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Part I.

General Introduction

1. Soils and the global carbon cycle

There has been growing interest in recent decades to improve understanding of the global carbon cycle due to the awareness that its perturbation by anthropogenic activities has far reaching consequences for earth's atmosphere and climate system (Treut et al., 2007; IPCC, 2013). Earth's carbon is cycled through four major pools: rocks and sediments, oceans, the terrestrial biosphere, and the atmosphere (Reeburgh, 1997). Rocks and sediments contain more than 99% of total carbon, but turnover is slow and takes place on geological timescales (i.e., 10th to 100th of millions of years); yet very little carbon is exchanged between the rock and sediment pool and the atmosphere. Most of the current carbon exchange takes place between the atmosphere, the terrestrial biosphere and the ocean surface waters, and it is the balance between these pools that affects climate on a timescale from decades to millennia (Jobbágy et al., 2000; Sabine et al., 2004; IPCC, 2007; Chapin et al., 2012). Human enterprises have altered the global carbon cycle through activities such the burning of fossil fuels, cement production and land use change, adding an average flux of 9.1 Gt C $year^{-1}$ to the atmosphere in the years from 2000–2006. Around 4.1 Gt of this carbon input is stored in the atmosphere, 2.2 Gt are taken up by the oceans and 2.8 Gt by the terrestrial biosphere (Canadell et al., 2007; Le Quéré et al., 2009; IPCC, 2007; Chapin et al., 2012).

Carbon enters terrestrial ecosystems through photosynthesis of plants, using atmospheric carbon dioxide and energy from sunlight to produce biomass. Of the carbon fixed by photosynthesis (gross primary production), around half is

respired by plant tissues and thereby returned to the atmosphere (Gruber et al., 2004). Most of the remaining carbon (net primary production) enters the soil as leaf, wood, and root litter, as well as root exudates (Chapin et al., 2012).

Organic carbon entering the soil system is decomposed and fed upon by animals and heterotrophic microorganisms, to support their growth. As this soil organic matter (SOM) is cycled through the decomposer biomass, it becomes successively mineralized to CO_2, accounting for the other half of the carbon fixed during gross primary production (Gruber et al., 2004). The mean residence time of SOM, before it is respired, can vary from weeks to millennia (Schmidt et al., 2011) and total organic soil carbon stocks are estimated to be between 1,500-2,400 Gt globally, with an additional 1,700 Gt of organic carbon stored in perennially frozen soils (IPCC, 2013). Controls on the activity and physiology of decomposers can affect the balance between net primary production and decomposition and thereby the carbon storage potential of soils (Colman and Schimel, 2013).

2. Microbial carbon use efficiency

Carbon taken up by heterotrophic microorganisms can be either respired to CO_2 or CH_4, assimilated into biomass (growth), or excreted. While CH_4 production can be high under anaerobic conditions, carbon is usually completely oxidized to CO_2 under aerobic conditions (Martink and Stahl, 2012).

The partitioning of carbon between respiration and biomass production of heterotrophic microorganisms is termed carbon use efficiency (CUE, sensu Giorgio and Cole, 1998), and is defined as:

$$CUE = \frac{Microbial\ production}{(Microbial\ production\ +\ Microbial\ respiration)}$$

Terminology and definitions vary, however, depending on author and method used for measuring CUE. Alternative terminologies include substrate use efficiency (Schimel and Weintraub, 2003; Cotrufo et al., 2013), microbial efficiency (Frey et al., 2013) microbial growth efficiency (Six et al., 2006), or growth yield efficiency (Thiet et al., 2006). As carbon inputs into ecosystems are metabolized by microorganisms and stable SOM is mainly derived from microbial products, CUE determines the amount of carbon potentially available for long term storage in soils (Cotrufo et al., 2013; Rumpel and Kögel-Knabner, 2010).

It has long been recognized that CUE strongly affects the estimation of SOM storage in biogeochemical models (Parton et al., 1987), as model predictions of are sensitive to small changes in CUE (Six et al., 2006). The majority of biogeochemical models assume that CUE is constant, but values ranging from 0.15 to 0.6 have been used in different models (Manzoni et al., 2012).

Most of the early empirical estimates of CUE came from bacterial cultures and aquatic ecosystems, partly due to the methodological challenges of measuring CUE in a complex matrix such as soil (Giorgio and Cole, 1998; Manzoni et al., 2012). The mean estimates for CUE in aquatic and terrestrial ecosystems are

0.26 and 0.55, respectively, with large variations in both systems. Based on theoretical considerations, Sinsabaugh et al. (2013) have attributed this discrepancy to methodological limitations leading to inflated values in terrestrial systems and proposed that broad-scale biogeochemical models with fixed CUE should assume a value of 0.3.

3. Controls on microbial carbon use efficiency

Both theoretical considerations and empirical data from terrestrial and aquatic ecosystems suggest that microbial CUE varies in response to environmental factors as well as substrate properties (Manzoni et al., 2012).

Organisms can be described in terms of their elemental composition. Most heterotrophic organisms need to maintain the ratio of the elements in their bodies within relatively narrow limits, a trait known as stoichiometric homeostatis (Sterner and Elser, 2002). In his seminal work, Redfield (1958), demonstrated that carbon, nitrogen, and phosphorus in marine plankton has on average a ratio of 106:16:1, with little variation across the world's oceans. Similarly, an average C:N:P ratio 60:7:1 has been found for soil microbial biomass in a global dataset (Cleveland and Liptzin, 2007). Plants are non-homeostatic organisms and are more flexible in their stoichiometry in response to nutrient availability than microorganisms and generally have wider elemental ratios (Sterner and Elser, 2002). When there is a mismatch between the elemental ratios of a homeostatic microorganism and the resources it consumes, one ore more of

the elements will become limiting to its growth. The elemental composition where limitation switches from one element to another is known as the threshold elemental ratio (TER) (Urabe and Watanabe, 1992). In order to maintain stoichiometric homeostasis, i.e., because the limiting element determines the ability of an organism to grow, elements in excess have to be eliminated. If the carbon:nutrient ratio is below TER, the microorganism is carbon limited and will mineralize the excess nutrient. When the carbon:nutrient ratio of the substrate is above TER, excess carbon is either respired through overflow ("waste") respiration, or excreted. Nutrient limitation thus reduces CUE.

CUE also depends on the chemistry of the substrate being utilized. Complex substrates that require a series of enzymatic reactions to breakdown may result in lower CUE (Manzoni et al., 2012). The efficiency with which substrates can be converted into biomass is also dependent on the metabolic pathways involved in their assimilation (Gommers et al., 1988). Finally, substrates differ in the chemical energy they contain, measured as the degree of reduction. The degree of reduction is defined as the number of moles of electrons available for transfer to oxygen per mole of carbon. The degree of reduction of microbial biomass is around 4.2. Substrates with a lower degree of reduction, such as most organic acids, will have a low efficiency of conversion to biomass as the incorporation of these substrates into biomass is energy limited (Roels, 1980).

Temperature affects microbial metabolism as well as the uptake of nutrients. The Arrhenius equation, which describes the relationship between chemical reaction rates and temperature, predicts that both microbial growth and respiration will increase with temperature. Due to the complexity of growth and

increasing cellular heat stress responses at higher temperatures, respiration tends to be more sensitive to temperature than growth. CUE would therefore be expected to decline as temperatures rise. A number of studies have found a negative correlation between temperature and CUE, with CUE decreasing by around 1% $^{\circ}C^{-1}$ (Tucker et al., 2013; Frey et al., 2013). However, the exact effects of temperature on CUE are unclear. Lopez-Urrutia and Moran (2007) have found that CUE decreases due to substrate limitation at higher temperatures, rather than temperature itself. Frey et al. (2013) reported that the effect of temperature on CUE is dependent on the substrate utilized as respiration costs due to enzyme production for the decomposition of more complex substrates increase with temperature. There is also evidence that acclimation of CUE to seasonal changes occurs as well as to long term increases in temperature (Tucker et al., 2013; Frey et al., 2013).

CUE can also be affected by microbial community composition. It has long been assumed that fungi have a higher CUE than bacteria (Parton et al., 1987). However, recent studies have found no effect of soil fungal:bacterial ratios on CUE (Thiet et al., 2006; Dijkstra et al., 2011). On the other hand, it has been shown that communities adapted to different levels of substrate availability differ in their CUE. Under conditions of abundant resources, fast growing opportunistic (zygmogenous) communities with low CUE develop. When resource availability is low, communities shift towards slow growing (autochthonous) microorganisms with high CUE (Shen and Bartha, 1996; Lipson et al., 2009).

4. Estimating carbon use efficiency using stable isotopes

Stable isotopes can be used to trace the flow of matter through biological systems in two ways. First, by measuring variations in the natural abundance of isotopes, which arise as the result of fractionation during chemical reactions. Second, by introducing compounds that are artificially enriched in heavy isotopes (labeled) and following the fate of these tracers in various system components. To measure microbial CUE in terrestrial environments, soil, sediment, or litter samples are incubated with a substrate enriched in the heavy stable carbon isotope ^{13}C. At the end of the incubation, the ^{13}C content of the microbial biomass as well as the respired CO_2 is measured. CUE can then be calculated as

$$CUE = \frac{Microbial\ ^{13}C}{\left(Microbial\ ^{13}C + Respired\ ^{13}C\right)}$$

This approach has been recently questioned as only the short term uptake and respiration of added substrates are measured which does not fully capture microbial growth and respiration (Sinsabaugh et al., 2013). It can therefore be considered a measure of microbial substrate use efficiency (Sinsabaugh et al., 2013), which is used as a proxy for CUE (Frey et al., 2013)

5. Study aims

Productivity and nutrient availability in ecosystems are strongly determined by climate. In arctic and subarctic ecosystems, plant productivity is limited

by low temperatures, as is decomposition. While the soils of the northern biomes, tundra and taiga (boreal forest), contain vast stores of organic carbon, they are poor in reactive nitrogen (Schimel and Bennett, 2004; Meyer et al., 2006). These ecosystems are of particular interest as they are disproportionately affected by climate change (IPCC, 2013). As a result, decomposition rates may increase, which could lead to the release of large amounts of CO_2 (Weintraub and Schimel, 2003; Davidson et al., 2006; Billings et al., 2010). It is therefore important to improve our understanding of microbial carbon cycling in these ecosystems.

The aim of this study was to investigate patterns in CUE across a range of ecosystems along a latitudinal transect. We specifically focused on the effect of nitrogen availability on CUE, both along the transect and within the soil profile. We expected that CUE would increase with nitrogen availability from north to south. Similarly, we expected that CUE would increase with soil depth as plant litter inputs are successively decomposed and elemental ratios decrease. To test our hypotheses, we established a 1,500 km latitudinal transect through West Siberia that ranged from the Tasovskiy peninsula in the North, to the border of Kazakhstan in the South. Samples were collected from six ecosystems in four major biomes along the transect: tundra, taiga (northern taiga, middle taiga, southern taiga), forest steppe and steppe. Soil samples from the top three soil horizons at each site were sampled and CUE measured as the partitioning of label between biomass production and respiration in incubation with a mixture of ^{13}C labeled substrates.

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Part II.

Manuscript

1. Abstract

Soils represent the largest terrestrial pools of organic carbon (C), and arctic and sub-arctic ecosystems, where decomposition is thought to be mainly limited by climate and low nitrogen (N) availability, store more C in their soils than the whole atmosphere. As stable soil organic matter is largely derived from microbial compounds, the partitioning of C uptake by microorganisms into growth and respiration determines the C storage potential in soils. To investigate the effect of nitrogen availability on soil microbial C cycling we established a 1,500 km latitudinal transect through West Siberia and measured microbial carbon use efficiency (CUE), as well as C and N pools and extracellular enzyme activities in the top three horizons of seven sites along the transect. We found that while C:N ratios decreased with soil depth, CUE was similar in the organic topsoil and upper mineral horizon but lower in the deeper mineral horizon, which is counter to an expected increase predicted by stoichiometric theory. Potential oxidative enzyme activities increased with soil depth while cellobiosidase:phenoloxidase ratios decreased, indicating reduced substrate quality and/or accessibility in lower horizons. Within horizons, CUE was always negatively related to oxidative enzyme activity, as well as to dissolved

and total C in the organic horizons and to C:N ratios in the upper mineral horizons. We conclude that substrate quality is an important control on CUE in all soil horizons. We further conclude that microorganisms in deeper soil horizons are limited in their growth by substrate limitation and chemical complexity.

2. Introduction

Soils are the largest terrestrial store of organic carbon (Gruber et al., 2004) and the decomposition of soil organic matter (SOM) and subsequent mineralization to CO_2 by microorganisms constitutes a major flux of carbon (C) between the biosphere and the atmosphere (Houghton, 2007). Heterotrophic microorganisms partition the C they take up between growth, respiration, and sometimes excretion. This partitioning is described by the microbial carbon use efficiency (CUE), also referred to as substrate use efficiency (Schimel and Weintraub, 2003), microbial growth efficiency (Six et al., 2006), or growth yield efficiency (Thiet et al., 2006). CUE is defined as the fraction of the total C uptake that is allocated to growth (Giorgio and Cole, 1998). CUE determines the C storage potential of soils as stable SOM is mainly derived from microbial compounds (Cotrufo et al., 2013; Rumpel and Kögel-Knabner, 2010).

Most biogeochemical models assume CUE to be constant (Manzoni et al., 2012), while small changes in CUE can strongly affect model estimates of respiration and soil C storage (Six et al., 2006). Empirical estimates of CUE from litter, soil,

and aquatic ecosystems show large variability depending on resource chemistry and stoichiometry as well as environmental conditions (Manzoni et al., 2012). Substrates differ in their enzymatic breakdown, the metabolic pathways through which they are assimilated and the chemical energy contained, with generally lower CUE during the decomposition of more recalcitrant substrates (Ågren and Bosatta, 1987; Gommers et al., 1988; Roels, 1980). Nutrient availability, particularly of nitrogen (N) and phosphorus (P), control CUE through the relationship between substrate and decomposer stoichiometry (Manzoni and Porporato, 2009). Microorganisms need to maintain the C:nutrient ratios of their biomass within physiological boundaries and show little variability in their elemental ratios, irrespective of stoichiometry of the substrate they consume (Cleveland and Liptzin, 2007; Manzoni et al., 2010). If the substrate C:nutrient ratio exceeds a threshold or critical value, excess C is respired through overflow respiration as microorganisms become nutrient limited. If the C:nutrient ratio is below the critical value however, microorganisms become C limited and nutrients are mineralized (Sinsabaugh et al., 2009; Larsson et al., 1995). In addition, nutrient limitation may lead to increased extracellular enzyme production, increasing the supply of limiting nutrients (Moorhead et al., 2012). However, the production and excretion of extracellular enzymes also reduces CUE through the required investment of C, nutrients and energy. Temperature can also alter CUE as microbial respiration tends to be more sensitive to higher temperatures than growth (Apple et al., 2006) and increasing temperatures have been shown to decrease CUE (Steinweg et al., 2008; Apple et al., 2006; Frey et al., 2013). Based on theoretical considerations, CUE in terrestrial systems has been estimated at ~ 0.3, while the mean for reported values is ~ 0.55, a

discrepancy attributed to methodological limitations of the measurement of CUE in terrestrial systems (Sinsabaugh et al., 2013).

With differences in environmental conditions, in substrate inputs through vegetation, and in nutrient availability, CUE can be expected to vary across ecosystems. Productivity and nutrient status of ecosystems are strongly determined by climate and follow latitudinal patterns at a large scale. Within ecosystems, conditions also change in the soil profile. C:nutrient ratios decrease with soil depth, as C is successively respired and the chemical composition of SOM changes from primarily plant derived compounds to primarily microbial derived compounds (Rumpel and Kögel-Knabner, 2010). Siberian ecosystems belong to several of the world's largest biomes; tundra, taiga (boreal forest), forest steppe and temperate steppe, containing a vast amount of organic C with potentially large repercussions for global climate when decomposed (Billings et al., 2010; Tarnocai et al., 2009; Davidson et al., 2006; Weintraub and Schimel, 2003). These ecosystems differ in their productivity and nutrient dynamics, with northern ecosystems being severely N limited due to low litter inputs and quality and slow decomposition (Schimel and Bennett, 2004; Meyer et al., 2006). As northern regions are also disproportionately impacted by climate change (IPCC, 2007), it is important to improve the understanding of soil microbial C cycling in these ecosystems that span a large climate gradient.

The aim of this study was to investigate patterns of CUE across a range of ecosystems along a continental north-south transect, with a particular focus on the effect of nitrogen availability on CUE. To this end, a 1,500 km latitudinal transect through West Siberia was established that corresponds to a

threefold decrease in topsoil C:N ratios and spans four major biomes: tundra, taiga (northern taiga, middle taiga, southern taiga), forest steppe and steppe. Specifically, we focused on stoichiometric controls on microbial CUE and hypothesized that (1) CUE increases with soil depth as organic matter becomes successively enriched in N with depth, (2) CUE increases from north to south with increasing soil N availability, and (3) this latitudinal effect is less pronounced in the mineral horizons than in the organic topsoil as, environmental influences are attenuated and the substrate properties are less dependent on the vegetation in deeper soil parts. To test these hypotheses, we measured CUE in samples collected along the transect from three soil horizons using a mixture of ^{13}C labeled substrates at constant temperature and measured total and labile C and N pools as well as nutrient acquiring enzymes to assess the effects of nutrient limitation on CUE.

3. Materials and methods

3.1. Site description

Soil samples for this study were collected in the frame of the CryoCARB project which aims at investigating long term carbon storage in arctic soils (www.univie.ac.at/cryocarb). Samples were taken from 7 sites along a 1,500 km latitudinal transect in West Siberia, spanning from the Tasovskiy peninsula in the North, to the border of Kazakhstan in the South. The transect spans a range of climate and vegetation zones, from southern tundra, dominated by subarctic conditions, to semiarid steppe in the South (Table 1). Mean annual temperatures (MAT) increased along the transect from $-7.6\,^{\circ}\mathrm{C}$ to $1\,^{\circ}\mathrm{C}$. Mean annual precipitation (PPT) was 391 mm in the tundra, peaked at 437 mm in the middle taiga and declined to 309 mm in the steppe (climate data were derived from Stolbovoi and McCallum, 2002). Elevation was similar across all sites, ranging from 30 m to 106 m (Table 1).

3.2. Sampling

Soils were sampled during August 2012, proceeding from north to south along the transect in order to sample under phenologically similar conditions. At each site, samples were collected from 5 representative soil pits, located at least 2 m from the nearest tree. Soil cores were taken from the top three horizons. Live roots were removed (judged by color and elasticity), samples were homogenized or sieved to 2 mm where appropriate.

3.3. Carbon use efficiency

Samples were incubated with a mixture of uniformly ^{13}C-labeled sugars, amino sugar, organic acids and amino acids (Table 2), enriched at 10.4 at%. The overall C:N ratio for the mixture was 20, the overall degree of reduction, a measure of the chemical energy per unit mole of C, was 4.0. This mixture was chosen to approximate the properties of low molecular weight compounds available in soils for microbial consumption (Hees et al., 2005; Manzoni et al., 2012).

Two (organic topsoil and upper mineral horizon) or four gram (lower mineral horizon) of soil were weighed into 20 ml scintillation vials and placed into 250 ml or 100 ml glass bottles, respectively. Different weights and bottle volumes were chosen to account for differences in respiration rates between soil horizons. The dissolved substrate mixture equivalent to 400 µg C, 40 µg C and 4 µg C were added to organic, upper mineral and lower mineral horizon

samples, respectively. These quantities were chosen to be smaller than microbial biomass C (C_{mic}), as adding high amounts of labile C may alter microbial metabolism and CUE (Manzoni et al., 2012; Sinsabaugh et al., 2013).

The bottles were sealed with Butyl rubber plugs (Glasgerätebau Ochs Laborfachhandel e. K., Germany). Preceding tests indicated that these plugs do not leak CO_2. Using a syringe, 20 ml headspace samples were taken from the bottles and transferred to evacuated Exetainers® (Labco Ltd., UK), directly after adding the ^{13}C labeled mixture. The syringe was purged with ambient air between samples. The air removed from the bottles was replaced from a gas bag with known CO_2 concentration and carbon isotope composition. Samples were incubated at 15 °C for 24 h, after which a second set of gas samples was taken. The microbial biomass carbon (C_{mic}) was estimated by chloroform fumigation extraction (CFE) according to Jenkinson and Powlson (1976) at the end of the incubation period. Soil samples were split into equal portions and one of the aliquots was extracted with 13 mL 0.5 M K_2SO_4 for 1 h on a horizontal shaker and filtered through ashless paper filter (Whatman Ltd., UK). The second aliquot was placed in a desiccator over ethanol-free chloroform for 24 h to lyse microbial cells and subsequently extracted as described above. Dissolved organic C (DOC) and total dissolved N (TDN) in the extracts was determined using a TOC/TN analyzer (Shimadzu TOC-VCPH/CPNTNM-1, Shimadzu corporation, Japan). Aliquots of the K_2SO_4 extracts were used to determine $\delta^{13}C$ of DOC, by direct injection (without column, direct mode) on a HPLC (Dionex Corporation, Sunnyvale, CA, USA) connected through a Finnigan LC-IsoLink Interface (Thermo Fisher Scientific, Waltham, MA, USA)

to a Finnigan Delta V Advantage Mass Spectrometer (Thermo Fisher, Bremen, Germany). Stable isotopes in CO_2 (^{13}C, ^{12}C) of air samples were analyzed by headspace gas sampler (GasBench II, Thermo Fisher, Bremen, Germany) coupled to an Isotope ratio mass spectrometer (Delta V Advantage, Thermo Fisher, Bremen, Germany). CO_2 reference gas was calibrated using ISO-TOP gas standards (Air Liquide) with certified ^{13}C concentrations.

3.4. Bulk carbon and nitrogen

Dried samples of soil were ground in a ball mill to a fine powder and weighed into tin capsules. Bulk analysis of soil for total N and C and nitrogen (^{15}N, ^{14}N) and carbon isotopes (^{13}C, ^{12}C) was conducted using an Elemental analyzer (EA 1110, CE Instruments, Milan, Italy) interfaced via a ConFlo III device (Thermo Finnigan, Bremen, Germany) to a continous flow stable isotope ratio mass spectrometer (DeltaPLUS, Thermo Finnigan, Bremen, Germany). A mixture of proline and sucrose was used as a lab standard which was regularly calibrated against international standards (IAEA, Vienna, Austria) for ^{15}N and ^{13}C and against atropine for total content of N and C.

3.5. Potential enzyme activities

Potential enzyme activities of β-1,4-Cellobiosidase (”cellobiosidase”), β-1,4-N-acetylglucosaminidase (”exochitinase”), chitotriosidase (”endochitinase”),

leucine aminopeptidase ("protease"), and phosphatase were measured using microplate fluorometric asseys, as described in Kaiser et al. (2010). Substrates used were 4-Methylumbelliferone-cellobioside, 4-Methylumbelliferone-N-acetyl-ß-D-glucosaminid, 4-Methylumbelliferone-triacetylchitotrioside, l-Leucine-7-amido-4-methyl coumarin and 4-Methylumbelliferone-phosphate, respectively. Phenoloxidase and peroxidase activities were measured photometrically, using L-3,4-dihydroxyphenylalanin as substrate, according to Kaiser et al. (2010).

3.6. Calculations

CUE was calculated as:

$$CUE = \frac{^{13}C_{mic}}{(^{13}C_{respired} + ^{13}C_{mic})} \quad (1)$$

where $^{13}C_{respired}$ is the cumulative respired ^{13}C and $^{13}C_{mic}$ is the ^{13}C incorporated into biomass. Biomass incorporation was calculated as the difference between ^{13}C in DOC of chloroform-fumigated and non-fumigated samples.

The initial CO_2-C content in the glass bottles was corrected for the replacement of the air sampled at the beginning of the incubation:

$$C_{initial} = C_{start} - C_{sample} + C_{replaced} \quad (2)$$

were C_{start}, C_{sample} and $C_{replaced}$ are the CO_2-C content of the bottle at the time of sampling, the sampled air and the replacement air, respectively.

To correct the initial at% values for the replaced air, a two-source mixing model was calculated:

$$at\%_{initial} = \frac{at\%_{start} \times \left(C_{start} - C_{sample}\right) + at\%_{replaced} \times C_{replaced}}{C_{initial}} \quad (3)$$

where $at\%_{start}$ and $at\%_{replaced}$ are the at% values for the initial sample and the replacement air, respectively.

Similarly, the final at% values were corrected for the initial ones to calculate the at% of respired CO_2:

$$at\%_{respired} = \frac{at\%_{end} \times C_{end} - at\%_{initial} \times C_{initial}}{\left(C_{end} - C_{initial}\right)} \quad (4)$$

where $at\%_{end}$ are the at% ^{13}C at the end of the incubation and C_{end} is the final CO_2-C content of the bottle.

To determine the contribution of the added substrate to ^{13}C CO_2 and biomass production, atom percent excess was calculated by subtracting an average natural abundance value, of bulk C, of 1.078 at% from all measured values.

3.7. Statistical analysis

One way analysis of variance with Tukey HSD was used to test for differences in CUE and soil parameters between sites and horizons. Data were checked for normality and homoscedasticity and transformed when necessary. Kruskal-Wallis tests with Mann–Whitney–Wilcoxon tests were used when normality and homoscedasticity could not be achieved. Linear regression analysis (least square regression) was used to relate CUE and soil characteristics (C, N, DOC, TDN, and their ratios), C_{mic}, potential enzyme activities, latitude and MAP. All statistical analysis were performed in R 3.0.1: R Development Core Team, www.R-project.org .

4. Results

4.1. Soil characteristics

The transect was chosen so that its sites would display similar soil properties. Soils were generally acidic with the exception of carbonate containing horizons in the forest steppe and steppe, which are characteristic for theses systems (Table 3). Water contents within horizons were comparable, clay content was similar among tundra and taiga sites but was lower in forest steppe and steppe. In the organic topsoil, C content was high in tundra and northern taiga (308 mg g^{-1} and 448 mg g^{-1}, respectively) and decreased from there towards the South with a minimum of 202 mg g^{-1} in the forest steppe meadow (Table 4). As the topsoil horizon of the steppe had a C content of only 35 mg g^{-1} and a C:N ratio of 11.0, it was treated as an upper mineral horizon in subsequent data analysis. DOC in the topsoil, as well as TDN and microbial biomass (C_{mic}) were highest in the southern taiga, indicating high concentrations of substrate available for microorganisms at this site.

4.2. CUE across sites and soil horizons

CUE varied both across sites and across soil horizons within sites, ranging from 0.42 in the southern taiga organic horizon to 0.78 in the steppe upper mineral horizon (Fig. 1). The lower mineral horizons showed the clearest pattern in CUE across the transect, with the two northernmost sites, tundra and northern taiga, displaying significantly lower values than the two southernmost sites, forest steppe and forest meadow (Tukey HSD, $p < 0.05$). Steppe lower mineral horizon was excluded from analysis due to marginal microbial respiration. Across all sites, upper mineral horizons exhibited the highest CUE (mean $\pm$ SD = 0.69 $\pm$ 0.12), followed by organic horizons (0.63 $\pm$ 0.12) and lower mineral horizons (0.56 $\pm$ 0.13); but only the difference between lower and upper mineral horizons was statistically significant (Tukey HSD, $p < 0.001$).

4.3. Effects of latitude and climate on CUE

CUE showed significant relationships with latitude and climate along the transect. As there is a near perfect negative correlation between latitude and mean annual temperature (MAT) as well as potential evapotranspiration for the study sites (r = -0.99), the use of these variables in correlation analysis is equivalent. While there was no relationship between latitude and CUE in the organic horizons, there was a significant negative relationship in the upper mineral and an even stronger negative relationship in the lower mineral horizon (Fig. 2). Significant negative relationships with MAP were observed in

all horizons, but were stronger in the mineral horizons. MAP increases from 391 mm the tundra to 438 mm the middle taiga and then decreases towards the South to 309 mm in the steppe. Despite these marginal differences in precipitation, CUE is linked to MAP more strongly than to temperature or latitude.

4.4. Effects of carbon and nitrogen pool sizes on CUE

Counter to our expectations, soil C:N ratio only showed a significant negative regression with CUE in the upper mineral horizon and a marginally significant (p = 0.084) negative regression in the lower mineral horizon (Fig. 3). The ratio of DOC and TDN, as a measure of available substrate C:N, also showed a weak negative relationship in the upper mineral horizon. In the organic horizons, CUE displayed negative relationships with total C and DOC (Fig.4), C_{mic} (R^2 = 0.33, $p < 0.001$) and TDN (R^2 = 0.46, $p < 0.001$), none of which showed significant correlations in the mineral horizons (Appendix A Tables 6 and 7).

4.5. Relationships between potential enzyme activities and CUE

We measured potential extracellular enzyme activities to assess relationships between CUE and microbial nutrient acquisition. All enzyme activities were calculated per g C. In the organic horizon, there was a strong negative relationship

between CUE and phenoloxidase (Fig. 6), as well as a weak negative relationship with cellobiosidase. (Fig. 5). In the mineral horizons, phenoloxidase and peroxidase were both negatively related to CUE, while endochitinase and cellobiosidase showed positive relationships with CUE. Hydrolytic enzyme activity was comparable in all horizons and showed little variation between sites; by contrast, phenoloxidase and peroxidase activity increased 25-fold and 33-fold, respectively, from the organic to the lower mineral horizon. There were no significant relations between CUE, exochitinase and protease.

5. Discussion

This study aimed to elucidate trends in CUE in response to changes in N availability along latitudinal gradients as well as within the soil profile. CUE was expected to show a negative relationship with soil C:N ratio as the relative availability of N for microbial decomposer communities is known control to partitioning of C between growth and respiration (Manzoni et al., 2012).

While CUE was related to the C:N ratio in the upper mineral horizons, no such relationship could be observed across all horizons ($R^2 = 0.03$, $p > 0.5$). According to the stoichiometric theory, the organic horizon should exhibit lower CUE values than the mineral horizons due to a stronger N limitation, but this was found to be true only for the southern taiga (Figure 1). Moreover, even though C:N ratios decreased within the soil profile, the lower mineral horizon displayed the lowest mean CUE. This suggests that C:N ratio alone is not an adequate indicator of N availability and/or that factors other than N availability exerted a stronger control over CUE at the study sites. It also suggests that controls over CUE may be substantially different between horizons.

The high CUE in the organic topsoil compared to the mineral soil may occur as organic horizons are generally richer in labile nutrients and nutrient availability can be decoupled from elemental ratios (Fierer et al., 2003). A decrease of CUE within the mineral horizons could occur for several reasons: First, microorganisms in deeper soil horizons may subsist under conditions of energy limitation as organic matter is scarce and can be physically disconnected from decomposers or protected through interactions with soil minerals (Schmidt et al., 2011); additionally the accessible C may have a low energy content (Fontaine et al., 2007). Under such conditions, less C would be available to allocate to biomass production after meeting the demands of maintenance respiration (Hoehler and Jørgensen, 2013). Second, substrate limitation or lower quality substrates in deeper soil may require enhanced enzyme production causing increased C and energy costs, again decreasing CUE. Third, despite a low C:N ratio, the microbial community in deep soil may be N limited if its bioavailability is low (Fierer et al., 2003). This can occur when N is mainly present in recalcitrant molecules, requiring the production of oxidative enzymes to access it. Oxidative enzyme production is associated with a higher metabolic investment to solubilize a unit of N, decreasing microbial growth (Sinsabaugh and Follstad Shah, 2011).

It has to be considered that the method used in this study measures short term uptake and respiration of added substrates. This does not fully capture microbial growth and respiration, or the utilization of complex SOM as substrate, and therefore does not quantify the effects of substrate quality on CUE. This could lead to a relative overestimation of CUE in soils containing highly processed

complex organic matter with a low degree of reduction, as it is found in deep soil. Also, since the added compounds contain N, CUE may be overestimated in severely N limited soils.

While C:N ratios in the organic and upper mineral horizons varied by a factor of two and a half, only the upper mineral horizon exhibited a significant negative relationship between CUE and C:N ratio and a weak negative relationship with DOC:TDN ratio (Fig. 3). In the organic horizons, were C is in excess and the availability of labile substrates was highest, CUE was negatively related to DOC and to a lesser extent to total C (Fig. 4), and C_{mic} ($R^2 = 0.33$, $p < 0.001$). C_{mic} was also correlated with DOC, but not total C (Appendix A Table 5).

This indicates that C in DOC is more easily available than bulk C and drives both microbial productivity and excess C availability. Surprisingly, CUE was negatively related to TDN ($R^2 = 0.46$, $p < 0.001$), which is likely due to the fact that DOC and TDN are highly correlated ($r = 0.95$, $p < 0.001$).

In addition to driving nutrient limitation, DOC concentrations could also affect CUE through changes in the microbial community, as high availability of labile C has been shown to shift soil microbial communities from slow growing decomposers with high CUE to fast growing opportunists with low CUE (Shen and Bartha, 1996; Lipson et al., 2009).

There was no significant relationship between CUE and any of the indicators of C and N pools size and stoichiometry in the lower mineral horizon. Moreover, variability of these measures between sites was low, while variability of CUE

was comparable to the upper horizons, indicating that CUE in this horizon is dependent on other factors.

Soil microorganisms decompose SOM and acquire soluble substrates for assimilation through the production of extracellular enzymes (Sinsabaugh et al., 2008). Enzyme activity and CUE are linked in two ways: First, enzyme activities are indicators of microbial nutrient or C demand (Olander and Vitousek, 2000; Schimel and Weintraub, 2003; Caldwell, 2005; Sinsabaugh et al., 2008) as specific enzymes are produced to acquire C, N or P (Sinsabaugh and Follstad Shah, 2011; Moorhead and Sinsabaugh, 2006). Second, the production of extracellular enzymes incurs a C and N cost and energy investment for microorganisms, which can constitute a substantial amount of their total C and/or N budget (Tholudur et al., 1999; Schimel and Weintraub, 2003; Moorhead and Sinsabaugh, 2006). Increasing enzyme production to alleviate C or nutrient limitation therefore reduces CUE, at least in the short term.

CUE was negatively related to phenoloxidase activity in all horizons and to peroxidase activity in the mineral horizons, while there was a manifold increase in the activity of both enzymes with horizon depth (Fig. 6). Both oxidative enzymes catalyze the degradation of recalcitrant phenolic compounds such as tannins and lignins (Mayer and Staples, 2002; Hofrichter, 2002), as well as range of other compounds that are believed to be part of polymeric SOM (Sinsabaugh and Follstad Shah, 2011; Moorhead and Sinsabaugh, 2006). Oxidative enzyme activity has also been linked to the detoxification of phenolic compounds and mediation of oxidative stress (Sinsabaugh, 2010). Across all horizons, oxidative enzyme activity was always highest in the taiga and tundra

ecosystems, even when compared on a dry matter basis. These ecosystems are generally characterized as strongly N limited by high C:N input ratios, and low quality litter inputs (Schimel and Bennett, 2004; Berg, 2000). CUE in northern ecosystems may therefore be reduced by low substrate quality, as well as nutrient limitation.

The increase in oxidative enzyme activity with depth is likely the result of an increase in the structural complexity of residual soil organic matter (Rumpel and Kögel-Knabner, 2010; Moorhead and Sinsabaugh, 2006), which decreases the efficiency of the deconstruction of organic matter by hydrolytic enzymes, necessitating oxidative enzymes. Additionally, C concentrations in the lower mineral horizons were low, ranging from 0.41% to 1.67% with an average of 0.75% (Table 4). Microbes themselves occupy only a minute portion of the soil volume, and both microbes and SOM are heterogeneously distributed in deeper soil. Under such conditions, a physical disconnection between decomposers and SOM becomes therefor more frequent (Schmidt et al., 2011). This requires increased enzyme production as enzymes have to diffuse through a larger volume of soil to reach a substrate compared to topsoil with a higher C content. Microbial communities under these conditions are thought to be dominated by slow growing nutrient miners with a high metabolic investment in oxidative enzyme production (Sinsabaugh and Follstad Shah, 2011). The high oxidative enzyme activity in the lower mineral horizons, particularly in the tundra and taiga ecosystems, might therefore help to explain the lower CUE in these sites.

While the activity of the hydrolytic enzymes cellobiosidase and endochitinase

did display significant relationships with CUE, there was little variability between sites (Fig. 5). Clear patterns, as with oxidative enzyme activity could therefore not be observed.

Contrary to the oxidative enzymes, hydrolytic enzyme activities did not increase with depth. The cellobiosidase to phenoloxidase ratio, on average, decreased by a factor of five from the organic to the upper mineral horizon, and by a factor of six from the upper to the lower mineral horizon. This ratio is an indicator for SOM recalcitrance (Sinsabaugh and Follstad Shah, 2011), and further confirms unfavourable substrate conditions in the lower mineral horizon.

CUE generally decreased with increasing latitude (except for the organic horizons) and with MAP (Fig. 2). This is likely the result of lower C:N ratios and higher quality of plant litter inputs, as well as more favorable environmental conditions, both increasing decomposition rates (Aerts, 1997; Jobbágy et al., 2000; Allison, 2006). C:N and DOC:TDN ratios were also positively correlated with latitude and MAP, i.e. lower ratios in warmer, dryer sites (Appendix A Tables 5-7

Counter to the expectation that CUE in the topsoil would be most related to climate through latitudinal differences in vegetation and decomposition status, CUE was more strongly related to latitude (MAT) and MAP in the mineral horizons. This clearly indicates that other factors, such as plant species composition and the quality of organic matter inputs, exert stronger controls over CUE than environmental factors. With increasing soil depth, the quality and nutrient

content of organic matter changes from plant- to microbial-dominated and converges towards a common quality. As such, climatic factors may become more important controls with depth.

In summary, when comparing soil horizons the results of our study demonstrate that CUE is not primarily controlled by substrate stoichiometry. Instead, substrate limitation (physical disconnection between substrate and decomposers or inaccessibility) and chemical complexity appear to decrease CUE in lower soil horizons, despite low bulk C:N ratios. It seems probable that changes in stoichiometric and energetic constraints across horizons are accompanied by changes in microbial community composition, which might in turn also affect CUE. Comparing the same horizons along the transect, controls on CUE were different in the three horizons. Negative relationships with oxidative enzyme activities in all horizons indicate that CUE is dependent on chemistry and/or N content of the substrate. However, while CUE in the upper mineral horizon was also determined by bulk SOM stoichiometry, in the organic horizon it was negatively related to the amount of soluble and total organic matter, pointing to differences in substrate utilization between horizons. Ultimately, the proximate controls on CUE are subject to state factors like climate, which regulate interconnected ecosystem properties such as vegetation type, productivity, as well as the physical and chemical properties of soils. Furthermore, the effects of climate and vegetation on CUE appear to persist into lower soil horizons, where organic matter has been turned over repeatedly, and were environmental conditions are more stable, indicating that there are intrinsic differences in CUE between ecosystems.

6. Tables and figures

6.1. Tables

Table 1.: Sampling sites along a latitudinal transect through West Siberia

Ecosystem	Coordinates	MAT [a] (°C)	MAP [a] (mm)	Plant community
Tundra	67°16′N 78°50′E	-7.6	391	Shrubby lichen tundra
Northern taiga	63°17′N 74°33′E	-4.6	430	Spruce forest
Middle taiga	60° 9′N 71°43′E	-2.2	438	Boreal coniferous forest
Southern taiga	58°18′N 68°35′E	-0.5	396	Abies forest with *Carex macroura* dominance
Forest steppe				
Forest	56°14′N 70°43′E	0.7	340	Broad leaf hemi-boreal forset
Meadow	56°14′N 70°43′E	0.7	340	Dry forest meadow
Steppe	54°41′N 71°38′E	1.0	309	True steppe

[a] Climate data from: Stolbovoi V, McCallum I (2002) Land resources of Russia (CD). International Institute for Applied Systems Analysis and the Russian Academy of Science, Laxenburg, Austria .

Table 2.: Composition of universally labeled ^{13}C substrate mix

Substance	% of total	C:N ratio	Degree of reduction
Benzoic acid	5.0	-	4.3
Glucosamine	15.0	6	4.0
Glucose	40.0	-	4.0
Mannose	20.0	-	4.0
Sodium acetate	10.0	-	4.0
Alanine	1.1	3	4.0
Arginine	0.5	2	3.7
Aspartic acid	0.9	4	3.0
Glutamic Acid	0.9	5	3.6
Glycine	1.0	2	3.0
Histidine	0.2	2	3.3
Isoleucine	1.0	6	5.0
Leucine	1.0	6	5.0
Lysine	0.7	3	4.7
Methionine	0.1	5	4.4
Phenylalanine	0.4	9	4.4
Proline	0.5	5	4.4
Serine	0.4	3	3.3
Threonine	0.5	4	4.0
Tyrosine	0.3	9	4.2
Valine	0.6	5	4.8
Mean		20	4.0

Table 3.: Soil profiles along a latitudinal transect through West Siberia

Site	Soil type[a]	Horizon[b]	Depth (cm)	Clay (%)	pH_{KCl}	Water content[c] (% fresh matter)
Tundra	Tundra Gleysem	O	0.5		3.8	63.5±9.4 a
		A	4	65.7	3.7	27.5±2.4 b
		Bg/BCg	8	73.9	3.9	16.4±1.2 c
Northern taiga	Gleyic	Oi/Oe	3		2.8	68±4.6 a
	podsolized soil	EA/AE	16	61.4	3.1	25.6±3.4 b
		Bg	22	70.7	3.7	18.1±2.2 c
Middle taiga	Deeply	Oi	0		3.7	56.9+7.1 a
	podsolized soil	AE/EA	7	74.8	3.3	29.9±15.7 ab
		E/EB/EA	13	69.3	3.5	13.3±1.1 ab
Southern taiga	Podsolized soil	Oi	0		4.3	67.3±8.0 a
	with second	A/AE	5	60.0	3.6	17.6±1.5 a
	humus horizon	EA/E	15	60.7	3.8	20.1±11.3 bc
Forest steppe	Leached	Oa/O	0.5		6.6	58.3±3.8 a
Forest	Chernozem	A	8-41	47.0	4.3	17.8±2.1 a
		B	61	37.4	4.1	11.2±1.2 a
Meadow	Podsolized	Oa	0		5.5	54.5±5.7 a
	Chernozem	A	5-25	56.9	4.1	16.8±1.0 a
		Bt	32	43.3	4.0	12.3±0.6 a
Steppe	Southern	OA	0	41.1	4.6	24.3±15.1 a
	Chernozem	Ak	11-29	31.8	5.1	27±18.0 ab
		Bk	38	24.9	7.9	9.9±1.9 a

[a] Soils named according to Russian Soil Classification

[b] When more than one horizon type was found in different pits, all types are given.

[c] Mean ± standard deviation; different letters indicate significant differences within horizons at $p < 0.05$ (Mann–Whitney–Wilcoxon test).

Table 4.: Total C, dissolved C, dissolved N and microbial biomass along a latitudinal transect through West Siberia

Biome	Horizon[a]	C (mg C/g)	DOC µg C/g	TDN (µg N/g)	Cmic µg C/g
Tundra	O	307.9±83.5 cd	587.7±162.1 b	53.7±15.4 b	3787.4±804.7 bc
	A	30.4±6.8 ab	34.5±14.7 ab	4.4±2.0 a	408.2±260.7 a
	Bg/BCg	4.1±1.2 a	4.7±2 a	nd	24.2±9.3 a
Northern taiga	Oi/Oe	448.4±15.6 e	1384.4±456.2 cd	134.4±26.1 c	2562.1±428.1 ab
	EA/AE	37±7.0 bc	79.3±17.6 c	9.7±2.1 b	144.7±54.9 a
	Bg	8.2±3.8 a	35.5±10.0 c	3.1±1.4 a	68.2±43.8 a
Middle taiga	Oi	426.1±54.7 e	1799.8±534.4 d	181.5±47.8 c	5697.5±1451 cd
	AE/EA	74.7±38.6 bc	196±131.2 c	29.6±20.2 c	666.7±509.2 a
	E/EB/EA	16.7±8.4 a	59.4±44.0 c	6.4±4.1 a	141.5±52.6 a
Southern taiga	Oi	398.2±40.9 de	3961±1516.7 e	411.5±202.1 d	7944.9±3093 d
	A/AE	43.4±8.1 bc	109.1±51.4 c	16.6±6.3 c	382.8±60.2 a
	EA/E	4.8±0.7 a	25.6±5.8 c	2.5±0.9 a	68.9±16.6 a
Forest steppe	Oa/O	292.9±53.8 c	735.1±654.1 bc	117.5±100.8 bc	5100.5±943 bcd
Forest	A	45.6±10.1 c	25±4.2 a	8.8±2.0 ab	196.1±41.8 a
	B	5.2±0.3 a	11.9±1.1 b	2.6±0.9 a	46.1±12.7 a
Meadow	Oa	202.1±50.7 b	511.7±201.7 b	83.9±38.1 bc	4417.3±1141 bc
	A	24.5±3.5 a	45±13.1 a	6.3±1.2 a	272.5±85.5 a
	Bt	5.8±0.8 a	10.4±1.2 b	2.4±0.4 a	59.4±13.7 a
Steppe	OA	35.3±12.0 a	22.8±7.4 a	12.8±7.4 a	656.5±233.7 a
	Ak	20.1±6.1 a	22.1±7.2 a	8.3±2.7 ab	364.4±107.6 a
	Bk	7.2±1.8 a	21.9±10.8 c	4.2±0.7 a	52.4±14.3 a

[a] When more than one horizon type was found in different pits, all types are given.

Values show Mean ± standard deviation; different letters indicate significant differences within horizons at $p < 0.05$ (Tukey HSD or Mann–Whitney–Wilcoxon test).

6.2. Figures

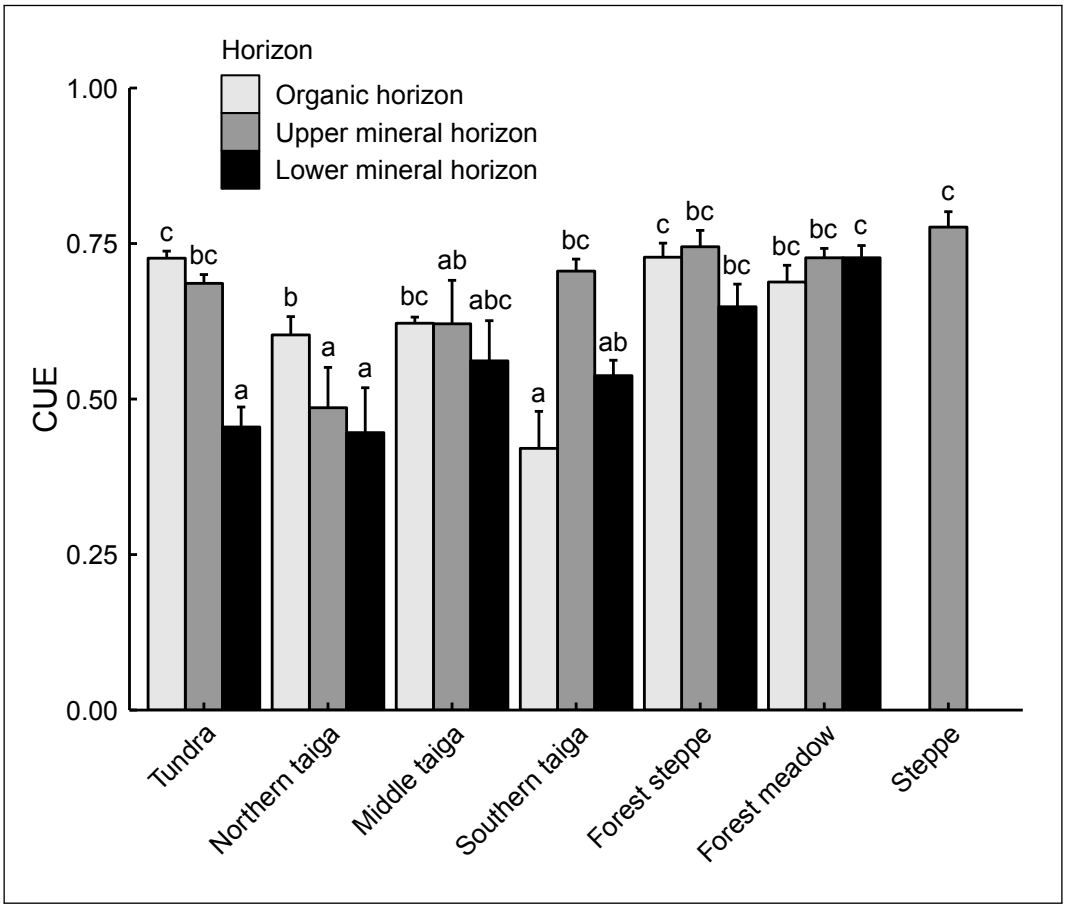

Figure 1.: CUE in top three soil horizons of a latitudinal transect through West Siberia. Error bars show SEM, different letters above bars indicate significant differences within a horizon at $p < 0.05$ (Tukey HSD)

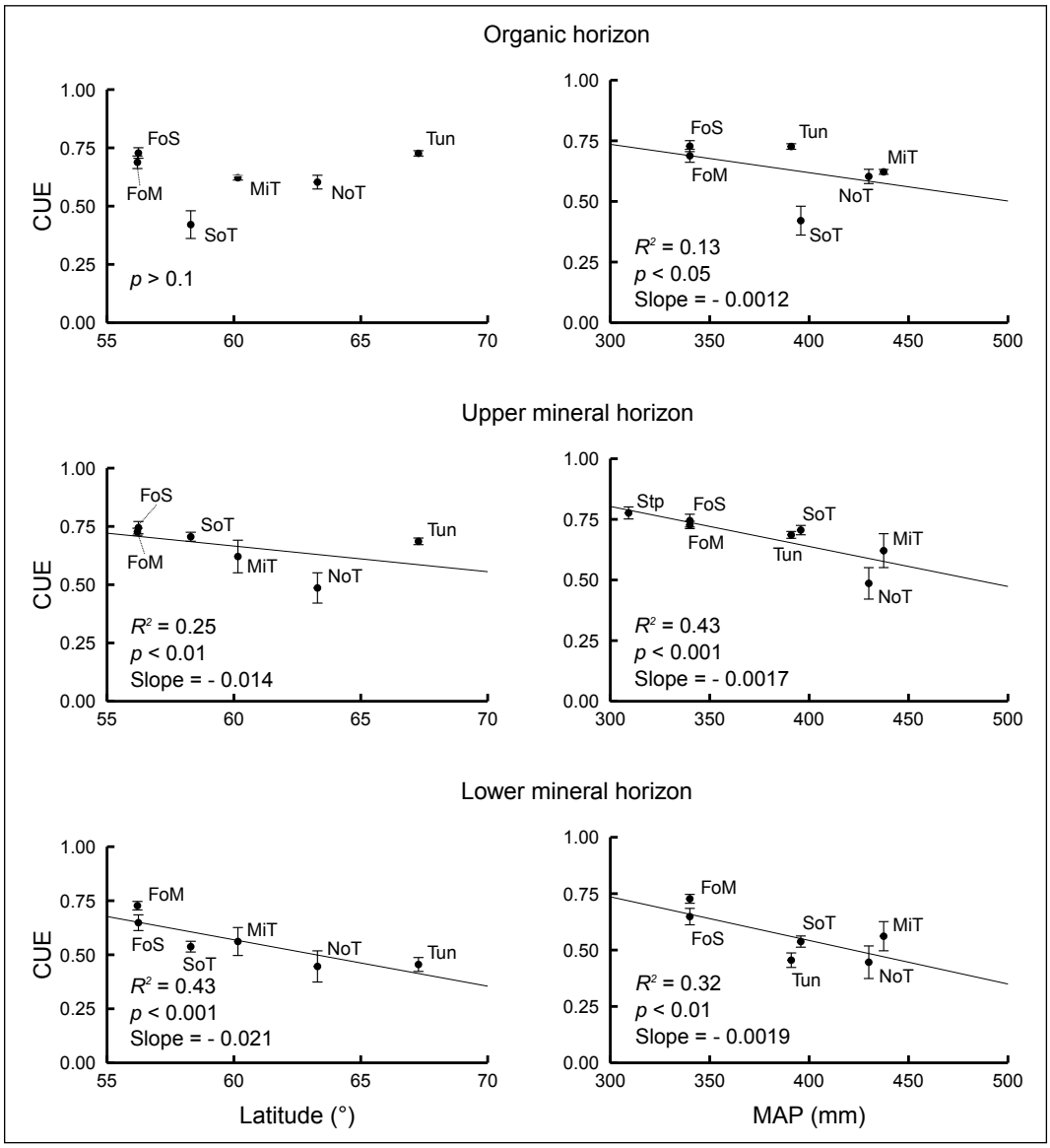

Figure 2.: CUE along a latitudinal transect through Western Siberia in relation to latitude and MAP. Sites: Tun (tundra), NoT (northern taiga), MiT (middle taiga), SoT (southern taiga), FoS (forest steppe forest), FoM (forest steppe meadow). Points and error bars show site mean and SEM; Regressions are based on individual data points.

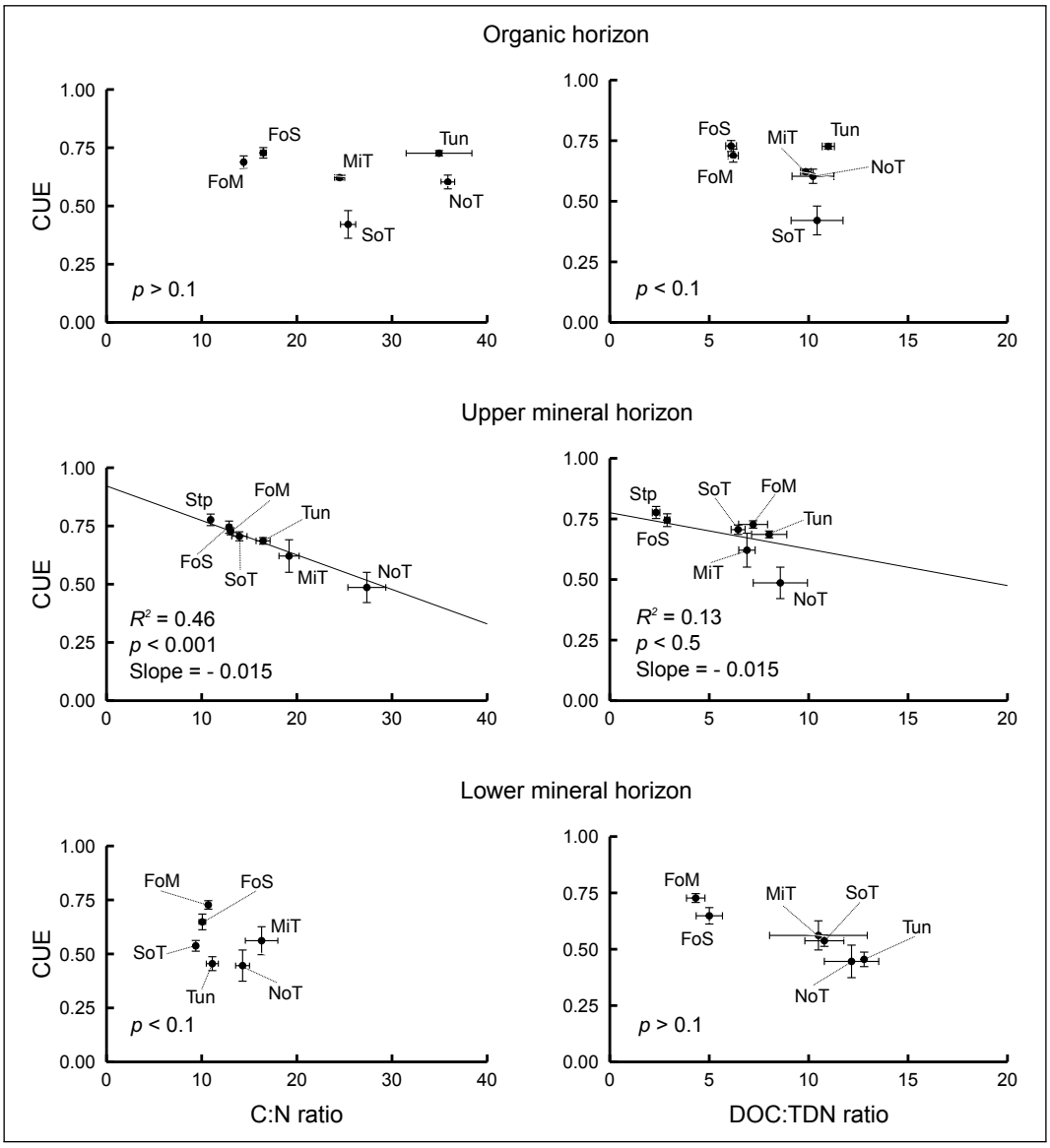

Figure 3.: CUE along a latitudinal transect through Western Siberia in relation to mass based C:N ratio and DOC:TDN ratio. Sites: Tun (tundra), NoT (northern taiga), MiT (middle taiga), SoT (southern taiga), FoS (forest steppe forest), FoM (forest steppe meadow). Points and error bars show site mean and SEM; Regressions are based on individual data points.

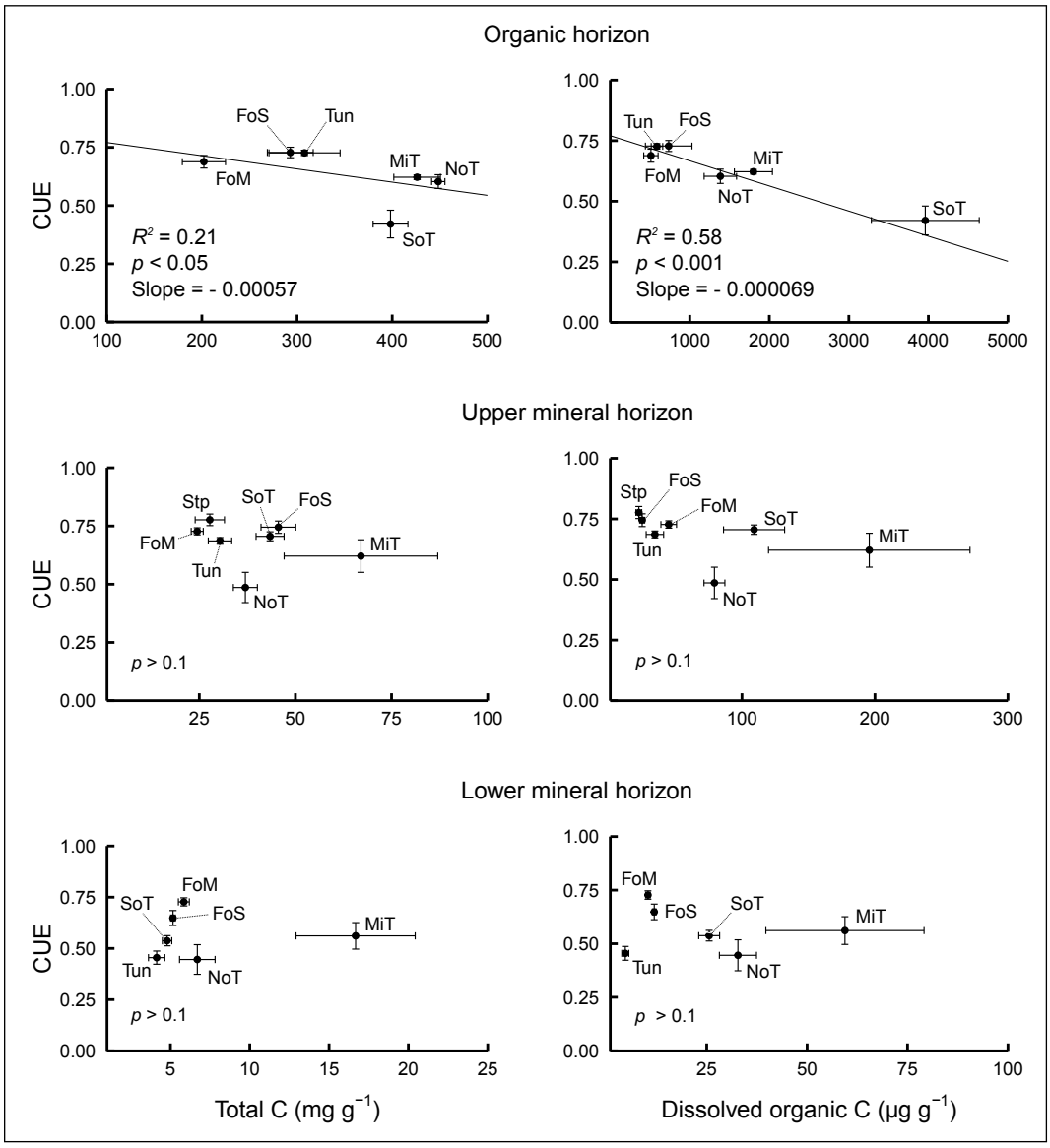

Figure 4.: CUE along a latitudinal transect through Western Siberia in relation to total C and and DOC. Sites: Tun (tundra), NoT (northern taiga), MiT (middle taiga), SoT (southern taiga), FoS (forest steppe forest), FoM (forest steppe meadow). Points and error bars show site mean and SEM; Regressions are based on individual data points.

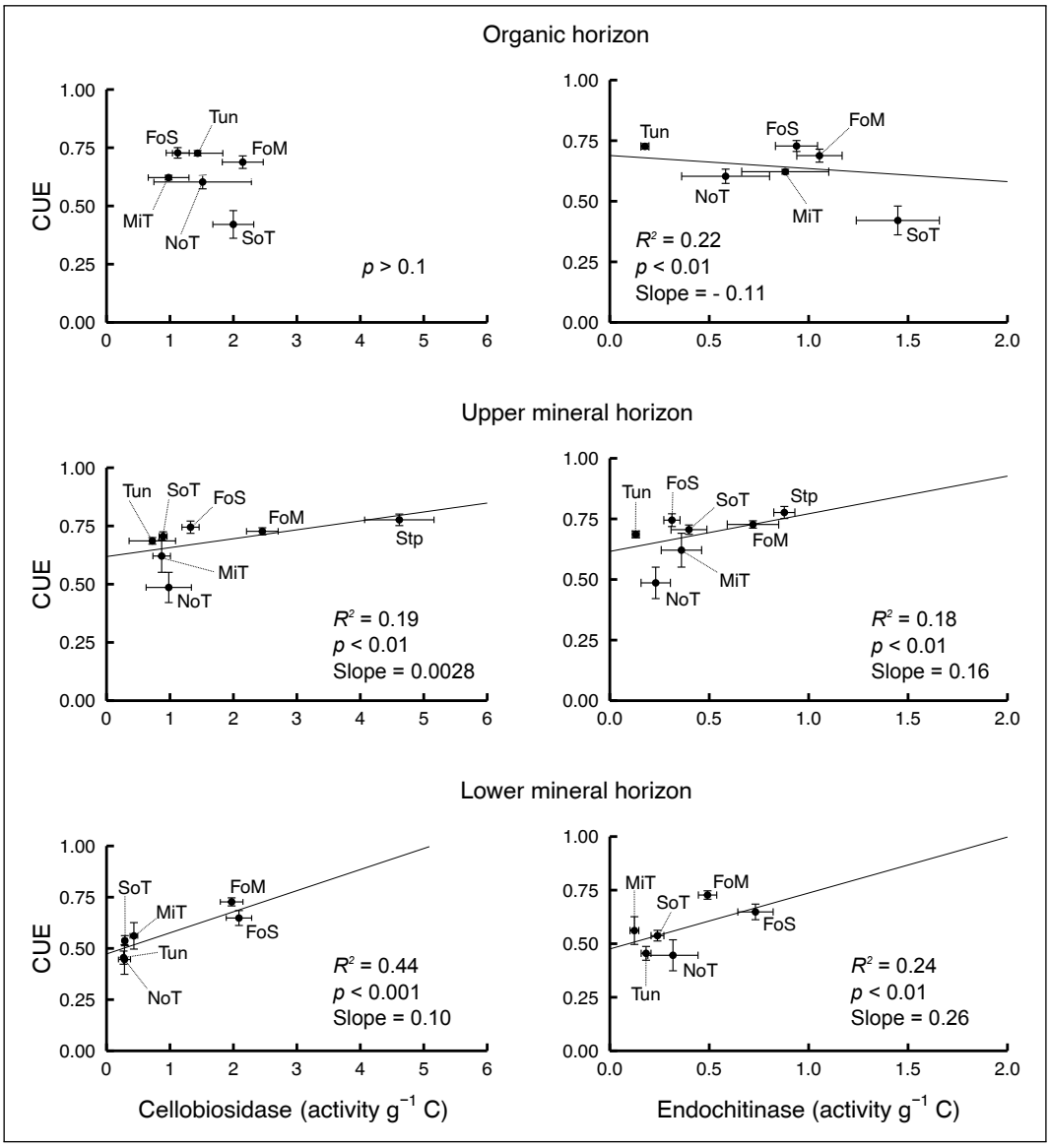

Figure 5.: CUE along a latitudinal transect through Western Siberia in relation to cellobiosidase and endochitinase activity. Sites: Tun (tundra), NoT (northern taiga), MiT (middle taiga), SoT (southern taiga), FoS (forest steppe forest), FoM (forest steppe meadow). Points and error bars show site mean and SEM; Regressions are based on individual data points.

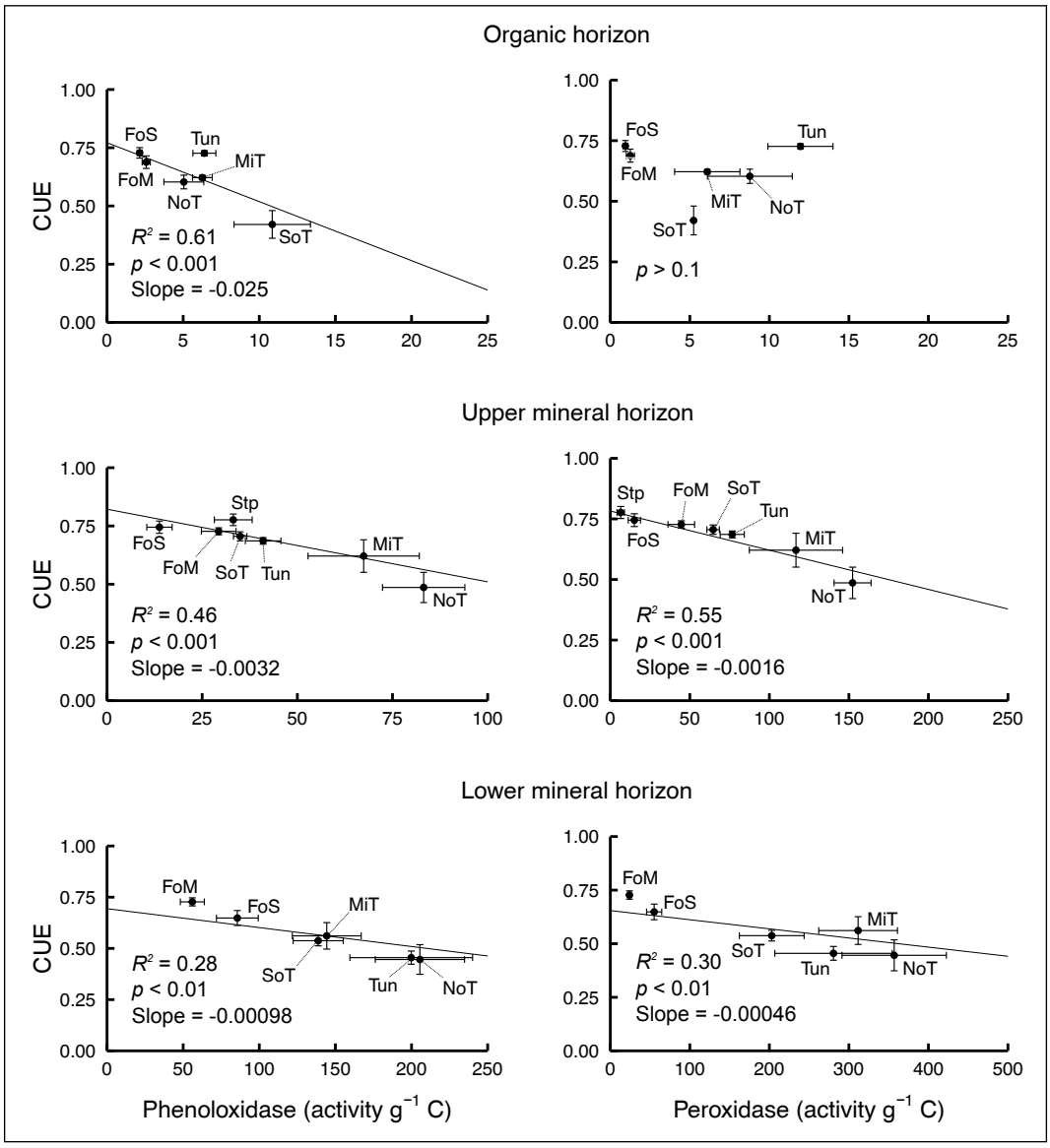

Figure 6.: CUE along a latitudinal transect through Western Siberia in relation to phenoloxidase and peroxidase activity. Sites: Tun (tundra), NoT (northern taiga), MiT (middle taiga), SoT (southern taiga), FoS (forest steppe forest), FoM (forest steppe meadow). Points and error bars show site mean and SEM; Regressions are based on individual data points.

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Appendix

Appendix A.

Supplementary data

Table 5.: Correlation table for organic horizon

	CUE	Lat	MAP	pH	DOC	TDN	DOC:TDN	Cmic	N	C	C:N	CBH	ECH	XCH	AP	POX	PER	LAP
CUE																		
Lat	0.13																	
MAP	-0.37*	0.56**																
pH	0.32	-0.70***	-0.87***															
DOC	-0.76***	-0.14	0.35	-0.23														
TDN	-0.68***	-0.24	0.22	-0.09	0.95***													
DOC:TDN	-0.31	0.64***	0.67***	-0.73***	0.32	0.08												
Cmic	-0.58***	-0.38*	-0.05	0.21	0.58***	0.52**	0.03											
N	-0.24	-0.68***	-0.09	0.36*	0.38*	0.46*	-0.37*	0.53**										
C	-0.46*	0.31	0.79***	-0.61***	0.56**	0.49**	0.45*	0.17	0.31									
C:N	-0.11	0.86***	0.69***	-0.77***	0.11	0.00	0.68***	-0.28	-0.53**	0.61***								
CBH	-0.20	-0.11	-0.16	0.00	0.06	-0.05	0.22	0.10	-0.29	-0.31	-0.09							
ECH	-0.47**	-0.64***	-0.18	0.24	0.42*	0.43*	-0.12	0.52**	0.45*	-0.02	-0.45*	0.52**						
XCH	-0.36	-0.26	0.17	-0.15	0.30	0.21	0.29	0.12	0.20	0.29	0.02	0.42*	0.54**					
AP	-0.28	0.43*	0.30	-0.37*	0.34	0.26	0.54**	0.26	-0.25	0.12	0.27	0.02	0.06	-0.10				
POX	-0.78***	0.22	0.42*	-0.40*	0.62***	0.54**	0.39*	0.43*	-0.02	0.35	0.25	0.18	0.25	0.05	0.53**			
PER	-0.19	0.77***	0.53**	-0.63***	0.05	-0.10	0.52**	-0.42*	-0.60**	0.23	0.61**	-0.03	-0.53**	-0.20	0.48*	0.87***		
LAP	-0.28	-0.39*	-0.42*	0.28	0.25	0.26	-0.17	0.44*	0.03	-0.47**	-0.49**	0.46*	0.42*	-0.09	0.20	0.19	-0.31	
CBH:POX	0.04	-0.26	-0.40*	0.23	-0.14	-0.18	-0.10	0.05	-0.23	-0.54**	-0.32	0.82***	0.41*	0.18	-0.02	0.01	-0.17	0.50**

CBH (cellobiosidase), ECH (endochitinase), XCH (exochitinase), AP (phosphatase), POX (phenoloxidase), PER (peroxidase), LAP (protease)

Table 6.: Correlation table for upper mineral horizon

	CUE	Lat	MAP	pH	DOC	TDN	DOC:TDN	Cmic	N	C	C:N	CBH	ECH	XCH	AP	POX	PER	LAP
CUE																		
Lat	-0.50**																	
MAP	-0.66***	0.74***																
pH	0.65***	-0.68***	-0.89***															
DOC	-0.12	0.18	0.59***	-0.45**														
TDN	0.00	-0.07	0.32*	-0.20	0.90***													
TOC:TDN	-0.36*	0.69***	0.72***	-0.70***	0.35*	-0.03												
Cmic	0.27	-0.09	-0.05	0.13	0.57***	0.74***	-0.15											
N	0.23	-0.32*	-0.09	0.10	0.43**	0.65***	-0.37*	0.57***										
C	-0.11	0.10	0.43**	-0.34*	0.83***	0.86***	0.08	0.60***	0.78***									
C:N	-0.68***	0.64***	0.79***	-0.75***	0.42**	0.18	0.69***	-0.11	-0.26	0.32*								
CBH	0.43**	-0.61***	-0.72***	0.66***	-0.32*	-0.06	-0.51***	0.31	-0.04	-0.34*	-0.47**							
ECH	0.42**	-0.72***	-0.68***	0.61***	-0.22	-0.04	-0.41**	0.22	0.02	-0.29	-0.50**	0.77***						
XCH	0.15	-0.27	-0.22	0.24	-0.06	-0.02	-0.07	0.09	-0.27	-0.21	0.05	0.58***	0.60***					
AP	-0.01	0.33*	-0.01	-0.02	-0.08	0.02	0.04	0.46**	-0.09	-0.14	-0.10	0.35*	0.09	0.08				
POX	-0.68***	0.46**	0.63***	-0.48**	0.20	0.03	0.39*	-0.21	-0.51***	-0.07	0.63***	-0.26	-0.34*	0.10	0.02			
PER	-0.74***	0.63***	0.85***	-0.85***	0.29	0.05	0.62***	-0.27	-0.46**	0.02	0.76***	-0.53**	-0.54**	-0.09	-0.03	0.91***		
LAP	0.16	-0.35*	-0.51***	0.39*	-0.24	-0.01	-0.34*	0.39*	-0.01	-0.26	-0.40*	0.73***	0.64***	0.31	0.62***	-0.25	-0.43*	
CBH:POX	0.51***	-0.74***	-0.74***	0.65***	-0.27	-0.06	-0.44**	0.30	0.11	-0.23	-0.48**	0.87***	0.79***	0.48**	0.12	-0.43**	-0.56***	0.61***

CBH (cellobiosidase), ECH (endochitinase), XCH (exochitinase), AP (phosphatase), POX (phenoloxidase), PER (peroxidase), LAP (protease).

Table 7.: Correlation table for lower mineral horizon

	CUE	Lat	MAP	pH	DOC	TDN	DOC:TDN	Cmic	N	C	C:N	CBH	ECH	XCH	AP	POX	PER	LAP
CUE																		
Lat	-0.66***																	
MAP	-0.56**	0.55**																
pH	0.30	-0.28	-0.80***															
DOC	-0.27	-0.03	0.58***	-0.72***														
TDN	-0.33	0.07	0.42*	-0.55**	0.90***													
DOC:TDN	-0.35	0.64***	0.69***	-0.57**	0.28	-0.12												
Cmic	0.05	-0.22	0.45*	-0.51**	0.42*	0.45*	0.03											
N	-0.05	-0.24	0.37*	-0.59***	0.82***	0.90***	-0.06	0.71***										
C	-0.20	-0.04	0.48**	-0.64***	0.88***	0.93***	0.02	0.65***	0.95***									
C:N	-0.33	0.25	0.64***	-0.62***	0.78***	0.80***	0.15	0.53**	0.72***	0.87***								
CBH	0.67***	-0.70***	-0.84***	0.63***	-0.30	-0.19	-0.71***	-0.17	-0.05	-0.17	-0.33							
ECH	0.49**	-0.55**	-0.71***	0.69***	-0.39*	-0.32	-0.53**	-0.30	-0.31	-0.37*	-0.41*	0.80***						
XCH	0.06	0.09	0.20	0.03	-0.05	-0.21	0.31	-0.02	-0.24	-0.16	0.05	-0.03	0.36					
AP	-0.52**	0.57**	0.51**	-0.22	-0.04	-0.22	0.75***	-0.21	-0.39*	-0.28	-0.15	-0.69***	-0.39*	0.24				
POX	-0.53**	0.69***	0.58***	-0.38*	-0.02	-0.15	0.62**	-0.06	-0.29	-0.15	0.10	-0.63***	-0.38*	0.29	0.64***			
PER	-0.54**	0.62***	0.77***	-0.62***	0.25	0.14	0.57**	0.24	0.05	0.16	0.37	-0.71***	-0.56**	0.18	0.48**	0.91***		
LAP	0.26	-0.06	-0.64***	0.76***	-0.75***	-0.75***	-0.24	-0.63***	-0.78***	-0.78***	-0.76***	0.36	0.47**	0.11	0.22	-0.07	-0.40*	
CBH:POX	0.69***	-0.69***	-0.79***	0.55**	-0.27	-0.20	-0.62**	-0.13	-0.05	-0.14	-0.30	0.95***	0.77***	0.02	-0.61***	-0.56**	-0.66***	0.37*

CBH (cellobiosidase), ECH (endochitinase), XCH (exochitinase), AP (phosphatase), POX (phenoloxidase), PER (peroxidase), LAP (protease).

Appendix B.

Zusammenfassung

Böden stellen den größten terrestrischen Speicher führ organischen Kohlenstoff dar. Dabei ist alleine in den Böden arktischer und subarktischer Ökosysteme mehr Kohlenstoff gespeichert, als in der gesamten Atmosphäre, was darauf zurückgeführt wird dass der Abbau organischen Materials in diesen Ökosystemen durch ungünstige klimatische Bedingungen und Stickstofflimitierung gehemmt wird. Langfristig stabile organische Substanz in Böden entsteht großteils aus den Überresten mikrobieller Biomasse und deren Ausscheidungen. Daher ist die Partitionierung von aufgenommenem Kohlenstoff in Respiration und Wachstum durch Mikroorganismen bestimmend für das Potenzial von Böden Kohlenstoff zu speichern.

Um den Effekt von Stickstoffverfügbarkeit auf den Kohlenstoffumsatz von Mikroorganismen zu untersuchen, wurden in dieser Studie Proben der obersten drei Bodenhorizonte in sechs Ökosystemen entlang eines 1.500 km lan-

gen Nord-Süd Transekts in Westsibirien genommen. An den Proben wurde die mikrobielle Kohlenstoffnutzungseffizienz (CUE) mittels Inkubation mit ^{13}C markiertem Substrat gemessen. Des Weiteren wurden Kohlenstoff- und Stickstoff-Pools, sowie die Aktivität extrazellulärer Enzyme bestimmt.

Die Ergebnisse zeigten, dass die CUE im organischen Oberboden und dem obersten mineralischen Horizont ähnlich wahr, aber im unteren mineralischen Horizont tiefere Werte annahm, obwohl das C/N Verhältnis mit der Tiefe enger wurde. Dieses Ergebnis stand im Gegensatz zu der Erwartung, dass aufgrund erhöhter Stickstoff- und abnehmender Kohlenstoffverfügbarkeit die CUE mit der Horizonttiefe zunehmen würde. Die potentielle Enzymaktivität von Phenoloxidase und Peroxidase nahm mit der Horizonttiefe zu, während das Cellobiosidase:Phenoloxidase Verhältnis abnahm. Dies deutet darauf hin, dass die Substratqualität und/oder Substratverfügbarkeit mit zunehmender Bodentiefe abnimmt. Innerhalb der Bodenhorizonte bestand in allen Horizonten eine negative Korrelation zwischen der CUE und der Aktivität der oxidativen Enzyme. Des Weiteren waren CUE und gelöster organischer Kohlenstoff in den organischen Horizonten, sowie C:N Verhältnis in den oberen mineralischen Horizonten, negativ korreliert.

Diese Ergebnisse zeigen, dass die Substratqualität in allen Horizonten einen wichtigen Einfluss auf die CUE hat. Des Weiteren führen sie zu dem Schluss, dass Mikroorganismen in tieferen Bodenhorizonten in ihrem Wachstum durch Substratmangel und die chemische Komplexität des Substrats gehemmt sind.

Appendix C.

Curriculum vitae

Mounir Takriti

Education

2012–present	Diploma thesis at the Division of Terrestrial Ecosystem Research, including development of a stable isotope technique to measure microbial carbon use efficiency and field field work in West Siberia Title: ”Microbial Carbon Use Efficiency along a Latitudinal Transect through West Siberia”
2006–present	Degree program in Biology with focus on Ecology at

	the University of Vienna
2005	GCE A Level exams with Edexcel International

Work experience

2013	Teaching assistant for the course ″Stoffkreisläufe Terrestrischer Ökosysteme″ Teaching assistant for the course ″Stabile Isotope in der Ökologie″ Laboratory analysis and sample preparation of soil samples for various projects at the Division of Terrestrial Ecosystem Research
2012	Teaching assistant for the course ″Stoffkreisläufe Terrestrischer Ökosysteme″