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Temperature sensitivity of soil organic matter decomposition in boreal soils

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ABSTRACT

The temperature sensitivity of decomposition of different soil organic matter (SOM) fractions was studied with laboratory incubations using ^{13}C and ^{14}C isotopes to differentiate between SOM of different age. The quality of SOM and the functionality and composition of microbial communities in soils formed under different climatic conditions were also studied. Transferring of organic layers from a colder to a warmer climate was used to assess how changing climate, litter input and soil biology will affect soil respiration and its temperature sensitivity.

Together, these studies gave a consistent picture on how warming climate will affect the decomposition of different SOM fractions in Finnish forest soils: the most labile C was least temperature sensitive, indicating that it is utilized irrespective of temperature. The decomposition of intermediate C, with mean residence times from some years to decades, was found to be highly temperature sensitive. Even older, centennially cycling C was again less temperature sensitive, indicating that different stabilizing mechanisms were limiting its decomposition even at higher temperatures. Because the highly temperature sensitive, decadally cycling C, forms a major part of SOM stock in the organic layers of the studied forest soils, these results mean that these soils could lose more carbon during the coming years and decades than estimated earlier.

SOM decomposition in boreal forest soils is likely to increase more in response to climate warming, compared to temperate or tropical soils, also because the Q_{10} is temperature dependent. In the northern soils the warming will occur at a lower temperature range, where Q_{10} is higher, and a similar increase in temperature causes a higher relative increase in respiration rates. The Q_{10} at low temperatures was found to be inversely related to SOM quality. At higher temperatures respiration was increasingly limited by low substrate availability.

Keywords: soil respiration, carbon dioxide, Q_{10}, ^{13}C, ^{14}C, soil organic matter fractions

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Copenhagen, May 2010, Kristiina Karhu

LIST OF ORIGINAL ARTICLES

This thesis consists of an introductory review followed by six research articles. The articles in the review are referred to by their Roman numerals. The articles are reprinted with kind permission of the publishers.

I Vanhala, P., **Karhu, K.**, Tuomi, M., Sonninen, E., Jungner, H., Fritze, H & Liski, J. 2007. Old soil carbon is more temperature sensitive than young in an agricultural field. Soil Biology and Biochemistry 39: 2967-2970.
doi:10.1016/j.soilbio.2007.05.022

II Conen, F., **Karhu, K.**, Leifeld, J., Seth, B., Vanhala, P., Liski, J. & Alewell, C. 2008. Temperature sensitivity of young and old soil carbon – Same soil, slight differences in 13C natural abundance method, inconsistent results. Soil Biology and Biochemistry 40: 2703-2705.
doi:10.1016/j.soilbio.2008.07.004

III Vanhala, P., **Karhu, K.**, Tuomi, M., Björklöf, K., Fritze, H & Liski, J. 2008. Temperature sensitivity of soil organic matter decomposition in southern and northern areas of the boreal forest zone. Soil Biology and Biochemistry 40: 1758-1764.
doi:10.1016/j.soilbio.2008.02.021

IV **Karhu, K.**, Fritze, H., Hämäläinen, K., Vanhala, P., Jungner, H., Oinonen, M., Sonninen, E., Tuomi, M., Spetz, P., Kitunen, V. & Liski, J. 2010. Temperature sensitivity of soil carbon fractions in boreal forest soil. Ecology 91: 370-376.
doi:10.1016/j.soilbio.2007.05.022

V **Karhu, K.**, Fritze, H., Tuomi, M., Vanhala, P., Spetz, P., Kitunen, V. & Liski, J. 2010. Temperature sensitivity of organic matter decomposition in two boreal forest soil profiles. Soil Biology & Biochemistry 42: 72-82.
doi:10.1016/j.soilbio.2009.10.002

VI Vanhala, P., **Karhu, K.**, Tuomi, M., Björklöf, K., Fritze, H., Hyvärinen, H. & Liski, J. 2010. Transplantation of organic surface horizons of boreal soils into warmer regions alters microbiology but not the temperature sensitivity of decomposition. Global Change Biology (In press).
doi:10.1111/j.1365-2486.2009.02154.x

AUTHOR'S CONTRIBUTIONS

I alone am responsible for the summary of this thesis. I did most of the data analysis and interpretation of the results in Paper I, where the planning of the study and measurements had been already carried out by others. I had a major contribution to the discussion of the results and writing of Paper II. I was responsible for planning and conducting the laboratory analysis related to SOM fractionation in Papers III, IV and V. In Papers IV and V, I was the person mainly responsible for the writing of the article and I was the corresponding author in article V. I further developed the idea of Paper V on looking at the temperature sensitivity of SOM decomposition in relation to changing SOM quality, labile substrate availability and microbial community composition during the long-term laboratory incubation. In article VI, I conducted part of the statistical analyses, contributed to the discussion of the results and made figures to the article.

TABLE OF CONTENTS

LIST OF TERMS AND ABBREVIATIONS

AMS	accelerator mass spectrometry
ANOVA	analysis of variance
Biolog	analysis of carbon source utilization patterns by microbial communities
C	carbon
CO_2	carbon dioxide
C3 plant	a plant that utilizes the C_3 carbon pathway to fix CO_2 in photosynthesis
C4 plant	a plant that utilizes the C_4 carbon pathway to fix CO_2 in photosynthesis
$\delta^{13}C$	the ratio of the stable isotopes ^{13}C to ^{12}C in a sample, compared to an international standard
DOC	dissolved organic carbon
DCA	detrended correspondence analysis
MAT	mean annual temperature
MOM	mineral-associated organic matter
N	nitrogen
OM	organic matter
PCA	principal component analysis
PLFA	phospholipid fatty acid
pMC	percent modern carbon, an unit to express ^{14}C activity in a sample
POM	particulate organic matter
SOC	soil organic carbon
SOM	soil organic matter, SOC and SOM are used as synonyms
WHC	water holding capacity
soil respiration	the term refers to the sum of heterotrophic respiration (decomposition of litter and SOM by heterotrophic micro-organisms) and autotrophic respiration (root respiration). In this study, plant roots were always excluded when measuring soil respiration, so only heterotrophic respiration originating from decomposition of SOM was measured
k	rate constant, is independent of the concentrations of reactants but depends on the temperature. The concentration of reactants (raised to a power depending on the order of the reaction) multiplied by rate constant, gives the reaction rate of a reaction
r	reaction rate or decomposition rate. For first-order reactions, the rate of reaction is directly proportional to the concentration of the substrate S; $r = k[S]$. In soil carbon

	models SOC decomposition is assumed to follow first-order kinetics
Q_{10}	the proportional increase in soil respiration when temperature increases by 10 °C
R_0	respiration rate at 0 °C, the so-called basal respiration rate (can be calculated also in some other reference temperature than 0 °C)
MRT	mean residence time, or turnover time, is the average time that carbon resides in soil, in a SOM fraction or in a (conceptual) SOM pool
half-life	a time after which the activity of a sample has decayed to half of its original value, for example the half life of ^{14}C is 5730 years.
elementary reaction	a chemical reaction in which one or more of the chemical species react directly to form products in a single reaction step and with a single transition state

1 INTRODUCTION

Soils contain globally two to three times more carbon (C) than the atmosphere or terrestrial vegetation (Schlesinger 1977, Jobbagy and Jackson 2000), and the yearly flux of carbon dioxide (CO_2) from heterotrophic soil respiration to the atmosphere is almost 10 times larger than the CO_2 emitted from burning of fossil fuels (IPCC 2007). Therefore, even slight changes in the rate of soil organic carbon (SOC) decomposition can significantly affect the concentration of CO_2 in the atmosphere. Whether soils will amplify or retard climate warming will depend on the balance between increased plant growth (due to increased CO_2 concentrations and warming), and thus litter input into the soil, and increased SOC decomposition. It has been hypothesized, that SOC decomposition can be more temperature sensitive than net carbon fixation by plants, and increased CO_2 emissions from soils due to climate warming could exceed the increased CO_2 uptake of plants (Schimel et al. 1994, Kirschbaum 2000), leading to a positive feedback to climate change (Cox et al. 2000, Kirschbaum 2006).

Current global studies predict a positive feedback from the terrestrial ecosystems to climate change. Estimates on the magnitude of this effect range from 20 to 200 ppm increase in atmospheric CO_2 concentrations by 2100 (Friedlingstein et al. 2006). A recent observational study has estimated this feedback to be at the lower end of this range (Frank et al. 2010). However, the sensitivity of the carbon cycle feedbacks in a future warmer climate may not be the same as in the pre-industrial conditions investigated in the study. For example, there might be thresholds for boreal forest growth after which temperature does not increase tree growth, but growth may even start to decline (D'Arrigo et al. 2004). The uncertainty of the temperature sensitivity of SOC decomposition is a major contributor to this high variability in current estimates of terrestrial carbon balance (Cox et al. 2000, Friedlingstein et al. 2006).

Boreal forests are especially important in this picture, because they cover 16 million square km - 14.5% of the earth's land surface area (Gower et al. 2001) - and contain high concentrations of SOC compared to other terrestrial ecosystems (Raich and Schlesinger 1992). Approximately 24% of global terrestrial carbon is stored in the cool soils of tundra and boreal forests (Schlesinger 1977). Boreal forests are an important terrestrial carbon sink (Bolin et al. 2000, Liski et al. 2003), but the large C storage of these forest soils can also be especially vulnerable to climate warming. Thus, there is a risk of these ecosystems turning from carbon sinks to sources (Lindroth et al. 1998) when the climate warms. Climate warming is predicted to be most pronounced in northern regions (IPCC 2007). Therefore, the soil carbon pool residing in boreal forests will be subject to a proportionally larger warming impact compared to soils in temperate or tropical regions. Temperature is the most significant factor controlling soil organic matter (SOM) decomposition in boreal forest soils, although moisture and nutrient availability are also important (Eliasson 2005).

It has been suggested that much of the SOC in northern soils is available for the microbes to decompose and has been stored in the soil not because it is inherently too recalcitrant or stabilized with minerals, but rather because of the environmental conditions being sub-optimal for decomposition. This carbon could thus be lost when the climate warms (e.g. Trumbore 2000, Weintraub and Schimel 2003, Biasi et al. 2005). It is likely that the increase in temperatures has already increased decomposition and release of C as CO_2 to the atmosphere (Trumbore 2000) or as dissolved organic carbon (DOC) to streams and lakes (Porcal et al. 2009). In Finland, increased C losses are observed during wet and

warm autumns (Piao et al. 2008), because autumn warming increases respiration more than photosynthesis.

Soil C is not a homogeneous pool (Trumbore 2000), but consists of a continuum of thousands of different substances from simple sugars to complex humified molecules, with turnover rates ranging from days to millennia (Trumbore 1997). The picture is even more complicated by the protection of SOM from decomposition inside soil aggregates or through association with mineral surfaces. To simplify the situation, soil carbon models divide SOM into conceptual pools with different decomposition rates and thus different mean residence times (MRT) (e.g. Parton et al. 1987, Coleman and Jenkinson 1996, Liski et al. 2005). Current soil carbon models assume that all soil C pools have the same temperature sensitivity. Moreover, this temperature sensitivity is determined based on bulk soil respiration measurements (field measurements or short-term laboratory incubations) (Kirschbaum 1995), which only give information on the temperature sensitivity of the more labile fractions (Liski et al. 1999, Trumbore et al. 2000). This fast cycling C is a major source of CO_2 from soil respiration, but comprises only a small fraction of total soil C (Schimel et al. 1994, Trumbore 2000). Most soil carbon is decades or hundreds of years old (Trumbore 2000) and the long-term effect of climate warming on soil carbon stocks will be largely determined by the temperature sensitivity of this more recalcitrant fraction. The temperature sensitivity of this old carbon is less well known.

Based on chemical and enzyme kinetics, more complex, slowly decomposing recalcitrant compounds should have higher temperature sensitivities of decomposition (Bosatta and Ågren 1999, Davidson and Janssens 2006). This basic principle may be hampered by other environmental factors limiting decomposition (Davidson and Janssens 2006) and by the different magnitude of confounding factors affecting the results in different experimental studies (Kirschbaum 2006). The temperature sensitivity of the slowly decomposing fractions is difficult to study, because the signal from their decomposition is easily masked by the decomposition of more labile fractions that produce a large part of the CO_2 (Søe et al. 2004, Davidson and Janssens 2006). These are some of the probable reasons why results from empirical and modeling studies on the temperature sensitivity of different SOM fractions are still controversial. Results from these studies have been interpreted to show that recalcitrant C is either more (Knorr et al. 2005, Leifeld and Fuhrer 2005, Fierer et al. 2006), less (Liski et al. 1999, Giardina and Ryan 2000) or equally (Fang et al. 2005, Reichstein 2005) temperature sensitive compared to the labile C. Whether or not these pools have differing temperature sensitivities will greatly affect the magnitude and even sign of the feedback between soil carbon and climate change, and is thus a question of great importance. Information on the temperature sensitivity of decomposition of different SOM fractions is needed for improving soil carbon models, in order to achieve more accurate predictions of the effects of climate warming on soil carbon stocks and the ensuing feedback to the climate system. In addition to improving the ability to predict what will happen to the soil C storage when the climate warms, increased knowledge on soil C cycling can help manage soil C stocks to mitigate climate change.

2 OBJECTIVES

The overall aim of this thesis was to study how SOM quality affects the temperature sensitivity of its decomposition. In this study, SOM was conceptually divided into three pools (labile, intermediate and stabilized/humified pools) that are different in turnover time and quality. The turnover times of the labile, intermediate and stabilized/humus pools are from days to years, years to decades and decades to centuries (or even millennia), respectively (Parton et al. 1987, Trumbore et al. 1996, Torn et al. 1997, Trumbore 2000). The specific objectives in the sub-studies were:

- To quantify the temperature sensitivity of decomposition of labile vs. intermediate SOM pools (**Study I, Study II**)
- To quantify the temperature sensitivity of decomposition of labile, intermediate and humified/stabilized SOM pools (**Study IV**)
- To study how the temperature sensitivity of bulk soil CO_2 production is related to SOM quality and substrate availability (**Study V**)
- To study the effect of climate on the amounts of labile SOM fractions, microbial community composition and function, and temperature sensitivity of SOM decomposition. The aim was to find out how the prevailing climatic conditions have affected these factors (**Study III**), and how climate warming would change them (**Study VI**)

3 FACTORS AFFECTING SOIL ORGANIC MATTER DECOMPOSITION

3.1 General

Soil organic matter decomposition is controlled by temperature, moisture, chemical quality of litter, and composition and dynamics of decomposer communities (Swift 1979). The decomposability of SOM, determined by its chemical quality, is modified by several stabilization processes (Sollins et al. 1996). When microbes decompose SOM, they incorporate some of the C and N into their biomass (growth), some is released as CO_2, and some transformed into more complex and recalcitrant materials (by-products). Microbes preferentially decompose the more labile substrates (Sollins et al. 1996), which leads to the build-up of a pool of SOC consisting mainly of recalcitrant, slowly decomposing substances (Trumbore 2000). Radiocarbon measurements of respired CO_2 show that in the absence of labile C, also the older, more recalcitrant C can be decomposed (Dörr and Munnich 1986), although some recalcitrant C fractions (e.g. lignin) may be efficiently decomposed only when there is also labile C available as an energy source (Kirk et al. 1976).

Sollins et al. (1996) define degradation of SOM as depolymerization and oxidative processes, where relatively large molecules are converted into smaller, simpler molecules (carboxylic acids, amino acids, CO_2). Degradation outside the cells occurs via the activity

of extracellular enzymes, which microbes excrete into the soil (Allison 2006). This enzymatic degradation of larger molecules into smaller molecules, which can then be taken into the microbial cells, is considered to be the rate-limiting step for consumption of SOC (Allison 2006, Sinsabaugh 2008). Most of the decomposition reactions in soils are enzyme-mediated. Synthesis is the reverse process, where the simpler molecules become linked to form larger molecules (e.g. poly-saccharides, poly-aromatics). When synthesis occurs outside the microbial cells, it is called condensation (Sollins et al. 1996). It has been suggested that humic substances in soil are formed by condensation of small molecules (Leenheer and Rostad 2004). Most recalcitrant molecules in SOM are not plant structural compounds, even though they originate from plants, but compounds formed in the microbial decomposition processes in soil (Allison 2006).

3.2 The temperature sensitivity of SOM decomposition

Arrhenius and Michaelis-Menten kinetics

The temperature sensitivity of SOM decomposition is often described with a Q_{10} value, which is the factor by which the respiration rate (r) increases, when the temperature (T) increases by 10 °C:

$$Q_{10} = r(T+10)/r(T) \quad (1)$$

According to current knowledge the following factors affect the temperature sensitivity of SOM decomposition:

1) SOM stability,

2) substrate availability, which is determined by the balance between input of organic matter (e.g. leaf and root litter, root exudates), decomposition and stabilization of SOM,

3) the physiology, substrate utilization efficiency and temperature optima of soil microbes,

4) physicochemical controls of destabilization and stabilization processes (von Lützow and Kögel-Knabner 2009). Because of the complexity of the soil system and the large amount of factors possibly affecting the temperature sensitivity, there is no general theory that could be used to describe the temperature sensitivity of organic matter decomposition (Kirschbaum 2006).

In their review, Davidson and Janssens (2006) described the basic kinetic principles and environmental constraints, which can be used as a framework for studying SOM decomposition. The Arrhenius equation

$$k = Ae^{(-Ea/RT)} \quad (2)$$

, where k is the rate coefficient, R is the universal gas constant, T is the temperature (in Kelvin), E_a is the activation energy of the reaction and A is the so-called pre-exponential factor (Arrhenius 1889), describes the temperature sensitivity of elementary chemical reactions. If the reaction is first order with respect to the substrate concentration $[S]$, the reaction rate r is equal to $k[S]$. According to the Arrhenius equation, more complex, slowly

decomposing substrates with high activation energy (E_a) should have higher temperature sensitivity (Davidson and Janssens 2006). It also predicts that the Q_{10} is temperature sensitive itself, decreasing with increasing temperature. Davidson and Janssens (2006) call this temperature sensitivity determined by the molecular structure of the compounds and ambient temperature the "intrinsic temperature sensitivity". The Arrhenius equation applies for chemical elementary reactions, but also for enzymatic reactions when substrate availability is abundant. Enzyme-mediated reactions are not qualitatively different from any other catalytic chemical reactions. In enzymatic reactions, the enzyme is the catalyst decreasing the activation energy of the reaction, so that it can take place at ambient temperatures.

Michaelis-Menten kinetics can be used to describe enzymatic reactions in conditions of limiting substrate availability (Michaelis and Menten 1913):

$$r = V_{max} * [S]/(K_m + [S]) \quad (3)$$

Michaelis-Menten kinetics describes the rate of a decomposition reaction (r) as a function of substrate availability *[S]* at an active site of an enzyme. When plotted against *[S]* equation 3 gives a saturating curve. The maximum reaction rate at a given temperature (V_{max}) is reached, when all active sites of enzymes are bound to substrates. When substrate is abundant, the term K_m is insignificant. In the equation, the ratio of V_{max} to K_m is the rate coefficient (k) of the reaction. In soils, substrate availability is often low, and the term K_m (Michaelis constant or half-saturation constant, the enzyme concentration at which reaction rate is $V_{max}/2$) in the equation becomes significant. Since V_{max} increases with temperature, and also K_m of most enzymes increases with temperature (Davidson et al. 2006, Davidson and Janssens 2006), their temperature sensitivities can neutralize each other, causing low apparent Q_{10} values at low substrate concentrations (Davidson et al. 2006, Davidson and Janssens 2006). Davidson and Janssens (2006) call the observed Q_{10} in conditions where environmental constraints limit decomposition the "apparent Q_{10}", and state that basically all these constraints (e.g. physical or chemical protection, drought, flooding or freezing), act by decreasing substrate concentrations at active sites of the enzymes.

Arrhenius kinetics applies for chemical elementary reactions, and also the Michaelis-Menten kinetics is limited only to very simple situations, assuming constant enzyme concentrations. So, even these two combined may not always describe soil respiration (Davidson and Janssens 2006). The measured CO_2 production is a sum of innumerable different decomposition reactions, each with different activation energies (E_a) and thus different Arrhenius - type rate expressions. Therefore, the Arrhenius equation may not represent the best fit to any measured respiration data, and for modeling soil respiration, empirical models that best fit the data have to be used instead (Kirschbaum 2000, Tuomi et al. 2008).

Despite their limitations in modeling soil respiration, the basic principles of Arrhenius and Michaelis-Menten kinetics probably still apply also for complex soil environments. According to Bosatta and Ågren (1999), the quality of the soil organic matter can be defined as the total number of enzymatic steps required to mineralize carbon to the end product CO_2. For the decomposition of complex substrates, more reaction steps (and more different enzymes) are needed than for simpler substrates. Thus, there are more possible rate limiting steps (Bosatta and Ågren 1999), and the effective activation energy (obtained e.g. by fitting the reaction rate to the Arrhenius equation) is likely to be higher. Therefore,

decomposition of SOM of lower quality should have higher temperature sensitivity, as long as other factors are not limiting decomposition (Davidson and Janssens 2006).

Comparison of empirical models

Although it has been known for a long time that Q_{10} is not constant, but decreases with temperature, and is near 2 only over a limited temperature range (see studies reviewed in Lloyd and Taylor 1994, Atkin and Tjoelker 2003, Davidson and Janssens 2006), the exponential model (van't Hoff 1898) is still often used in many applications to model soil respiration rate (r) due to its simplicity. The model

$$r = ae^{(bT)} \quad (4)$$

, where the coeffient a (often named R_0) is the respiration rate at 0 °C and b is the temperature dependence coefficient, gives a constant Q_{10} ($Q_{10} = e^{(10*b)}$). Note that here the pre-exponential term already includes the concentration of decomposing substrates, while the pre-exponential factor A in the Arrhenius equation is independent of concentration. Furthermore, while the temperature in the Arrhenius equation has to be given in Kelvin, T in equations 4 and 5 is often given in Celsius. At a limited temperature range, the Arrhenius equation produces fits that are very similar to the exponential model, but both models are inadequate especially at low temperatures (Lloyd and Taylor 1994). At the southern border of the boreal forest zone, soil temperature in the mineral soil is most of the time below 10 °C also during the growing season (e.g. Pumpanen et al. 2008), and when studying these soils it is thus important to use a function that can well describe soil respiration at lower temperatures. Based on the knowledge of generally temperature dependent Q_{10} (e.g. Tjoelker et al. 2001), models allowing the Q_{10} to vary with temperature are preferable. Different authors have compared models describing the temperature sensitivity of soil respiration (e.g. Lloyd and Taylor 1994, Tuomi et al. 2008). Tuomi et al. (2008) found that the Gaussian model

$$r = ae^{(bT+cT^2)} \quad (5)$$

, was better in describing the temperature sensitivity of soil respiration than the other often used models, and this model is thus used in many of the sub-studies of this thesis (**Study III, V, VI**). In the model, where $a > 0$, $b > 0$ and $c < 0$, are fitter parameters, a is the respiration rate at 0 °C and b and c are the temperature dependence parameters. In addition to producing best possible fit to the data, without being over-parameterized, one criterion for a goodness of a model is its biological meaningfulness. The Gaussian model can well describe the faster increase in soil respiration at low temperatures and also settling down towards an optimum temperature and decline after it, which makes it biologically meaningful, although the model parameters do not have a direct biological or chemical meaning like the parameters of the Arrhenius equation. In this thesis, temperature dependent Q_{10} curves were calculated based on the fitted parameters of the Gaussian model

(**Study III, V, VI**). This serves the purpose of showing that Q_{10} is temperature-dependent itself, but using still the familiar concept of Q_{10} values.

3.3 Mechanisms of SOM stabilization

Soil organic matter can be stabilized in soil, so that its decomposition is limited and the temperature sensitivity of its decomposition differs from the intrinsic temperature sensitivity determined by its chemical structure (Davidson and Janssens 2006). In addition to effects of low temperature, low O_2 and too high or low moisture contents, which Trumbore (2009) calls climatic stabilization, there are different theories or explanations for why some part of SOM is not decomposed, and accumulates in soil. Sollins et al. (1996) divides the stabilizing mechanisms into three groups: changes in recalcitrance, interactions or accessibility. In other words, SOM can become biochemically, chemically or physically protected during the decomposition process in soil (Six et al. 2002).

Some compounds are long-lived in soils due to their intrinsic recalcitrance, for example black carbon (Preston and Schmidt 2006) and some lipid compounds (Mikutta et al. 2006). More recalcitrant compounds are formed during the decomposition process, i.e. SOM can become biochemically stabilized (Six et al. 2002, Allison 2006). It is possible, that the quality of SOM is so poor, that its decomposition does not produce enough energy for microbial growth (Allison 2006). On the other hand, microbes may not decompose the most recalcitrant substrates to get energy, but they are cometabolically decomposed at the same time when labile substrates are decomposed (Kirk et al. 1976). Thus, limited labile substrate or nutrient availability especially in deeper soil layers may be the reason for preservation of SOM (Fontaine et al. 2007), because it limits the production of extracellular enzymes (Allison 2006). According to Allison (2006), the decomposition of subunits of humified (and lignin-type) substances produces sufficient energy for microbial growth. The more likely reason for the slow decomposition of the humified molecules is their complex, random structure, which makes them difficult to decompose enzymatically. Compounds with random structures (e.g. humic acids, plant lignins) are degraded by oxidative enzymes that catalyse depolymerization via free-radical mechanisms (Allison 2006). Because of the nonspecific reaction mechanism, the oxidative enzymes may not decrease the activation energy enough for the degradation of some substrates to occur efficiently (Allison, 2006). Thus, in theory these fractions could have high intrinsic temperature sensitivities (high E_a), but if the substrate does not meet the active site of an enzyme, or E_a is so high that the reaction rate is practically zero in the natural conditions, the apparent temperature sensitivity would be low.

The strength of chemical stabilization depends on the type of interaction between the OM and mineral surfaces: organic material can be more loosely bound through cation bridging or hydrogen bonding, or more strongly bound through ligand-exchange (Kleber et al. 2007). Physically stabilized SOM is protected from decomposition inside soil (micro)aggregates (Six et al. 2002), or inside small pores of soil minerals (Zimmerman et al. 2004). Changes in accessibility (Sollins et al. 1996) or inhibition of microbial activity/inaccessibility (Trumbore 2009) are often mentioned as a separate class of stabilization mechanism, although these mechanisms are closely linked to physical and

chemical stabilization. For example, a mineral-bound compound cannot diffuse and thus reach the active site of a mobile enzyme (Sollins et al. 1996).

Many of the mechanisms work together, for example the decomposition of humified molecules can be even more slowed down by their association with mineral surfaces (Allison 2006). These different stabilizing mechanisms may themselves respond more to temperature than the enzyme-mediated decomposition processes (Thornley and Cannell 2001), have different importance in different climates (Leifeld et al. 2009), and work on different timescales (Trumbore 2009). Little is known about the temperature sensitivities (activation energies) of these stabilization and destabilization processes (Thornley and Cannell 2001), and thus the changes in them due to climate warming. The decomposition rate of litter depends on its chemical quality (Liski et al. 2005), but it is less clear, how the original litter quality affects the stability of the residue remaining after several years of decomposition (Sollins et al. 1996). Although litter with low carbon to nitrogen (N) ratio decomposes faster during early stages of decay, a higher proportion of it could eventually become stabilized (Berg et al. 2000). In theory, C/N ratios of litter could increase due to climate change (increased CO_2 concentrations), but experimental results are contradictory, reporting either increase, decrease or no change in C/N ratios of litter (Gifford et al. 2001). The effect of these changes on SOM stabilization is not known.

3.4 Microbial communities

Sources of carbon and carbon use efficiency

The effectiveness of microbial substrate utilization can be defined as the metabolic quotient [qCO_2] (Anderson and Domsch 1993), or its synonym R_{mass} (Bradford et al. 2008), which both describe the heterotrophic soil respiration rate per unit microbial biomass. The yield coefficient [*Y*], which describes the proportion of decomposed C immobilized to microbial biomass, is another measure for this efficiency (Anderson and Domsch 1993). Fungi have higher substrate utilization efficiencies compared to bacteria (Paul and Clark 1996). K-strategists, which are thought to utilize more recalcitrant substrates, have a higher carbon use efficiency than r-strategists, which depend on more labile substrates (Insam and Haselwandter 1989). For example, Gram-negative bacteria have been found to prefer recent plant material as C source, while Gram-positive bacteria use substantial amounts of more recalcitrant C (Kramer and Gleixner 2006), due to their ability to produce exoenzymes (Biasi et al. 2005).

Most substrates can be decomposed by many microbial species (Setälä and McLean 2004), although there are exceptions. For example, the basidiomycetes within the fungal community are one of the few taxa that can efficiently degrade lignin (Kirk and Farrell 1987, Rabinovich 2004). However, the high amount of different microbial species in soil, the large variety of different enzymes microbes can excrete, and the non-specificity of a large part of these enzymes, leads to functional redundancy of the SOC decomposing microbial community as a whole (e.g. Nannipieri et al. 2003, Setälä and McLean 2004, Salminen et al. 2010). From this, it follows that microbes have a great potential for adapting to changing conditions, but also that it is not likely that small changes in microbial community composition change its function as a whole (Nannipieri et al. 2003).

Temperature optima of microbes

Generally, it is thought that all microbes have a minimum, optimum and maximum temperature for growth (e.g. Dalias et al. 2001, Petterson and Bååth 2003), and these cardinal points depend on the temperature range that the microbes have adapted to live in (Bradford et al. 2008). Different microbial groups are thought to have different temperature optima, and thus changes in microbial community composition with changing climate could change the temperature optima of the whole community (Petterson and Bååth 2003). However, there is actually little direct information on the temperature optima of different microbes (Pietikäinen et al. 2005). Pietikäinen et al. (2005) found that in top-layers of boreal soils, fungi were better in growing at low temperatures, and bacteria were less adversely affected by high temperatures, but both groups had quite similar optimum temperatures of growth between 25-30 °C. Heterotrophic soil respiration continued to increase at least to 40 °C or over, so there was an uncoupling of soil respiration from microbial activity at high temperatures (Pietikäinen et al. 2005). The increase in CO_2 production beyond this optimum temperature for microbial growth is probably due to exoenzymes in soils (Pietikäinen et al. 2005), the activity of which depends on temperature, and can increase until higher temperatures, where the enzymes start to denature. Also Bárcenas-Moreno et al. (2009) found similar temperature optima of about 30 °C for both fungi and bacteria growing on tree litter. In studies from different ecosystems and climates optimum temperatures for microbial growth have been quite similar (around 30 °C) and always higher than the prevailing *in situ* soil temperatures in nature, at least for the arctic, boreal and temperate soils (Dıáz-Raviña et al. 1994, Pietikäinen et al. 2005, Rinnan et al. 2009, Balser and Wixon 2009, Bárcenas-Moreno et al. 2009). This appears to be a common characteristic in environments with fluctuating temperatures (Bárcenas-Moreno et al. 2009).

Suggested mechanisms of thermal adaptation

It has been suggested that, because plants acclimate to higher temperatures (Atkin and Tjoelker 2003), microbes would do the same (Bradford et al. 2008). Atkin and Tjoelker (2003) define acclimation as the adjustment of respiration rates to compensate for a change in temperature, which would lead to reduction in long-term temperature sensitivity of respiration, and thus a smaller positive feedback to climate warming. Because acclimation usually refers to physiological responses of individuals, Bradford et al. (2008) have, in the case of soil microbes, started to use the term thermal adaptation, which includes also genetic changes and shifts in species composition.

The mechanisms for the suggested thermal adaptation are based on changes in the effectiveness of substrate utilization (qCO_2, R_{mass}, Y) by microbes. Bradford et al. (2008) define thermal adaptation as "a decrease in heterotrophic soil respiration rates per unit microbial biomass (R_{mass}) in response to a sustained increase in temperature." The long-term adaptation to higher temperature could show up as 1) a lower Q_{10} but a similar respiration rate at low temperatures (i.e. only Q_{10} changes, not R_0), 2) a lower respiration rate at all temperatures (Q_{10} does not change, basal respiration changes) (Atkin and Tjoelker, 2003), or 3) as change in the optimum temperature for respiration (Bradford et al. (2008). All these result in lower respiration at a standard measuring temperature

(intermediate temperature) (Atkin and Tjoelker, 2003). The change in optimum temperature would most likely involve a shift from cold-adapted populations to warm-adapted populations, while adaptation types 1) and 2) could result also from physiological changes in individuals (Bradford et al. 2008).

For individual plants, the reason for down-regulating respiration with increasing temperature is to retain a positive carbon balance (Hartley et al. 2008). But according to Hartley et al. (2008), free living microbes in soil would have no benefit for down-regulating their respiration, when temperatures increase. Hartley et al. (2007, 2008, 2009) argue that R_{mass} or qCO_2 should increase with temperature, as has been observed in several studies (Insam 1990, Sand-Jensen et al. 2007). No physiological acclimation in response to short-term temperature variations (7 days) was observed by Malcolm et al. (2009a) for litter decomposing microbial community. The Q_{10} of respiration was similar independent of the previous incubation temperature. Hartley et al. (2008) argue that instead of causing acclimation, temperature increase would make recalcitrant substrates with high E_a available to decomposition. Thus, microbes would take the advantage of the temperature increase to decompose substrates that are not always available. Therefore, the increasing temperature would increase the amount or activity of microbes (in a population) that can decompose these recalcitrant substrates (K-strategists) (Hartley et al. 2008, Biasi et al. 2005). This could lead to an even higher positive feedback to climate change.

Hatrley et al. (2008) also point out that acclimation is not needed to explain the results from experimental studies (e.g Luo et al. 2001, Melillo et al. 2002), where respiration rates have been found to decline with time during experimental warming, after an initial increase. A competing hypothesis of depletion of labile substrate pools can equally well explain the observed results (Kirschbaum 2004, Eliasson 2005). Actually, depletion of labile pools could also cause the observed decrease in qCO_2 (Bradford et al. 2008), because a decline in qCO_2 has been observed with soil depth in forest soils (Scheu and Parkinson 1995, Dilly and Munch 1998), or within the litter decay continuum (Dilly and Munch 1996), indicating a more efficient C use by microbes at later stages of decay. Acclimation to temperature has not been observed in arctic soils (Hartley 2008) or peat soils (Vicca 2009), with a large amount of relatively labile C. There is little evidence for thermal acclimation from natural conditions, when increases in temperature are small, and overall temperatures are below the optimum for microbial growth (Rinnan et al. 2009). Seasonal fluctuation in temperatures has been shown to change microbial community composition in some studies (Monson et al. 2006), but not in others (Sand-Jensen et al. 2007). Evidence for thermal acclimation/adaptation of heterotrophic microbial respiration and its relevance with respect to anticipated changes due to climate warming thus remains weak (e.g. Hartley et al. 2009).

4 METHODS

Different experimental methods, together with modeling approaches, are needed to get a consistent picture on the temperature sensitivity of SOM decomposition. Generally, the temperature sensitivity of SOM has been studied by measuring soil respiration at different temperatures in the laboratory (Kirschbaum 1995) or in the field with seasonally varying temperatures (Lloyd and Taylor 1994). Soils could be warmed long-term in situ in the field (Rustad et al. 2001) or in the laboratory (Fang et al. 2005). Soil carbon models (e.g. CENTURY, RothC, Yasso) can be used to model these experiments, and predict the effects

of warming on soil carbon stocks. Observations on geographical relationships between SOM stocks and climate have also been used to make conclusions on the temperature sensitivity of SOM decomposition (Post et al. 1982). Fractioning of SOM into physico-chemical fractions that can be compared along climate gradients (Trumbore et al. 1996) or incubated separately in the laboratory (Leifeld and Führer 2005) has been used to study the temperature dependence of different SOM fractions. Carbon isotope measurements have been combined with field measurements or short-term or long-term laboratory incubations to compare temperature sensitivities of younger and older C (Dioumaeva et al. 2003, Bol et al. 2003, Waldrop and Firestone 2004, Conen et al. 2006). Von Lutzow and Kögel-Knabner (2009) define that a short-term experiment is less than 100 days in laboratory incubations and less than 10 years *in situ*, and these definitions are used in this thesis when talking about short- and long-term incubations.

In this thesis the measurements on temperature sensitivity of total heterotrophic soil respiration were complemented by measurements on the temperature sensitivity of different SOM fractions. Together these parameters were studied by:

1) Differentiating sources of respired CO_2 at different temperatures using ^{13}C and ^{14}C isotopes and modeling mean residence times of different SOM age-fractions
2) Following changes in SOM quality, CO_2 production and its temperature sensitivity during long-term laboratory incubation of different soil horizons
3) Taking soil samples from different climatic conditions and measuring the soil heterotrophic respiration, and its temperature sensitivity in controlled conditions
4) Characterizing the SOM quality, and structure and function of microbial communities of soils from different climatic conditions
5) Transplanting soil samples to warmer climatic conditions to simulate climate warming, and measuring the CO_2 production and its temperature sensitivity from the transplanted samples in controlled conditions.

All these methods, their background and use in the **Studies I - VI** are described in more detail below. This thesis concentrated on laboratory incubations in controlled conditions, although soil respiration could also be measured in the field. This choice is justified, because many researchers have addressed the need for studies, where many of the factors affecting temperature sensitivity that covary in situ could be controlled (e.g. Kirschbaum 2000, 2006, Davidson et al. 2006, Trumbore 2006). Kirschbaum (1995, 2000, 2006) considered laboratory incubations to give the least-biased estimation of the temperature dependence of SOM decomposition. In field measurements, there are more confounding factors, e.g. contribution of root respiration (Dalias et al. 2001), the timing of litter inputs (Gu et al. 2004, Kirschbaum 2006) and occurrence of drought (Kirschbaum 2000, Wan and Luo 2003).

In incubations conducted under controlled conditions, the effect of moisture limitations can be restricted by incubating the soils at 60 % water holding capacity (WHC) (**Study III, VI**), which is commonly considered optimal for microbial respiration (Howard and Howard 1993). Drying of the soils during long-term incubations is avoided by adding water based on weight loss of the samples during the incubation (Hartley and Ineson 2008, **Study V**). In field measurements, the temperature sensitivity of older SOM fractions cannot be measured because the high CO_2 production from labile C is masking the signal from their decomposition. For example in **Study IV**, the soils needed to be incubated in the laboratory for 1.5 years to decompose the most labile C, before the temperature sensitivity of SOM

fractions cycling on decadal or centennial timescales could be measured. This could not have been done in the field. However, there are also shortcomings in the laboratory incubation methods, such as exclusion of plants and disruption of soil structure by sieving.

4.1 Differentiating younger and older C with ^{13}C natural abundance (Study I, II)

C3 plants discriminate substantially against $^{13}CO_2$ during photosynthesis, while C4 plants discriminate much less (Ehleringer and Osmond 1989). Thus, their litter labels SOM with a different $^{13}C/^{12}C$ ratio. The concentration of ^{13}C isotope in a sample is described by delta values ($\delta^{13}C$) in per mil (‰), which is the deviation of the $^{13}C/^{12}C$ molar ratio (R) of the sample from the $^{13}C/^{12}C$ ratio of an international standard (Vienna-Pee Dee Belemnite, V-PDB):

$$\delta^{13}C(‰) = (R_{SAMPLE}/R_{STANDARD} - 1)*1000 \quad (6)$$

For example, the $\delta^{13}C$ value of C4 plants is on average -12 ‰, while the $\delta^{13}C$ value of C3 plants is on average -27 ‰ (Deines 1980). Less negative δ values mean a higher concentration of ^{13}C. Consequently, at a site where vegetation has changed from C3 to C4 vegetation, SOM of different age has a different $^{13}C/^{12}C$ ratio, and this can be used to study C cycling (e.g. Balesdent et al. 1987). The stable isotope of carbon, ^{13}C, has been used to calculate the amount of soil C derived from C4 versus C3 vegetation (Balesdent and Mariotti 1996). Similarly, the contribution of C4 vs. C3 derived SOM decomposition to respired CO_2 can be calculated (John et al. 2003, **Study I**). This is possible because the isotopic signature of the respired CO_2 resembles that of the respective C source in the soil (Amundson et al. 1998), i.e. discrimination against ^{13}C during microbial respiration is negligibly small (e.g. Santruckova et al. 2000). If two C pools have different enough $\delta^{13}C$ values, their contribution to CO_2 production can be calculated based on a two-pool mixing model:

$$f_1 = (\delta_{SAMPLE} - \delta_{SOURCE2})/(\delta_{SOURCE1} - \delta_{SOURCE2}) \quad (7)$$

, where f_1 is the proportion of CO_2 coming from pool 1 (SOURCE1), δ_{SAMPLE} in this case is the $\delta^{13}C$ value of the respired CO_2, and $\delta_{SOURCE1}$ and $\delta_{SOURCE2}$ are the $\delta^{13}C$ values of the two SOM pools.

In **Study I**, the temperature sensitivity of young, labile C (younger than 5 years) was compared to that of older, more recalcitrant C (> 5 years). This was done by taking soil samples from a field turned to maize cultivation (a C4 crop) 5 years ago, and from an adjacent field still growing a C3 crop. Carbon dioxide production and its $\delta^{13}C$ value were measured from these soil samples incubated at different temperatures in the laboratory. These measurements were repeated after storing the samples at 4 °C for 2 months. The measurement sets 1 and 2 showed the reproducibility of the results, and yielded additional information on the temperature sensitivity of labile C. In the maize field, the maize litter had labeled SOM younger than 5 years with a different $^{13}C/^{12}C$ ratio compared to the older SOM originating from C3 vegetation. A change in the $^{13}C/^{12}C$ ratio of respired CO_2 from

this maize field soil with changing incubation temperature would indicate that the decomposition of C in these two pools is differently sensitive to temperature (**Study I, II**). In the control field, both young and old C should have on average the same $\delta^{13}C$ value corresponding to C3 vegetation, and there should be no change with temperature in the $^{13}C/^{12}C$ ratio of CO_2 respired from the control samples. Because the $\delta^{13}C$ value of CO_2 produced by the maize field soils decreased with temperature, and there was no trend in the $\delta^{13}C$ values from control samples (Figure 1 in Study I), it was possible to calculate the fraction of produced CO_2 that originated from the younger and older SOM pools of the maize field soil at different temperatures (Eq. 7). Next, it was calculated how much the decomposition of these two pools, in terms of their Q_{10} values, increased with increasing temperature (**Study I**). Monte Carlo sampling was used to obtain probability distributions (95%) for the Q_{10} values.

Study II was an inter-laboratory comparison with the same soil as in **Study I**, but using a slightly different method compared to **Study I**. In **Study II**, the soil samples were incubated at different temperatures for different time-periods (3-105 hours), to collect the same amount of CO_2 at each temperature as in Conen et al. (2006). The aim was to avoid substrate depletion in the warmer temperature and compare similar SOM quality. This approach differed from that used in **Study I**, where the soils were incubated in water baths for 24 hours, the time needed to collect enough CO_2 for the ^{13}C analysis at all temperatures. The assumption in **Study I** was that exhaustion of the labile substrates would not be a problem during the 24 hour incubations used. **Study I** aimed at answering the question which kind of C substrates are decomposed during a warm day vs. during a cold day. During a colder day, the temperature sum received by the soil is smaller than during a warmer day. Thus, in the approach of **Study I**, incubation time was kept constant, but the temperature sum the soils received was higher at a higher incubation temperature. In the incubation approach of **Study II**, keeping the collected CO_2 amount constant, but letting the incubation time vary, lead to short incubation times at higher temperatures (3 h at 35 °C). This probably caused the measurement results in **Study II** to differ from those in **Study I**. The sampling season was also different, which might have caused differences in available C sources and thus affected the results.

In case of C3/C4 shifts, the different $^{13}C/^{12}C$ ratios of younger and older SOM fractions can be used to study the temperature sensitivity of decomposition of labile vs. intermediate C, i.e. to compare SOM cycling on yearly vs. decadal timescales on places where there has been a change in vegetation from C3 to C4 or vice a versa (Trumbore 2000). The exact differentiation point between younger and older SOM depends on the time when the conversion occurred (for example 5 years in **Study I**). In **Study I**, the C3 signal stems from both intermediate and stabilized/humified pools, so it cannot be used to differentiate between them. However, since the large intermediate pool contributes significantly to CO_2 production, and the production of CO_2 from the stabilized/humified pools during this 24 h incubation is probably negligible, it can be said that this study compares the temperature sensitivity of decomposition of labile and intermediate pools. Natural abundances of ^{13}C cannot be used in ecosystems where there is no change between C3 and C4 vegetation, like the boreal forest ecosystems (Trumbore 2009). Thus, ^{14}C measurements were needed to compare the temperature sensitivities of older, stabilized or humified SOM, intermediate and labile SOM in forest ecosystems (**Study IV**).

4.2 Differentiating younger and older C with ^{14}C natural abundance (Study IV)

Soil organic carbon of different age has a different $^{14}C/^{12}C$ ratio, because ^{14}C decays radioactively and additionally its concentrations in the air have varied since the 1950s as a result of nuclear weapons testing (Trumbore 2000). Radiocarbon is a naturally occurring radioisotope, which is created in the upper atmosphere due to cosmic rays at a rather constant rate (Trumbore 2000). Due to the nuclear weapons testing, the ^{14}C activity of the atmosphere about doubled from the pre-1950 values, peaked in year 1964, and has been steadily decreasing since that (Levin and Hesshaimer 2000). (**Figure 1**)

Radiocarbon measurements can be used to trace the fate of the "bomb carbon" in soils, and its incorporation into SOM can be used to study soil carbon cycling on timescales from years to decades (Baisden and Parfitt 2007, Trumbore 2000). ^{14}C is one of the only tools to study the dynamics of C in soils also on decadal to millennial timescales (Trumbore 2009), and was used in **Study IV** to compare temperature sensitivities of labile C, intermediate C (decadally cycling) and old, humified or stabilized C. Measuring the ^{14}C activity of CO_2 respired at different temperatures can provide evidence for shifts in substrate utilization of microbes (Trumbore 2009).

In **Study IV**, soil samples were taken from two boreal forest sites located in southern Finland; one Scots pine (*Pinus sylvestris* L.) -dominated and one Norway spruce (*Picea abies* (L.) Karst.) -dominated site. Individual 10 dm^3 samples were taken from the organic and two mineral soil layers (0–15 and 15–30 cm). Based on calculations with the Yasso model, 1.5 years pre-incubation was needed to decompose the most labile C, so that the signal from the decomposition of the older SOM could be detected.

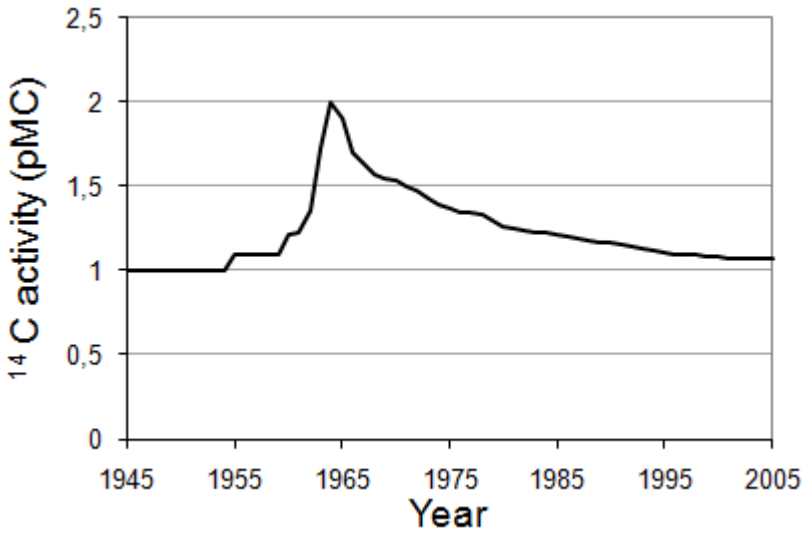

Figure 1. ^{14}C activity of the atmosphere, pMC = percent modern carbon (increase from 100 pMC to the maximum of 200 pMC in year 1964). (Hua and Barbetti 2004, Levin and Kromer 2004)

Thus, the soils were pre-incubated at 25 °C for 1.5 years before making the ^{14}C measurements (**Study IV**). After this pre-incubation, CO_2 respired from the same soil samples at 8 and 25 °C was collected into a molecular sieve. Respiration was assumed to increase exponentially between these temperatures. The collected CO_2 was graphitized, and its $^{14}C/^{12}C$ ratio was measured with accelerator mass spectrometry (AMS) (**Study IV**).

The ^{14}C activity of the sample is expressed as percent modern carbon (pMC), which is the $^{14}C/^{12}C$ ratio in the sample as a percentage of the $^{14}C/^{12}C$ ratio in the international oxalic acid standard (NBS SRM 4990 C), corrected for photosynthetic isotopic fractionation i.e. normalized for ^{13}C content (Stuiver and Polach 1977, Donahue et al. 1990). Another unit often used in ^{14}C studies is $\Delta^{14}C$ (e.g. Gaudinski et al. 2000, Trumbore 2000). These units can be converted to each other. pMC is defined as $A_{SN}/A_{abs}*100$ and $\Delta^{14}C = (A_{SN}/A_{abs}-1)*1000$, where A_{SN} is the normalized ^{14}C activity of the sample and A_{abs} is the absolute activity of the international standard (the activity of the oxalic acid standard in year 1950) (Stuiver and Polach 1977). Values over 100 pMC indicate incorporation of "bomb carbon" and thus a C fraction fixed post-1955. Values below 100 pMC indicate that a large part of the C has resided in soil for long enough for significant radioactive decay to take place (^{14}C half-life = 5730 yr) (Trumbore 2000). Recently fixed C has ^{14}C signature close to the present atmosphere (Trumbore 2000, Gaudinski 2000). The ^{14}C activity of atmosphere was 107 pMC in year 2005, when the soil samples for **Study IV** were taken.

From the changes in ^{14}C activity of respired CO_2 with temperature, it could be deduced whether the decomposition of younger or older SOM was more temperature sensitive in each soil layer. In **Study IV**, the ^{14}C activities of bulk organic layer samples and two fractions in mineral soil, particulate organic matter (POM; >63 µm, <1.85 g/cm^3) and mineral associated organic matter (MOM; <63 µm, >1.85 g/cm^3) (Cambardella and Elliott 1992), were also measured. Particulate organic matter is considered to be an intermediate pool with chemical characteristics still resembling those of the original litter input, and is less mediated by microbial decomposition than the MOM (Six et al. 2001). Particulate organic matter has been shown to have shorter MRT than total SOM (Gregorich and Janzen 1996). Mineral associated matter has longer MRT due to stabilization with minerals (Hakkenberg et al. 2008). Through modeling, MRTs and Q_{10} values for different SOM age-fractions (labile-intermediate-stabilized/humified) were obtained (**Study IV**).

When calculating the MRT of a SOM pool, to describe its average stability, the following assumptions were made:

1) that the soil storage (and size of each SOM pool) is in equilibrium with the litter inputs, i.e. steady state is assumed,
2) the size of litter input was assumed to have been constant, i.e. interannual variability in litter inputs was not considered,
3) the litter decomposes according to 1st order kinetics,
4) the different lag times that carbon has resided in the plant biomass depends on the vegetation type and were taken into account when resolving the MRT for a SOM fraction as described below (see also Bruun et al. 2005, Hakkenberg et al. 2008).

The flux model used for calculating the MRT of different SOC fractions in **Study IV** can be written as (Fontaine et al. 2007):

$$A_{SOC}^{14}(t) = \frac{\sum_{i=b}^{p}\left[M_i e^{-(p-i)/MRT} \times A_i^{14} e^{-(p-i)\lambda}\right]}{\sum_{i=b}^{p} M_i e^{-(p-i)/MRT}} \quad (8)$$

, where $A^{14}{}_{SOC}$ (t) is the measured or modeled ^{14}C activity of a SOC fraction, A_i^{14} the atmospheric ^{14}C activity in year i and λ the radioactive decay rate of ^{14}C (1/8268 y^{-1}), p is the year of soil sampling (2005 in our study), and b the year of starting the calculation (10 000 years before present). The annual new SOC input M_i was assumed constant in this study. A 3 year lag was applied in the A_i^{14} values at the pine site and a 6-7 year lag at the spruce site (Liski et al. 2006) (**Study IV**), i.e. the ^{14}C activity of the litter cohort in each year is the ^{14}C activity of the atmosphere corrected with this lag time. Then the MRT of a SOM fraction was numerically solved. In case of two possible solutions for the MRT the other one can usually be discarded based on knowledge on rates of litter input to the soil (and thus CO_2 production, if these are in equilibrium) (e.g. Fontaine et al. 2007, Leifeld et al. 2009, **Study IV**). For example if a shorter MRT would need an irrationally high litter input to the soil, the longer MRT can be chosen as a probably more correct one.

4.3 Long-term laboratory incubations (Study V)

Changes in respiration rate, SOM quality and microbial community composition and their interactions during the 1.5 years incubation conducted for the forest soil samples in **Study IV** are described in more detail in **Study V**. When soils are incubated in the laboratory, they are disconnected from the plants, and labile C input from the roots ceases. The root exudates are a very small pool, so cessation in their production cannot alone explain the reduction in CO_2 production during the incubation, but other labile and also more recalcitrant SOM pools are being increasingly depleted as the incubation continues. Controlled laboratory incubation can be thought of as a means to biologically fractionate between labile and intermediate/slow SOM pools, assuming that in the beginning of the incubation CO_2 comes mostly from the labile pool, and after respiration has settled, the CO_2 comes mostly from the intermediate pool (Townsend et al. 1997, Fissore et al. 2009).

The assumption in long-term incubation experiments, used for studying the temperature sensitivity of SOM decomposition, is that as the labile C is consumed from the soil, a larger portion of the produced CO_2 comes from decomposition of more recalcitrant fractions. If labile and recalcitrant pools have different temperature sensitivities, this should cause a change in the Q_{10} of total heterotrophic soil respiration (e.g. Fang et al. 2005, Conant et al. 2008a). However, even after a long-term incubation, the CO_2 produced is still a sum of decomposition of SOM with different decomposition rates (Trumbore 2000). Thus, both in short- and long-term laboratory incubations, ^{13}C and ^{14}C isotope measurements, SOM fractionation and modeling are still needed to quantify the temperature sensitivity of SOM fractions with different turnover times.

Kirschbaum (2000) pointed out that all measurements offer only a snapshot of the system, and the researcher has to be aware that the studied system may change during the measurement period. Comparing heterotrophic soil respiration at a higher and at a lower temperature can lead to comparing decomposition of different SOM pools at different temperatures, because the labile C pools are faster depleted at higher temperatures. This problem is smaller in short-term incubations (**Study I**), but to be able to study the decomposition of the more recalcitrant fractions, long-term incubations are needed. In long-term incubations, the results are confounded by the different SOM quality if respiration rates of soils kept at a lower and at a higher temperature are compared (Kirschbaum 2006, Reichstein et al. 2000). The use of this kind of parallel incubations (another soil sample incubated long-term e.g. at 15 °C and another at 25 °C, and Q_{10} calculated as the respiration at 25 °C divided by respiration at 15 °C) has been questioned frequently (Leifeld 2003, Leifeld and Fuhrer 2005, Reichstein 2005), since it leads to underestimation of Q_{10} (Dalias et al. 2001). In **Study V** this problem was minimized by incubating the samples at a same temperature (T = 25 °C) to let the labile C decompose, and taking sub-samples during the incubation for measuring CO_2 production at different temperatures to determine the short-term temperature sensitivity of SOM decomposition (see also Hartley and Ineson 2008). Short-term temperature sensitivity was measured by incubating these sub-samples in water baths for 24 h at different temperatures (5-26 °C) and measuring the CO_2 produced at different temperatures with gas chromatography. Heterotrophic respiration was modeled with the Gaussian function, and differences in the temperature sensitivity parameters *a* and *b*, and thus in the temperature-dependent Q_{10} curves, between different soil layers and different incubation stages, were compared.

Soil sub-samples were frozen, and later analyzed for microbial community composition (phospholipid fatty acids, PLFA's) and SOM quality (relative amounts of different SOM fractions) to relate the changes in respiration rate and Q_{10} during the incubation to changes in these factors. Their relations were tested with Pearson correlations. In the mineral soil, the measured SOM fractions were POM, MOM, sand-associated OM, dissolved organic carbon (DOC) (<0.45 µm) and cellulose content of the POM fraction. In the organic layers, SOM was chemically fractionated into water- and ethanol-soluble compounds, acid-hydrolysable compounds and a non-hydrolysable residue. The quality of the water-soluble fraction was characterized by measuring the content of sugar monomers and lignin-type compounds (**Study V**).

4.4 Climatic gradient and transplantation studies (Study III, VI)

Studies on climatic gradients can be used to address the questions: 1) How do soils formed at different climatic conditions respond to temperature changes? 2) If there is a difference in the temperature sensitivity of SOM decomposition, is it due to different quality distribution of SOM, or adaptation of microbes to the prevailing temperature conditions?

Since decomposition rates are higher at high temperatures, soils from colder climates have been hypothesized to contain a relatively larger pool of labile, incompletely decomposed C, which has been accumulated in the soils due to unfavorable decomposition conditions (Ågren and Bosatta 2002). This follows from the different decomposition rates (slow decomposition of low quality substrates and fast decomposition of labile, good

quality substrates), at least if nearly similar temperature sensitivities of decomposition are assumed. This is the basis for the assumption that northern soils would contain a larger pool of labile C. On the other hand, much higher temperature sensitivity for the decomposition of recalcitrant fractions could lead to an accumulation of low-quality substrates in colder climates (Leifeld and Fuhrer 2005). Thornley and Cannel (2001) hypothesized that stabilization of SOC increases at warm temperatures, despite the positive effect of temperature on litter decomposition, because the mechanisms stabilizing C could be more temperature sensitive than the enzyme-mediated decomposition reactions. Leifeld et al. (2009) hypothesized that in colder climates, also other unfavorable environmental conditions than low temperatures, e.g. low pH or small amounts of labile C, hinder the transformation of SOM into stabilized fractions.

A problem with wide climatic gradients is that with changing latitude also rain patterns, nitrogen deposition, soil mineralogy, vegetation type and other factors than temperature affecting SOM quality and decomposition may change (e.g. Callesen et al. 2003). Altitudinal gradients on mountain regions can also be used to study the effect of temperature on SOM decomposition in otherwise similar environments (e.g. Niklinska and Klimek 2007, Leifeld et al. 2009), but can also be confounded by changes in mineralogy along the gradient. Therefore, the boreal forest sites used in **Study III and VI** were selected so that other factors than temperature affecting soil C (vegetation, soil age, parent material, pH, development since the latest glaciation, etc.) remain as similar as possible (Liski and Westman 1997). There were 12 forest sites included in the study in total, half of the sites were located in southern and half in northern Finland, and were either Norway spruce- or Scots pine-dominated. The difference in mean annual temperature between the northern and southern sites was 4.5 °C, which is in the middle of the range of possible climate warming scenarios for Finland during the coming 80 years (2.4-7.4 °C) (Jylhä et al. 2004).

In **Study III**, the heterotrophic respiration rate was measured from samples originating from different geographic origins (see above) and incubated at different temperatures in the laboratory. The respiration rate and its temperature sensitivity were modeled with the Gaussian function. Amounts of labile C fractions (cold water soluble C, hot water soluble C and acid soluble C) were compared in the organic layers of boreal forest soils from southern and northern borders of the boreal forest zone. These chemical extractions were chosen because they are thought to correspond to C available for microbes (McLauchlan and Hobbie 2004). Microbial biomass C, mineralizable C and other labile C fractions are often highly correlated with the amount of total SOC (Franzluebbers 2001). Thus, in order to study the effect of climate on these labile fractions, their amounts need to be expressed per unit of total SOC. As the CO_2 produced during short-term laboratory incubation comes mostly from the most labile C, the mineralizable C normalized for OM or C content can also be considered as a measure of labile C (**Study III**). Microbial communities were characterized using the phospholipid fatty acid (PLFA) method, which is a broad measure of microbial community composition and carbon utilization potential method (Biolog), which describes what kind of carbon substrates can be utilized by the soil microbial community. Principal component analysis (PCA) was used in statistical analysis of these results. Differences in PCA scores, and amounts of labile C and microbial biomass between the northern and southern sites were compared using one-way analyses of variance (ANOVA) followed by Tukey's test.

Transferring of soil sections from colder to warmer climate regions (Rey et al. 2007), either southwards along a latitudinal transect (Bottner et al. 2000) or from higher elevation to lower elevation (Zimmermann et al. 2009) can be used to mimic the effects of a warming

climate on soil biology and chemistry. In **Study VI**, soil organic layer sections from the same northern sites as in **Study III** were transplanted to the southern sites. The aim was to study whether changes in surface vegetation in a warmer climate, and thus litter inputs to soil, would also change microbial communities and alter the temperature sensitivity of SOM decomposition in the transplanted samples. The effect of transplanting was differentiated from the effect of warmer climate by transplanting control samples at the site of origin (**Study VI**). After two years in a warmer climate, soil microbial community composition (PLFA's), carbon source utilization patterns (Biolog), heterotrophic respiration rate and its temperature sensitivity were compared between the soil sections transplanted at site and transferred to south, using the same methods as in **Study III**. A detrended correspondence analysis (DCA) was performed for interpreting changes in the ground vegetation.

5. RESULTS AND DISCUSSION

5.1 Definitions and difficulties in comparing results

The results from earlier studies on the temperature sensitivity of decomposition of different SOM fractions are contradictory (e.g. review by Davidson and Janssens 2006). It is difficult to compare studies with different methodology, and experimental conditions, where different confounding factors may have a smaller or larger effect on the results (Kirschbaum 2006). Even in studies conducted in controlled conditions in the laboratory, slight differences in the methods used can cause the results to be inconsistent (**Study I**, **Study II**). The Q_{10} values of different studies are difficult to directly compare, because the Q_{10} value increases with decreasing temperature (e.g. Tjoelker et al. 2001, Dalias et al. 2001, Biasi et al. 2005, Kirschbaum 2006, **Study III, V, VI**). Thus, the temperature range at which the measurements were made, affects the Q_{10} values (**Study V**). Also, the choice of function used to describe the temperature sensitivity of SOM decomposition, and the way of fitting the function to data, has an effect (Tuomi et al. 2008).

Different model structures can make it difficult to compare the results from theoretical or modeling studies (e.g. Liski et al. 1999, Giardina and Ryan 2000, Knorr et al. 2005). For example, Knorr et al. (2005) estimated on an theoretical basis that slowest cycling C should be most temperature sensitive, but did not take into account the possibility that different stabilization mechanisms could limit the decomposition of the oldest C. Giardina and Ryan (2000) found the decomposition rates not to be related to temperature along a gradient of mean annual temperature (MAT), but assumed a single-pool model in calculations of turnover time for soil C. This approach omits the heterogeneity of SOM and cannot give information about the temperature sensitivity of different SOM fractions.

Some of the controversy may also be due to inconsistent use of the terms labile/active, intermediate/slow/recalcitrant, and resistant/humified/stable/stabilized/passive carbon pools (Kirschbaum, 2006). Different authors may have different definitions for them. The dispute often is whether a small pool of young/labile C is more temperature sensitive than old/ stabilized C. Use of three pools instead of two might help reduce the controversy: 1) labile C (1-5% of SOM, containing soluble C and easily decomposable parts of litter) 2) intermediate/recalcitrant C (The large part of SOM that is chemically recalcitrant, but can

be enzymatically decomposed) and 3) stabilized C (old C that is either biochemically, chemically or physically stabilized) (Trumbore et al. 1996, Torn et al. 1997). According to Trumbore (2006), the problem is that there are no good definitions for these different pools, especially for the large and heterogeneous intermediate pool, the behavior of which is most crucial for the soil carbon – climate feedback. The matching of these conceptual pools in soil carbon models to measured SOM fractions in nature has also been only partly successful (e.g. Zimmermann et al. 2007). The division to (at least) three conceptual pools is still useful, because it shows that the labile pool is too small, and the stabilized pool decomposes too slowly, to have an important effect on the climate during coming years and decades (Trumbore 2006).

5.2 Incubation studies using ^{13}C (Study I, II)

In **Study I**, the older, recalcitrant C was found to be more temperature sensitive than the younger, more labile C. The mean Q_{10} values (at T = 20 °C) for younger, maize-derived C were 2.4-2.9 and for older C3-derived C 3.6 (**Figure 2**). The Q_{10} of the total CO_2 production was 3.4-3.6 (calculated for the full temperature range). The difference between the temperature sensitivity of older and younger C decreased between measurement sets 1 and 2, when the soils were stored for 2 months at 4 °C. This indicates that especially the decomposition of the most labile C was less temperature sensitive. The amount of this fraction probably decreased during the storage. Other studies using ^{13}C have also found that older, recalcitrant C is more efficiently utilized at higher temperatures (Andrews et al. 2000, Bol et al. 2003, Waldrop and Firestone 2004, Biasi et al. 2005). Contradictory to these studies, Conen et al. (2006) concluded that decomposition of recalcitrant and labile C is equally temperature sensitive.

Study II shows how the contradictory results in Conen et al. (2006), **Study I** and **Study II** could be due to small differences in experimental setup. The measurement results from **Study II** could not be used to calculate Q_{10} values for C fractions younger and older than 5 years as in **Study I**, since in **Study II** there was no trend in the $\delta^{13}C$ values of respired CO_2 with increasing temperature from the maize soils (Figure 1 in Study II). Instead, there was an increasing trend in the control soil. If the values of control soil also exhibited no trend with temperature, these results of **Study II** could be inferred as younger and older C having similar temperature sensitivity, which was the conclusion of Conen et al. (2006). Partly these differences in results could be due to different sampling season (October in **Study I** and April in **Study II**). If there was an increased availability of ^{13}C enriched labile substrates in both soils after winter (mobilized after freeze-thaw cycles), and these sources contributed a high proportion to produced CO_2, this could have masked the temperature sensitivity of older C. However, the increasing trend in the control soil, but not in the maize soil, raises concern of an artifact due to the way the incubations and ^{13}C measurements were conducted in **Study II** and by Conen et al. (2006). The reason for this increase in the control soil is not clear, and Conen et al. (2006) did not investigate the reason for this trend either. However, since there was an increasing trend in the ^{13}C values of respired CO_2 in the control soils also in the original study of Conen et al. (2006), where the soils were sampled in winter, it may be small differences in experimental setup that cause this trend in the control soil measurements.

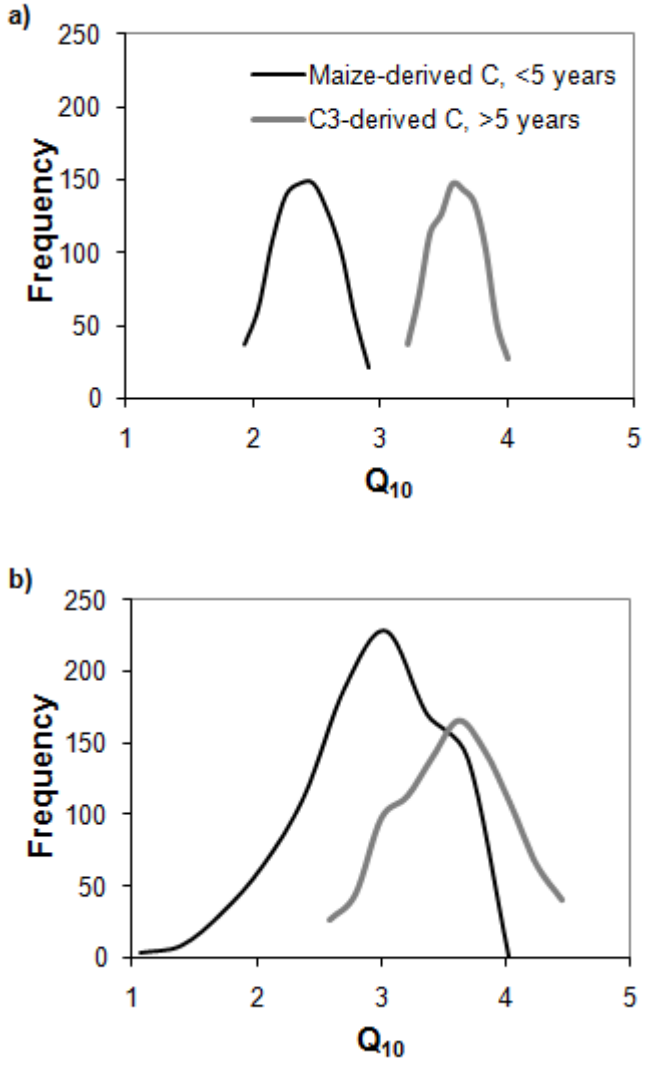

Figure 2. The Q_{10} values (95% of the probability distributions) for SOM younger than 5 years (black line) and older than 5 years (grey line), from a) the first measurement set, b) the second measurement set (**Study I**).

Biasi et al. (2005) showed that even after 6 weeks incubation at different temperatures, when a soil sample incubated at 24 °C was transferred to 12 °C, it had similar $\delta^{13}C$ of respiration as the sample originally incubated at 12 °C. This indicates that labile substrates were not exhausted even during 6 weeks incubation. This gives support to the conclusion that the decreasing $\delta^{13}C$ with temperature in **Study I** was really due to a shift in substrate utilization caused by the temperature and not caused by labile substrates being exhausted at

higher incubation temperatures during the 24 hours incubation. Therefore, the approach used in **Study II** is not necessarily needed. Comparing very short incubation times at a high temperature (3 hours at 35 °C) to longer incubation times at lower temperature is not biologically meaningful, and may superimpose other mechanisms that disturb measurements on which substrates can be decomposed at different temperatures. The more efficient recalcitrant substrate decomposition at higher temperatures may be due to increased exo-enzyme activity and an increase in the activity of microbes capable of decomposing complex substrates (Biasi et al. 2005). The 3-hour measurements in **Study II** could be too short-term to measure this effect. Instead, they could capture only the response of the fastest growing microbes, which may preferentially decompose labile substrates.

Biasi et al. (2005) and Andrews et al. (2000) have measured both the change in $\delta^{13}C$ of respired substrates and the change in microbial community structure in response to temperature increase, and link these changes together. Their results support the view that as temperature increases, more and increasingly recalcitrant substrates become available to microbes. Andrews et al. (2000) claim that the increase in available C with temperature could be explained by changes in the structure and size of the active microbial population. Another way to think of this would be through the activation energy of the decomposition reactions: when temperature increases, more recalcitrant substrates become available for decomposition. Microbes adapt to this change in environmental conditions. Thus, the structure and size of the active microbial population changes, i.e. the amounts and activity of microbes capable of decomposing recalcitrant substrates increases. These explanations are not contradictory but complementary.

5.3 Differentiating SOC age-fractions using ^{14}C (Study IV)

In **Study IV**, the ^{14}C activity of SOM and respired CO_2 were higher at the spruce-dominated site, compared to the pine-dominated site, reflecting the longer residence time of C in trees in spruce forests (Liski et al. 2006). The ^{14}C signature of respired C changed with increasing temperature in both the spruce- and pine-dominated site, indicating different temperature sensitivities for SOM fractions of different age.

The ^{14}C activity of the CO_2 respired by the organic layers in **Study IV** was higher than the activity of the atmosphere at the time of sampling (**Figure 3**). This means that there is a SOM fraction with mean residence time from some years to decades that is significantly contributing to heterotrophic respiration (**Study IV**, Trumbore 2000, Gaudinski 2000). Because the ^{14}C activity of the CO_2 respired was lower than the ^{14}C activity of SOM on average, a more labile C fraction that is younger than the SOM on average is dominating the respiration. This can be deduced, because older, pre-1950 C is not a significant fraction in the organic layers.

In the mineral soil layers, the ^{14}C activities of MOM and POM were lower than that of the present atmosphere (with the exception of POM in the upper mineral soil layer of the spruce-dominated site), indicating a remarkable share of older, pre-1950 carbon. The ^{14}C activity of respired CO_2 was also below the atmospheric level in 2005 at the Scots pine site, indicating contribution from decomposition of older, pre-1950 SOM to soil respiration. When taking account the longer lag time of carbon in spruce trees, the same could be concluded for the Norway spruce site. However, this ^{14}C activity of respired CO_2 was

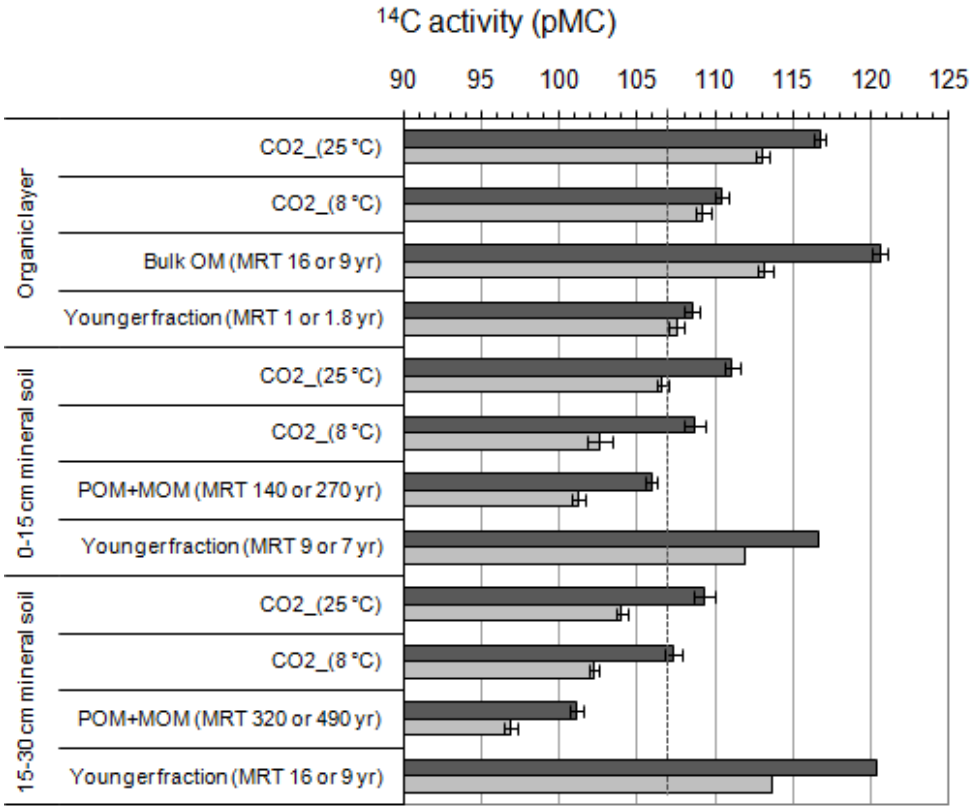

Figure 3. ^{14}C activity of different SOM fractions and CO_2 of produced at 8 and 25 °C for the Norway spruce-dominated site (dark grey) and for the Scots pine-dominated site (light grey). Error bars represent AMS measurement errors (0.4–0.8 pMC), and standard error of the estimate for the younger fraction in organic layers. (For the younger fraction of the mineral soil layers, only a value based on the model-calculated median ^{14}C activity is presented.) Modeled MRT's based on the ^{14}C activity (eq. 8) are also indicated for spruce-dominated site, and pine-dominated site respectively (eg. 16 or 9 years for organic layers).

higher than the ^{14}C activity of the combined MOM+POM fractions (**Figure 3)**, showing that a younger, post-1950 C was important for the CO_2 production (**Study IV,** Trumbore 2000**)**. In all soil layers in **Study IV**, the measured ^{14}C activity of CO_2 increased at the higher measurement temperature (**Figure 3**). From this it was deduced that decomposition of the fraction with MRT from some years to decades increased more with temperature than the decomposition of more labile C (MRT 1-2 years) in the organic layers, or than that of the more stable C (MRT hundreds of years) in the mineral soil layers. In the mineral soil, the amount of this decadally cycling fraction is probably small, so that it does not largely affect the ^{14}C activity of the bulk SOM or SOM fractions, but it can still significantly contribute to CO_2 production (Trumbore 2000, **Study IV**).

In **Study IV**, the contributions of younger and older SOM fractions to CO_2 production at 8 and 25 °C and their Q_{10} values were calculated similarly as in **Study I**. The pools

compared in the organic layers were the labile C pool (estimated to have the ^{14}C activity of recent litter input) vs. more recalcitrant C (with the measured ^{14}C activity of bulk organic matter in the layer). In the mineral soil layers, POM was always younger than MOM, but since the MRTs of these fractions were close to each other, they were combined to form the older fraction in mineral soils. This older fraction, with MRT of several centuries, was compared to a faster-cycling fraction, which had median MRTs from some years to a decade. Probability distribution of the ^{14}C activity of the younger fraction in the mineral soils was modeled based on the total CO_2 production at 25 °C and CO_2 production from the decomposition of the combined POM+MOM fractions during the 1.5 years incubation, and their ^{14}C activities (**Study IV**).

The most labile C had quite low temperature sensitivity (Q_{10} < 2), while more recalcitrant decadally cycling C was highly temperature sensitive (Q_{10} = 4.2 to 6.9), and the even older, centennially cycling C was again less sensitive (Q_{10} = 2.4 to 2.8) (median Q_{10} values from **Study IV**). The Q_{10} of total heterotrophic respiration varied from 2.7 to 3.2 between all the soil layers. The observed high temperature sensitivity of the pool cycling on timescales from years to decades (**Study IV**) would imply that it is chemically rather recalcitrant material, and that it is not strongly stabilized by association with minerals. The source of the decadally cycling C in mineral soil could be either DOC transported downwards in the soil profile, or decomposition of fine roots (Gaudinski et al. 2000, Trumbore 2000). Some stabilizing mechanism is probably responsible for the lower Q_{10} of the centennially cycling C, but based on the results of **Study IV** it cannot be said, which is the relative importance of the possible stabilizing mechanisms: biochemical stabilization/inherent recalcitrance (Six et al. 2002), absence of labile C and nutrients (Fontaine et al. 2007), or association with minerals (e.g. Six et al. 2002). Probably all these mechanisms play a role. **Study IV** shows that these boreal forest top-soils have a decadally cycling C fraction that can be more efficiently decomposed at high temperatures, and C from this fraction can thus be lost as the climate warms. Whatever the stabilizing mechanism is for the centennially cycling C, our results imply that short-term increases in temperature do not lead to relatively large destabilization and rapid decomposition of this old C.

The results of **Study IV** show that using the same Q_{10} (determined based on total heterotrophic soil respiration) for all SOM fractions underestimates the response of SOM decomposition to climate warming on the short term, during coming years and decades, and overestimates the long-term response on centennial timescales, as also suggested by Trumbore (2000). Based on the fraction-specific Q_{10} values instead of the Q_{10} of total heterotrophic soil respiration, and comparing soil C stocks at steady states, it was calculated that in response to climate warming (a predicted warming of 5.1 °C, Jylhä et al. 2004) the organic layers would lose 30-45 % more carbon, if there is no change in carbon input (**Study IV**). This is because most carbon in the organic layers belongs to the highly temperature sensitive decadally cycling pool. Because the mineral soils contain only a small fraction of the temperature sensitive decadally cycling C, and consists mainly of the less temperature sensitive C cycling on centennial timescales, the mineral soils would lose 4-17 % less carbon.

Several other studies using the ^{14}C natural abundance observed no change in the ^{14}C activity of respired CO_2 in response to increasing temperature (Dioumaeva et al. 2003, Czimczik and Trumbore 2007, Cisneros-Dozal et al. 2007). Their results indicate that there was no shift in the source of substrates being respired at different temperatures. Cisneros-Dozal et al. (2007) conclude that slowly cycling C is at least as temperature sensitive as the

faster cycling C. The crucial difference between these studies is that in **Study IV** the soils were first incubated for 1.5 years to let the most labile C decompose to be able to study the temperature sensitivity of decadally vs. centennially cycling C (i.e. intermediate vs. stabilized/humified pools). This difference in the results may be due to a higher proportion of the CO_2 coming from relatively labile C in their studies compared to **Study IV**. Thus, the decomposition of labile substrates was probably masking the signal from the decomposition of the more recalcitrant substrates, so that the proportionally higher increase in recalcitrant C decomposition could not have been detected even if it existed. Boddy et al. (2008) showed, through addition of ^{14}C labeled labile substrates, that the decomposition of labile C (low-molecular weight compounds in DOC) was not temperature sensitive, but the decomposition of more complex microbial compounds formed in the decomposition process was temperature sensitive, which is consistent with **Study IV**.

The assumption when calculating the MRT of a SOM fraction is that the isolated fraction is homogeneous with respect to decomposition rates (Trumbore 2000). Different fractionation methods try to distinguish between SOM fractions of varying stability, taking into account one or several possible stabilization mechanisms. However, like the pools of soil carbon models, also the soil fractionation techniques average over processes, and cannot adequately describe the continuum of SOC (Paul et al. 2006). The fractionation of SOM into functional pools with distinct turnover times has been problematic, and most studies show that differentiated SOM fractions still comprise a mixture of old and young C (e.g. Madig et al. 1996, Olk and Gregorich 2006, von Lützow et al. 2007). According to Trumbore (2009), it should not even necessarily be expected for the operationally defined SOC fractions to be homogenous with respect to age. Instead, monitoring ^{14}C in labile components can provide information about shifts in microbial substrate utilization, and indicate destabilization of older C pools. The ^{14}C activity is a direct measure for how long ago the carbon in SOM or respired CO_2 was fixed from the atmosphere, but as such it integrates over several processes, e.g. different stabilization mechanisms (Trumbore 2009). Microbial C, which is considered a labile C fraction, can contain old C, or new C can become associated with minerals and become stabilized. On average, however, older C is either more recalcitrant or tightly associated with minerals (Trumbore 2009).

Besides showing the problems in extracting SOM fractions with different MRTs, the quite similar ^{14}C activities for POM and MOM (MRT ranging from 110-250 years for POM in the 0-15 cm layer, 310-330 years in the 15-30 cm layer, and for MOM 160-280 years in the 0-15 cm layer and 320-560 years in the 15-30 cm layer) in **Study IV** reveal some information about the mechanisms of C cycling and stabilization at these sites. This could imply that both biochemical and physical stabilization mechanisms play an important role in these soils, or that the role of stabilization by association with minerals is smaller than found in studies from warmer climates (e.g. Conen et al. 2008, Leifeld et al. 2009). Also other studies have found quite old ^{14}C ages for POM (100 years or several hundred years) at higher altitudes in grasslands in the Swiss Alps (Conen et al. 2008, Leifeld et al. 2009) and forest sites in the Italian Alps (Hakkenberg et al. 2008), especially in the deeper (20-30 cm) mineral soil layers, although studies from temperate grasslands report MRTs of only few years for this fraction (e.g. Cambardella and Elliott 1992). Conen et al. (2008) argue that when the ^{14}C age of MOM relative to POM is small (i.e. the factor how much more stable MOM is compared to POM), accumulation of SOM is due to incomplete transformation of plant residues, and not strongly related to mineral interactions of microbial-derived products. According to Conen et al. (2008) SOM at such sites would be more vulnerable to

loss due to climate warming than SOM at sites where the high stability of MOM implies efficient stabilization of microbial-derived decomposition products.

5.4 Changes in Q_{10} during a long-term incubation (Study V)

In **Study V**, the temperature sensitivity of SOM decomposition (Q_{10}) of the organic layers increased during the long-term incubation (**Figure 4**). This is probably because there was a shift towards utilization of more complex substrates, when the amounts of more labile substrates decreased. The initial decrease in heterotrophic soil respiration during laboratory incubation has been thought to reflect the depletion of labile SOM pools, and the change in the dominant source of CO_2 to more recalcitrant SOM pools (Townsend et al. 1995, 1997). Based on laboratory incubations, the amount of labile C has been estimated to be 0.7–4.3% of total soil C (Townsend et al. 1997). In **Study V**, the loss of initial organic C during the first three months incubation varied from about 6 % in the organic layers to about 1% in the deeper mineral soil layers. The slower decrease in respiration rates in the mineral soil layers implies that most of the SOM is already of rather low quality. In **Study V**, the increase of temperature sensitivity with incubation time was observed in organic horizons, but there was no clear trend in Q_{10} of the mineral soil layers.

Results from **Study V** support the theory (Davidson and Janssens 2006) that the decomposition of recalcitrant C is more temperature sensitive than that of the labile C. This is consistent with the results from **Studies I** and **IV**. Some other long-term laboratory incubation studies have also observed an increase in Q_{10} with incubation time (Hartley and Ineson 2008, Conant et al. 2008a, 2008b). However, there are also several studies where no change in Q_{10} with incubation time has been observed (e.g. Townsend et al. 1997, Fang et al. 2005, Reichstein et al. 2005), and from this the authors have concluded that decomposition of labile and recalcitrant C is equally temperature sensitive, which contradicts the kinetic theory. It is possible that these incubations were too short-term to give information on the temperature sensitivity of more stable SOM, and decomposition of labile pools was still masking the decomposition of a large, slow pool (Davidson et al. 2000). A larger depletion of labile C in Conant et al. (2008a, 2008b) and **Study V** compared to e.g. Fang et.al. (2005) and Reichstein (2005), probably enabled to observation of a statistically significant increase in Q_{10}. Another possible explanation would be a smaller confounding effect of association with minerals. Studying the organic layers in **Study V** gave the possibility to study the temperature sensitivity without the limiting effect of association with minerals. The temperature sensitivity of decomposition of litter and substrates added to soil has been also found to be inversely related to their quality (Fierer et al. 2005). These studies support the hypothesis of Davidson and Janssens (2006) that the more recalcitrant C is more temperature sensitive, and this can be observed when association with minerals is not limiting decomposition.

Studies I, IV and several other studies have also shown that even if the Q_{10} of total heterotrophic respiration remains similar during a laboratory incubation, or is similar for different soil layers, different SOM fractions can still have remarkably different temperature sensitivities (Leifeld and Fuhrer 2005, Feng and Simpson 2008). Feng and Simpson (2008) measured varying temperature sensitivities for different SOM components during a long-term incubation. For example, lignin monomers had higher temperature sensitivity than solvent extractable compounds. Leifeld and Fuhrer (2005) incubated

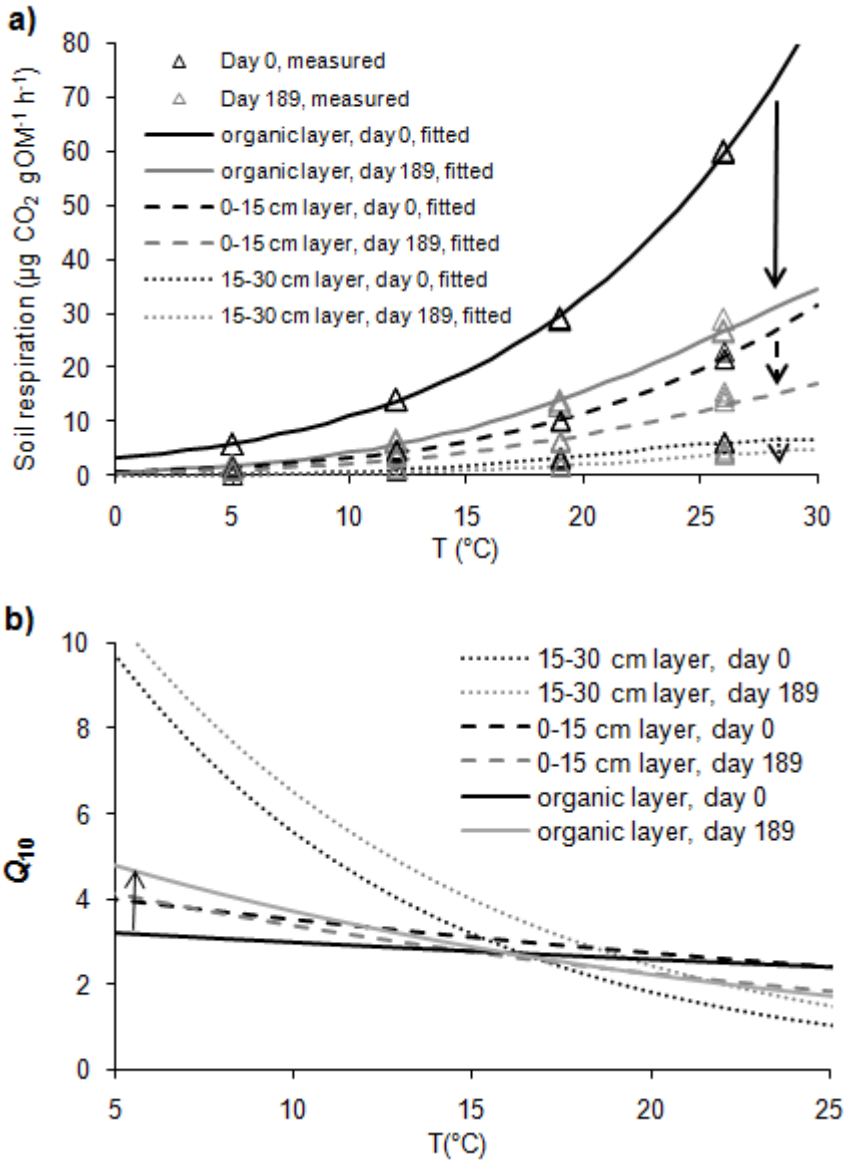

Figure 4. a) Measured and modeled soil respiration and b) temperature-dependent Q_{10} curves calculated based on the fitted values of parameters *a* and *b* of the Gaussian model for different soil layers of the spruce-dominated site (for incubation days 0 and 189). The figure shows the decrease in soil respiration rate with time (clearest in the organic layer). Initially the temperature sensitivity of the organic layer differed from the mineral soil layers (day 0). The increase in Q_{10} of the organic layer (day 0 → day 189) is statistically significant. On day 189 there are no statistically significant differences in the temperature sensitivities between the layers.

separated SOM fractions, and found different temperature sensitivities for fractions with varying stability. These studies demonstrate that the Q_{10} of total heterotrophic soil respiration is not an adequate measure for the temperature sensitivity of different SOM fractions. Even if there is no statistically significant change observed in the Q_{10} of total heterotrophic soil respiration during incubation, this does not mean that there are no differences between the temperature sensitivities of different fractions. It may be that the relative amounts of different fractions have not changed enough to show up as a change in the Q_{10} of total heterotrophic respiration. A decrease in C availability can also decrease Q_{10}, confounding the effect of more recalcitrant substrates tending to be respired later during an incubation.

Factors controlling the Q_{10} of bulk heterotrophic soil respiration

The temperature-dependent Q_{10} curves in **Study V** give more information about the processes affecting the temperature sensitivity of SOM decomposition than Q_{10} values calculated at one temperature or averaged over a wide temperature range. The Q_{10} curves of the mineral soil layers were steeper (decreased faster with increasing temperature) compared to organic layers in the beginning of the incubation. The Q_{10} curves of the organic layers became steeper, and thus more similar to those of the mineral soil layers, with increasing incubation time (**Figure 4**).

Although there is increasing evidence on a generally temperature dependent Q_{10}, only few attempts have been made to explain what regulates Q_{10} at different temperatures (Atkin and Tjoelker 2003, Davidson et al. 2006, **Study V**). Similarly to **Study V**, Atkin and Tjoelker (2003) claim that respiration would more likely to be limited by maximum catalytic enzyme activity at low temperatures, and by substrate availability at intermediate temperatures. Intermediate temperature here means intermediate between 0 °C and the optimal temperature for respiration. At temperatures higher than the optimal temperature (and at least after the temperature where enzymes start to denature) limitations in enzyme capacity would again be important. "The temperature dependence of Q_{10} is linked to shifts in the control exerted by maximum enzyme activity at low temperature, and substrate limitations at high temperature" (Atkin and Tjoelker, 2003). Thus, the steeper Q_{10} curves of mineral soil layers in **Study V** could reflect a higher recalcitrance of SOM (higher E_a and thus higher Q_{10} at low temperatures), and lower substrate availability (relatively lower Q_{10} at intermediate temperatures) (**Figure 4**). In organic layers, where substrate availability is less limiting, the Q_{10} decreases relatively less with increasing temperature. Also Malcolm et al. (2009b) found that temperature-dependent Q_{10} curves became steeper with depth in the organic layers of a pine forest soil, and argued that this was probably due to lower SOM quality in the deeper layers. Pumpanen et al. (2008) found higher Q_{10} values for deeper soil layers at low temperatures *in situ* at the same site, where samples for **Studies IV** and **V** were collected. The effect of limiting substrate availability on the form of temperature-dependence indicates that the often used exponential equation is least appropriate for soils with low substrate availability, such as most mineral soils (**Study V**, Gershenson 2009).

If the microbes in deeper soil layers of **Study V** had lower temperature optima, it could partly explain the initial difference in Q_{10} curves between the organic and mineral soil layers. However, differences in SOM quality and substrate availability are a more likely explanation. At least the changes in the shape of Q_{10} curves in each soil layer with time are

related to changes in SOM quality and substrate availability (**Study V**). In **Study V**, this change in SOM quality is seen as the driver that changes the microbial community structure, as the change in microbial communities is larger in the soil layers, where changes in SOM quality were also larger. Thus, although changes in microbial community composition can affect the temperature sensitivity of SOM decomposition, the SOM quality was the ultimate reason behind the changes in Q_{10} is this study. With increasing incubation time the substrates decomposed are of lower quality, leading to higher E_a and higher Q_{10}.

When substrate availability is low, it limits decomposition rates regardless of temperature (Atkin and Tjoelker 2003). Wan and Luo (2003) showed in a field-study that reduced labile C inputs decreased respiration rate and Q_{10}. Addition of labile substrates to soil, where substrate availability is limiting decomposition, has been shown to increase the Q_{10} of respiration (Larionova 2007, Gershenson 2009), which is consistent with Michaelis-Menten kinetics. At low substrate concentrations, Q_{10} have been found to be positively correlated with the amount of soluble sugars in soil (**Study V**) or in plants (Atkin and Tjoelker 2003, Covey-Crump 2002). Variation in substrate availability can explain variation of apparent temperature sensitivities in the field, and omitting it can be a reason for some of the inconsistencies in temperature sensitivities of labile and more recalcitrant C (Gershenson 2009). How it should be taken into account in models is a tricky question, since the substrate availability to microbes is very difficult to measure directly.

5.5 Climatic gradient- and translocation studies (Studies III and VI)

SOM quality along gradients of MAT (Study III)

In **Study III**, no differences were found in the amounts of labile SOC fractions per total C between the southern and northern forest sites. In the Norway spruce forest, there was more microbial biomass per total OM content in the northern sites compared to southern sites, but no similar trend was found in the Scots pine forests. Concentrations of cold- and hot water soluble C were correlated with CO_2 production rates. Higher amounts of cold water soluble C in the spruce-dominated sites, compared to pine dominated-sites, may thus partly explain their higher CO_2 production (basal respiration rate, R_0). Within each forest type, the basal respiration rate (R_0, respiration at 0 °C, determined from laboratory incubations at the same temperature range 5-33 °C) did not differ between north and south. Tree species affected microbial community composition more than the climatic conditions. The microbial community composition differed between northern and southern sites for the spruce forests but not for the pine forests. The carbon utilization patterns were dependent on climate and also on the forest site type.

Despite these differences in microbial community structure and carbon utilization potentials, there were no differences in the temperature sensitivities of heterotrophic respiration between tree species or climatic conditions (**Figure 5**). This implies that the amount and quality of microbially available C are more important for determining the temperature-dependent Q_{10} curves than the microbial community composition. This would support the idea of functional redundancy of the SOM decomposing microbial community (e.g. Nannipieri et al. 2003, Setälä and McLean 2004, Salminen et al. 2010). Also Waldrop and Firestone (2006a) found that microbial community composition differed between plant overstory communities, but that these microbial communities were functionally similar.

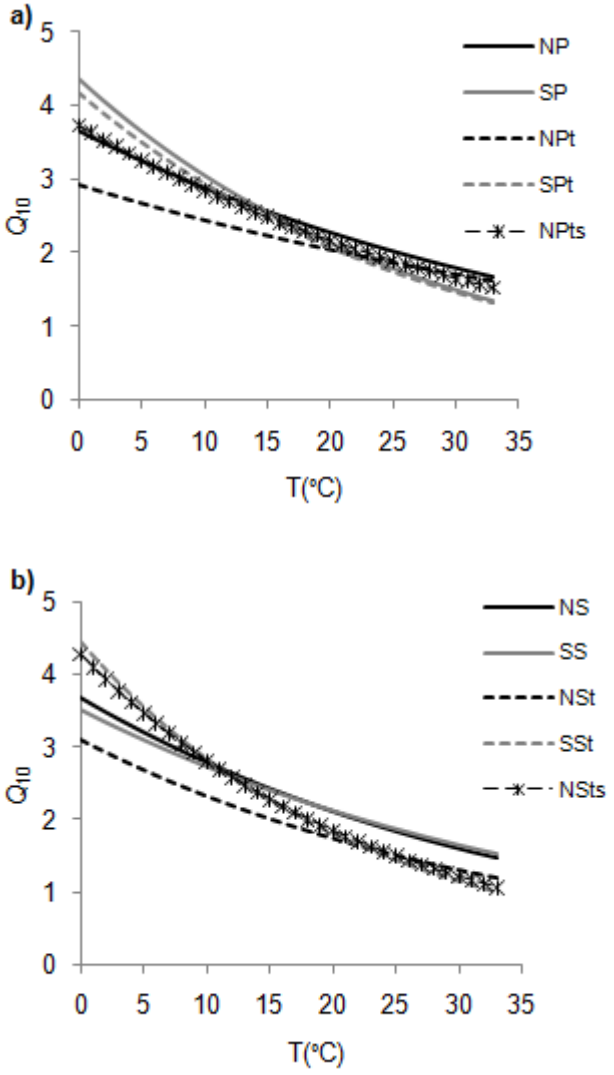

Figure 5. The temperature-dependent Q_{10} curves for organic layers of the a) pine-dominated and b) spruce-dominated forest sites (**Study III, VI**). NP = north pine, SP = south pine, NPt =north pine transplanted at site, SPt = south pine transplanted at site, NPts = north pine transferred to south. NS = north spruce, SS = south spruce, NSt = north spruce transplanted at the site, SSt = south spruce transplanted at the site, NSts = north spruce transferred to south. Only NSt differed statistically significantly from the other spruce sites.

The results from **Study III** are consistent with results from studies **I** , **IV** and **V** in that the decomposition of the most labile C is not especially temperature sensitive, and thus its amount is not largely affected by climate. Because the sizes of these pools are small and they are rapidly replenished, a 4.5 °C difference in MAT is probably too small to cause a statistically significant effect. Fissore et al. (2008) reported a decrease in SOM quantity and quality with increasing MAT (22 °C gradient) along a forested gradient in the United States. They also found a small decrease in the labile C (MRT 33 days, 2% of tot C) with increasing temperature. In previous studies, the microbial C to total C ratio has been found to either increase (Insam et al. 1989, Santruckova et al. 2000, Franzluebbers 2001) or decrease (Insam 1990, Grisi et al. 1998) with increasing MAT.

Generally, soil carbon stocks have been found to increase with decreasing temperatures, and be largest in colder and wetter climates (e.g Jenny 1941, Post 1982, Jenkinson 1988). Although this is probably true globally, on regional scale opposing trends with temperature have been found (Liski and Westmann 1997, Callesen et al. 2003, Egli et al. 2007) and the effect could depend on the soil texture and tree species on the gradient (Callesen et al 2003, Fissore et al 2009). When comparing the results from studies that have measured the amounts of different SOM fractions along climatic gradients, the comparison is complicated by different operational definitions for "labile", "intermediate" and "stabilized" SOM. However, several studies have found that the proportion of C stock in stabilized fractions (e.g. heavy fractions, mineral associated fractions) increases with temperature, while the proportion of litter, light fraction or POM decreases (Jenny 1950, Zimmermann et al. 2007, Wagai et al. 2008, Leifeld et al. 2009).

Studies that have measured ^{14}C activities of the different fractions have found that the MRT's of litter, light fraction or POM strongly decrease with MAT, implying that their decomposition is temperature sensitive (Vitousek et al. 1994, Townsend et al. 1995, Trumbore et al. 1996, Wang et al. 2005, Leifeld et al. 2009). The decomposition of the most labile C has not been found to be especially temperature sensitive along climatic gradients (eg. Couteaux et al. 2002). Amounts or MRT's of mineral associated SOC have not been related to MAT (Trumbore et al. 1996, Liski et al. 1999, Giardina and Ryan 2001, Wang et al. 2005, Wagai et al. 2008, Leifeld et al. 2009). Instead, in a study of Leifeld et al. (2009), the MRT of mineral associated organic matter was positively related to soil mineral surface area, suggesting that stabilization through organo-mineral associations was retarding decomposition. These results are generally consistent with the results form **Studies I** and **IV,** while the exact temperature sensitivities obtained for SOM fractions in gradient studies may be over- or underestimations due to co-variation of other factors with temperature along the gradient, e.g. litter production, moisture, pH, N availability or quality of the extracted fractions (e.g. Vitousek et al. 1994, Kirschbaum 2000, Leifeld et al. 2009).

When comparing SOM quality, i.e. the amounts of different SOM fractions along the climate gradients, it should be remembered that "It is the carbon that has already left the soil (at warmer climates) that may reveal the latitudinal importance of temperature on SOM dynamics" (Davidson et al. 2000). Vancampenhout et al. (2009) found no evidence of a higher proportion of chemically recalcitrant compounds at warmer climates compared to colder climates, which would have been the case if labile and recalcitrant pools had similar temperature sensitivities. Extractable SOM from colder climates resembled more the composition of litter, and in warmer climates increased microbial degradation had altered SOM chemistry more. SOM in tropics was low in lignins, indicating that its chemical recalcitrance does not lead to accumulation in soil under favorable decomposition conditions. Incubation studies have found that organic matter in tropical soils is more

degraded or humified than in temperate soils, based on the lower cumulative respiration per initial C, and a smaller decrease in microbial biomass during 150 day laboratory incubation (Grisi et al. 1998). Garcia-Pausas et al. (2008) found that cumulative CO_2 production per total C during 28 days incubation was lower from soils from warmer and wetter sites along the climate gradient in the Pyrenees. Niklinska et al. (1999) found that respiration rates from northern soils remained relatively similar during a 14-week laboratory incubation, but decreased fast in soils from the southern border of the climatic transect from Sweden to the Pyrenees. They concluded that the SOM from the north was more uniform in quality, mostly consisting of compounds relatively resistant to decomposition, while central European soils consisted of two different pools: a labile pool that was depleted early during the incubation, and a resistant, slowly decomposing pool. This could be interpreted so that northern soils have a larger intermediate C pool. Soils in warmer climates have a smaller pool of intermediate C, because this highly temperature sensitive fraction is more efficiently decomposed at warmer sites, and a larger pool of stabilized C. The larger pool of labile C in warmer sites could be due to longer growth periods and larger labile C inputs to soil (Franzluebbers et al. 2001).

Although there are numerous studies that have measured the amounts of different SOM fractions along gradients of MAT, there is still uncertainty on how these C stocks formed at different climatic conditions will change in response to climate warming, because the lack of process-based understanding (Trumbore 2009). The effect of warming on soil C storage may depend on different controlling factors at the studied sites, e.g. effect of soil mineralogy, vegetation (C quality and substrate availability), moisture, nutrient limitation (Rustad at al. 2001, Fissore et al. 2008, 2009). Experimental warming and translocation studies have been made to study the effect of climate change on soil C storage in different ecosystems.

Translocation of soil sections to warmer climate (Study VI)

Initially there were differences in surface vegetation, microbial community structure and carbon utilization patterns of the microbes between the northern and southern sites (**Study III, VI**). Two years after a transfer into a warmer climate, these ecological indicators in the transferred samples had slightly changed towards those of the southern sites (**Figure 6**). However, both the basal respiration rate at 19 °C and the temperature sensitivity modeled with the Gaussian function (**Figure 5**) were unaffected by translocation to the south. This indicates that the change in the quality of C inputs or the increased SOM decomposition due to warmer climate had not changed the SOM quality enough to change the respiration rate and its temperature sensitivity.

These results support the conclusions from **Study III** that similar C quality and availability leads to similar respiration rates and temperature sensitivities regardless of differences in the microbial community structure and climatic conditions where the SOM has been formed. Also a study of Tuomi et al. (2009) has shown that Yasso07 soil carbon model can adequately predict litter decomposition rates across the global climate conditions, based on the chemical quality of litter and temperature and precipitation at a site, despite possible differences in microbial communities. The implication of these results for soil carbon modeling is that the temperature sensitivity of SOM decomposition could be described with the same temperature response function also when simulating the effect of

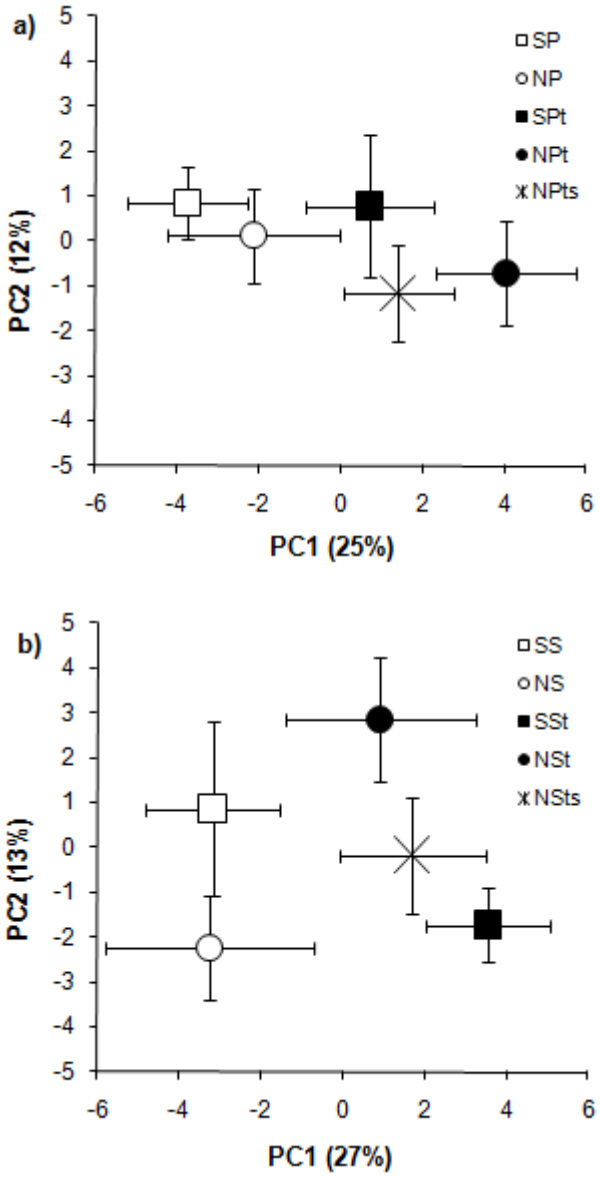

Figure 6. PCA scores of the phospholipid fatty acids (PLFAs) of the soil samples (n=27) (**Study VI**). The error bars represent standard deviation. a) NP = north pine, SP = south pine, NPt =north pine transplanted at site, SPt = south pine transplanted at site, NPts = north pine transferred to south. b) NS = north spruce, SS = south spruce, NSt = north spruce transplanted at the site, SSt = south spruce transplanted at the site, NSts = north spruce transferred to south.

climate change, although it causes changes in surface vegetation and soil biology. Observed changes in the microbial community composition in samples transferred south (**Study VI**) may be due to changed litter inputs and higher MAT, but this change did not lead to lower basal respiration rates or lower Q_{10}. Thus, these results do not support the "thermal adaptation" hypothesis of Bradford et al. (2008). Because Q_{10} generally increased towards lower temperatures (**Study III**, **VI**), increases in temperature would cause higher proportional increase in C decomposition at sites, where soil temperatures are the lowest (**Study VI**). This shows that when modeling the effects of climate warming on soil carbon storage, it is important to use Q_{10} values calculated at temperature ranges naturally occurring in the soil, as discussed in **Studies V** and **VI**.

Zimmermann et al. (2009) came to similar conclusions in their study, where soils were transferred from a colder climate to a warmer climate along an elevation gradient. Since Q_{10} is temperature dependent, it was higher for the higher elevation sites, when calculated for the mean soil temperature at the site. Several studies have found no difference in temperature sensitivity of soil respiration for soils collected along altitudinal or latitudinal gradients, when Q_{10} values were calculated for the same temperature range (**Study III**, Rey and Jarvis 2006, Niklinska and Klimek 2007, Zimmermann et al. 2009). Thus, these studies show that different Q_{10} values measured *in situ* for different soils, may be just due to different temperature ranges used for measurements, and do not necessarily imply differences in SOM quality or different temperature optima for microbial respiration. For relating differences in Q_{10} to SOM quality, the measurements should be conducted in controlled conditions using the same temperature range.

The amplitude of intra-annual temperature variations is large in boreal soils (Kähkönen et al. 2002, Pumpanen et al. 2008). The responses of microbial communities to these seasonal variations may be more important for the function of the community than the increase in MAT. Waldrop and Firestone (2006a) found that, based on enzyme essays, there were seasonal fluctuations in the potential of the microbial community to decompose different C substrates. This seasonal fluctuation in the functioning of microbial community was largely due to changes in soil temperature. Also other studies show that microbial communities may fluctuate during the year, so that different microbes dominate during different seasons (Monson et al. 2006). This is consistent with the laboratory incubation study of Biasi et al. (2005), where changes in the microbial community structure induced by incubation at a higher temperature for 6 weeks, were reversible when temperatures were decreased again. Recalcitrant substrates are more efficiently decomposed at higher temperatures (**Study I**, **IV**, Waldrop and Firestone 2004, Biasi et al. 2005), and if climate change increases the amount of warm days during the year, it would increase the decomposition of recalcitrant C.

However, it is not likely that a small increase in MAT changes the optimum temperature of respiration, and thus the temperature response of total soil heterotrophic respiration in the boreal forest soils. Shifts in the optimum temperature of microbial growth have been observed in laboratory incubations, where soils have been incubated at temperatures outside the cardinal points (Ranneklev and Bååth 2001, Bárcenas-Moreno et al. 2009), but incubations at or below optimum temperature have induced only minor shifts in the temperature response of the microbial community (Petterson and Bååth 2003). Larger changes in microbial community composition occur when it experiences extreme conditions outside the "life history" of the community (Waldrop and Firestone 2006b). Because the warming in the boreal region will change soil temperatures towards the optimum for microbial activity (within the range of temperature variations the microbes are

used to), it is not likely that this will largely shift the optimum temperature for respiration. This is consistent with our results that temperature sensitivity of heterotrophic respiration was not changed due to the 4.5 °C increase in MAT (**Study III, VI**).

Experimental warming studies

The effect of climate warming on soil respiration has also been studied by artificially warming the soils *in situ*, either using heating cables buried in soil (e.g. Melillo et al. 2002, Eliasson et al. 2005), heating air above the plots by infrared radiators (Luo et al. 2001) or by building open-top chambers (Rinnan et al. 2009) or greenhouses over the studied plot (e.g. Allison and Treseder 2008). Many experimental warming studied have found that the response of soil CO_2 efflux to a step increase in temperature declines over time (e.g. Rustad et al. 2001, Melillo 2002, Eliasson et al. 2005). This has been hypothesized to be due to microbial acclimation to new temperature conditions (Bradford et al. 2008, Luo et al. 2001, Reichstein et al. 2005). Another, more plausible, explanation is an initial increase in labile C decomposition, but a decrease in respiration rate after the small labile C pool has been depleted during the first decade of warming (Peterjohn et al. 1994, Eliasson et al. 2005, Knorr et al. 2005, Kirschbaum 2004, 2006). In nature, the substrate availability is determined by a balance between input (litter, root exudates) and output. Net primary productivity will often increase with warming and increased CO_2 concentration, and thus also C input to soil should increase. Therefore, a depletion of a C pool means that its decomposition is faster than new C input into this pool.

In addition to increased basal respiration rate during the experimental warming, many studies have reported a decrease in (seasonal) Q_{10} (Luo et al. 2001, Niinistö et al. 2004, Zhou et al. 2006). This has been interpreted as the labile C being highly temperature sensitive and more recalcitrant C being less temperature sensitive (Davidson and Janssens 2006). This could also indicate a limiting effect of substrate availability after depletion of the most labile C (**Study V**), or limiting effect of drought in the warmed treatment. Drought can also decrease substrate availability due to decreased diffusion of substrates. According to Michaelis-Menten kinetics, the substrate concentration that is required to saturate r increases with increasing temperature (Atkin and Tjoelker 2003). Thus, decreasing labile C pools in the warmed treatment could explain the relatively higher decrease in respiration at higher temperatures and thus observed decreases in apparent Q_{10}, when calculated with the exponential equation over the whole temperature range (Luo et al. 2001, Niinistö et al. 2004, Zhou et al. 2006). Because Q_{10} its temperature dependent, the observed decrease in Q_{10} in these experimental warming studies *in situ* could also partly be due to the different temperature ranges used for calculating Q_{10}'s (less low temperatures and more high temperatures included in the measurements from warmed plots).

In the study of Niinistö et al. (2004) of a boreal forest, soil warming had as high increasing effect on soil respiration during the 4th year of experiment as in the 1st year. Reth et al. (2009) recently showed in a 10-year experimental warming study, that soil respiration was still higher in the warmed treatment after 10 years. These results imply that it is not necessarily the decrease in the most labile C that is most relevant for explaining the different results of warming studies. The results of Reth et al. (2009) are consistent with the results of **Study IV**, showing that the intermediate C cycling on decadal time scales is highly temperature sensitive. If a soil contains a large pool of "intermediate" SOM that is biochemically recalcitrant, but not effectively stabilized with minerals, then soil respiration

could remain elevated for decades. This might be the case for a large portion of SOM in coarse textured boreal forest soils, especially in the organic layers, or tundra soils (Biasi et al. 2005, Niklinska et al. 1999, Weintraub and Schimel 2003, Shaver 2006), which contain a large amount of relatively labile C that is not stabilized through association with minerals.

Recent modelling studies have shown that a model with a small labile pool and a larger more recalcitrant pool that is also temperature sensitive, but decomposes much more slowly, can also fit the experimental data well (Eliasson et al. 2005, Kirschbaum 2004). Thus, the observed changes in respiration rate and Q_{10} in experimental warming studies can be explained based on changes in relative amounts of different SOC pools, and could be modeled with multi-pool soil carbon models (Knorr et al. 2005, Kirschbaum 2004, Rey et al. 2007). Neither a high temperature sensitivity for the most labile C and a low sensitivity for the more recalcitrant fractions, nor temperature acclimation of microbes, is needed to explain the observations (Davidson and Janssens, 2006).

Applicability of the short-term temperature sensitivities determined in laboratory

Ågren and Bosatta (2002) suggest that comparing the MRT of soil C at different latitudes gives a more correct estimate for the long-term temperature sensitivity than measuring the short-term temperature sensitivity at a common temperature range in the laboratory, where the soils are perturbed from their native temperature conditions. Kirschbaum (2006) has an opposing view that comparing the decomposition rate of soils formed in different climates underestimates the temperature sensitivity, because SOM of lower quality (slower decomposition rate) at a high temperature and of higher quality (higher decomposition rate) at a low temperature are then being compared. The less temperature-sensitive Q_{10} curves obtained this way are thus due to different SOM pools being compared. This error is similar to comparing the heterotrophic soil respiration of two soils incubated long-term at two different temperatures, in the so-called parallel incubations (Kirschbaum 2006). Thus, according to Kirschbaum (2006), laboratory incubations give a more correct estimate of the temperature sensitivity. If climate warming is fast, it can also be seen as a perturbation of the soils from their natural temperature conditions, and thus the laboratory incubations give information on how the active part of soil C (with MRTs small enough to be able to respond to warming during the course of the experiment) will react to this perturbation. If there is a shift in substrate utilization with temperature, the incubation at a higher temperature gives information on which kind of substrates can be decomposed during a warmer day, compared to a colder day.

By definition the short-term temperature sensitivity of SOM decomposition measured in the laboratory (e.g. 24 hour incubations) does not take into account possible microbial adaptation developing after longer exposure to higher temperatures. However, **Studies III** and **VI** show that such a phenomenon does not have a measurable effect in the studied soils. Thus, with certain precautions, the short-term temperature sensitivities measured in controlled conditions can be used to predict CO_2 fluxes from SOM decomposition in the field. Sieving of soils could disrupt soil structure and make available SOM that is not available for decomposition in the field. However, since the studied forest soils do not have a strong soil structure, this effect was probably small. Also, soil respiration measured at the natural temperature range *in situ* has been shown to give high Q_{10} values, especially for

deeper mineral soil layers (Pumpanen et al. 2008), which is compatible with the steepness of the temperature dependent Q_{10} curves measured in the laboratory (**Study III, V, VI**).

Warming in northern soils will happen on a temperature range from sub-optimal temperatures towards the optimal temperature for microbial growth. When extrapolating from laboratory incubations to natural conditions, it would be thus important not to include temperatures above the optimal temperature for soil microbes when fitting the temperature dependence functions. Including high temperatures, and fitting a constant Q_{10} for this long temperature range, leads to an underestimation of the Q_{10} of microbial respiration (e.g. Fang et al. 2005), and its detachment from SOM quality, and microbial activity (Pietikäinen et al. 2005). The temperature-dependent Q_{10} curves are steeper in boreal areas with low temperatures (Chen and Tian 2005). Thus, the use of a flat temperature response function (fixed Q_{10} of 2 used in many ecosystem models) would underestimate the temperature sensitivity most in the boreal biome, while the error is probably smaller for tropical soils (Chen and Tian 2005). Using spatially variable Q_{10} values for different biomes (e.g. higher for high-latitude soils, lower for deserts) has been shown to lead to an overall stronger modeled positive feedback from soil carbon decomposition to climate warming, than using a same global mean value for all regions (Zhou et al. 2009).

6 CONCLUSIONS

Different SOM fractions were found to have varying temperature sensitivities, despite the quite similar Q_{10} values of total heterotrophic respiration for the studied soils. The Q_{10} of total heterotrophic soil respiration from laboratory incubations or field measurements is thus an inadequate measure for the temperature sensitivity of different SOM fractions. Assuming a homogeneous pool of SOM leads to either underestimation or overestimation of soil carbon-climate feedback depending on soil layer and timescale. The most labile C is not very temperature sensitive, but is utilized irrespective of temperature (**Studies I, III, IV, VI**). Decomposition of more recalcitrant, intermediate C (MRT from years to decades) was highly temperature sensitive (**Studies I**, **IV** and **V**). The older, stabilized C has again lower, but still moderate temperature sensitivity (**Study IV**). A multiple pool approach is thus needed for estimating soil carbon cycle – climate feedbacks. Using the same Q_{10} for all soil C pools leads to erroneous estimates on the effects of climate warming on soil carbon stocks. The magnitude of this error depends on the relative abundances of different SOM pools with varying kinetic properties and temperature sensitivities in different soils.

Based on the results of this thesis, SOM decomposition in the surface layers of boreal forest soils could increase more than earlier estimated as a result of climate warming during the coming decades. Thus, a positive feedback to climate warming from the boreal forest soils is a concern. The timescale of this possible positive feedback is problematic. Due to the high temperature sensitivity of the intermediate, decadally cycling fraction, these soils could release more CO_2 to the atmosphere during the time, when the anthropogenic CO_2 emissions should be sharply decreased in order to keep the rise in global average temperature below 2 °C. On longer, centennial timescales, these C losses are probably balanced by the lower temperature sensitivity of older C fractions (**Study IV**). These fractions may be of too low quality to be efficiently consumed by the microbes, at least in the absence of labile C substrates, or they may be stabilized through association with minerals.

The Q_{10} values were found to decrease with increasing temperature, which is consistent with earlier observations and chemical kinetics. This relative decrease in the Q_{10} with temperature was higher for mineral soil layers than for organic layers in the studied forest soils (**Study V**), which probably reflected the lower C quality and lower substrate availability in the mineral soil. There is increasing evidence of this temperature-dependent Q_{10} also on the global scale. The use of a constant Q_{10} of 2 for soils from different climate regions in global climate models, e.g. HadCM3LC, is thus not appropriate. When modeling soil carbon – climate feedbacks a function taking into account the temperature- dependence of Q_{10} should be used instead, as is already done in many soil carbon models (e.g. Roth C, original Century, and Yasso07). The Q_{10} values from a temperature range natural for each climatic region should be used in global climate models. In the studied boreal soils, Q_{10} values around 2 were found only after temperatures from 20 °C upwards, which seldom occur in the forest soils of the boreal regions. The Q_{10} values at lower temperatures were much higher, suggesting that decomposition in these soils could increase more than earlier estimated, because the temperature increase due to climate change occurs at a lower part of the curve. Thus, in addition to the different temperature sensitivities of different SOM fractions, the error from using a constant Q_{10}, instead of a temperature-dependent Q_{10} for a correct temperature range, is also critical for modeling the soil carbon – climate feedback.

Short-term temperature sensitivity of SOM decomposition measured in controlled conditions did not depend on the previous temperature range the soils had experienced (southern or northern Finland) (**Study III**). Transplanting of soil sections from north to south did not change the temperature sensitivity of heterotrophic respiration, although the transfer to warmer climate changed the microbial community composition (**Study VI**). The same temperature sensitivity function could be applied in changing climatic conditions, despite the possible effect of changing climate on C inputs and microbial community structure. Based on these results, it seems that a decrease in the amounts of labile SOM, rather than microbial acclimation to higher temperature, is responsible for the decreased response of soil respiration to warming after an initial spike in some soil warming experiments. A multi-pool soil carbon model, with different decomposition rates and temperature sensitivities for different pools, could explain the observations from warming studies correctly. Thus, it is important to further study the mechanisms that control the decomposition, stabilization and destabilization of different SOM fractions in soils, and incorporate this knowledge into soil carbon models.

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