable and more susceptible to priming.

Both MRB7 and MRB6 soils showed evidence for priming in Chapter 2, and soils from both these sites (MRB6 active layer and near-surface permafrost; MRB7 active layer soils only) display significantly higher respiration patterns in the biodegradability experiment. The similarities between all soils included in the experiments can eliminate carbon content, age, type of surface vegetation, and depth of soil from factors that influence priming effects in these peat soils. I did not account for changes in microbial populations over the course of the substrate addition experiment in Chapter 2, however the use of an inoculum in the present Chapter minimized the difference in microbial communities present in each soil. Despite this uniform starting point, the sites displayed differences in respiration with significant differences in total cumulative respiration at the conclusion of the experiment. Assuming the inoculum was representative of the microbial communities and microbial abundance, similar CO_2 production patterns would have indicated similar inherent biodegradability of soil organic matter because the initial microbes were experimentally equalized, and therefore shows non-microbial differences in soil organic matter chemistry. There is however evidence that the starting point of the soil organic matter was different across the sites; with varying $\delta^{13}C$, bulk density, and respiration patterns that suggest MRB6 contains a soil environment with a higher abundance of isotopically lighter compounds such as lipids and lignin.

Conclusion

The biodegradability in the northern most permafrost peatland soils in the Mackenzie River Basin locked in near-surface permafrost was greater than that of active layer soils, indicating the potential for a surprisingly reactive organic carbon pool in these sites that may become available to microbes should active layer depths increase. This may be a particular concern for northern permafrost peatlands with shallow (<30cm) active layers, where warmer air may result in warmer soils and oxygen availability does not limit the rate of decomposition. Organic soils in the active layer in southern most sites were more susceptible to microbial decomposition, and demonstrated more near surface permafrost carbon stability. This could imply that surface inputs moving through the active layer to be incorporated to the near-surface permafrost might already have undergone decomposition and the material remaining is less degradable.

In Chapter 2, evidence for a priming effect was seen in two of the soils with the highest and lowest biodegradability. The near-surface permafrost soil at site MRB6 showed the strongest apparent priming effect (Figure 2.5), however the biodegradability of this site did not suggest a link between priming and microbial utilization of carbon. MRB6 shows the highest overall biodegradability of CO_2 compared to the other sites, this is evidence that this soil ecosystem has all the requirements for an ideal soil microbial environment. This is the opposite of what priming theory suggests; that soils susceptible to priming have limits on microbial respiration due to lack of necessary energy or nutrients.

The global soil carbon pool contain twice as much carbon as the atmosphere making it vital to understand processes that control carbon release from soils (Nottingham et al., 2009). If priming effects potentially contribute to the release of permafrost peat carbon, then exploring how and why different soils exhibit different degrees of susceptibility would help identify areas that are vulnerable to carbon loss. These studies demonstrate that priming mechanisms are driven by something other than soil biodegradability and underline the heterogeneity of permafrost peatland soils.

The approaches used in this study to examine biodegradability have some limitations when looking to better examine more specific controls on CO_2 production in these permafrost peatlands. The contrasting depth effects seen between northern and southern sites (Figure 3.2) could potentially illustrate the differences in organic matter chemistry. These are all *Sphagnum fuscum* dominated sites specifically chosen for their visible similarities, however, differences in moss and vascular plant inputs could affect decomposition (Treat et al., 2014). If the colder northern sites had a higher abundance of *Sphagnum*, the active layer peat might have higher abundance of complex compounds such as lignin, which can slow microbial decomposition (Rinks et al., 2014). In contrast, the southern site active layers may have a higher abundance of vascular plant inputs that are high in polysaccharides and a preferred substrate for soil microbes (Dai et al., 2002). Knowing the peat type, the abundance of other plants, and the influence their inputs have on peat chemistry and decomposition would have provided a more complete description of carbon mineralization processes in these soils. However, the overall pattern of the depth effect across latitude was clearly describes in the cumulative respiration generated at the same incubation temperature, and can provide a complete comparison of biodegradability between sites.

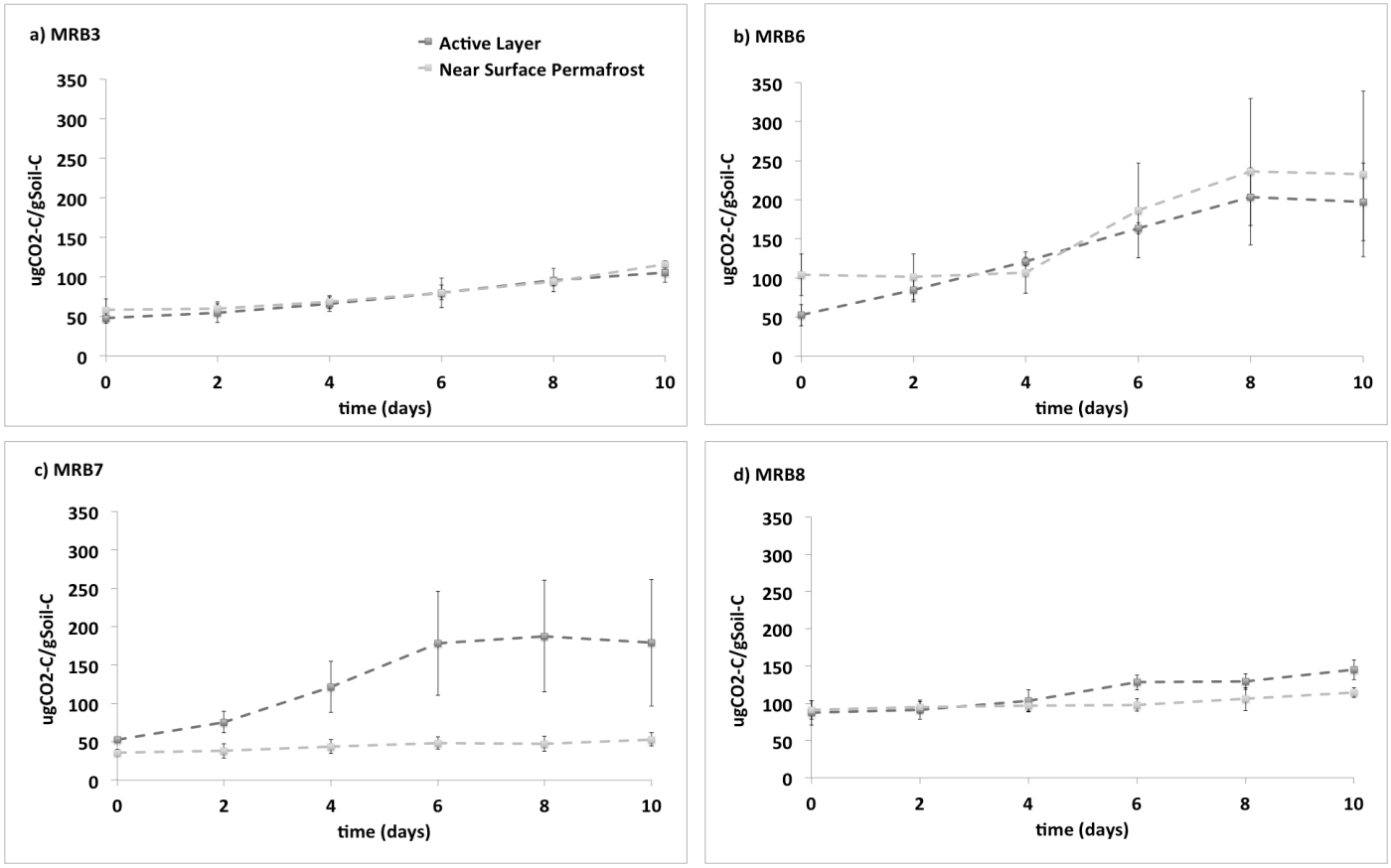

Figure 3.1: Cumulative respiration over the 10 day incubation period. Curves are expressed as respired CO_2 as µg CO_2-C g-1 Soil-C from the four incubated sites from the Mackenzie River Basin. Points represent averages from three replicates +/- standard error.

Table 3.1: Table with results from Two-Way ANOVA comparing incubation data from the four sites and two depths. There is not a significant interaction between site and depth at the 0.05 significance level. There is a strong site influence on total cumulative respiration ($p<0.05$).

	Df	SumSq	MeanSq	F value	Pr(>F)
Site	3	637622	212541	8.04	0.00172**
Depth	1	63282	63282	2.394	0.14137
Site:Depth	3	356427	118809	4.494	0.01805*
Residuals	16	422989	26437		

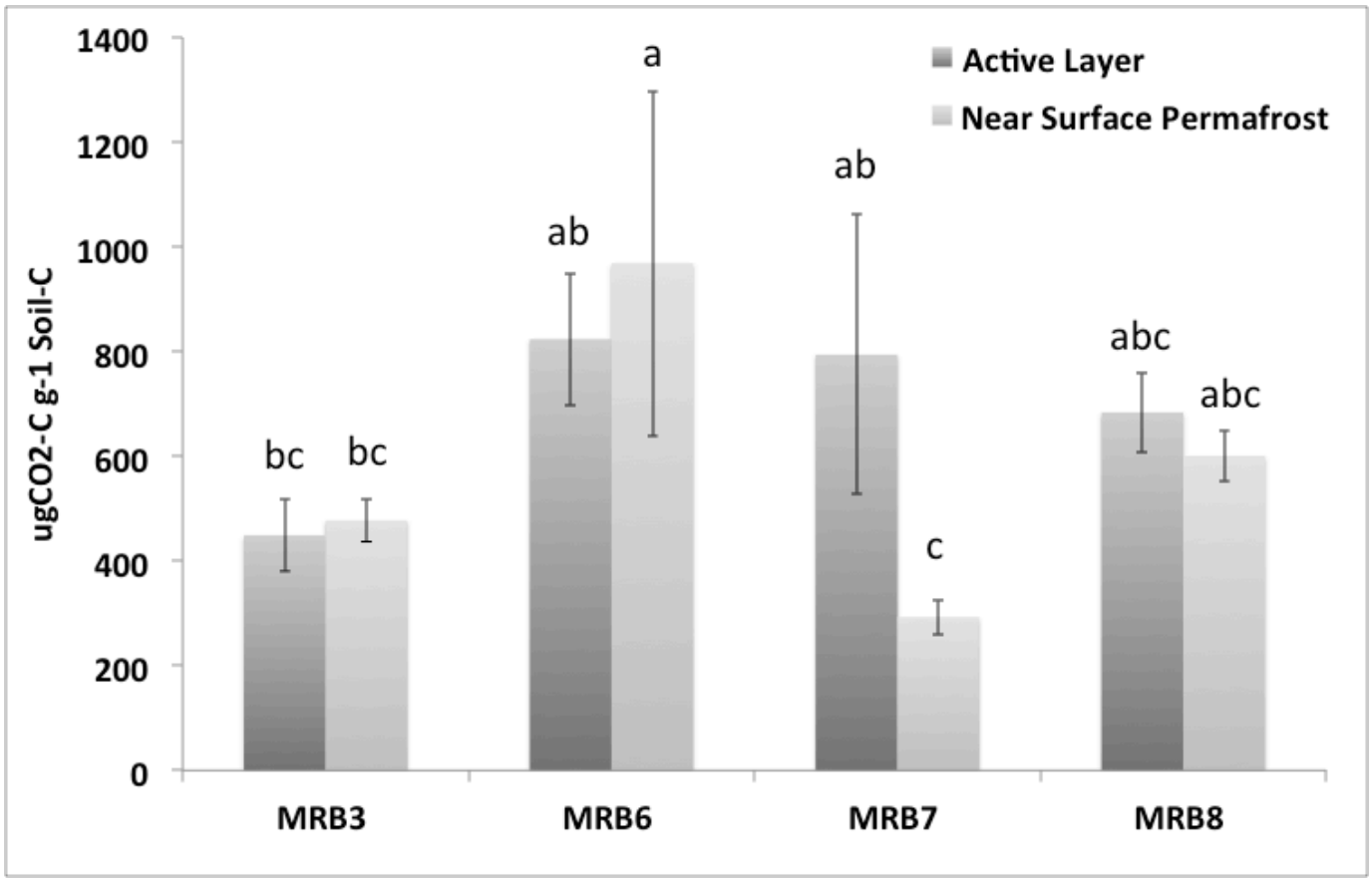

Figure 3.2: Total Cumulative CO_2 after the completed 10 day incubation across the four sites from the two incubated depths. Bars represent averages from three replicates +/- standard error. Bar pairs (active layer and near surface permafrost from single sites) are labeled with different letters to show significant difference ($p<0.05$).

Chapter 4: General Discussion

Summary and Synthesis

Arctic permafrost peatlands store a substantial part of the Earth's soil organic carbon, equaling 1/3 of the CO2 carbon in the atmosphere (Tarnocai et al., 2009). Sixteen gigatonnes of this Arctic carbon is stored in the peat soils of the Mackenzie River Basin (Vitt et al. 2005; Figure 1.1). The carbon storage of the Mackenzie River Basin makes this region an important element of the Arctic Carbon Feedback response to climate change (McGuire et al., 2009). The results from Chapter 2 are the first, as far as I know, to examine the potential for the priming effect to affect Arctic permafrost peatland soils. Wild et al. (2014) suggested that non-peatland permafrost soils with low carbon content (0.6-9.4%C) may be susceptible to priming. Particularly the mineral subsoil, where rates of soil organic matter derived carbon exceeded topsoil rates after substrate addition. Basiliko et al. (2007) in their incubation experiments using temperate non-permafrost peat soils found some evidence for priming from the addition of a synthetic root exudate solution (solution of glucose, acetic acid, and an amino acid solution). However, the total magnitude of the effects were not significantly greater than baseline respiration and microbial mineralization rates observed in the study site, and therefore was assumed to not represent an important additional carbon cycling process. In Chapter 2, I presented data that glucose addition to soils from four permafrost peatland sites stimulated an observable priming effect in only two sites. In one of these sites, MRB7, the excess CO_2 suggests that priming may have occurred in a very small amount, and arguably within the uncertainties of the measurements and methods. Demonstration of the priming effect, or absence of priming requires the subtraction of averages from control and treated sample cumulative respiration, these averages both contain variability that could effect a priming signal that is relatively small in size. The apparent priming effect seen at MRB6 near-surface permafrost is arguably too large to be affected by this variability. However, despite the extra 2770.0 μCO2-C produced with the addition of glucose, the difference between substrate addition and control respiration was found to be insignificant ($p>0.05$). The addition of an easily degradable substrate was insignificant on overall respiration across the sites ($p >0.05$; Table 2.4). This supports the findings of Basiliko et al. (2007) in that even when substrate addition samples produced more carbon than controls this difference in respiration was statistically insignificant.

The biodegradability study presented in Chapter 3 further explored the inherent decomposability of permafrost peatland soils in the context of the observed differences in priming effects seen in Chapter 2. I found that soils showing positive priming contained highly decomposable organic matter compared to the other soils. Soils from MRB6, which showed some evidence for priming, had the highest cumulative microbial respiration in both the active layer (823.6 ± 126.4 μCO_2-C) and near-surface permafrost (968.4 ± 329.7 μCO_2-C), indicating that priming can occur in peat sites with varying degrees of degradability.

The priming effect has been studied in a wide variety of soils with varying results. Sistla et al. (2013) found that carbon storage below ground in mineral subsoil horizons was increased with inputs associated with increased plant productivity at the surface. Whereas Hartley et al. (2012) saw carbon losses with substrate addition in both organic birch forest and

heath soils. However, in the two completed priming studies conducted in peat soils by Basiliko et al. (2007) and myself, the results are supportive of an overall priming robustness. In this thesis underscores the heterogeneity of soil response to the priming effect by showing a lack of relationship between soil characteristics and susceptibility. The only soil included in this experiment to show evidence of an apparent priming effect was both similar in soil characteristics and higher in biodegradability compared to the other soils, showing that predicting soil vulnerability to priming is more complicated than described by original priming theories. This shows a need to further investigate other driving mechanisms of the priming effect in soils before it is possible to include or ignore this process in global carbon models.

The four sites used in the experiment span the zones of permafrost occurrence however the sample collection sites were far from zone boundaries that are arguably going to experience the greatest amount of change in carbon dynamics as conditions change in the Arctic. This could suggest that areas with currently more consistent seasonal thaw depths and temperatures located more centrally in these zones are less vulnerable to environmental change (Koven et al., 2015). The southern boundaries where thawing events would lead to a transition from permanently frozen to permanently unfrozen would drastically change the soil environment and potentially enhance the permafrost carbon feedback (Koven et al., 2015). As soils thaw and new vegetation regimes move north with increased temperatures, deeper permafrost soils along the southern boundary of the permafrost zones could be regions where the priming effect would promote more carbon released to the atmosphere.

Considerations for future research

SOM quality and soil environment

Biodegradability is an important characteristic controlling soil organic matter processes and dynamics in carbon rich soils. Hypothesized priming effect mechanisms have been explored by various studies, and one of the suggested drivers of extra carbon mineralization is nutrient mining by soil microbes. Organic molecules in soil contain bonded nutrients such as N, P, S, and soil organic matter dynamics and turnover will therefore also affect the mobility and availability of these nutrients (Marschner and Kalbitz, 2003). Soils with different biodegradability by definition have either different rates of mineralization or different processes by which original compounds are taken up and broken down within the soil. This is in part driven by the actual chemical composition of the compounds present in soils. By examining intrinsic soil carbon quality parameters such as molecular size or chemical structure we can better understand similar priming effect responses in soils with different biodegradability potentials. This would address the theory that priming effects are caused by pool substitution, or a preferential shift from complex native carbon to labile carbon that would be seen in an initial pulse of CO2 originating from the new added material.

The indigenous microbial communities that are responsible for the break down and the ultimate degree of degradation of soil carbon, influence biodegradability and the general soil ecosystem. If there is a tie between priming effects and biodegradability, then there is a fundamental link between microbial utilization of soil carbon and the potential for priming in susceptible soils (Nottingham et al., 2009). Permafrost ecosystems are currently stable environments where conditions have limited the accessibility and potential for resident microbial group to decompose soil organic carbon. Permafrost up to 3 million years in age has been found to contain a variety of viable microbes that upon thaw could renew or accelerate the

physiological activity (Coolen et al., 2011). The heterogeneity of permafrost environments with respect to geographic distribution, vegetation cover, geochemistry, and biological factors make predicting permafrost response to the priming effect even more complex. This thesis focused on the general susceptibility to priming and biodegradability of these permafrost peatlands. The results resented here suggest that priming potentials are not directly tied to the carbon and nitrogen content in these soils, or age of material, or the microbial utilization potential of the soil organic matter. However, a sensitive way to deconstruct the microbial influence in these soils is to examine the bioavailability of complex soil organic matter in these soils.

Microbial Influence on Priming Effects

Priming effects have also been hypothesized to be driven by an increase in enzyme production in soils following the addition of easily degradable carbon inputs (Kuzyakov et al., 2000; Nottingham et al., 2009). This is the theory that extra mineralization of native carbon is due to new substrate addition providing energy to microbes to generate enzymes needed to break down the complex soil organic matter to supply the population with necessary nutrients. Extracellular enzymes, which are released by microbes to cleave organic matter into smaller molecules, contribute to a soils bioavailability or the potential of microorganisms to metabolize soil substances. Peat carbon includes various abundance of major plant compounds such as cellulose /hemicellulose, polysaccharides, lignin, lipids, phenols, and proteins (Tveit et al., 2013; Treat et al., 2014; Benner et al., 1987). The percent abundance of the individual compounds depends on the peat type (ex. plant and moss peat have higher abundance of polysaccharides and proteins, where amorphous peat has a higher abundance of lignin (Treat et al., 2014)). The degradation of these to oligomeric and monomeric compounds is catalyzed by a diverse set of extracellular enzymes produced by microbes (Kotsyurbenko, 2005; Tveit et al., 2013). The native microbial communities and their genetic potential, or ability to degrade soil organic matter, will therefore theoretically drive the priming effect of permafrost peatlands.

Broad and non-specific studies have examined the biogeography of soil bacteria communities and the dynamics of Arctic soil microbial communities in relation to the composition of surface plant communities (Waldrop et al., 2010; Coolen et al., 2011; Tveit et al., 2013), however only recently have metagenomics and metatranscriptomics developed into powerful tools for soil scientists to study microbial ecology. Now studies can used general non-targeted methods to examine genetic potential, gene expression, and microbial community composition in soils relatively easily (Tveit et al., 2013). The results presented in this thesis have shown that priming is related to something other than controls on soil organic matter degradability and I believe by answering the following research questions using new and easy application technologies will bring us further to understanding priming mechanisms in these sites:

1) Are microbial communities and extracellular enzyme potentials for degradation similar across the sites and between the active layer and near surface permafrost? How do these communities change with exposure to a labile substrate and over the course of a priming experiment?

2) Assuming the composition of soil organic compounds in soil determines microbial dynamics (Tveit et al., 2013; Treat et al., 2014) then examining microbial efficiency and substrate preference would shed light on microbial priming mechanisms. Is the presence of priming related to the genetic repertoire of microbial enzymes present in the soil? Is priming related to the native microorganism substrate preference? *Sphagnum fuscum* dominated sites

have higher abundance of complex compounds such as lignin and lipids, which can slow microbial decomposition (Rinks et al., 2014). In contrast, peatlands with higher abundance of vascular plant inputs that are high in polysaccharides and a preferred substrate for soil microbes have higher rates of decomposition(Dai et al., 2002). Knowing the peat type, the abundance of other plants, and the influence their inputs have on peat chemistry and decomposition could provided a more complete description of carbon mineralization processes in these soils. Specifically with respect to the priming effect in carbon rich peatlands, the type of carbon compounds present might be a more important identifier of priming susceptibility than carbon content or soil nutrients.

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