Dissertationes Forestales 288

Carbon dynamics in forest fire affected permafrost soils

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Academic dissertation

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Northern Hemisphere permafrost soils store approximately 50% of the global soil carbon (C), a quarter of which could thaw by the end of the century. Thawing exposes previously frozen soil organic matter (SOM) to decomposition, resulting in release of greenhouse gases (GHG) from the soils. Vast areas of permafrost soils are covered by boreal forests currently acting as sinks of C. As global warming is strongest at northern latitudes, the occurrence of boreal forest fires may increase. Forest fires further advance permafrost thaw and forest soils may turn from sinks to sources.

This thesis examines how forest fires affect the quality of SOM and GHG emissions from permafrost soils in boreal forests by conducting chemical fractionation of SOM and soil incubations, as well as manual chamber measurements of GHGs.

Forest fires increased the active layer depth on top of permafrost, altered species composition of vegetation and affected the organic layer depth and the SOM pools. Fires decreased the quality of SOM, observed as reduction in the proportional amount of labile SOM fraction and increased SOM temperature sensitivity, as well as enrichment with heavier isotopes of ^{13}C and ^{15}N. GHG measurements showed that fire initially decreased carbon dioxide flux from the soil and it returned to its pre-fire status approximately 50 years after the fire. The effects of fires on methane and nitrous oxide fluxes were not significant.

Forest fires have significant effects on the release of GHGs from permafrost soils. In the future, the fate of permafrost stored SOM is dependent on its degradability, the frequency of fire events and the ability of forests to regenerate, allowing permafrost recovery, in the changing climate. There is a demand for further studies investigating the specifics of different permafrost ecosystems and building a complete picture to estimate total emissions from permafrost regions.

Keywords: Q_{10}, ^{13}C, ^{15}N, soil respiration, soil organic matter, greenhouse gas emissions

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The journey leading to this dissertation was somewhat of a surprise even for myself. Though nature and science always fascinated me, I did not plan to begin a PhD, which I saw as the most challenging and arduous path one could take. When Professor Jukka Pumpanen asked me if I was interested in doing a PhD in their new project, I remember saying yes, while trying to look like I had some idea about the topic and silently thinking I was just selling my soul to the doom of endless hours of statistics, revisions and a lifetime spent in the windowless lab. Lucky for me I did find out, that while my prejudices are somewhat an unavoidable part of the journey to a dissertation, there are also much more positive sides, such as the people you work with, all the adventures you experience and the passion you can find for your research.

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LIST OF ORIGINAL PUBLICATIONS

This thesis consists of four research articles preceded by an introduction. Throughout the thesis the articles are referred to by their Roman numerals and the original articles have been reprinted to the theses with the kind approval of the publishers.

I. Aaltonen, H., Köster, K., Köster, E., Berninger, F., Zhou, X., Karhu, K., Biasi, C., Bruckman, V., Palviainen, M. and Pumpanen, J. (2019). Forest fires and soil organic matter in Canadian permafrost region: The combined effects of fire and permafrost dynamics on SOM quality. Biogeochemistry 143 (2): 257-274. https://doi.org/10.1007/s10533-019-00560-x

II. Aaltonen, H., Palviainen, M., Zhou, X., Köster, K., Köster, E., Berninger, F. and Pumpanen, J. (2019). Temperature sensitivity of soil organic matter decomposition over a forest fire chronosequence in Canadian permafrost region. Journal of Environmental Management 24: 637-644. https://doi.org/10.1016/j.jenvman.2019.02.130

III. Köster, E., Köster, K., Berninger, F., Aaltonen, H., Zhou, X. and Pumpanen, J. (2017). Carbon dioxide, methane and nitrous oxide fluxes from a fire chronosequence in subarctic boreal forests of Canada. Science of the Total Environment 601:895-905. https://doi.org/10.1016/j.scitotenv.2017.05.246

IV. Köster, E., Köster, K., Berninger, F., Prokushkin, A., Aaltonen, H., Zhou, X., Pumpanen, J. (2018). Changes in fluxes of CO_2 and CH_4 caused by fire in Siberian boreal forest with continuous permafrost. Journal of Environmental Management 228: 405-415. https://doi.org/10.1016/j.jenvman.2018.09.051.

Author's contributions

I am responsible for the summary of this thesis. In Study I, I was responsible for data analysis, writing of the manuscript and was the corresponding author. I was mainly responsible for the planning and implementation of the soil organic matter fractionation and practical work in the laboratory. The planning of field sampling had already been done by others when I joined the project. In Study II, I was involved in the planning of the incubation method and was responsible for the actual incubation measurements. I did most of the statistical data analysis and was the corresponding author for this article. For Study III I was responsible for the laboratory incubation measurements and determining $Q_{10,}$ and participated in the writing of the manuscript. I was also responsible for supervising laboratory measurements performed by a trainee. In Study IV I participated actively in field measurements in Russia, including measuring the greenhouse gas fluxes. I also performed and supervised basic laboratory experiments and took part in the manuscript writing.

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List of terms and abbreviations

C	carbon
CH_4	methane
CO_2	carbon dioxide
CUE	carbon use efficiency
$\delta^{13}C$	ratio of isotope ^{13}C to ^{12}C
$\delta^{15}N$	ratio of isotope ^{15}N to ^{14}N
GHG	greenhouse gas (CO_2, CH_4, N_2O)
LMM	linear mixed model, a statistical model containing both fixed and random effects
N	nitrogen
N_2O	nitrous oxide
OM	organic matter
Pyrogenic compounds	compounds formed by burning of organic matter, often quite resistant to decomposition
Q_{10}	proportional increase in soil respiration if temperature increases 10 ˚C
qCO_2	the microbial metabolic quotient, ratio of microbial respiration to microbial biomass
SOC	soil organic carbon
Soil autotrophic respiration (R_a)	respiration caused by plant roots
Soil heterotrophic respiration (R_h)	respiration caused by heterotrophic micro-organisms decomposing organic matter
SOM	soil organic matter

1 INTRODUCTION

Permafrost soils overlap noticeably with the boreal forest zone, resulting in a peculiar interaction of forest fires and permafrost dynamics, with around 80% of the world's boreal forests growing on permafrost soils (Helbig et al. 2016). Global warming is not only causing permafrost thaw on the northern hemisphere (Guo and Wang 2017; Oliva and Fritz 2018; Strauss et al. 2017), but also increasing the frequency of forest fires (Kelly et al. 2013; Veraverbeke et al. 2017). What makes fires in boreal forests on permafrost soils unique are the soil carbon (C) stores preserved in the frozen soil. Permafrost soils have been estimated to contain between 50 and 60% of global soil C reserves (Tarnocai et al. 2009). This significant store is endangered by the thawing caused by the combined effects of global warming and forest fires. The decomposition of the previously frozen soil organic matter (SOM) would facilitate possibly large emissions of greenhouse gases (GHGs) and positive feedback to global warming (Schädel et al. 2016).

The permafrost thaw is advanced by the direct and indirect effects of the fire and the changes in forest soils caused by the fire. An intense forest fire may directly consume the soil organic layer almost totally. This layer typically acts as an insulator that keeps the soil underneath cooler, and removal of this layer by fire leads to increased temperatures in the soil (Fisher et al. 2016). As the organic soil layer burns, the remaining soil surface has an albedo (reflectivity) that is lower than that of an unburned forest (Bret-Harte et al. 2013; French et al. 2016), allowing heat radiation to be absorbed in the soil more effectively. Soil temperatures are increased even more after stand replacing fires, as lack of forest canopy increases solar radiation on the soil surface (Fisher et al. 2016; Jorgenson et al. 2010). During winter the lack of canopy allows a thicker snow layer to accumulate on the forest floor, and this insulation restricts the freezing of the underlying soil (Brown et al. 2015). These indirect effects of forest fires lead to the deepening of the seasonally freezing and thawing active layer on top of the permafrost (Fig. 1).

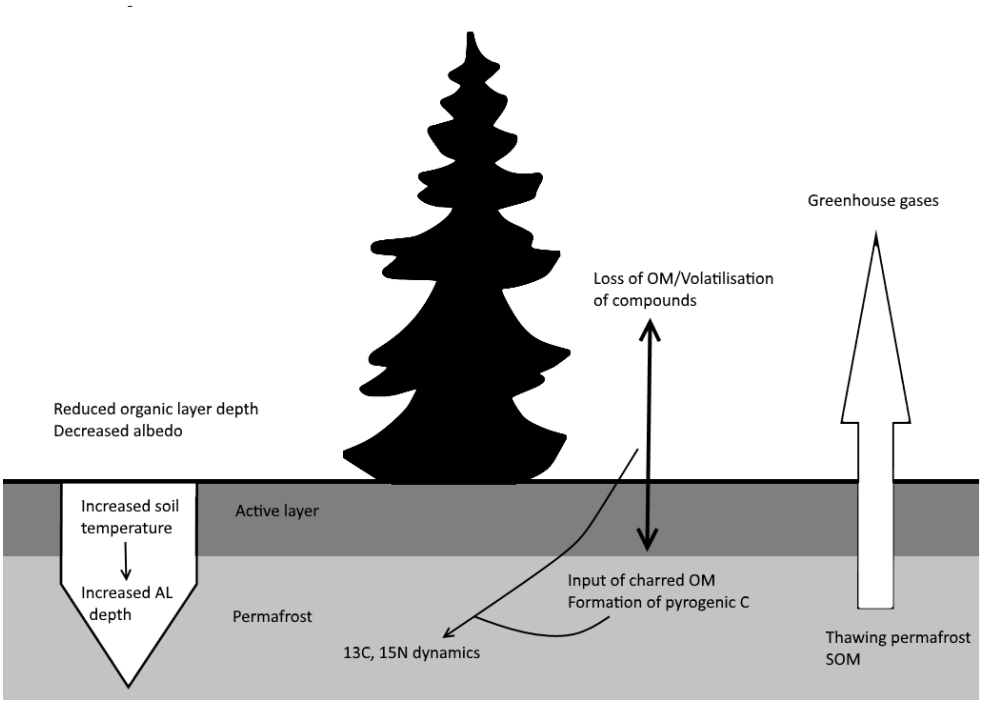

Figure 1: The processes taking place on permafrost soils after forest fire, where OM relates to organic matter, SOM is the soil organic matter and AL is the active layer.

Soil organic carbon (SOC) is a significant component of SOM. The SOC stored in soil originates from above- and belowground litter, exudates or animal residues that become decomposed by soil microbes (Cotrufo et al. 2015). At the same time, SOC is lost from the soil via root- and microbial respiration and leaching. The degree of decomposition and leaching depends on the nature of the nutrient, litter type and site conditions (Berg and Mcclaugherty 2014). The components of incoming organic matter (OM) change with forest succession: in the early stages, the incoming litter consists mostly of foliar matter, while the proportion of woody debris increases with stand age (Berg and Mcclaugherty 2014). As woody debris has a higher lignin content and lower nitrogen (N) content than foliar litter, it also decomposes more slowly (Berg et al. 1982; Gonçalves et al. 2007). Additionally, different nutrients leach at different rates and in different stages of decomposition. As the most soluble materials are readily leached, other components are released and consumed via microbial degradation. During this process, carbon dioxide (CO_2) is released. Soil CO_2 respiration is divided into two components: the soil heterotrophic respiration (R_h) originating from soil microbial decomposition and soil autotrophic respiration (R_a) caused by plant roots and mosses (Czimczik et al. 2006). The autotrophic respiration may form up to 50% of total soil respiration in mature boreal forest (Högberg and Read 2006; Pumpanen et al. 2015), although the share of the heterotrophic and autotrophic components from the total respiration vary seasonally (Pumpanen et al. 2015). The autotrophic respiration, for example, follows the C allocation pattern of trees (Pumpanen et al. 2015).

The decomposability of the SOM stored in permafrost is affected by several factors, such as the recalcitrance of SOM, possible physical protection by soil particles, soil temperature and soil moisture (Schmidt et al. 2011). Therefore, one of the key questions in recent years has concerned the quality of the frozen SOM as the frozen reservoirs might contain

significant amounts of labile SOM. Forest fires add another factor to the SOM quality in soils. They may change the SOM quality by burning the vegetation and litter- and organic layers, causing a loss of easily degradable material (Certini 2005; Jiménez-González et al. 2016). At the same time, the byproducts of burning yield partly charred material and recalcitrant compounds, also known as pyrogenic C (Knicker 2007) and this post-fire SOM may undergo changes in the abundance of the heavier isotopes ^{13}C and ^{15}N. These factors together may reduce soil respiration for extended periods.

The effects of forest fires on soil GHG fluxes (CO_2, methane (CH_4) and nitrous oxide (N_2O)) have been studied fairly actively in recent decades (Kim and Tanaka, 2003; Levine et al. 1988; Morishita et al. 2015; Veraverbeke et al. 2015; Walker et al. 2018). While fire has often been found to decrease CO_2 flux rates from soil, the CO_2 fluxes have also been found to increase or maintain pre-fire levels at least temporarily (Burke et al. 1997; Muñoz-Rojas et al. 2016). The studies have also shown that after forest fire the soils are greater sinks of CH_4 (Kulmala et al. 2014; Morishita et al. 2015; Taş et al. 2014), while N_2O fluxes have been thought to decrease (Kim and Tanaka 2003; Levine et al. 1988).

The reduced soil respiration rates are affected by multiple factors following fire, such as SOM quality, quantity, soil temperature (Lloyd and Taylor 1994; Muñoz-Rojas et al. 2016), soil moisture (Muñoz-Rojas et al. 2016) and the possible demise of decomposing microbes (Dooley and Treseder 2012; Köster et al. 2016). Therefore, the estimation of possible GHG emissions from post-fire stands on permafrost soils also requires knowledge of SOM quality (post-fire and permafrost stored), as well as factors affecting it, and the changes in different SOM pools in the years following fire.

Forest fires and their effects on forest regeneration and soil physical and chemical characteristics in boreal regions have been studied quite comprehensively, which is not surprising as wildfires consume around 5-20 million ha of boreal forest each year (Flannigan et al. 2009; Kasischke and Stocks, 2000). Several studies have also specifically concentrated on boreal forests on permafrost soils, but these studies usually deal with the physical changes (Fig. 1) caused by the forest fires that affect the permafrost depth and permafrost C pool as a whole (Brown et al. 2015; Harden et al. 2000; Loranty et al. 2016; Yoshikawa et al. 2002). Other studies, again, have focused on the SOM quality of permafrost soils in tundra areas (De Baets et al. 2016; Uhlířová et al. 2007; Walz et al. 2017; Weintraub and Schimel 2003) and only a few articles have actually combined the effects of fire on forest SOM quality in the permafrost region (Masyagina et al. 2016; O'Donnell et al. 2009; Taş et al. 2014). Therefore, it appears that there is a need for studies that deal with the collective, long term, effects of forest fires and permafrost dynamics on SOM quality and different SOM pools.

Figure 2: Forest area burned in 2012, captured in 2018 (Yukon, Canada). Sampling took place in 2015.

1.1 Quality of soil organic matter

The quality and quantity of SOM in soil are one of the key factors affecting SOM decomposition and the following release of GHGs from the soil ecosystem. The methods currently used to determine SOM lability include studies on the temperature sensitivity of SOM, fractionation of different SOM pools and the determination of soil isotopic composition (chapter 1.3). The previous studies on permafrost SOM quality have yielded somewhat differing results. Traditionally the SOM stored in permafrost soils has been considered labile as it has not been affected by microbial decomposition and is thought to have no physical protection (Davidson et al. 2006; Schuur et al. 2008; Zimov et al. 2006). However, possible dissimilarities may arise from the differences between studied ecosystems, such as vegetation and hydrology.

One of the measures used to describe SOM lability is the temperature sensitivity of decomposition (Q_{10}), which conveys the rate of change of soil respiration when the temperature is increased by 10 °C (Lloyd and Taylor 1994). The Q_{10} values are typically derived from laboratory incubation studies by fitting a model to measured CO_2 flux data. If the effect of plant material, such as roots, is removed, the flux measured is the heterotrophic respiration. The interpretation of Q_{10} is not always straightforward, and differing results have been reported in the literature (Gillabel et al. 2010). Quite often the higher Q_{10} values have been connected to more recalcitrant material and lower values to labile material (Conant et

al. 2008; Vanhala et al. 2007; Waldrop and Firestone 2004). This interpretation is in line with the kinetic theory: a more complex compound requires more activation energy to break down than a simpler compound (Davidson and Janssens 2006). This is, however, challenged by the metabolic theory, which states that the temperature sensitivity is not dependent on OM quality itself, but rather on the sensitivity of microbial metabolism to the temperature (Yvon-Durocher et al. 2012).

Many studies have found the Q_{10} values to increase with depth in soil profiles (Fierer et al. 2003; Jin et al. 2008; Lomander et al. 1998), with deeper soil profiles usually thought to contain older, more resistant SOM. Yet, some studies have observed a decrease in Q_{10} with depth or no change at all (Leifeld and Fuhrer 2005; Rey et al. 2008; Winkler et al. 1996). In addition to variations between ecosystems, the differing results might be caused by different methods used in laboratory experiments. Another reason might be that factor other than the recalcitrance of SOM is affecting Q_{10}. A study by Gillabel et al. (2010) proposed that Q_{10} values can be decreased by the physical protection of SOM by soil particles, meaning that the magnitude of Q_{10} of a recalcitrant SOM is masked by the effect of physical protection. This kind of protection would occur especially in silt and clay soils (Gillabel et al. 2010). The magnitude of Q_{10} could also be affected by microbes: since microbial biomass and composition vary along the soil profile (Blume et al. 2002; Fritze et al. 2000), microbes in the deeper soil may have lower thermal optima than those in the surface soil (Fierer et al. 2003). In addition, substrate availability may decrease with depth (Jobbágy and Jackson 2001).

Chemical fractionation is a method that enables separation of different SOM pools, or fractions, based on the solubility of SOM in different solvents (Abbott et al. 2016; Berg and Ekbohm 1991; Mikutta et al. 2005). The method of Berg and Ekbohm (1991) is based on extracting the soluble material with water, ethanol and sulphuric acid and allows the separation of SOM to four pools: water soluble (sugars, low levels of fatty acids and protein remains), ethanol soluble waxes and fats, acid soluble (hemicellulose, cellulose) and insoluble fraction (lignin and humified material) (Berg and McClaugherty. 2008; Berg and Ekbohm 1991; Trofymow 1998).

SOM is a variable combination of different compounds from simple, small structures to complex aromatic polymers, such as lignin. Traditionally these can be classified into different groups: 1. simple compounds of sugars, amino acids, 2. humic substances which are complex and varying group of polydispersed materials: plant lignin and products, polysaccharides, melanin, cutin, proteins, lipids, nucleic acids and fine char particles (Fisher 1995; "What are humic substances" 2007). The different substances have their inherent decomposition rates and may be divided from fast to slow as follows: sugars, starches, simple proteins, crude proteins, hemicellulose, cellulose, fats, waxes, resins and lignins (Osman 2013). SOM decomposition rates in different ecosystems have been studied with soil decomposition models, including Yasso (Liski et al. 2005) and Century (Parton et al. 1983), both of which divide SOM into pools with different decomposition rates. In Yasso model, the pools are named as extractives (decomposition rate in conifer needle 0.48 $year^{-1}$), celluloses (0.30 $year^{-1}$), lignin-like materials (0.22 $year^{-1}$), humus 1 (0.012 $year^{-1}$) and humus 2 (0.0012 $year^{-1}$) (Liski et al. 2005). The Century model, on the other hand, divides the pools into active (turnover of months to a few years), slow (20-50 years) and stable (400-2000 years) (Metherell et al. 1993). The different SOM pools relating to these could roughly be thought to be sugars (active pool), fats, waxes and cellulose (slow pool) and lignin (stable pool) (Bot and Benites 2005; Kutsch et al. 2009).

SOM fractionation aims to separate the different SOM fractions into different pools much like the soil C models and although the pools in models and SOM chemical fractions are not quite directly comparable, the basis is the same. From the soil C models it can be seen that the decomposition rates of different SOM pools have a vast range and give some indication on how long the different SOM fractions might take to decompose. For example, the water-soluble SOM, consisting of low molecular weight, simple compounds would belong to the fastest cycling pool, whereas lignin-like, high molecular weight and complex materials would persist for a long time as slow-cycling/stable pool.

1.2 Post-fire greenhouse gas emissions

Soil GHG fluxes are measured with either automatic or manual chambers. In the case of CO_2, the measured flux corresponds to total soil respiration ($R_a + R_h$). The changes in GHG fluxes are very much dependent on the severity of fire and through this the quality of decomposing SOM and microbial activity (Holden et al. 2016; Knicker 2007). As the GHG fluxes are also greatly dependent on soil temperature and moisture conditions, disturbances affecting these will also alter the GHG fluxes (Hashimoto et al. 2011).

Forest fires, in general, have been observed to have a negative effect on soil CO_2 effluxes (Burke et al. 2004; Köster et al. 2016; Morishita et al. 2015), although also at least temporary increases after fire have been observed (Burke et al. 2004; Muñoz-Rojas et al. 2016). The decreased CO_2 emissions from soils post-fire have been attributed to decreased root respiration and microbial activity (Kim and Tanaka 2003; Morishita et al. 2015; O'Neill et al. 2006), while increases have been connected to increased soil temperatures (O'Neill et al. 1997). Additionally, the parts of soil respiration originating from different sources may cause even more varying results. The two different components of soil respiration, heterotrophic and autotrophic respiration, can behave in different ways (increase or decrease) after fire and thus the changes in the soil respiration could be dependent on the source of the respiration (Hu et al. 2017).

Autotrophic respiration may follow post-fire forest regeneration so that it peaks decades after the fire (Gower et al. 2001), while heterotrophic respiration can reach its maximum fairly shortly after fire when the soil is warmer and fire residues are present (Litvak et al. 2003; Wang et al. 2002). As noted by Hu et al. (2017) the majority of the decrease has been linked to decreased autotrophic respiration, while the decrease in heterotrophic respiration in their study was found to be much milder. The released amount of CO_2 from heterotrophic respiration is connected to microbial C use efficiency (CUE), i.e. how effectively the microbes assimilate C (Rutigliano et al. 2007). This is measured by CUE or qCO_2 (Pinzari et al. 2017; Rutigliano et al. 2007). CUE is determined as a ratio between C allocated to growth and C uptake (Spohn et al. 2016), while qCO_2 is the respiration rate per microbial biomass C (Anderson and Domsch 1993). Furthermore, the qCO_2 value is the opposite of CUE: when CUE is high, qCO_2 is low and the microbial growth is efficient, with only low amounts of C being released as respiration (Manzoni et al. 2012; Rutigliano et al. 2007). Studies have reported increased qCO_2 values after burning (Fritze et al. 1993; Rutigliano et al. 2007) and thus qCO2 has been seen as an indicator of stress in the soil (Anderson and Domsch 1993). The reason for this is suggested to be pioneer microbial species having high respiration rates (Pietikäinen and Fritze 1995).

CH_4 is another of the three GHGs possibly affected by fire. Boreal forests are usually sinks for CH_4, unless the area is governed by waterlogged conditions (Kulmala et al. 2014).

This sink ability may even be enhanced after fire for a short period of time before returning to the original levels (Kulmala et al. 2014; Taş et al. 2014), which has been connected to a fast recovery of the microbial community post-fire (Hamman et al., 2007; Kulmala et al., 2014). For example, Morishita et al. (2015) found that fire driven changes led to increased temperature in the soil, which then increased the activity level of methanotrophs. Hence, the CH_4 fluxes are dependent on soil temperature and moisture, time since last fire and the availability of soil C (Poth et al., 1995; Sullivan et al., 2011). Sometimes permafrost soils have also been noted to become sources of CH_4 because of permafrost thaw (Kim and Tanaka, 2003). Permafrost soils are often prone to CH_4 production, as the soils may be waterlogged due to permafrost surface that restricts drainage (Schuur et al. 2015), further reinforced by permafrost thaw (Wei et al. 2018). Therefore, the CH_4 stored and produced in permafrost peatlands and soils has raised concerns about permafrost thaw resulting in positive feedback to climate warming via increased CH_4 emissions (Christensen et al. 2004; Smith et al. 2004; Wei et al. 2018).

N_2O, the third GHG discussed here, differs from the two others as it is produced both in aerobic and anaerobic conditions, these pathways being nitrification and denitrification, respectively (Megonigal et al. 2003; Oertel et al. 2016). Previous studies have observed decreased trends in post-fire N_2O fluxes (Kim and Tanaka 2003; Morishita et al. 2015), although also increased fluxes have been reported (Karhu et al. 2015). As denitrification and nitrification are both processes governed by soil temperature and moisture, the effects of fire also on N_2O fluxes probably take place partly due to post-fire changes in soil temperature and moisture conditions (Morishita et al. 2015). In addition to these also pH and mineral N concentrations have been observed to affect the N_2O fluxes after fire (Karhu et al. 2015).

1.3 Fire and soil isotopic composition

Separate parts of plants, plant species and soil depths can have different isotopic compositions. These compositions originate from many different processes that often favour one isotope over the other, typically the lighter isotope in favour of the heavier one (Farquhar et al. 1989). This kind of discrimination leads to enrichment of source material with heavier isotopes and depletion of the product caused by the reaction rate: a heavy isotope requires more energy to complete the reaction than a light isotope (O'Leary 1988; Davidson and Janssens 2006). Soils, for example, often have increasing (less negative) $^{13}C/^{12}C$ values with depth (Boström et al. 2007). Different processes, one of which is the Suess effect (Diochon and Kellman 2008), may cause such enrichment. The depletion of atmospheric CO_2 of ^{13}C with the burning of depleted fossil fuels (the Suess effect) (Balesdent et al. 1990; Trolier et al. 1996) may appear as deeper soil layers having similar ^{13}C values as the atmosphere at the corresponding time (Ehleringer et al. 2000).

For N, one of the reasons for varying soil $^{15}N/^{14}N$ values may be that ammonification, nitrification and denitrification favour the lighter isotopes, forming depleted NO_3^-, NH_4^+ and N_2O, while leftover material is enriched with ^{15}N (Girona-García et al. 2018). Hence, the material that is comparably enriched with a heavier isotope may be thought to be more recalcitrant as it has been processed further or is a residual of some process. The enrichment of heavier isotopes in the soil might also evolve from changes in species composition of N fixing fungal species since the discrimination against ^{15}N is also affected by the type of mycorrhiza (Michelsen et al. 1998). The ^{15}N values could also be affected by root activity (Pumpanen et al. 2017).

Forest fires have been observed to change both ^{15}N and ^{13}C signatures in the soil, but even though fires have been observed mainly to cause enrichment with ^{15}N, the pattern for ^{13}C enrichment/depletion is not as clear (Beuning and Scott 2002; Boeckx et al. 2005; Högberg 1997; Hyodo et al. 2013). During a fire, organic C and N are lost both from growing vegetation and the soil organic layer. This leads to two types of factors taking place: material that is perhaps depleted with isotopes is lost in fire (Högberg 1997), while enriched material is being formed due to volatilization of lighter isotopes (Saito et al. 2007; Boeckx et al. 2005; Cook 2001) or nitrification processes (Pardo et al. 2002). Also, increased leaching after fire causes loss of ^{15}N-depleted NO_3^- (Pardo et al. 2002). As different compounds have their specific $^{13}C/^{12}C$ (or $^{15}N/^{14}N$) ratios, the isotopic composition of post-fire litter depends on what kind of material is lost. For example, polysaccharides (such as cellulose) and amino acids tend to be enriched compared with lignin and lipids (Loader et al. 2003; Rumpel and Kögel-Knabner 2011). Thus, fire might cause relative depletion of ^{13}C, as cellulose is lost more than lipids and lignin. Contrastingly, post-fire litter may also have higher $\delta^{13}C$ values than pre-fire litter (Alexis et al. 2010).

2 OBJECTIVES

The aim of this thesis was to study how forest fires on permafrost soils, and the interaction of fire and permafrost thaw, affect the quality and changes in SOM pools and GHG emissions from the soil. In addition, the aim was to determine the factors most affecting the aforementioned variables. The objectives of the sub-studies were:

- To examine how the effects of fire change the proportions of recalcitrant and labile fractions of SOM and how they change with forest succession. The aim was also to determine the most important factors affecting the size of the most recalcitrant SOM fraction (Study I)
- To determine the heterotrophic respiration and SOM quality and how they change with time since fire (Study II)
- To determine how forest fires affect the GHG emissions and how they change with time after fire, including what the most important factors affecting the fluxes are in Canadian permafrost region (Study III)
- To determine how forest fires affect the GHG emissions and how they change with time after fire, including what the most important factors affecting the fluxes are in the Siberian permafrost region (Study IV)

The hypothesis related to each separate study were as follows:

- Study I: I hypothesized that the effects of fire would be evident on the proportions of different SOM chemical fractions, since fire can simultaneously decrease the total amount of SOM and produce recalcitrant SOM from burning vegetation and heat-induced chemical transformation. These changes would be observable in the chronosequence, with the proportional amount of recalcitrant SOM decreasing with time since fire. The effects of fire could also be seen in the ^{15}N and ^{13}C isotopic composition of SOM as found by previous studies (Beuning and Scott, 2002; Hyodo et al., 2013; Rumpel et al., 2007).

- Study II: I expected forest fire to decrease R_h and affect the Q_{10} of SOM with the fire-induced decreases in the quality of SOM. In addition, I hypothesized that the qCO_2 of microbes would increase as found by previous studies (Fritze et al., 1993; Rutigliano et al., 2007).

- Study III: We hypothesized that the GHG fluxes would change due to fire, and these changes would correlate with the active layer depth and time since fire. We also expected that the most significant changes would be seen in CO_2 and CH_4, rather than N_2O. This is because sparse N availability and generally low fluxes of N_2O from boreal permafrost soils.

- Study IV: We expected the fluxes of CO_2 and CH_4 to be apparent with fire related permafrost thaw, again correlating with time since fire. The fluxes would also positively correlate with the depth of the active layer and the changes in the magnitudes of the fluxes would follow the recovery of vegetation.

3 METHODS

3.1 Study design

All studied areas had the same study design. The study areas were located in permafrost underlain boreal forest regions of Canada (Studies I, II, III, Fig. 3) and Siberia (Study IV, Fig. 4). In both places, fire chronosequences were formed by choosing forests with similar site conditions, but burned at different times. The unmanaged burned forests included to the fire chronosequence were chosen based on GIS-maps of burned areas (Studies I, II and III) and tree ages that we further determined from cored tree rings. In Study IV the areas were selected based on forest inventory data with recordings of time and area of fire and satellite images. The same hierarchical sampling method was applied in all study areas: sampling lines were divided into three plots and samples were collected from these plots. The sampling method is described in more detail in the following chapter.

3.1.1 Canadian sites

The study areas were set along the Dempster Highway (Fig. 3) in the vicinity of Eagle Plains (66º22' N, 136º43' W) and Tsiigethchic (67º26' N, 133º 45'W). These forest areas formed a fire chronosequence of forest stands with fire 3, 25, 46 and over 100 years ago. These areas are hereafter referred to as $FIRE_3$, $FIRE_{25}$, $FIRE_{46}$ and $FIRE_{100}$ as they are in publications I and II (in publication III they are referred to areas burned 3, 25, 46 or over 100 years ago). In each of the $FIRE_3$, $FIRE_{25}$ and $FIRE_{46}$ areas three lines were established (150 m apart from each other) with three sampling plots (400 m^2 each)per line (50 m from each other). In total there were 9 sampling plots per forest stand (fire chronosequence). One soil pit was excavated in the middle of each plot, from which the soil samples were collected for Study I, Study II and Study IV. The soil samples were collected with a steel corer from the vertical face of the pit. In the vicinity of each of the three fire areas, one line was established in a forest stand

with no fire for at least the last 100 years ($FIRE_{100}$), so that these sampling lines ($FIRE_{100A}$, $FIRE_{100B}$ and $FIRE_{100C}$ in Fig. 3) together also totaled to nine sampling plots forming the $FIRE_{100}$ year area used in the analysis. The sampling scheme for the $FIRE_{100}$ area was set like this to represent a geographically balanced composition of old forests. All areas were chosen so that they represented as similar ecosystems as possible in terms of terrain, vegetation, precipitation and soil characteristics.

The ecosystems in our Canadian sites are characterized by underlying continuous permafrost and thus the soils are classified into belonging to the Cryosols (IUSS Working Group WRB 2014). The soil texture was silty clay loam. The climate in this area is predominantly cold continental with mean annual temperature of -8°C and annual precipitation of 248 mm (Environment Canada 2009). The area belongs to the taiga, which is dominated by evergreen conifers *Picea mariana* (Mill.) BSP and *Picea glauca* (Moench) Voss. The ground vegetation consists of mosses, lichens and dwarf shrubs, such as *Sphagnum* sp., *Cladonia* sp., *Cladina* sp., *Vaccinium vitis-idaea* L., *Rhododendron groelandicum* Oeder., *Rubus chamaermorus* L. and *Vaccinium uliginosum* L (Meikle and Waterreus, 2008). Stand characteristics were measured in sample plots, including ground vegetation biomass, cover and species composition, living and dead tree biomasses and densities, as well as tree height, crown height and crown diameter.

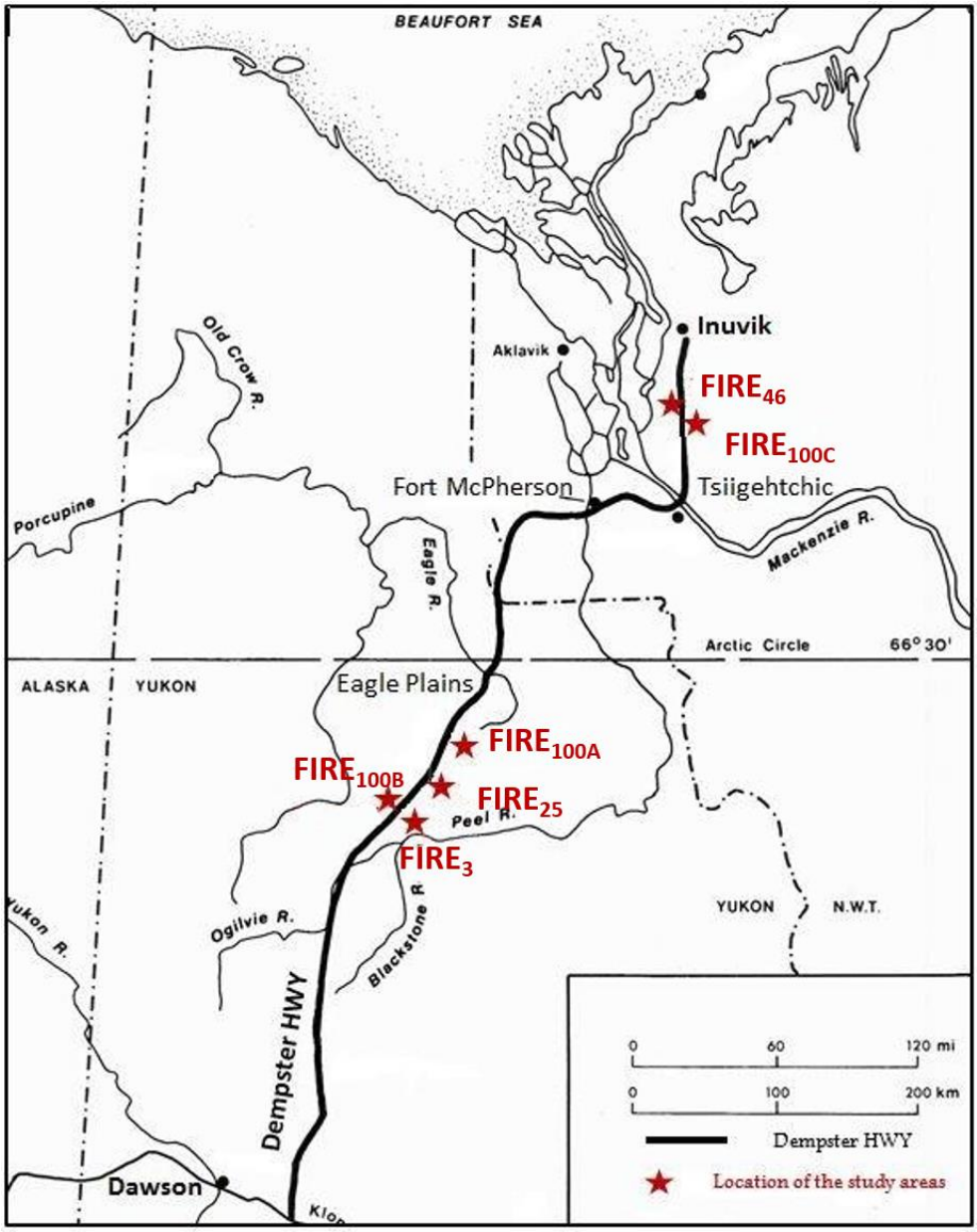

Figure 3: The locations of sampled fire areas along the Dempster Highway in the Northwest Territories of Canada in Studies I, II and III (modified based on Köster et al. (2017).

3.1.2 Siberian sites

The study areas were situated in the vicinity of Tura (Fig. 4), set in the Evenkiyski district of Krasnoyarsk Kray in the Russian Federation (64º16' N, 100º 13' E). Forest areas chosen for the study lie within the basin of the Nizhnyaya Tunguska and Kochechum rivers. The area is governed by cold continental climate, with an annual mean temperature of -9.5ºC and a mean annual precipitation of 250-390 mm (kharuk et al. 2011; prokushkin et al. 2006). soils area

characterized by a noticeable proportion of gravel with low or medium clay content (Prokushkin et al. 2006) and belong to the permafrost-affected taiga soils. These soils are dominated by cryozems and podburs, as well as shallow permafrost (Startsev et al. 2017).

Trees in the forest areas were mostly larch (*Larix gmelinii* Rupr.) with occasional birch (*Betula pubescens* Ehrh.), spruce (*Picea obovata* Ledeb.) and shrub alder (*Duschekia fruticose* Rupr.). The ground vegetation was formed by dwarf shrubs (such as *Ledum palustre* L., *Vaccinium vitis-idaea* L., *Vaccinium uliginosum* L.), mosses (*Pleurozium schreberi* (Brid.), *Aulacomnium palustre* (Hedw.) Schwaegr.) with some lichens (*Cladina* spp. and *Cetraria* spp.).

The study areas in Siberia formed a fire chronosequence that followed the same hierarchical sampling method as described previously with three different aged forest fire areas consisting of three sampling lines each (n=9) and adjacent lines in forest areas with no fire in the last 100 years. The chosen forest areas had burned 1, 23 and 56 years before sampling. The fire areas in this thesis are hereafter referred to $FIRE_1$, $FIRE_{23}$, $FIRE_{56}$ and $FIRE_{100}$ for uniformity. The same stand, vegetation and soil characteristics were measured from the plots as in Canada and the soil sampling also followed the same methods. The following stand characteristics were measured from the sample plots: ground vegetation biomass, coverage, species composition, and living and dead tree biomass, including tree species composition.

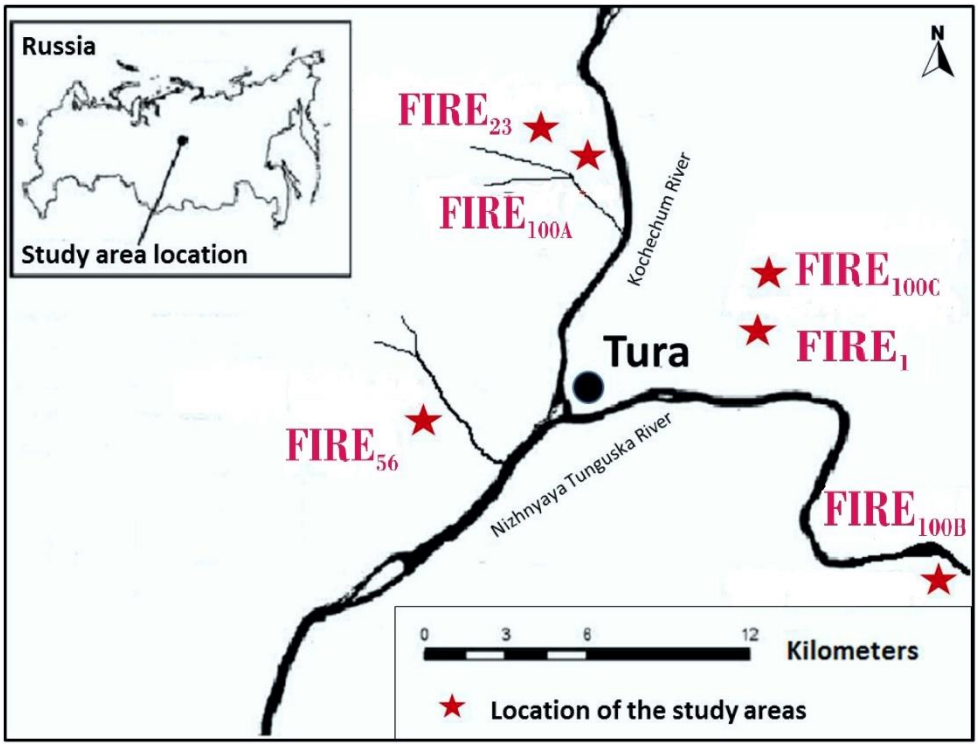

Figure 4: Locations of sampled fire areas (Study VI) along Nizhnyaya Tunguska and Kochechum Rivers, northern Central Siberian Plateau in Russia (modified based on Köster et al. 2018).

3.2 Soil characteristics

Soil pH and electrical conductivity were measured from a soil-water solution (1:2.5 soil to ultrapure water ratio) with glass electrode (Standard pH meter, Radiometer Analytical, Lyon France) and electric conductivity meter (JENWAY 4010 Conductivity, TER Calibration, Wigan, UK). Soil dry weights were determined by drying the samples at 105 ˚C. Soil organic content was further analysed at the loss on ignition test at 550˚C for 3 h in a furnace. Also soil C and N contents were measured from sieved (2 mm) and ground (mechanic ball grinder) soil samples with an Elementar analyser (Variomax CN elemental analyser, Elementar Analysensysteme, Germany). In addition, soil particle sizes were determined from sieved and dried samples with laser diffraction (LS 230, Beckman Coulter, USA).

3.3 Soil organic matter fractionation

There are several methods, both physical and chemical for extraction of different SOM fractions. Physical fractionation is based on the density analyses and particle size, whereas chemical fractionation separates different SOM fractions based on their solubility to solvents (von Lützow et al. 2008). In study I we used a chemical fractionation method by Berg and Ekbohm (1991) and Karhu et al. (2010) by extracting SOM to water, ethanol and sulphuric acid. Soil samples (from depths 5, 30 and 50 cm) were air dried at 40°C and sieved through a 2 mm sieve. The water and ethanol soil solutions were sonicated in an ultrasonic bath for 90 min and filtered through glass crucibles and dried at 105°C to constant weight and the water/ethanol soluble fraction was detected as mass loss in the sample. The sulphuric acid soil solutions were also placed in the ultrasonic bath for 1h and then autoclaved at 125°C for 1h before drying and weighing. Mineral soils were centrifuged instead of being filtered through crucibles due to fine soil material.

3.4 Determination of Q_{10}

Soil temperature sensitivity was determined with laboratory incubation of soil samples collected from 5, 10 and 30 cm depths. The aim (Study II) was to compare the differences of the two youngest fire areas with the oldest. The incubation was performed in a climatic chamber (WEISS WK11 340, Weiss Klimatechnik, Germany) at 1, 9, 19 and 19°C, for 24h at each temperature following the method of Riikonen et al. (2017). Before incubation, visible roots were removed from the soil samples and around 25 ml of sample was inserted in a 100 ml glass bottle capped with a rubber stopper. Empty bottles were used as blanks. Before closing, the bottles were flushed with technical air (Technical air 320020, AGA, Finland). The flushing was performed after every change of temperature. Samples were collected through the rubber stopper with a 60 ml syringe (BD Plastipak 60, BOC Ohmeda, Helsingborg, Sweden) and inserted into 12 ml vials (Soda glass Labco Exetainer®, Labco limited, UK). Sample CO_2 concentrations were analysed with a gas chromatographer (Agilent Gas Chromatograph 7890A Agilent Technologies, USA). R_h was expressed as μgCO_2 per gram of soil C. Q_{10} was acquired from a fitting made to the soil respiration data with Python (Python Software Foundation, version 2.7).

$$R_h = R_{ref} Q_{10}^{\frac{T-T_{ref}}{10}} \quad (1)$$

where R_h is the measured heterotrophic respiration rate (μgCO_2 g C^{-1} h^{-1}) at different temperatures T (°C), and R_{ref} is the reference respiration at the reference temperature T_{ref}.

3.5 Measuring greenhouse gas fluxes

Both Studies III and IV focused on GHG fluxes from the soil after a forest fire and hence very similar measurements were performed. For the GHG measurements of Studies III and IV, 18 metal collars were inserted into each forest chronosequence. The gases were measured from these with a cylindrical, aluminium foil covered chamber equipped with a small fan to circulate the air. In Study III the CO_2 flux was measured with non-dispersive infrared probe (GMP343, Vaisala, Helsinki, Finland) at 5 s intervals for 4 min. The chamber was placed in position for 5 min, but the first 30 s were excluded from the measurements due to possible disruptions caused by the setting up of the chamber. The CH_4 and N_2O fluxes were measured from the same chamber by taking sample from the chamber headspace with a syringe at 0 min (at chamber placement) and after 1, 5, 10 and 20 min. Soil temperature (with temperature probe P300W, Dostmann Electronic GmbH, Germany) and moisture (with soil moisture sensors: Thetaprobe ML2x and ML3, Delta-T Devices Ltd, Cambridge, UK connected to HH2 moisture meter, Delta-T Devices Ltd., Cambridge, UK) were also measured from 0.1 m depth during the chamber measurement.

In Study IV the CO_2 and CH_4 fluxes were measured from samples taken with a syringe from the chamber headspace. The first gas sample was taken before placing the chamber (at 0 min) and the following samples were taken at 1, 5, 10 and 20 min after the placement of chamber and inserted into glass vials. In both studies the gas samples were later analysed with a gas chromatograph (Study III: Agulent 7890A, Agilent Technologies, USA) and Study IV (Agilent 6890 N, Agilent Technologies Inc., USA). A six-point standard curve was used to analyse the samples (Pihlatie et al., 2013).

3.6 Statistical methods (Studies I, II, III, IV)

A linear mixed model (LMM) was used in all studies. LMM is a statistical model including both fixed and random effects often used for data sets that might have nonindependence in the data. The analyses were performed either with R (R version 3.3.2) (Studies I, III and IV) or SPSS (Study II) (SPSS Statistics 24.0 IBM Corporation, Armonk, New York, USA). The SOM fractions, heterotrophic soil respirations and temperature sensitivities were compared with the LMM between years of fire (or soil depths) with multiple comparison (Bonferroni/Tukeys) using the sampling line as a random factor to account for possible dependency of sampling areas on each other. All data was checked for normality with the Shapiro-Wilk test. The GHG gas fluxes (Studies III and IV) between fire areas were compared with ANOVA followed by Tukey's honestly significant difference test.

LMM was also used in the studies to compare explanatory factors to find the best describing model. This was done by using Akaike's information criteria (Akaike, 2011), AIC value with drop1 function (Chambers and Hastie, 1992) in R ("lme4" package (Bates et al., 2015). The dependent factor was, depending on the study, either SOM fraction, Q_{10}, R_{ref} or

GHG. These were explained by fixed factors, such as time since fire, active layer depth, biomass, pH etc.

4 RESULTS

Studies from both Canada and Russia have shown that forest fire increases the active layer depth and the recovery of the permafrost to its original state takes several decades. The thickest active layers were observed in the areas with most recent fire occurrences and the shallowest in the areas with no fire in the last 100 years (Table 1). In both Canadian and Siberian fire chronosequences, the organic layer thickness was reduced in the youngest fire areas compared with the older areas (Fig.5). Consequently, also the soil temperatures followed the same trend, with highest soil temperatures measured in the most recent fire areas and lowest temperatures in the oldest areas. This same trend was also followed by the measured soil moisture, with soil moisture increasing with time since fire. In Study III, the pH was found to be lowest in the most recent fire areas, but in Study IV there were no clear differences. Both studies, however, showed that vegetation cover was dependent on the time since fire, as could be expected.

Table 1*:* Mean soil pH, active layer thickness (m), soil temperature (C) and soil moisture at 10 cm depth from all measurement areas.

Area	Depth (cm)	pH	Active layer thickness (m)	Soil temperature (ºC)	Soil moisture (%) at 10 cm depth
Canada					
FIRE$_3$	5	4.5	1.01	7.2	37.2
	30	5.2		4.0	
	50			2.5	
FIRE$_{25}$	5	4.8	0.88	7.1	40.3
	30	5.3		3.6	
	50			3.5	
FIRE$_{46}$	5	6.6	0.49	8.9	49.1
	30	7.0		2.8	
	50			1.1	
FIRE$_{100}$	5	4.7	0.28	6.9	54.9
	30	5.6		-0.1	
	50			0.0	
Siberia					
FIRE$_1$	5	5.8	1.01	16.0	23.6
	30	6.3		12.0	
	50			10.1	
FIRE$_{23}$	5	5.7	0.88	8.0	36.1
	30	6.5		3.3	
	50			2.6	
FIRE$_{56}$	5	5.1	0.49	9.9	30.4
	30	6.1		2.3	
	50			0.9	
FIRE$_{100}$	5	5.5	0.28	11.3	40.1
	30	6.5		0.8	
	50			0.1	

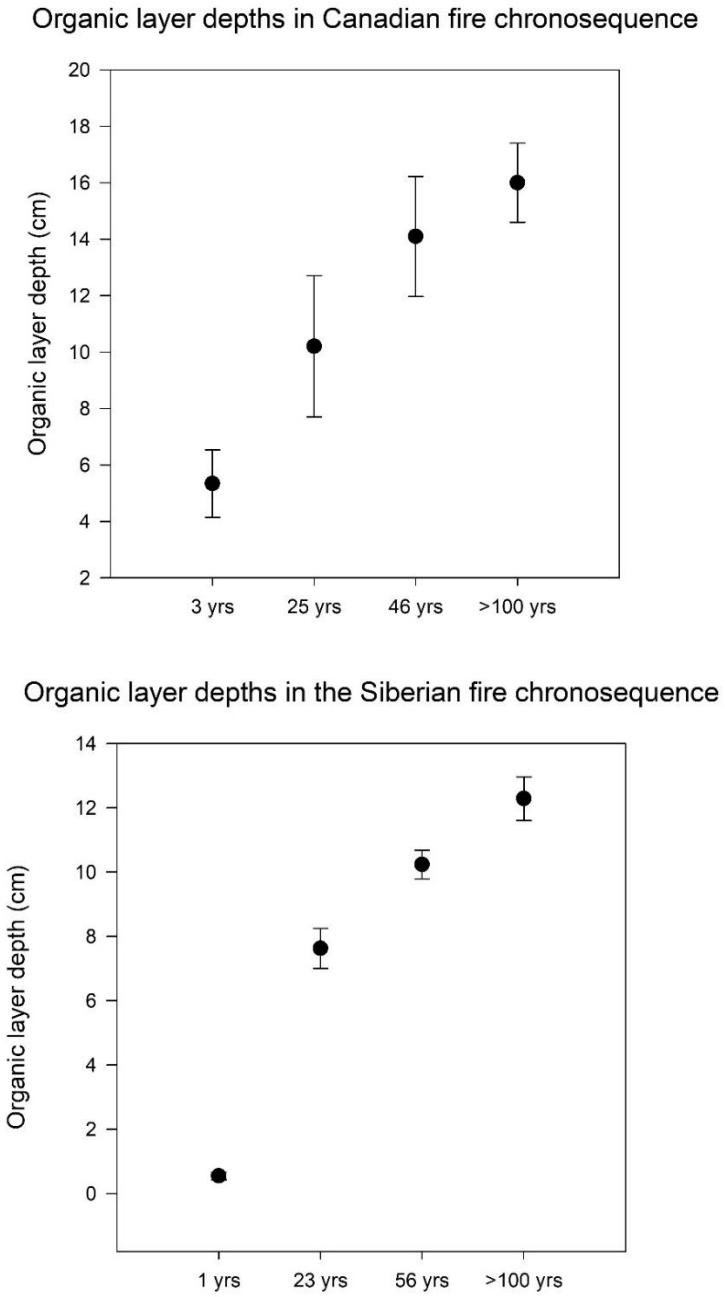

Figure 5: Soil organic layer depths (cm) in the fire chronosequences in the measurement areas in Canada and Siberia. The error bars represent the standard errors.

4.1 Soil organic matter chemical fractions and soil isotopic composition

The different soil depths showed differing distribution of SOM (Study I) with fractions at 5 cm depth having much larger soluble fraction sizes (65 %) compared with the insoluble fraction (35 %) (Fig. 6). At the 30 cm and 50 cm depth the soluble fractions together only totaled 16-18 % of SOM, while the insoluble fraction totaled to 82-84 %. The most noticeable changes in the fractions with time since fire were observed in the water- and ethanol soluble fractions at the 5 cm depth. However, at the 30 and 50 cm depths, the effects of fire were not nearly as clear.

In the water-soluble fraction sizes (at 5 cm depth) the $FIRE_3$ and $FIRE_{100}$ area did not differ from each other, but both $FIRE_{25}$ and $FIRE_{46}$ had significantly higher water-soluble fractions ($P<0.05$) than FIRE3. In the ethanol soluble fractions, both $FIRE_3$ and $FIRE_{25}$ had smaller fraction sizes than $FIRE_{46}$ and $FIRE_{100}$ ($P<0.001$). There were no significant differences between the acid- and insoluble fractions. At the 30 cm depth, the main differences were that $FIRE_{100}$ had a higher fraction of ethanol soluble material than $FIRE_3$ and $FIRE_{25}$ ($P<0.05$) and both $FIRE_3$ and $FIRE_{100}$ had larger acid soluble fractions than $FIRE_{25}$ and $FIRE_{46}$ ($P<0.001$). In addition, $FIRE_{25}$ had a higher insoluble fraction than any other area. Finally, at the 50 cm depth (permafrost depth for $FIRE_{46}$ and $FIRE_{100}$) the only notable difference was $FIRE_{46}$ having a higher fraction of ethanol soluble material than any other area.

Also, the bulk soil isotopic compositions ($\delta\ ^{15}N$ and $\delta\ ^{13}C$) showed some age-related differences (Fig. 7 and Fig. 8). The $\delta^{15}N$-values in the $FIRE_3$ area were enriched compared with $FIRE_{100}$ ($P<0.05$) at 5 cm soil depth and the same trend was observed at the 30 cm depth ($P=0.06$). At the 50 cm soil depth, there were no significant differences as was also the case between soil depths within each age class. The $\delta\ ^{13}C$-values showed a similar pattern to $\delta\ ^{15}N$ with $FIRE_3$ and $FIRE_{25}$ being enriched compared with $FIRE_{100}$ and $FIRE_{46}$ in the 5 cm soil depth ($P<0.05$). This was not the case at the deeper soil depths, where in general there were no significant differences. Yet, there was a depthwise enrichment with the 5 cm soil depth being more depleted of ^{13}C than the 30 and 50 cm depths ($P<0.001$).

The LMM revealed that the changes in the size of the insoluble SOM fraction were best described (at 5 cm soil depth) by active layer depth and biomass. These explained 22% of the variation. For 30 cm soil depth the best predictors were biomass and the C:N ratio, explaining 85%, while at 50 cm depth the best explanatory factor was the C:N ratio, which explained 10%. The changes in microbial biomass C were best described by the size of the insoluble SOM fraction at the 5 and 30 cm depths, explaining 27 and 97% of the variation, respectively. At 50 cm depth, none of the models were significant, thus failing to explain variations in microbial C.

Sensitivity analyses conducted on the best models for insoluble SOM showed that a 10% change in active layer depth or biomass resulted in a 1.5-2.0% change in the SOM fraction size (5 cm soil depth). For the 30 cm soil depth changing the factors in the best model (biomass and C:N ratio) lead to a 0.1-0.6% change in the size of the insoluble SOM fraction. Both aforementioned models were slightly more sensitive to changes in biomass. A 10% change in the C:N ratio at 50 cm soil depth caused a 1.2% change in insoluble SOM.

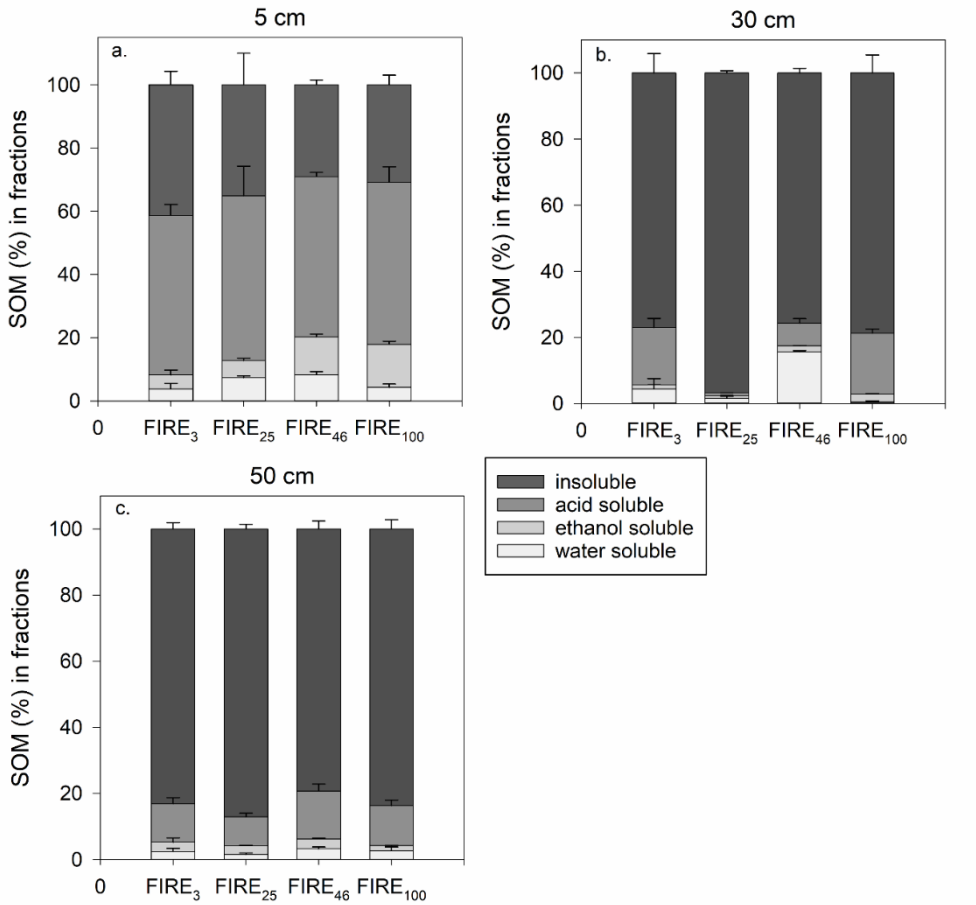

Figure 6: Chemical fractions of SOM from the 5, 30 and 50 sampling depths, presented as percentage of total SOM (Study I). The error bars show standard errors of mean (Aaltonen et al., 2019a).

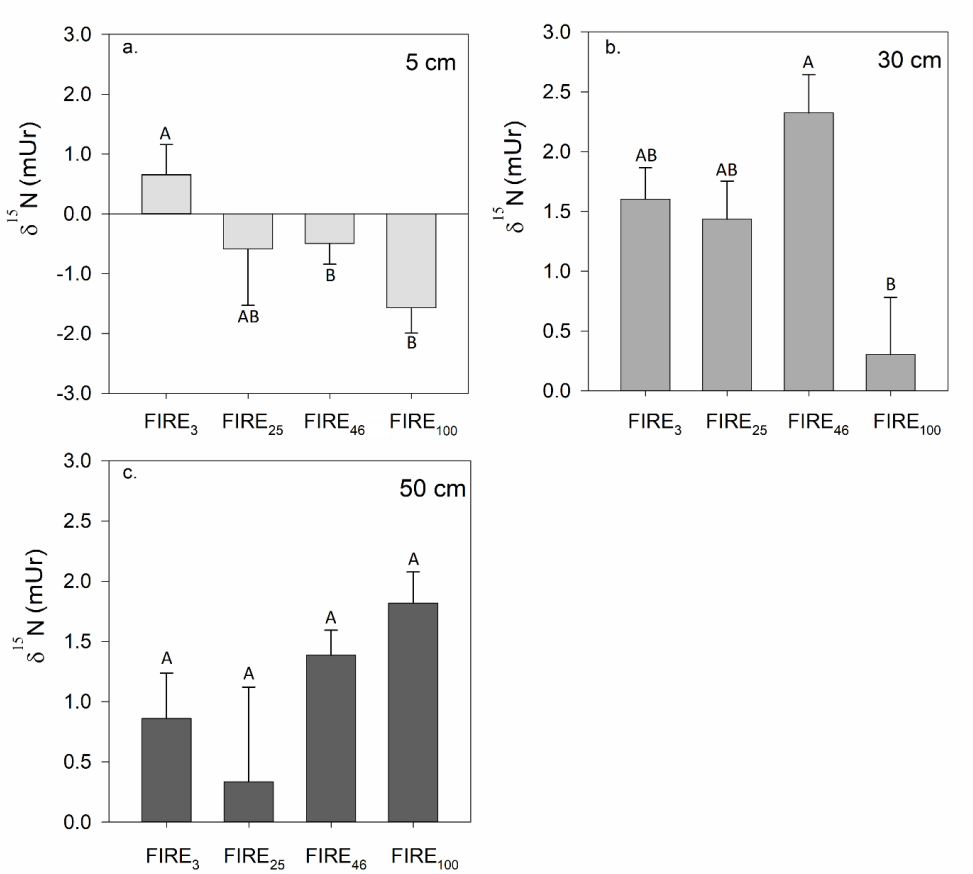

Figure 7: Natural $\delta^{15}N$-values of bulk soil samples at 5, 30 and 50 cm depths from each fire area (Study I). The letters denote significant differences between age classes and error bars represent standard errors (Aaltonen et al., 2019a).

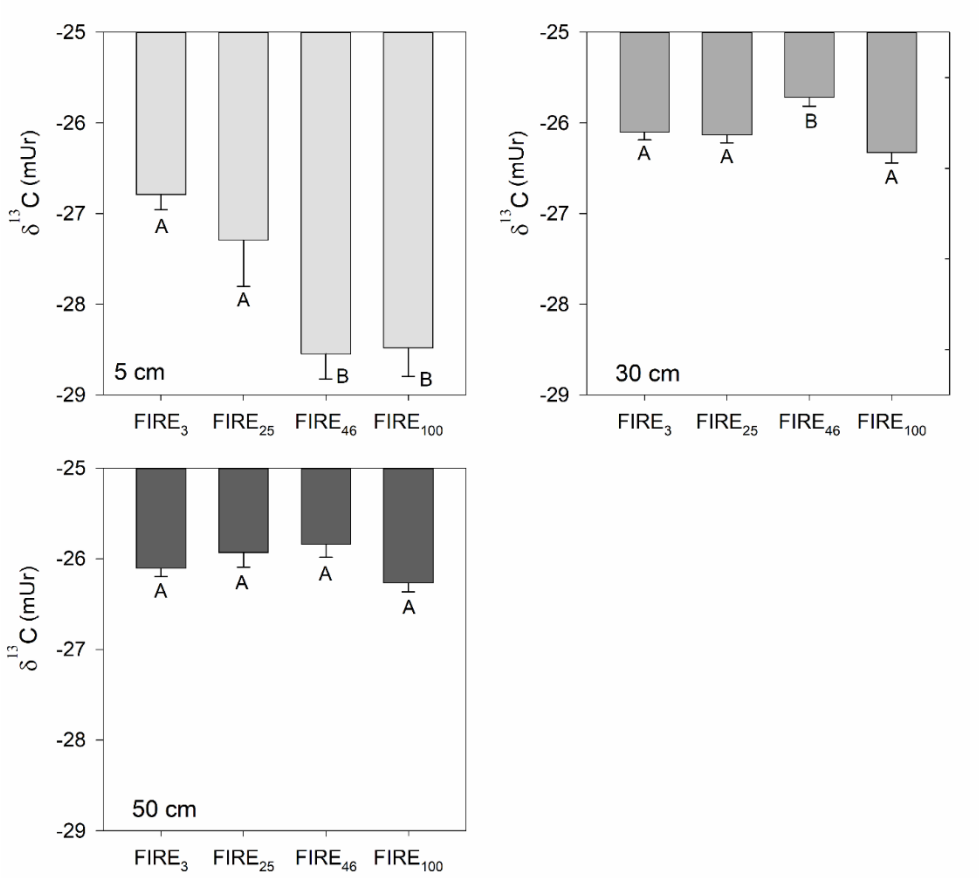

Figure 8: Natural $\delta^{13}C$-values of bulk soil samples at 5, 30 and 50 cm depths from each fire area (Study I). The letters denote significant differences between age classes and error bars represent standard errors (Aaltonen et al., 2019a).

4.2 Temperature sensitivity of soil heterotrophic respiration and microbial efficiency

The Q_{10} values (Study II) showed differences both in time since fire and soil depth (Fig. 9). In area $FIRE_3$, Q_{10} was higher at all three soil depths than in area $FIRE_{100}$. While both the $FIRE_{25}$ and $FIRE_{100}$ areas demonstrated decreasing Q_{10} with depth, $FIRE_3$ showed a different kind of trend which all the three depths had similar Q_{10}. In area $FIRE_{100}$ the 30 cm depth was at permafrost depth, thus indicating also the temperature sensitivity of permafrost SOM. Fire seemed to have no significant effect on the heterotrophic respiration rates between fire ages. However, in all fire areas, the heterotrophic soil respiration decreased with depth.

Based on the LMM the Q_{10} values were best described by soil depth and ground vegetation biomass, which together explained 43% of the variation in Q_{10}. The Q_{10} values decreased with increasing soil depth and ground vegetation biomass. R_{ref}, on the other hand, was best explained (54%) by microbial biomass C, soil depth and the active layer depth. The microbial biomass C increased with increasing $R_{ref,}$ while R_{ref} decreased with increasing soil and active layer depths.

Fire increased the qCO_2 in (Fig. 10) area $FIRE_3$ compared with older fire areas. The difference was found to be significant in the 5 cm soil samples in all incubation temperatures except 13°C, while at 10 cm depth the differences were significant at all temperatures. Furthermore, at 30 cm depth the qCO_2 of area $FIRE_3$ was significantly higher at 1 and 7°C, but not at 13 and 19°C. In addition, there were no differences between areas $FIRE_{25}$ and $FIRE_{100}$ in any temperatures or sampling depths.

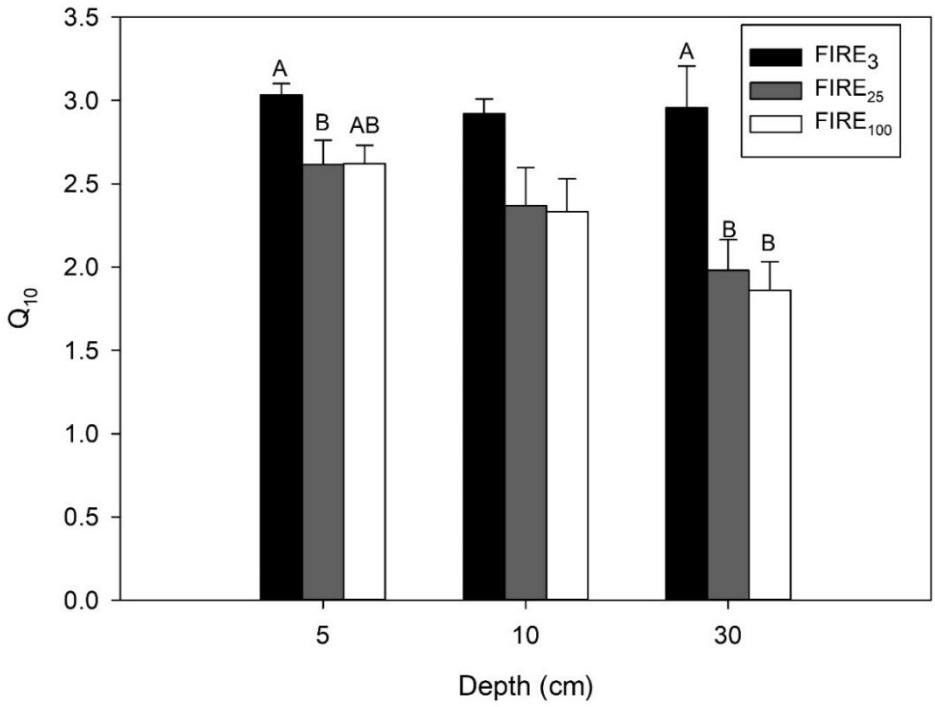

Figure 9: Mean (±SE) soil temperature sensitivities (Q_{10}) of samples from 5, 10 and 30 cm depths. Within a given group (between fire areas), bars with the same uppercase letter at their top do not differ statistically (Study II). If no letters are given, no significant differences were detected (Aaltonen et al., 2019b).

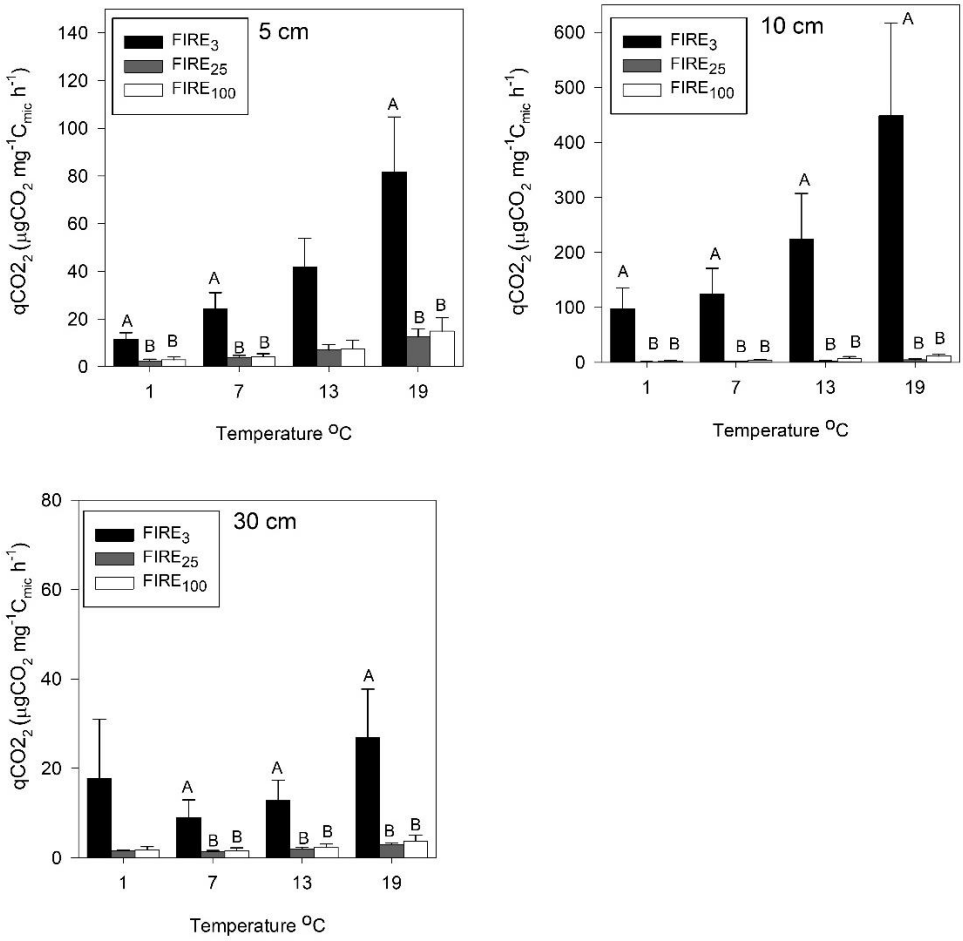

Figure 10: The metabolic quotient qCO_2 of fire areas in the soil depths of 5, 10 and 50 cm (Study II). Within a given group (between fire areas), bars with the same uppercase letter at their top do not differ statistically with error bars showing the standard errors. If no letters are given, no significant differences were detected (Aaltonen et al., 2019b).

4.3 Greenhouse gas fluxes in Canadian fire chronosequence

In the Canadian study areas (Study III), the CO_2 fluxes from the soil were decreased after fire with $FIRE_3$ having significantly lower fluxes than the rest of the fire areas (Fig. 11). The flux increased later, so that $FIRE_{25}$ and $FIRE_{46}$ had higher flux rates than $FIRE_{100}$. These would indicate that the CO_2 emissions reach the original levels within 50 years after fire. Based on the LMM the variation in CO_2 emissions was mainly caused by time since fire, which explained 50 % of the variation.

All fire areas were sinks for CH_4 and showed a slight increase in uptake after fire, but the only distinct difference was observed in area $FIRE_{25,}$ where the uptake was significantly greater than in other areas. The CH_4 fluxes were best predicted by the time since the last fire, the active layer depth and the tree biomass, explaining 33% of the variation. Furthermore, all the fire areas were sources of N_2O and a trend of decreasing efflux was observed after the fire. However, the decrease was statistically significant only in $FIRE_{25}$. The variation in N_2O was best expressed by the soil temperature, active layer depth and interaction between these two factors. They explained 30 % of the variation.

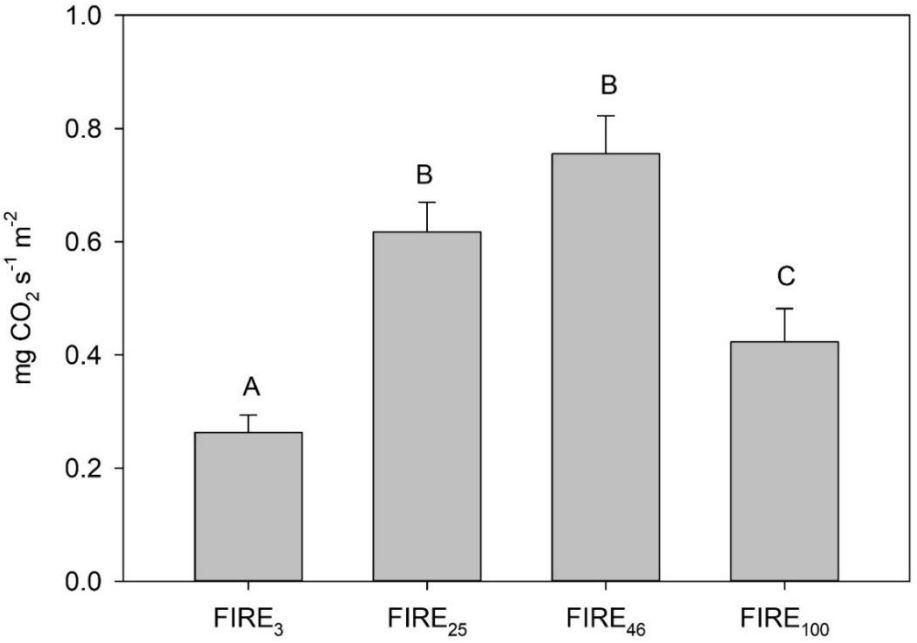

Figure 11: Averages of soil carbon dioxide fluxes of the Canadian fire chronosequence in Study III. Error bars represent standard errors, with letters indicating statistical differences (modified based on Köster et al. 2017).

4.4 Greenhouse gas fluxes in Siberian fire chronosequence

The measured CO_2 fluxes showed (Study IV), that all fire areas were sources of CO_2, but the emissions were reduced significantly after fire such that the $FIRE_1$ area had lowest and the $FIRE_{56}$ area highest emissions (Fig. 12). The CO_2 flux rates again increased after initial reduce. Therefore, it appeared that the CO_2 fluxes return to the original levels within approximately 50 years post-fire. The LMM showed that the CO_2 fluxes were best predicted by the pH of the top 5 cm of soil and the biomasses of birch, alder and vascular plant ground vegetation. This model explained 62 % of the changes in CO_2 fluxes. The effect of time since fire was tested separately and it explained 13 % of the variation.

In contrast to CO_2, all areas were found to be sinks of CH_4. On average area $FIRE_1$ was the largest CH_4 sink, while $FIRE_{56}$ was the lowest. These differences were not significant. Also, time since fire had no significant effect on the CH_4 fluxes, explaining a mere 0.6% of the variation in the CH_4 flux. Further analysis showed that CH_4 was best predicted by the pH of the mineral soil and the ground vegetation biomass of vascular plants, which together explained 23% of the variation. However, this model was not significant.

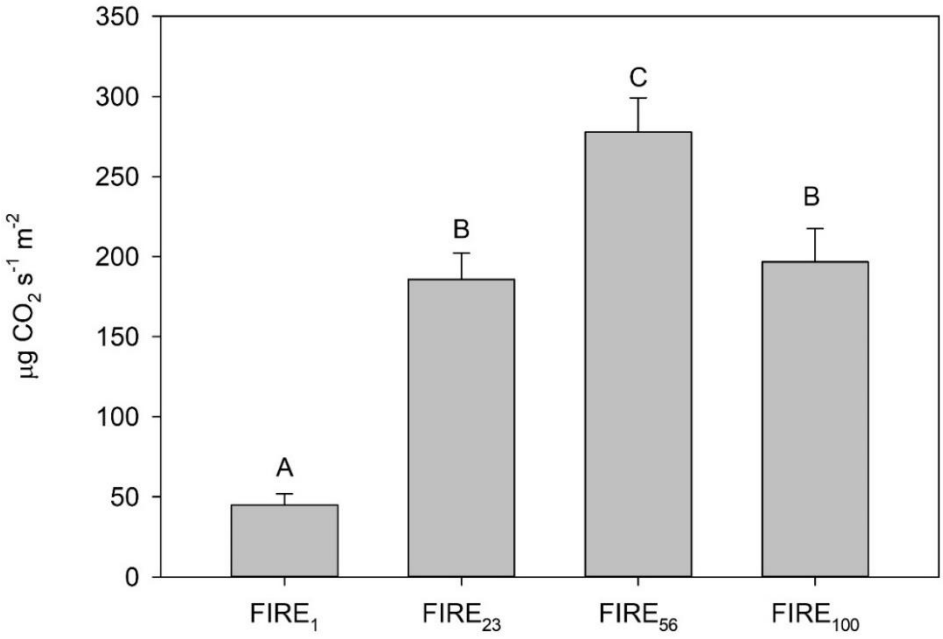

Figure 12: Averages of soil carbon dioxide fluxes of the Siberian fire chronosequence in Study IV. Error bars represent standard errors, with letters indicating statistical differences (modified from Köster et al. 2018).

5 DISCUSSION

The number of studies concerning wildfires and permafrost soils is increasing, as the topic is gaining more interest among the scientific community. Several separate studies have emerged in the recent couple years showing the timeliness of the topic in a changing climate (e.g. Ludwig et al. 2018; Potter and Hugny 2018). In this thesis, the effects fire on SOM quality were studied comprehensively with laboratory- and field measurements. The novelty of the thesis lies in the combination of methods that provide a comprehensive picture of long-term C dynamics through a forest fire chronosequence study. The decadal effects of forest fires, especially on permafrost soils, on SOM quality and GHG fluxes are still not well known, even though their importance in the global climate change scenario.

Forest fires have been observed to increase the active layer depth and reduce the organic layer thickness (Jafarov et al. 2013; Swanson 1996; Taş et al. 2014), as was also seen in the studies in this thesis. When fire frequency increases, the ability of forests to store C and the degree of permafrost recovery decrease (Hoy et al. 2016). Furthermore, survival and recovery of permafrost after fire are not only dependent on fire interval and intensity, but also the soil type and terrain (Jafarov et al. 2013; Swanson 1996). The permafrost of upland mineral soils with thin organic layers has been found to be vulnerable to forest fire more than the lowland soils with thicker organic layers (Jafarov et al. 2013). The permafrost thaw in the upland mineral soils studied in this thesis is a consequence of stand-replacing, severe fire that decreased the organic layer thickness, thus weakening the insulation of underlying soil.

The overall effects of forest fires on soils seemed to be limited to the soil surface. This was consistent with other studies stating that the direct heat from fire rarely reaches below 10 cm into the soil (Campbell et al. 1995; DeBano 2000), which may be the reason most of the changes observed in both studies I and II were in soil surface. Changes in SOM fractions, soil isotopic composition and temperature sensitivity of SOM were most apparent in the soil surface in the Canadian fire chronosequence. Fire both decreased the proportional amount of the labile fraction and increased SOM temperature sensitivity. Both of these reverted towards the assumed original stage with succession. The higher Q_{10} values of the youngest fire area were supported by the decreased proportional fraction of labile SOM at the 5 cm sampling depth.

One of the post-fire factors affecting the soil GHG fluxes is the ratio in which material is turned to recalcitrant and contrastingly how much easily decomposable material is released to forest floor from partly burned vegetation. In Study I, fire decreased the quality of SOM at soil surface: the proportional sizes of the most soluble fractions at 5 cm soil depth were smaller after fire, but there were no similar changes in the two deeper soil layers. For the water- soluble fraction the middle-aged areas had relatively higher water-soluble fractions, while areas $FIRE_3$ and $FIRE_{100}$ did not differ significantly from each other. This might be related to succession dynamics: in both recently burned and old forest, there are sources of less decomposable material. In a recently burned forest there might be a high amount of pyrogenic C (González-Pérez et al. 2004; Wardle et al. 2008), while in older forest the incoming litter might be less easy to decompose, such as from shrubs that decompose relatively slowly (Nilsson and Wardle 2005). The presence of such species might be observed in the sizes of the ethanol-soluble fraction (fats and waxes). The areas $FIRE_3$ and $FIRE_{25}$ had proportionally smaller ethanol-soluble fractions than two older areas. In older forests there are shrubs and coniferous trees with significant amounts of waxes in their cuticles (Dickinson and Pugh, 1974), which later end up as part of the SOM. The observed fractions might also

be affected by pyrogenic C, some of which is possibly water-soluble (Norwood et al. 2013). Pyrogenic C may also be transferred down the soil profile (Dai et al. 2005). Apart from fire effects, the chemical fractionation also seemed to imply, that a large fraction of SOM in these mineral soils, in the active layer and permafrost surface, is recalcitrant and enriched with heavier isotopes.

Previous studies of permafrost SOM quality have found somewhat varying results, which is not surprising as the permafrost region is a mosaic of peatlands, tundra and taiga, and also the study methods have varied. Noticeable amounts of labile SOM have been reported in deep permafrost of Siberian yedoma and thermokarst deposits (Strauss et al. 2015). Permafrost soils of drained lake basins in Alaska were also observed to contain labile SOM (Mueller et al. 2015). When the SOM pools are divided into fast (decay of days to weeks), slow (decay of years to decades) and passive pools, the permafrost soils have been found to contain less than 10% fast-cycling C (of the total C content), with the rest being slow-cycling C (Knoblauch et al. 2013; Schädel et al. 2014). Furthermore, the study of De Baets et al. (2016) revealed permafrost SOM to be similar to that of the SOM in the active layer and less labile than SOM close to the soil surface. However, many of the permafrost related studies are located in tundra (De Baets et al. 2016; Mueller et al. 2015; Strauss et al. 2015) or peatland sites, with forest areas remaining less studied.

In Study I the LMM analysis revealed that the most resistant fraction size was best explained by active layer depth and biomass (at 5 cm soil depth) and the biomass and C:N ratio (30 cm soil depth). Biomass is lost in the fire and on the other hand gained with forest succession, resulting in changes in incoming litter quality (Brassard and Chen 2006), thus also affecting the quality of SOM. The C:N ratio is also linked to the SOM quality and through it to the composition of biomass. The effects of active layer depth are also related to biomass as it affects the rooting depth and rate of decomposition through soil temperature. The biomass and C:N ratio had a negative effect on the size of the insoluble SOM fraction, which seems natural. The model failed to significantly explain the variation at 50 cm soil depth, perhaps because of the presence of permafrost or high soil water content.

Forest fires have been observed to change soil isotopic composition in several ways (Boeckx et al. 2005; Cook 2000; Loader et al. 2003; Rumpel and Kögel-Knabner 2011). In Study I fire was observed to increase the $\delta^{15}N$ values in the youngest fire area compared with the oldest area, possibly caused by the loss of ^{15}N-depleted leaf and litter biomass during fire (Hobbie et al. 2000; Sah and Ilvesniemi 2007) or due to increased leaching of NO_3^- post-fire (Pardo et al. 2002). While volatilization of lighter isotopes (Boeckx et al. 2005; Cook 2001) and possible fire-affected changes in the N fixing fungal community may also play a part, these effects would probably be secondary. In the youngest fire area, the soil profile was throughout enriched with ^{15}N, while the older fire areas showed depleted values in the uppermost depth but enrichment in the two deeper sampling depths. Though these depth-wise trends were not significant, they indicate a pattern where after a fire the soil surface becomes enriched with ^{15}N but turns depleted with forest succession as the relatively depleted litter again collects on the forest floor. In contrast, the deeper soil remains constantly enriched due to SOM that has already been processed by microbes.

The observed effects of fire on soil ^{13}C values are somewhat differing (Beuning and Scott 2002; Hyodo et al. 2013; Alexis et al. 2010). In Study I the ^{13}C abundance was increased by fire: the two most recently burned fire areas had less depleted values in the surface soil than the two oldest fire areas. This could be related to different compounds in SOM having differing $^{13}C/^{12}C$ ratios. If post-fire litter contains less cellulose (relatively enriched with ^{13}C compared to lipids) than more depleted lipids, this could be seen in the $^{13}C/^{12}C$ ratios. In the

case of lipids, it is then possible to draw a connection between the soil isotopic composition and chemical fractions: the ^{13}C depleted older fire areas also had proportionally larger ethanol-soluble fractions. This fraction includes lipids, which as mentioned, are depleted compared with cellulose. Some studies have also suggested that the SOC ^{13}C is affected by the fungal to bacteria ratio: fungi might prefer ^{13}C depleted substrates such as lignin, while bacteria would prefer ^{13}C enriched, leading to microbial biomass having the ^{13}C values of the preferred substrate (Glaser and Amelung 2002; Kohl et al. 2015; Osono 2007). Fire indeed decreased the fungal to bacterial ratio in the Canadian study areas (Zhou et al. 2018), perhaps that way somewhat contributing to the enrichment of SOC with ^{13}C after fire via a proportional increase in the relatively ^{13}C enriched bacterial biomass.

Typically, the δ ^{13}C also varies along with the soil profile. In Study I, the enrichment with ^{13}C increased with soil depth, as has been found by previous studies (Balesdent et al. 1993; Boström et al. 2007; Brüggemann et al. 2011; Krull et al. 2002). This way, both the enrichment of deeper soils with ^{13}C and the proportionally high recalcitrant SOM fractions of deeper soil both indicate the presence of resistant SOM in these soil layers. The ^{13}C enrichment of a soil profile with depth can be caused by several different factors, such as the Suess effect (Ehleringer et al. 2000), microbial preference of substrates (Ehleringer et al. 2000; Kohl et al. 2015), microbial fractionation of isotopes or soil mixing (Ehleringer et al. 2000; Natelhoffer and Fry 1988).

Fresh and old SOM may mix in permafrost soils. The permafrost soils are prone to cryoturbation, where the organic layer may become mixed into the underlying mineral soil through freeze-thaw cycles (Čapek et al. 2015). This way the soil at the permafrost surface can also include pockets of easily degradable OM (Čapek et al. 2015), while uplifted older material can be found at the soil surface. On the other hand, the isotopic composition and recalcitrance of SOM, and therefore Q_{10}, might be affected by transport of material/compounds from the soil surface. For example, some forms of pyrogenic compounds can be leached (Norwood et al. 2013) and transported in water. Pyrogenic compounds may move along the soil profile, as found in Siberian permafrost tundra forest ecotone (Guggenberger et al. 2008). The permafrost soils in this area were found to be stores of black C (Guggenberger et al. 2008). However, while the SOM fractionation in Study I showed recalcitrant material in mineral subsoils (30 and 50 cm) to be the proportionally highest fraction, this was not seen in the Q_{10} values of $FIRE_{25}$ and $FIRE_{100}$, though higher Q_{10} values could be expected for such material based on the kinetic theory. One of the possible explanations is that the low Q_{10} values were actually caused by aggregate protection (Gillabel et al. 2010). In such cases the physical protection of SOM leads to lower temperature sensitivity than expected.

The reduced quality of SOM post-fire at the soil surface, among other factors, became apparent in the CO_2 fluxes from the forest floor. The Canadian and Siberian study areas showed similar behavior in GHG fluxes after fire: the CO_2 emissions clearly decreased shortly after fire, whereas CH_4 fluxes were changed only mildly and most areas were sinks, rather than sources. In Canadian sites, the CO_2 fluxes were mostly affected by time since fire, while in Siberia the flux was best explained by the pH of the top 5 cm of the soil, the biomass of the alder and birch trees, and the biomass of vascular plants in the ground vegetation. The differences in the explanatory factors arise at least from the following differences: The Canadian study areas were mostly dominated by a single tree species (Black spruce), while in Siberia the tree composition consisted of few species (but mainly larch). Also, in the Canadian sites the pH (5 cm soil depth) of younger areas was either lower ($FIRE_3$) or at the same level ($FIRE_{25}$) as in older fire areas. At the same time in Siberian areas both younger

fire areas had higher pH than the two older areas. The time since fire affected the CO_2 flux in both the Canadian and Siberian areas, but the effect of time seemed to be more pronounced in Canada. It must also be noted that after the initial decrease in CO_2 fluxes, they increased in the following decades, most likely due to the appearance of pioneer species and recovering OM layer thickness.

Although the CO_2 flux from the soil column decreased shortly after fire, this was not quite the case with the heterotrophic soil respiration. The heterotrophic soil respiration showed some decrease, but was not significantly reduced. This could be attributed to qCO_2 values being higher after fire, meaning that after fire the microbes respire relatively more of the C they acquire. There are at least two underlying reasons for the higher qCO_2 after fire: the pioneering microbial species might have higher respiration rates (Pietikäinen and Fritze 1995) or there are changes in the fungal to bacterial ratio in the soil. The fungal to bacterial ratio has been found to decrease after fire (Zhou et al. 2018) and fungi in general respond more strongly to fire than bacteria (Mataix-Solera et al. 2009). Fungi have lower qCO_2 (Sakamoto and Oba 1994) and hence qCO_2 has been found to decrease with higher fungal to bacterial ratio (Sakamoto and Oba 1994). A decreased fungal to bacteria ratio after fire has also been reported in a study from the same study areas (Zhou et al., 2018) as used in this thesis. qCO_2 is also dependent on the soil C:N ratio: soil microorganisms have been found to respire more C per microbial biomass C if they are degrading substrate that has a poor N content (Spohn 2015), which may well be the case in post-fire soils with pyrogenic material.

Several previous studies have reported increased CH_4 uptake in soils after fire (Burke et al. 1997; Kim and Tanaka 2003; Morishita et al. 2015; Song et al. 2017; Sullivan et al. 2011; Takakai et al. 2008). Consequently, the forest areas were slightly greater CH_4 sinks shortly after fire in both Studies III and IV, but the differences were not significant. The slightly increased CH_4 uptake after fire is probably linked to increased soil temperatures and decreased soil moisture, as also noted by other studies (Burke et al. 1997; Kim and Tanaka 2003; Morishita et al. 2015; Song et al. 2017). This has been explained by increased methanotroph activity in drier and warmer conditions of post-fire soils (Kim and Tanaka 2003; Morishita et al. 2015; Takakai et al. 2008). In Study III, time since fire, soil temperature, active layer depth and tree biomass together explained 33% of the variation in CH_4 uptake. The soil temperatures correlated positively with the CH_4 uptake of the soil, while the increased uptake in the youngest fire area was also accompanied by the lower soil moisture than the other areas. On the other hand, in Study IV (Siberia) the CH_4 flux did not appear to be affected by any of the measured factors, as the best model was not significant. This might be at least partly due to different vegetation and soil conditions in Canadian (silt loam) and Russian (gravel with low to medium clay content) sites. The different soil types would affect, for example, the soil water holding capacity and thermal conductivity.

Fire on permafrost soils may also increase soil CH_4 efflux due to increased soil temperatures causing permafrost thaw leading to release of CH_4 from permafrost (Kim and Tanaka 2003). The soil moisture conditions after fire are governed by permafrost thaw, increased evaporation caused by the increased soil temperatures (Bond-Lamberty et al. 2009) and on the other hand by reduced transpiration as the vegetation is at least partly burned. In waterlogged permafrost soil, the thawing ice may further advance the anoxic conditions (Wei et al. 2018). The fluxes might also be affected by the increased diffusion of gases caused by the higher soil temperatures (Kim and Tanaka 2003), although this increase would be quite small and possibly decreased if soil water content increases. However, in both studies III and IV the soil moisture was reduced after fire compared with older areas.

A study from boreal region in Alaska reported significant decreases in N_2O fluxes from soil post-fire (Kim and Tanaka 2003). Also the N_2O fluxes measured in Study III showed some, but not consistent decreases after fire. Moreover, almost all the measured factors seemed to contribute to the prediction of N_2O flux: soil temperature and moisture, active layer depth and tree biomass. Time since fire did not have a significant effect. The N_2O flux has been shown to respond positively to increased temperatures (Kim and Tanaka, 2003; Smith et al. 1998). Soil temperature, moisture and active layer depth together probably affected the N_2O flux rate by affecting the microbial activity, whereas tree biomass may affect the microbial community. The small N_2O fluxes observed in the youngest fire area may then be related to the soil moisture content: the decreased soil moisture content after fire might limit the denitrification process. At the same time higher soil temperatures post-fire are connected to decreased soil moisture (Kim and Tanaka, 2003) and the net effect of these is dependent on the decreases in soil moisture, whether or not it will become the limiting factor for microbial activity.

If N is released after fire and the soil moisture content is suitable for nitrification, the soil N_2O fluxes may increase short term as N_2O is formed from NO_3. For example, Gathany and Burke (2011) stated that increases in N_2O fluxes post-fire in Ponderosa pine forest were diminished within five years. In some soils, the N_2O fluxes have been observed to increase after fire as a consequence of increased availability of mineral N from ash, increased pH and less competition of N reserves as plants are killed (Karhu et al. 2015; Levine et al. 1988). On the other hand, the flux could be limited by the presence of burned material on soil: biochar has been observed to decrease N_2O emissions due to its effects on soil quality and N immobilization (Bai et al. 2015; He et al. 2017). Of the three measured GHGs fire had a significant effect on CO_2 fluxes, but only tendential impact on CH_4 and N_2O. The boreal forest soils have reasonably low CH_4 and N_2O fluxes to begin with (Pihlatie et al. 2007; Savage et al. 1997), although permafrost adds its own aspect to boreal soil of the permafrost region. Still, our results indicate that subarctic forest on upland mineral soils will not be sources of N_2O and CH_4 after fire, but might rather slightly increase their sink ability.

Forest fires increase the active layer depth, leading to permafrost thaw and reduced SOM quality at the soil surface. Consequently, decreased SOM quality and the effects of fire on soil microbes and vegetation bring about at least initial decreases in CO_2 fluxes from soil column post-fire. So far, the changes caused by the fire have reverted to pre-fire stages with forest succession, allowing the permafrost depth to reach its original levels and protect the SOM from further decomposition. However, the warming climate and increased fire frequency may change this. The contribution of previously frozen SOM to GHG fluxes has also been observed to depend much on the oxic/anoxic soil conditions (Estop-Aragonés et al. 2018). Therefore, oxic forest soils would produce more CO_2 from thawing permafrost SOM compared with anoxic wetland or peatlands.

6 CONCLUSIONS

Forest fires significantly affect the C cycle of northern boreal forests in permafrost regions. Fires decrease the CO_2 flux for decades due to loss and decreased quality of SOM and changes to microbial community. The elevated temperatures in the soil profile following fire and the increased active layer depth following permafrost thaw enhance the decomposition of OM stored in the soil. However, while permafrost thaw was apparent after fire, the permafrost stored SOM did not appear to be especially labile or temperature sensitive. These lead to a conclusion that the CO_2 emissions from upland mineral soils underlain by permafrost are limited after fire due to decreased quality of SOM after fire and the limited decomposability of permafrost SOM. As significant amounts of C are released during fire, the balance between these different factors accounts for the net CO_2 emissions from the soil. Nevertheless, the phenomena linked to wildfires and permafrost soil interactions are complicated and cause partly opposite results. Fire had only a tendential effect on the CH_4 and N_2O fluxes. Although the CO_2 fluxes from burned permafrost soils have received attention among the scientific community, studies focusing on N_2O and CH_4 are less abundant, despite the greater global warming potential of these gases (Lashof and Ahuja, 1990). The effects of fire are dependent also on the frequency of fire events in the future and the ability of forests to regenerate in the changing climate. Moreover, the subarctic and arctic permafrost region is a mosaic of tundra, peatlands and taiga forests, which cannot be fitted into the same mold. Thus, there is a demand for further studies investigating the specifics of these ecosystems and building a complete picture of these pieces to estimate total emissions from permafrost regions

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