Nutrient availability and limitation within soils of polygonal tundra in the Sakha Republic, Russian Federation

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List of Symbols and Abbreviations

ALT	Active Layer Thickness
ANOVA	Analyses of Variances
a.s.l.	above sea level
b.s.	below surface
C	Carbon
$CaCl_2$	Calcium Chloride
CCSM	Community Climate System Model
CEC	Cation Exchange Capacity
CH_4	Methane
C_{labile}	Labile Inorganic Carbon
C_{mic}	Microbial Carbon
CO_2	Carbon Dioxide
C_{res}	Residual Carbon
Δ	Difference
DIN	Dissolved Inorganic Nitrogen
DOC	Dissolved Organic Carbon
DOM	Dissolved Organic Matter
DON	Dissolved Organic Nitrogen
DOP	Dissolved Organic Phosphorus
EC	Electrical Conductivity
Gt	Gigaton

h	hour
$\mathbf{H_2CO_3}$	Carbonic Acid
$\mathbf{H_2SO_4}$	Sulphuric Acid
M	Molar
N	Nitrogen
$\mathbf{N_2}$	Elemental Nitrogen
$\mathbf{N_2O}$	Nitrous Oxide
$\mathbf{NH_3}$	Ammonia
$\mathbf{NH_4^+}$	Ammonium
$\mathbf{(NH_4)_2S_2O_8}$	Ammonium Persulfate
$\mathbf{N_{labile}}$	Labile Inorganic Nitrogen
$\mathbf{N_{mic}}$	Microbial Nitrogen
NO	Nitric Oxide
$\mathbf{NO_2^-}$	Nitrite
$\mathbf{NO_3^-}$	Nitrate
$\mathbf{N_{res}}$	Residual Nitrogen
$\mathbf{K_2SO_4}$	Potassium Sulfate
$\mathbf{K_{labile}}$	Labile Inorganic Potassium
$\mathbf{K_{res}}$	Residual Potassium
pH	pH-value
Pg	Petagram
$\mathbf{P_{labile}}$	Labile Inorganic Phosphorus

P_{mic}	Microbial Phosphorus
PO_4^{3-}	Phosphate
P_{res}	Residual Phosphorus
RCP	Representative Concentration Pathway
S	Siemens
SOM	Soil Organic Matter
TC	Total Carbon
TN	Total Nitrogen
TOC	Total Organic Carbon
TON	Total Organic Nitrogen
TWINSPAN	Two Way Indicator Species Analyses
Vol.%	Volumetric Percentages
W	Watt
yr B.P.	Years Before Present

Summary

Arctic tundra ecosystems are characterized by short summers, low temperatures and low nutrient availability. Cold and long winters result in soils that are perennially frozen in their lower layers and seasonally frozen in their upper layers. As decomposition of organic matter is impeded by low temperatures in these permafrost-affected soils, they represent a significant global carbon reservoir. In the course of climate change, arctic ecosystems are expected to experience a rapid warming, considerably faster than the global average. This temperature increase will affect soil temperatures as well as growing season length. Increased carbon emissions due to higher microbial activity in response to higher temperatures are expected, representing a positive climate feedback mechanism. Moreover, increased microbial decomposition rates may also cause increased availability of nutrients, resulting in changes in the plant-species composition of this nutrient-deficient ecosystems.

An increase of woody plants in the arctic tundra is expected and can stimulate different negative climate feedbacks, including stabilization of the permafrost by increased shrub growth and compensation of increased soil carbon emissions by increased primary production. However, also positive climate feedbacks like reduction of the surface albedo of arctic permafrost landscapes are expected. Thus, nutrient availability indirectly controls the carbon and energy balance of arctic ecosystems and needs to be more intensively studied for a better assessment of the further development of the arctic tundra.

Though plant growth in the arctic tundra is commonly known to be limited by low availability of nitrogen, the factors causing the current shortage of nitrogen are comparatively less investigated. Many studies have been conducted in the last decades in order to characterize the circumpolar belowground carbon pools. These studies were conducted since thawing of the permafrost will mobilize these carbon pools, probably resulting in a significant positive climate feedback. On the other hand, the nitrogen pools of arctic permafrost-affected soils, as potentially mitigating factor for nutrient limitation in the arctic tundra, have received comparatively less attention.

The presented study was conducted to get a comprehensive overview on limiting and available nutrients in the soil-vegetation system of arctic polygonal tundra landscapes and to give an outlook into the future state of nutrient limitation in this ecosystem in the course of climate change. The objectives of this study were in detail: (1) To analyze availability and limitation of nutrients in the soil-vegetation system of an arctic polygonal tundra landscape, (2) to quantify pools of inorganic nitrogen within the perennially frozen ground and the active layer of different soils in the Siberian arctic, (3) to give an estimate of potential annual nitrogen release rates in the course of climate change, and (4) to assess the changes of microbial growth, microbial respiration and nitrogen availability in arctic soils in response to increased temperatures by a soil incubation study.

Three different sites in the Eastern Siberian arctic were investigated in this study. The westernmost study site was located on Samoylov Island in the Lena River Delta (72°22´N; 126°30´E). The second study area was located in the Indigirka Lowlands near the World Wildlife Fund station in Kytalyk (70°53’N; 147°48’E). The third and easternmost study area was located in the Kolyma River Delta in the vicinity of the small village Pokhodsk (69°04’N; 160°58’E). All three study areas were located in the Siberian zone of continuous permafrost and were characterized by polygonal tundra.

Limiting and available nutrients in the polygonal tundra in the Indigirka Lowlands were analyzed by a stoichiometric approach, based on the N/P ratios in the vegetation biomass, the microbial biomass, the pools of inorganic and organic nutrients and the total elemental pools. Eleven soil profiles down to one meter depth below surface at the three different study areas were studied to quantify pools of inorganic nitrogen in arctic permafrost-affected soils. Furthermore, the potential thickening of the seasonally unfrozen uppermost soil (active) layer under higher temperatures for the three study areas was modeled to estimate potential annual nitrogen mobilization from thawing permafrost soils in the course of climate change. In addition, soil samples of one peat-rich soil profile from the study area in the Indigirka Lowlands were incubated for six weeks at 5 °C and at 15 °C. During this incubation, emissions of CO_2 and CH_4 from the soil samples were measured. Changes in microbial biomass carbon and nitrogen (C_{mic} and N_{mic}), dissolved organic carbon and nitrogen (DOC and DON) and ammonium and nitrate (NH_4^+, NO_3^-) were determined subsequent to the sample incubation.

Currently, plant growth in the studied polygonal tundra of the Indigirka Lowlands appeared to be limited mostly by low availability of nitrogen. On the other hand, the molar-based amount of total phosphorus in the soils was approximately 30-fold lower than the amount of total nitrogen. Considering molar based mean N/P ratios of the vegetation between 15 and 25, there was an imbalance between the phosphorus demand of the vegetation and the potentially mineralizable phosphorus in the soils. As already up to 40 % of the total phosphorus were found as plant-available phosphorus, dissolved organic phosphorus and microbial phosphorus, the potentially mineralizable phosphorus is strongly restricted. Thus, increased availability of nitrogen eventually will lead to phosphorus limitation of this polygonal tundra ecosystem.

Furthermore, there were large amounts of inorganic nitrogen stored within the perennially frozen ground of arctic tundra landscapes in Eastern Siberia. As the projected climate warming will cause thawing of the permafrost, these nitrogen stores will become mobilized and can potentially mitigate the current nitrogen limitation of the arctic tundra. The results of this study suggest that the mean annual nitrogen mobilization due to thawing of the permafrost is up to 81 mg m^{-2}, which is almost in the same range of values than the annual nitrogen fixation rates as reported in the literature.

On the other hand, the results of the incubation experiment suggest that increased temperatures may not induce increased nitrogen mineralization by microbial communities in the short-term. Furthermore, though microbial production rates of CO_2 appeared to be increased under higher temperatures, net growth of the microbial biomass was significantly higher at the current soil temperature regime than at higher temperatures. Thus, higher temperatures probably will result in increased respiration rates of the microbial communities at the expense of their growth rates, indicating that they are not adapted to a warmer climate. Adaptation of the microbial communities to a warmer climate may result in mediated microbial respiration rates in the long-term, reducing the expected positive climate feedback of the large carbon stocks of arctic permafrost-affected soils.

This study highlights the importance of comprehensive analyses of the soil-vegetation system in arctic ecosystem, including plant communities, soil nutrients and the microbial biomass as well. This integrated approach led to more detailed conclusions aside of well-known findings like the nitrogen limitation of the arctic tundra and the temperature dependence of microbial respiration rates. The presented results of this study improve our understanding of arctic soil biogeochemistry and give an outlook into the future state of nutrient limitation in the arctic tundra.

Zusammenfassung

Das Ökosystem der arktischen Tundren zeichnet sich durch kurze Sommer, niedrige Temperaturen sowie geringe Nährstoffverfügbarkeit aus. Lange, kalte Winter führen zu ganzjährig gefrorenen Böden mit einer lediglich saisonal aufgetauten oberen Schicht. Da der Abbau organischen Materials durch die geringen Temperaturen in den von Permafrost beeinflussten Böden gehemmt ist, bilden diese Böden ein Kohlenstoffreservoir von globaler Bedeutung. Im Zuge des Klimawandels wird erwartet, dass die arktischen Ökosysteme im globalen Vergleich den größten Temperaturanstieg zu verzeichnen haben werden, was sich sowohl auf die Bodentemperaturen als auch auf die Dauer der Vegetationsperiode auswirken wird. Aufgrund der durch den Temperaturanstieg erhöhten mikrobiellen Aktivität werden verstärkte Kohlenstoffemissionen erwartet, welche dann einen positiven Rückkopplung-seffekt auf das Klima ausüben können. Darüber hinaus können erhöhte mikrobielle Zersetzungsraten auch zu einer erhöhten Nährstoffverfügbarkeit führen, welche sich dann wiederum auf die Zusammensetzung der Pflanzengesellschaften in diesen nährstoffarmen Ökosystemen auswirken kann.

Verstärktes Wachstum von Bäumen und Sträuchern wird in der arktischen Tundra erwartet was verschiedene negative Klimarückkopplungen wie beispielsweise die Stabilisierung des Permafrosts durch erhöhtes Strauchwachstum und die Kompensation erhöhter Kohlenstoffemissionen durch erhöhte Primärproduktion verursachen kann. Aber auch positive Klimarückkopplungen durch die Verringerung der Oberflächenalbedo der arktischen Permafrostlandschaften werden erwartet. Somit werden die Kohlenstoffbilanz und die Energiebilanz der arktischen Ökosysteme indirekt durch die Nährstoffverfügbarkeit gesteuert und ein tieferes Verständnis der Nährstoffverfügbarkeit ist vonnöten, um die zukünftige Entwicklung der arktischen Tundra besser abschätzen zu können.

Obwohl das Pflanzenwachstum in der arktischen Tundra allgemein als stickstofflimitiert gilt, sind die zugrundeliegenden Faktoren dieser Stickstofflimitierung vergleichsweise wenig untersucht. In den zurückliegenden Dekaden wurden viele Studien durchgeführt mit dem Ziel, die Kohlenstoffvorräte arktischer Böden zu charakterisieren. Hintergrund dieser Arbeiten sind die erwarteten positiven Klimarückkopplungen durch den potentiellen Abbau der Kohlenstoffvorräte beim Auftauen des Permafrosts. Die Stickstoffvorräte der arktischen Böden haben bislang weitaus weniger Aufmerksamkeit auf sich gezogen, obgleich diese das Potential hätten, die Stickstofflimitierung der arktischen Tundra zumindest teilweise auszugleichen.

Die vorliegende Studie wurde unternommen, um eine umfassende Übersicht über die

Nährstofflimitierung und Nährstoffverfügbarkeit im Boden-Vegetationssystem der arktischen Tundra zu erlangen. Darüber hinaus soll sie einen Ausblick auf die, im Zuge des Klimawandels, veränderte Nährstofflimitierung dieses Ökosystems geben. Die Ziele dieser Studie waren im Einzelnen: (1) Die Analyse der Nährstoffverfügbarkeit und -limitierung in der polygonalen Tundra, (2) die Quantifizierung anorganischen Stickstoffs im permanent gefrorenen und im saisonal aufgetauten Bereich verschiedener Böden der sibirischen Arktis, (3) die Abschätzung der potentiellen Stickstofffreisetzungsraten aus diesen Böden durch das Auftauen des Permafrosts, sowie (4) die Einschätzung der Veränderungen mikrobiellen Wachstums, der mikrobiellern Respiration und der Stickstoffverfügbarkeit unter erhöhten Temperaturen durch die Inkubation eines arktischen Bodenprofils.

Für die unterschiedlichen Abschnitte dieser Arbeit wurden drei verschiedene Standorte in der ostsibirischen Arktis untersucht. Der westlichste Standort lag auf der Insel Samoylov im Lena Delta (72°22´N; 126°30´E). Der zweite Standort lag im Tiefland der Indigirka bei der WWF Station in Kytalyk (70°53’N; 147°48’E). Der dritte und östlichste Standort lag im Kolyma Delta in der Umgebung des kleinen Örtchens Pokhodsk (69°04’N; 160°58’E). Alle drei Standorte lagen in der Zone des kontinuierlichen Permafrosts und waren durch polygonale Tundra charakterisiert.

Die limitierenden und verfügbaren Nährstoffe in der polygonalen Tundra des Indigirka-Tieflands wurden mittels eines Stöchiometrischen Ansatzes untersucht, welcher auf den N/P Verhältnissen in der Vegetationsbiomasse, der mikrobiellen Biomasse, den anorganischen und organischen Nährstoffvorräten sowie den Gesamtelementvorräten basierte. Elf Bodenprofile bis zu einem Meter Tiefe wurden an den drei verschiedenen Standorten untersucht um die Vorräte an anorganischem Sctickstoff in von Permafrost beeinflussten Böden Sibirirens zu quantifizieren. Darüber hinaus wurde die potentielle Erweiterung der jährlichen Auftautiefe unter höheren Temperaturen in diesen Böden modelliert um die potentielle Stickstofffreisetzungsrate durch das Auftauen des Perfmafrosts abschätzen zu können. Zusätzlichen wurden Bodenproben eines torfreichen Bodenprofils des Standorts im Indigirka-Tiefland für sechs Wochen bei 5 °C und bei 15 °C inkubiert. Während der Inkubation wurden die CO_2- und CH_4-Emissionen aus diesen Proben gemessen. Veränderungen im Gehalt an mikrobiellem Kohlenstoff und Stickstoff (C_{mic}, N_{mic}), gelöstem organischen Kohlenstoff und Stickstoff (DOC, DON) sowie Ammonium und Nitrat (NH_4^+, NO_3^-) wurden am Ende des Inkubationsversuches ermittelt.

Das Pflanzenwachstum in der untersuchten polygonalen Tundra im Indigirkatiefland schien hauptsächlich durch Stickstoff limitiert zu sein. Gleichzeitig war der Gehalt des Gesamtphosphors im Boden um etwa das dreißigfache geringer als der Gehalt des Gesamtstickstoffs. Im Vergleich mit mittleren molaren N/P Verhältnissen der Vegetation zwischen 15 und 25, bestand ein Ungleichgewicht zwischen dem Phosphorbedarf der Vegetation und dem Gehalt an potentiell mineralisierbaren Phosphors im Boden. Da bereits bis zu 40 % des Gesamtphosphors als pflanzenverfügbarer Phosphor, gelöster organischer Phosphor und mikrobieller Phosphor gefunden wurden, ist die Menge des potentiell mineralisierbaren Phosphors stark begrenzt. Erhöhte Stickstoffverfügbarkeit wird deshalb möglicherweise langfristig zur Phosphorlimitierung dieser polygonalen Tundra führen.

Darüber hinaus ließen sich große Mengen anorganischen Stickstoffs im permanent gefrorenen Boden verschiedener Tundralandschaften Ostsibiriens nachweisen. Da die erwartete Klimaerwärmung voraussichtlich zum Auftauen des Permafrosts führen wird, ist von einer Stickstofffreisetzung aus den bestehenden Vorräten auszugehen welche die momentane Stickstofflimitierung der arktischen Tundra potentiell abschwächen kann . Die Ergebnisse dieser Studie deuten darauf hin dass jährlich bis zu 81 mg N m^{-2} durch das Auftauen des Permafrosts freigesetzt werden können, was annähernd den Literaturwerten der jährlichen Stickstofffixierungsrate in arktischen Permafrostlandschaften entspricht.

Auf der anderen Seite scheinen erhöhte Temperaturen nicht zu einer kurzfristig erhöhten Stickstoffmineralisierung zu führen. Obwohl die mikrobielle Produktion von CO_2 bei höheren Temperaturen anzusteigen schien, war das Nettowachstum der mikrobiellen Biomasse unter den momentanen Bodentemperaturen signifikant höher als unter experimentell erhöhten Temperaturen. Höhere Temperaturen führen also möglicherweise zu erhöhten Respirationsraten der mikrobiellen Gemeinschaften, allerdings auf Kosten ihrer Wachstumsraten. Dies spricht dafür, dass die derzeitigen mikrobiellen Gemeinschaften nicht an ein wärmeres Klima angepasst sind. Die Anpassung dieser mikrobiellen Gemeinschaften an ein wärmeres Klima könnte dann langfristig zu abgeschwächten Respirationsraten führen, was die erwartete positive Klimarückkopplung durch die hohen Kohlenstoffvorräte der arktischen Böden reduzieren würde.

Die vorliegende Studie betont besonders die Wichtigkeit umfassender Untersuchungen des Boden-Vegetationssystems arktischer Ökosysteme, inklusive der mikrobiellen Biomasse in diesen Böden. Dieser integrierte Ansatz ermöglichte detaillierte Schlussfolgerungen abseits hinreichend bekannter Ergebnisse wie der Stickstofflimitierung der arktischen Tundra und der Temperaturabhängigkeit mikrobieller Respirationsraten. Die in dieser Arbeit vorgestellten Ergebnisse leisten einen wichtigen Beitrag zum Verständnis der Biogeochemie arktischer Böden und ermöglichen einen Ausblick auf die zukünftige Entwicklung der Nährstoffverfügbarkeit in der arktischen Tundra.

1 Introduction

1.1 Introduction and Objectives

The tundra biome covers the vast northern circumpolar areas beyond the climatic limit of the treeline and south of the polar deserts. The arctic tundra is characterized as a treeless ecosystem, dominated by ericaceous dwarf-shrubs, sedges, grasses, mosses and lichens. Temperatures are very and growing-seasons are short. Precipitation is low in the Arctic, which is resulting in a semi-desert like climate (Bliss and Matveyeva, 1992). Plant species diversity is low in the arctic tundra and plant-growth is limited by short-growing seasons, low temperatures and low availability of nutrients (Gurevitch et al., 2002).

Due to the cold temperatures and only short periods of summer, the soils in the arctic tundra do not thaw completely in the summer, resulting in soils that are perennially frozen in their lower layers and seasonally frozen in their upper layers. These soils are called permafrost soils if the soil within two meters remains frozen during two or more consecutive years (van Everdingen, 2005). The perennially frozen ground acts as a physical barrier - for root growth as well as for leaching of water and nutrients. As drainage is impeded by the underlying permafrost, the soils of the arctic tundra are characterized mostly by high water-contents, despite of the semi-desert like climate. More than 20 % of the northern hemisphere are underlain by permafrost (Zhang et al., 2000). Annual freeze-thaw processes in permafrost environments form different specific landscape elements like sorted stone circles, frost mounds and ice-wedge polygons (French, 2007).

These thermal-contraction-crack polygons are an ubiquitous landscape forming element in arctic wetlands (French, 2007). During winter, thermal-contraction leads to cracks in the soil which fill with re-freezing water from melting snow in spring. Annual repetition of this process leads to the formation of ice-wedges, and the connection of the single ice-wedges leads to the development of the distinct polygonal pattern (Chernov and Matveyeva, 1997; Mackay, 2000). The polygon centers are characterized by high soil water contents, the elevated ridges vary from a dry to a moderately moist water regime (French, 2007). The different hydrological properties cause a distinct plant-species composition for the different zones. The wet polygonal depressions are characterized by sedges and mosses, and the polygon ridges are usually characterized by lichens, mosses, herbs and dwarf-shrubs (French, 2007).

Arctic ecosystems are of particular interest within the context of global change. The global mean surface air temperatures over land and over oceans substantially increased by 0.85 °C between the years 1880 and 2012 (Cubasch et al., 2013). In contrast, temperatures in the arctic showed regional warming over the past three decades of 1 °C per decade, which was significantly higher than the global mean (Christensen et al., 2013) - a phenomena known as Polar Amplification (Manabe and Stouffer, 1980). Due to rising temperatures in the Arctic, substantial portions of the permafrost may thaw in the coming decades (Grosse et al., 2011b) and formerly frozen organic carbon and nutrients are likely to get mobilized (e.g. Kuhry et al., 2010). Increased temperatures probably will also stimulate microbial respiration rates and thereby will result in increased greenhouse gas emissions from the arctic tundra (e.g. Nadelhoffer et al., 1991; Johnson et al., 1996; Schuur et al., 2009; Tveit et al., 2013).

Aside of thawing of the permafrost and increased greenhouse gas emissions, higher temperatures will also have impacts on microbial mineralization rates and nutrient availability (MacDonald et al., 1995; Rustad et al., 2001; Schaeffer et al., 2013). Currently, plant growth in the Arctic is known to be limited by nitrogen (Mack et al., 2004; Weintraub and Schimel, 2005b; Reich et al., 2006) or co-limited by nitrogen and phosphorus (Chapin et al., 1995; Giesler et al., 2012). The supply of both, nitrogen and phosphorus is driven my microbial mineralization from the dead organic material (Fig. 1.1). However, whereas atmospheric nitrogen can also be transformed into mineral nitrogen by microbial fixation, the phosphorus cycle lacks an atmospheric component (Fig. 1.1B; Aber and Melillo, 2001). Input of phosphorus into pristine ecosystems occurs only by weathering of primary minerals like apatite, which is considered to be a minor process in periglacial environments (Allen et al., 2001). Thus, the availability of phosphorus in arctic soils is ultimately limited by the availability of primary minerals and the chemical weathering rates.

Higher nutrient availability will result in increased primary production and in changes in the plant species composition (Eriksson et al., 2010; Sistla et al., 2013). Increased shrub growth is already observed in the arctic tundra (Sturm et al., 2001; Tape et al., 2006) and an increase of woody cover by 50 % is projected until the year 2050 (Pearson et al., 2013). Changes in the plant-species composition of arctic ecosystems will have major impacts on different environmental factors (Foley, 2005): Trees and shrubs will amplify regional warming by reducing winter-and summer-albedo of the arctic tundra (Chapin et al., 2005; Loranty et al., 2011). Transition to shrubs and trees will also increase evapotranspiration and the concentration of water vapor in the atmosphere and thus will amplify the regional greenhouse-warming (Swann et al., 2010). However, shrub expansion may also reduce permafrost thaw by insulating the soils due to their higher snow-holding capacity (Sturm

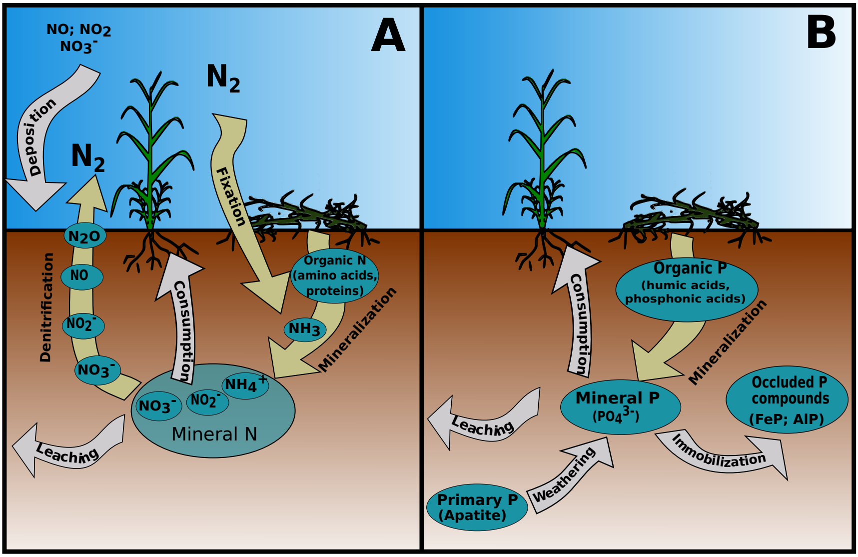

Figure 1.1 Main components of the terrestrial cycles of nitrogen (A) and phosphorus (B). Microbial processes are shown by green arrows, all other pathways are shown by grey arrows.

et al., 2005; Blok et al., 2010). By influencing plant species composition and primary production, changes in nutrient availability have substantial impacts on the carbon balance of arctic ecosystems: Experimental studies found that increased nutrient availability in high latitudes can compensate higher CO_2-emissions by increased primary production (Natali et al., 2012; Sistla et al., 2013).

In summary, nutrient availability indirectly controls different positive and negative feedback mechanisms to climate warming and is an important factor for the further progression of arctic ecosystems. Although the carbon pools in permafrost-affected soils have drawn much attention in the last decades (e.g. Post et al., 1982; Zimov et al., 2006; Tarnocai et al., 2009; Zubrzycki et al., 2014; Hugelius et al., 2014), comparatively little is known about the circumpolar nutrient pools. There are recent approaches to quantify the circumpolar belowground nitrogen pool, and the soils of Northern peatlands are currently estimated to store approximately 10 % of the global nitrogen (Limpens et al., 2006; Zubrzycki et al., 2013; Loisel et al., 2014). However, as mineralization rates are low in arctic ecosystems, only small proportions of this nitrogen are available for plant nutrition in form of dissolved inorganic nitrogen (Schimel and Bennett, 2004; Harms and Jones, 2012; Wild et al., 2013), and total nitrogen alone is not an appropriate measure to characterize the current nitrogen balance of arctic permafrost-affected soils.

As mentioned above, phosphorus have already been shown to be an important and limiting nutrient in arctic ecosystems for plant growth and microbial activity (Giesler et al., 2012; Gray et al., 2014). Recent Earth System Models consider phosphorus as an important factor for the terrestrial carbon cycle (Zaehle and Dalmonech, 2011; Perveen et al., 2014; Thomas et al., 2015). However, there are major uncertainties in the strength of the phosphorus limitation as there is only a limited number of studies investigating phosphorus availability and limitation, especially in arctic soils (Goll et al., 2012). Thus, an accurate characterization of the nutrient balance of arctic ecosystems is needed to understand recent constraints by nutrient availability on the carbon cycle in high latitudes.

Many studies have investigated the greenhouse gas balance of the arctic tundra in order to determine, whether the arctic tundra is currently a carbon sink or a carbon source (e.g. Kutzbach et al., 2004b; Sachs et al., 2010; Parmentier et al., 2011). Furthermore, microbial respiration rates have been shown to increase under higher temperatures in arctic soils (e.g. MacDonald et al., 1995; Jonasson et al., 1999; Mikan et al., 2002), resulting in a positive climate feedback to increased temperatures (Bardgett et al., 2008). However, as microbial growth in arctic soils may also be negatively influenced by increased temperatures (Santruckova et al., 2003), microbial growth and respiration as two independent processes should be investigated simultaneously. Though there are many studies investigating also the temperature dependence of microbial respiration in arctic soils, coupled observations of microbial respiration and changes in the microbial biomass and other relevant soil parameters like DOC, DON and inorganic nitrogen compounds (NH_4^+, NO_3^-) during incubation experiments are scarce (e.g. Nadelhoffer et al., 1991).

As microbial organisms not only act as nutrient suppliers but also actively compete with plants for nutrients, the microbial biomass should be considered when assessing the nutrient balance of arctic ecosystems (Jonasson and Shaver, 1999; Schimel and Bennett, 2004; Churchland et al., 2010). Thus, to give a qualified assessment on the further progression of arctic ecosystems in the course of climate change, integrated analyses of nutrient availability and microbial biomass with respect to rising temperatures are needed. These analyses should include microbial respiration rates, microbial growing conditions, nutrient limitation in the different compartments of the trophic web and nutrient pools in the perennially frozen ground.

This study presents the results of three field campaigns which were conducted in Eastern Siberia in the Lena River Delta, the lowlands of the Indigirka River and the Kolyma

River Delta within the years 2011 and 2012. These expeditions were conducted within the framework of the German-Russian joint project POLYGON (*Polygons in tundra wetlands - state and dynamics under climate variability in Polar regions*; Schirrmeister et al., 2012). The first study area was located on Samoylov Island in the Lena River Delta (72°22'N, 126°30'E). The second study area was located in the vicinity of the World Wildlife Fund station Kytalyk (70°53'N; 147°48'E) in the Lowlands of the Indigirka River. The third study area was located in the Kolyma River Delta near the village Pokhodsk (69°4'N; 160°57'E). All three study areas were located in the Siberian zone of continuous permafrost and were characterized by polygonal tundra. By containing different lacustrine and fluvial sediments as well as peat and pure ice, the different sites represent typical features of arctic periglacial landscapes.

The biogeochemical investigations in this study include stoichiometric analyses of nutrient availability in different compartments of the trophic web, the investigation of nutrient pools in permafrost soils and incubation of soil samples with coupled analyses of microbial biomass growth, microbial respiration and nutrient availability. The present study is aimed to contribute to a better understanding of the nutrient limitation and availability in arctic permafrost-affected soils by coupling the analyses of vegetation biomass, microbial biomass and soil nutrients. The objectives of this study were to:

- Identify limiting and available nutrients in the polygonal tundra by analyzing stoichiometric relationships within and between the vegetation biomass, the microbial biomass, the pools of dissolved inorganic and organic nitrogen and phosphorus as well as the total elemental pools,
- Assess pools of potentially available nitrogen within the perennially frozen ground of permafrost-affected soils,
- Analyze microbial feedback to climate warming by incubation experiments and to give an estimate how nitrogen availability may change under higher temperatures.

1.2 Chapter Overview

The work presented in this study is based on three different papers or manuscripts in different stages of the publication process in international peer-reviewed journals. The results of these three papers and manuscripts are presented in the chapters 5, 6 and 7. Each of these result chapters contains a separate introduction and discussion. However, repetition of general information may occur in the single chapters as the three manuscripts and papers are dealing with the overall topic of nutrient availability and limitation in the arctic tundra.

The chapter 2 - *Nutrient Availability in Arctic Peatlands* - introduces into the background of the following chapters. The current state of research is discussed here. The following chapter 3 - *Material and Methods* - summarizes all methods which were used for the analyses of soils and vegetation in this study. The chapter 4 - *Geographical Characterization of the Study Areas in the Sakha Republic* - gives an overview about the three different study areas in the Siberian Arctic. Characteristics of the study areas in the Lena River Delta, the Lowlands of the Indigirka River and the Kolyma River Delta are presented here. The different investigations are described in the three following chapters: Chapter 5 - *Stoichiometric Analysis of Nutrient Availability (N, P, K) within the Polygonal Tundra* - provides a detailed analyses of nutrient availability and limitation in a polygonal tundra landscape in the Indigirka Lowlands. A modified version of this chapter is already published in *Biogeochemistry* (Beermann et al., 2015). The results of this chapter have also been presented at the 4th European Conference on Permafrost in Évora, Portugal (Beermann et al., 2014). Chapter 6 - *Nitrogen Pools and Permafrost Thaw in Soils of Polygonal Tundra in Eastern Siberia* - shows pools of nitrogen within the perennially frozen ground of soils in the Lena River Delta, the Lowlands Indigirka River as well as soils in the Kolyma River Delta. Furthermore, potential nitrogen release rates due to permafrost thaw in the coming decades is analyzed here. The work presented in this chapter is currently under review for publication in *Biogeosciences* (Beermann et al., 2016). Parts of this study have also been presented at the Tenth International Conference on Permafrost in Salekhard, Russia (Beermann et al., 2012). In chapter 7 - *Effects of Different Temperatures on Soil Microbial Biomass, Microbial Respiration and Nutrient Availability* - the reactions of the microbial biomass, microbial respiration and nutrient availability to increased temperatures in an incubation experiment is shown. This chapter is currently in preparation for publication in *PLOS One*. The last chapter 8 - *Synthesis and Conclusions* - summarizes the results and interpretations of the previous chapters and points to open questions which could be subject to follow-up studies in the future.

1.3 Authors' Contribution

Due to the interdisciplinary and international character of this study, several co-authors contributed to the papers which are either published or still in preparation for publication. As first author of these manuscripts, Fabian Beermann designed the studies, conducted the literature review, collected the samples, conducted the laboratory analyses and most of the statistical analyses and the data evaluation and finally coordinated and wrote the publications.

The co-authors of the publication which is based on chapter 5 - *Stoichiometric Analysis of Nutrient Availability (N, P, K) within the Polygonal Tundra* - provided critical and helpful reviews. Furthermore, Annette Teltewskoi provided the figures 3.1, 5.1 and 5.2 and provided also the description of the vegetation in the section 5.2.1 - *Soil Profiles and Plant Communities*. Furthermore, this publication was critically discussed and reviewed by the co-authors. Chapter 6 - *Nitrogen Pools and Permafrost Thaw in Soils of Polygonal Tundra in Eastern Siberia* - is still in preparation for publication. All Co-Authors helped with critical reviews of the manuscript. Furthermore, Moritz Langer helped with modeling the increase of the active layer under different climate scenarios and provided the figure 6.2. Julia Boike, Lutz Schirrmeister and Sebastian Wetterich provided a monitoring of the soil thermal dynamics in all study areas; Sebastian Wetterich provided also the figures A.5. Additionally, Lutz Schirrmeister provided the figures A.1, A.2 and A.3. The publication based on chapter 7 - *Effects of Different Temperatures on Soil Microbial Biomass, Microbial Respiration and Nutrient Availability* was critically discussed and reviewed by the co-authors.

2 Nutrient Availability in Arctic Peatlands

2.1 Arctic Peatlands in the Climate System

2.1.1 Arctic Peatlands and their Carbon Balance

Peat develops when the decomposition rate of dead plant material does not keep pace with its addition to the soil. Low temperatures and anaerobic conditions due to high soil water contents impede decomposition processes and thus favor peat growth in arctic permafrost ecosystems. The amount of peat stored in boreal and arctic peatlands is estimated to account for 75 - 80 % of the global peat deposit (Frolking et al., 2011). The ubiquitous peat cover insulates arctic wetlands from summer heating and favors the aggradation of permafrost (Woo and Young, 2006).

High-latitude peatlands, with their large inventory of potentially mobilizable organic carbon, are a major factor in the global climate system with respect to climate active greenhouse gases. They represent a long-term carbon dioxide sink but are also a global source for methane (Smith et al., 2004; MacDonald et al., 2006). For instance, the development of arctic peatlands during the early Holocene contributed to a sustained peak in atmospheric methane concentration (Yu et al., 2013). Thus, many studies have been conducted in the last decades to quantify the belowground organic carbon pool of arctic permafrost-affected soils (e.g. Post et al., 1982; Ping et al., 2008; Tarnocai et al., 2009; Hugelius et al., 2013; Strauss et al., 2013; Zubrzycki et al., 2014). Currently, arctic permafrost-affected soils are estimated to contain approximately 1300 Pg carbon (1 Pg = 10^{15} g = 1 Gt) within the first 3 m of the soil (Hugelius et al., 2014). In the course of climate change, these carbon stocks are potentially vulnerable to microbial decomposition and can be a large source for increased atmospheric CO_2 and CH_4 concentrations (Kuhry et al., 2010; Schneider Von Deimling et al., 2012).

However, high-latitude peatlands are also highly sensitive to the projected changes in the regional climate: The three main general impacts of climate change on peatlands are (1) drainage, (2) permafrost thaw and (3) increased fire intensity (Frolking et al., 2011). Though fire intensity due do drought may not be a major factor for arctic peatlands, permafrost thaw and drainage are serious threats for these ecosystems. Major portions of the permafrost may thaw in the coming decades (Grosse et al., 2011a) and a large decrease of arctic wetlands by drainage is projected (Avis et al., 2011). On the other hand, soil moisture contents in large parts of the circumpolar arctic are also projected to increase in a warmer climate (Subin et al., 2013). Thus, the sustainability of arctic wetlands eventually depends on the balance between water supply and water losses by evaporation and lateral drainage (Woo and Young, 2006).

2.1.2 Permafrost Soils

A main characteristic of arctic peatlands is the underlying permafrost. More than 20 % of the northern hemisphere and even about 27 % of the landmass north of 50° N are underlain by permafrost (Zhang et al., 2000; Jones et al., 2010). The soils in these areas are called permafrost soils when they remain frozen within two or more consecutive years (van Everdingen, 2005). The annually thawing near-surface layer above the permafrost is called *Active Layer* (French, 2007). The active layer is the main zone of microbial activity and recent pedogenesis whereas the underlying frozen ground limits root growth and prevents leaching of nutrients

A unique soil forming process in permafrost environments is called cryoturbation. The term cryoturbation is used to describe soil movements due to frost actions. The main driving factor for this process is the different water capacity of different soil horizons and materials and their different expansions during the water-ice phase change (French, 2007). This process is most pronounced in mineral soils with a large number of freeze-thaw cycles and can lead to burying and conservation of soil organic material (Bockheim, 2007; Kaiser et al., 2007). Frost heave and sorting of soil materials due to cryoturbation can lead to the formation of distinct patterned ground like e.g. sorted stone circles (Kessler and Werner, 2003). Another distinct arctic soil pattern are thermal contraction-crack polygons which are formed by annual freezing and thawing of the soil.

The distinct pattern of polygonal tundra (Fig. 2.1A) results from thermal-contraction-cracks due to tensile stress induced by falling winter temperatures. These fractures partially fill with re-freezing snow melt water in spring. The resulting vertical ice-veins are zones of weakness to repeated cracking as the tensile strength of any frozen ground is greater than the tensile strength of ice (Lachenbruch, 1962). Thus, repetition of this process leads to the development of ice-wedges, 3 - 5 m deep (Fig. 2.1B). Connection of the ice-wedges leads to the formation of polygonal patterned ground. The spacing between the single ice-wedges depends on the sediment and the climatic conditions as well (Lachenbruch, 1962; Plug and Werner, 2002). As the soil between these ice-wedges extends during summer warming, it gets pushed above the ice-wedges and thus forms elevated polygon ridges above the ice wedges (Mackay, 2000).

Polygonal tundra occurs in the vast coastal plains of Siberia from the Gydan peninsula in the west over the Taymir peninsula, the Lena River Delta and the Yana-Indigirka

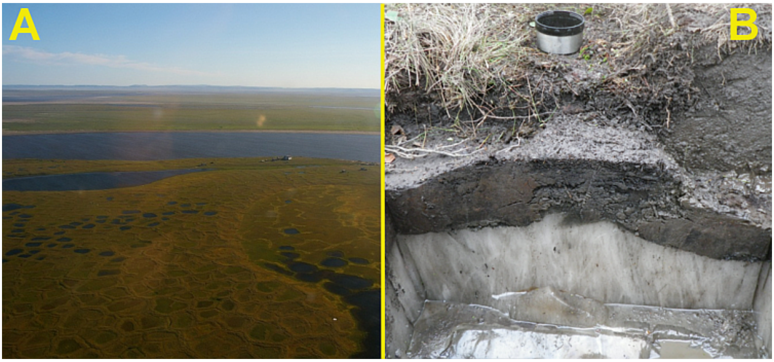

Figure 2.1 Photographs of polygonal tundra and an ice-wedge. **A:** Polygonal tundra in the Lena River Delta. Photo by courtesy of Sebastian Zubrzycki. **B:** Cross section through the upper part of an ice-wedge and the overlying frozen soil in the Kolyma River Delta

Lowlands to the Kolyma River Delta in the east. In North America, polygonal tundra is widespread along the northern coast of Alaska and North West Canada (c.f. Minke et al., 2007; de Klerk et al., 2014).

Following the US Soil taxonomy, there are three suborders within the soil order of Gelisols: namely *Histels*, *Turbels* and *Orthels*. *Histels* are defined as permafrost soils that comprise 80 % or more of organic material to a depth of 50 cm or to e.g. a glacic or lithic layer. When the soil comprise less than 80 % organic material but also shows influence of cryoturbation it is assigned to the great group *Turbels*. All other soils that do not meet the aforesaid criteria belong to the great group of *Orthels*. Within these suborders the soils are characterized into different Great Groups, for instance by the mineral composition of the soil, by water saturation and redox conditions and also by the state of decomposition of the organic material. In total, there are 20 different Great Groups within the soil order of the Gelisols (Soil Survey Staff, 2014).

2.1.3 Arctic Peatlands in a Changing Climate

The mean surface air temperature in the Arctic showed significant regional warming over the past three decades of 1 °C per decade, which is significantly higher than the mean global warming in this period (Christensen et al., 2013). Long-term warming in arctic peatlands will have multiple effects on these ecosystems, causing different positive and negative feedbacks on regional and global climate (Fig. 2.2). The main direct effect of higher temperatures on permafrost soils will be thawing of the permafrost and increased active layer thicknesses (Grosse et al., 2011a; Lawrence et al., 2012). This might lead to a rapid loss of organic carbon as the organic matter, previously locked in the perennially frozen ground, is highly vulnerable to microbial decomposition (Schmidt et al., 2011; Mueller et al., 2015). Thus, increased temperatures will probably result in increased greenhouse gas emissions from arctic soils (e.g. Nadelhoffer et al., 1991; Johnson et al., 1996; Dutta et al., 2006; Schuur et al., 2009) and also in increased nutrient availability in arctic soils (e.g. MacDonald et al., 1995; Rustad et al., 2001; Schaeffer et al., 2013). The input of easily available carbon and nitrogen will stimulate microbial decomposition again (Wild et al., 2014) and former carbon sinks are likely to become carbon sources (Hicks-Pries et al., 2011). Furthermore, following permafrost thaw and under higher temperatures, rapid shifts in the microbial community composition and functioning are expected, probably resulting in higher decomposition rates of carbon and nitrogen (Wallenstein et al., 2007; Graham et al., 2012).

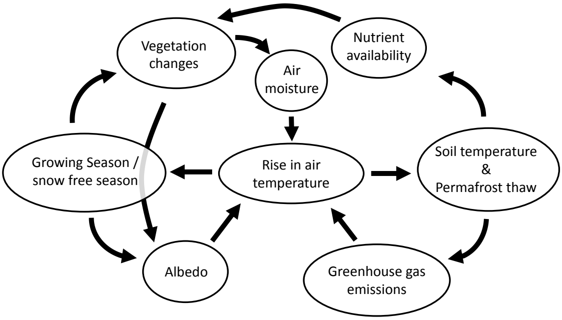

Figure 2.2 Summary of the main positive climate feedback mechanisms in arctic ecosystems.

Long term-warming and higher nutrient availability in arctic peatlands will influence the plant species diversity and composition of arctic ecosystems (Aerts, 2006; Eriksson et al., 2010). The dominance of woody plants probably will increase due to higher temperatures, extended growing season lengths and deeper thawed active layers (Foley et al., 1994; Vitousek et al., 1997; Sturm et al., 2005; Sistla et al., 2013). Increased shrubcover in the circumpolar Arctic is predicted (Pearson et al., 2013) and already reported (Callaghan et al., 2011). Shrub expansion will insulate the soils and increase soil winter temperatures by the high snow-holding capacity of the shrubs (Sturm et al., 2005; Lawrence and Swenson, 2011; Myers-Smith et al., 2011). Higher soil temperatures further increase microbial activity and microbial decomposition rates of the soil organic matter (Sturm et al., 2001; Schimel et al., 2004).

However, increased temperatures and permafrost degradation could also promote the carbon storage function of arctic peatlands: Increased growth of woody plants and increased nutrient availability due to permafrost thaw will enhance primary production and an increased net carbon storage in the vegetation could be promoted (van Huissteden et al., 2012; Sistla et al., 2013). Current satellite data already show an earlier onset of greenness and a longer growing season over the tundra biome (Jia et al., 2012). Lengthening of the growing season has a direct positive effect on plant carbon uptake and also on soil respiration (Euskirchen et al., 2006). Winter warming of the tundra could eventually increase the net primary productivity by 20 % (Natali et al., 2012). However, expansion of shrubs and trees will mainly reduce the winter albedo of these ecosystems, changing the radiative budget and amplifying regional warming (Chapin et al., 2000; Foley, 2005; Loranty et al., 2011). Furthermore, increased evapotranspiration by shrubs and trees will also increase the amount of water vapor in the atmosphere, strengthening the regional greenhouse-warming (Swann et al., 2010).

Thus, greenhouse-warming and the associated increases in nutrient availability will have major impacts on arctic peatlands. Furthermore, experimental studies showed that primary productivity is probably even more sensitive to changes in the nutrient availability than to higher temperatures (Zamin and Grogan, 2012). As the succession of plant-communities control different positive and negative climate feedback mechanisms, nutrient availability and limitation are major parameters to assess the further development of arctic ecosystems.

2.2 Nutrient Availability in Arctic Peatlands

2.2.1 Nitrogen

Northern peatland soils store 8-15 Gt nitrogen which accounts for approximately 10 % of the global soil nitrogen pool (Limpens et al., 2006; Loisel et al., 2014). However, as mineralization rates are low in arctic ecosystems, only small proportions of this nitrogen are available as dissolved inorganic nitrogen (Schimel and Bennett, 2004; Harms and Jones, 2012; Wild et al., 2013). Thus, nitrogen is known to be one of the main limiting nutrients for plant growth in the arctic tundra (Mack et al., 2004; Reich and Oleksyn, 2004; Weintraub and Schimel, 2005b; Reich et al., 2006).

Though plants preferentially use inorganic nitrogen forms like ammonium (NH_4^+), nitrate (NO_3^-) and nitrite (NO_2^-), they are also able to use organic nitrogen bound in amino acids (Schimel and Bennett, 2004). Thus, nitrogen uptake by plants is possible without microbial mineralization to inorganic nitrogen. Furthermore, plants and microbial organisms actively compete for soil organic nitrogen (Weintraub and Schimel, 2005a), and the soil microbial biomass represents a substantial sink-capacity for nitrogen in arctic ecosystems (Churchland et al., 2010; McLauchlan et al., 2013). However, only a small proportion of the dissolved organic nitrogen (DON) in arctic soils is available as amino acids (Jones and Willett, 2006), and the transformation of proteins to amino acids probably is the main limiting factor for nitrogen supply during the decomposition of soil organic matter to inorganic nitrogen compounds in arctic ecosystems (Jones and Kielland, 2002).

Microbial decomposition of the soil organic matter provides the main proportion of the annual nitrogen mobilization in arctic soils. The annual mineralization rate of nitrogen is between 50 and 500 mg m^{-2} (Nadelhoffer et al., 1992; Schmidt et al., 1999; Schimel and Bennett, 2004). Fixation of atmospheric nitrogen is the main external input of nitrogen in these ecosystems. The annual input of nitrogen into arctic soils by microbial nitrogen fixation amounts to approximately 80 to 130 mg m^{-2} (Hobara et al., 2006). The atmospheric deposition of inorganic nitrogen compounds (NO, NO_2, NO_3^-, NH_3, NH_4^+) accounts for additional 8 to 56 mg m^{-2} (Van Cleve and Alexander, 1981). On the other hand, the annual nitrogen demand of an arctic plant-community was estimated to be approximately between 750 and 2,000 mg m^{-2} (Chapin et al., 1988; Shaver and Chapin, 1991). Thus, the annual input and mobilization of inorganic nitrogen in arctic soils hardly meets the annual nitrogen demand of the vegetation, clearly illustrating the current nitrogen limitation of plant-growth in arctic ecosystems (Fig. 2.3).

However, also the growth and activity of the soil microbial biomass in arctic ecosystems may currently be limited by low availability of nitrogen (Schimel and Weintraub, 2003; Hartmann et al., 2013). By warming of arctic soils, increased microbial decomposition rates may follow and increased availability of nitrogen is expected (MacDonald et al., 1995; Rustad et al., 2001; Natali et al., 2012; Schaeffer et al., 2013). Increased nitrogen availability could probably cause a positive feedback by further stimulating microbial activity and decomposition of the soil organic matter (Stark et al., 2012; Wild et al., 2014). Thus, nitrogen availability plays a key role for plant growth and microbial activity in arctic ecosystems.

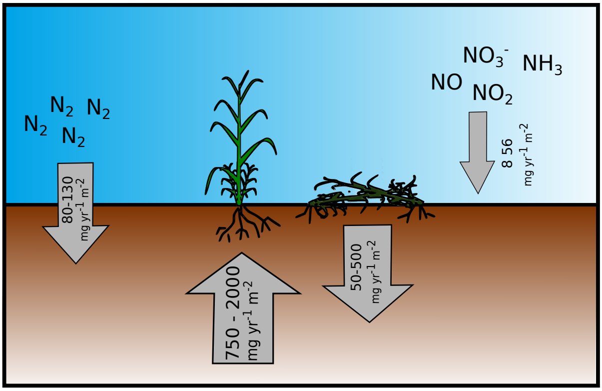

Figure 2.3 Overview on the main annual fluxes of nitrogen in arctic soils. Arrows represent from left to right (1) Nitrogen fixation (Hobara et al., 2006), (2) Annual nitrogen demand of the vegetation (Chapin et al., 1988), (3) Nitrogen mineralization (Nadelhoffer et al., 1992) and (4) Deposition of inorganic nitrogen compounds (Van Cleve and Alexander, 1981). The wider the arrow, the larger the annual flux.

2.2.2 Phosphorus

Several authors showed that phosphorus is at least as important as nitrogen for plant growth in the arctic tundra (Chapin et al., 1995; Giesler et al., 2012; Zamin and Grogan, 2012). Moreover, the availability of soil phosphorus also significantly influences microbial abundances in arctic soils (Gray et al., 2014). In contrast to the nitrogen cycle, the phosphorus cycle lacks a major atmospheric component (Aber and Melillo, 2001). Thus, chemical weathering of primary minerals like apatite is the main input of phosphorus in pristine ecosystems (Fig. 1.1). During the succession of ecosystems, phosphorus availability declines due to depletion (leaching) and occlusion of phosphorus in unavailable forms. A so-called Terminal Steady State is reached when the amounts of both available phosphorus and total phosphorus are strongly restricted (Fig. 2.4; Walker and Syers, 1976). As chemical weathering rates are very low in periglacial environments (Allen et al., 2001), phosphorus is currently overall a strongly finite resource in arctic soils.

The microbial biomass is the largest reservoir of potentially available phosphorus in arctic soils (Weintraub, 2011). Abiotic stresses like drying-rewetting and freezing-thawing contribute substantially to the solubilization of soil phosphorus (Blackwell et al., 2010), and periodic crashes of microbial communities provide most of the phosphorus inputs into the soil pool of plant-available nutrients (Chapin et al., 1978). As the input of phosh-

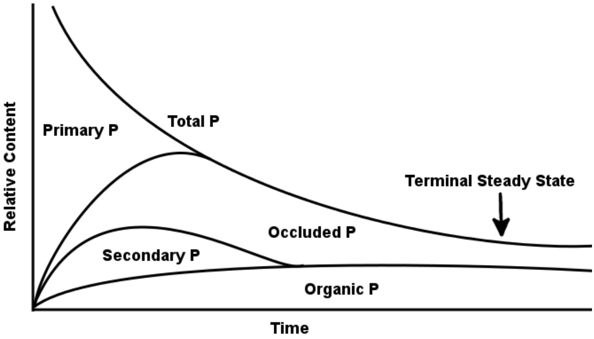

Figure 2.4 Changes in soil phosphorus availability over time. High amounts of primary phosphorus are transformed into other forms while the total amount of phosphorus declines over time (After Walker and Syers (1976))

porus in arctic soils is very low, higher decomposition rates of the soil organic matter in a warmer climate could lead in the long-term to phosphorus limitation of the arctic tundra due to low amounts of potentially mineralizable phosphorus (cf. Peñuelas et al., 2012). However, as the main control of chemical weathering of primary minerals is temperature, higher temperatures could also enhance phosphorus availability in arctic soils (Lasaga et al., 1994).

3 Material and Methods

3.1 Fieldwork

3.1.1 Active Layer Studies

In all three study areas, samples were taken from the active layer as well as from the permafrost. The location of the soil profiles in the different study areas is described in detail in chapter 4 - *Geographical Characterization of the Study Areas in the Sakha Republic*. The main focus of the active layer studies was on the study area in the Indigirka Lowlands (cf. Section 4.3, *Indigirka Lowlands - Kytalyk*). In one selected ice-wedge polygon (Lhc11; Figure 4.6), 23 soil profiles were sampled in a regular grid of 4*5 m across the polygon (Figure 3.1). Of each soil profile, all organic horizons of the thawed soil to a depth of up to 50 cm and the overlying vegetation were sampled. Measurements of heights of ground surface, frost table and water level were mapped in the same grid as the vegetation was mapped. Ground surface elevation, frost table height (i.e. elevation) and open water level were determined in the center of each square, relative to a horizontal reference level (Fig. 3.1).

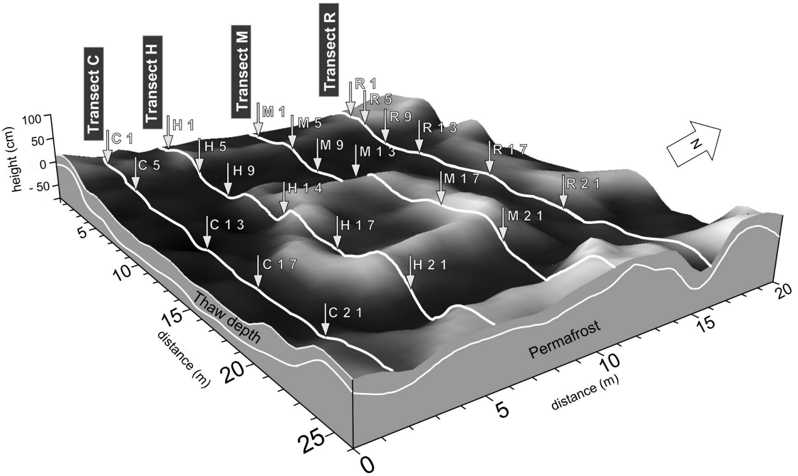

Figure 3.1 Microtopography of the investigated polygon Lhc11 in the Indigirka Lowlands. Surface height and thaw depth are shown. Locations of the soil profiles are marked by arrows

To ensure representativeness of the results from the polygon Lhc11, microtransects of four soil profiles from the polygon ridge into the polygonal depressions were sampled in seven additional polygons (IND-1-7) within the whole study area (20 km^2, Fig. 4.6). Sampling of these soil profiles were conducted as described before.

Furthermore, in the soil profile IND-3.4 nine soil samples were taken in each of the investigated soil horizons. The samples were taken within metal cylinders with a volume of 100 cm^3 and kept in an intact state of stratification until analyses of the soil samples (Fig. 3.2).

3.1.2 Permafrost Studies

Soil profiles including samples from the frozen ground were sampled in all three study areas (LEN-1-R, LEN-1-C, IND-R, KOL-1 - KOL-7). At the study area in the Lena River Delta, both investigated soil profiles (LEN-1-R, LEN-1-C) were sampled down to a depth of 1 m within the permafrost. At the site in the Indigirka Lowlands, one soil profile of a polygon ridge (IND-R) was sampled in August 2011 for analyses of the soil chemistry as well as for palaeoecological analyses. This profile was excavated from a pit, 1.1 m deep. A detailed description of the profile IND-R is given by (Teltewskoi et al., 2016).

Eight additional soil cores were drilled in duplicate form, 0.5 m to each other in the Kolyma River Delta near Pokhodsk. The duplicate soil cores were either labelled as KOL... or as 12P... The soil cores labelled as KOL... were used for analyses of the soil chemistry and the soil cores labelled as 12P... were used for cryolithological studies. Due to the duplicate sampling, description and analytical data from both cores are summarized. For drilling of the soil cores a portable permafrost auger set was used. This set contained a small engine STIHL BT 121 (Stihl Holding AG & Co. KG, Germany) as well as a Snow-Ice-Permafrost-Research-Establishment coring auger (Jon´s Machine Shop, Alaska; Zubrzycki, 2011). All soil cores were divided into subunits of 5 cm which were analyzed for their contents of extractable plant available ammonium and nitrate, for total carbon and nitrogen and for water content and bulk density.

Sediment and ice structures of all soil profiles which included permafrost samples were described, sketched and photographed in the field to document the stratigraphy of the soil profiles. These data were used as input data for the active layer thickness model (cf. section 3.4 - *Modeling Active Layer Thickness*). The different sediment layers of the soils were characterized using the grain size distribution, color, content and kind of plant remains as well as the amount and arrangement of segregation ice. Grain-size distribution was analyzed using a LS 200 laser particle analyzer (Beckman-Coulter, USA) and com-

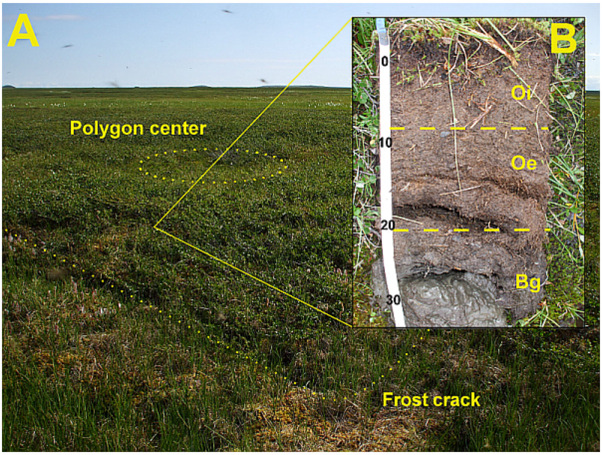

Figure 3.2 Location (A) and profile (B) of the investigated soil profile IND-3.4. The polygonal depression and the frost crack on the polygon ridge are marked by dotted lines. The investigated soil was located on the polygon ridge.

puted with GRADISTAT 4.0 (Blott and Pye, 2001). Volumetric contents of ice, sediment and organic C were calculated following Strauss et al. (2012; 2013), using absolute ice contents, total organic C contents and bulk density estimation.

3.1.3 Vegetation Sampling

At each investigated soil in the study areas in the Indigirka Lowlands and in the Kolyma River Delta, one plot (1*1 m) was sampled by noting all occurring vascular plants, mosses and lichen taxa as well as their estimated cover. For estimating cover and abundance of the species, a modified Braun-Blanquet scale was used (Reichelt and Willmanns, 1973). The vegetation was classified into two discrete units by a modified TWINSPAN analysis, using the program JUICE (Tichý, 2002). These two units represent roughly the polygon ridges and the polygon centers.

The vegetation of the polygon Lhc11 in the study area in the Indigirka Lowlands was continuously mapped in a grid of 1*1 m quadrats, covering an area of 26*21 m and resulting in 546 quadrats with information about identity and abundance of occurring plant species. Species coverage in the polygon Lhc11 was estimated into 15 cover classes after Londo (1976).

Unknown vascular species were determined by using the literature of Tolmachev and

Yurtsev (1974), Polunin (1959) and Rothmaler (2002); their nomenclature follows Czerepanov (1995). Moss and lichen species were identified and named after Frey (1995), Michaelis (2011) and Wirth (Wirth, 1995). Representative samples of the foliar biomass of the plant communities (including mosses) on each plot of the soil profiles in the study area in Kytalyk were sampled for further analyses.

3.1.4 Monitoring Soil Thermal and Hydrological Conditions

In order to assess current on-site physical soil conditions, annual monitoring of soil moisture and temperatures was conducted at all three sites in a soil profile on a polygon ridge (Fig. A.5). At the study site in the Kolyma River Delta, this monitoring included the active layer and the perennially frozen ground, whereas the monitoring at the two other sites was conducted only in the active layer. The longest record of ground temperatures and active layer depth for the Lena River Delta is available on Samoylov Island for the years between 1998 and 2011 (Boike et al., 2013). Comparable data for the Indigirka Lowlands is available between 2008 and 2009 (Parmentier et al., 2011) and between 2009 and 2011 (Iwahana et al., 2014).

The hourly climate data record (air temperature, net radiation, humidity, wind speed and direction, rainfall, snow depth) on Samoylov Island is derived from a weather station installed in 1998 (Boike et al., 2008). Continuous monitoring of soil temperatures and soil moisture was initiated in 1998. Soil temperatures were recorded using thermistors (107, Campbell Scientific Ltd., UK) and liquid water content was calculated from time domain reflectometry measurements (Tektronix 1502 and TDR100, Campbell Scientific Ltd., UK) using the semi empirical mixing model of Roth et al. (1990). Ice was included as the fourth phase (air, water, soil, ice) to account for the composition of permafrost soils.

The monitoring at the Kytalyk study site in the Indigirka Lowlands took place between July 2011 and July 2012 for temperatures and in July 2011 and August 2011 for soil moisture, and in the Kolyma River Delta in Pokhodsk between July 2012 and July 2013 for all measured parameters. The data sets were obtained by HOBO 12-Bit Temperature and Soil Moisture Smart Sensors (S-TMB-M002 and S-SMD-M005, Onset Computer Corporation, USA) at different depth below surface. All data loggers measured their specific value with a resolution of 30 minutes.

3.2 Laboratory Work

3.2.1 Nutrient Analyses

Initial analyses of the samples from the expeditions to the Indigirka Lowlands and the Kolyma River Delta were conducted directly in the field laboratory on dissolved inorganic nitrogen (DIN), which was considered as the sum of ammonium (NH_4^+) and nitrate (NO_3^-). Contents of total carbon (TC), total nitrogen (TN), dissolved organic carbon (DOC) and dissolved organic nitrogen (DON) were analyzed after transport in frozen state to the laboratories at the University of Hamburg. The samples from the Lena River Delta were measured after transport under frozen conditions to the laboratories at the University of Hamburg for all parameters. Contents of ammonium and nitrate in the soils were extracted by 0.0125 M $CaCl_2$. In the field laboratory these extracts were measured by using photometrical test-kits for Ammonium and Nitrate analyses (LCK304 and LCK339, HACH-Lange GmbH, Germany). In the laboratory, ammonium in these extracts was measured photometrically by the indophenolblue reaction (Selmer-Olsen, 1971). Extractable nitrate was measured in the same extracts using high pressure liquid chromatography (Agilent 1200 series, Agilent Technologies, USA).

Further analyses were conducted after transport under frozen conditions: total carbon, nitrogen, phosphorus and potassium as well as labile phosphorus (loosely bound inorganic phosphorus) and labile potassium (loosely bound inorganic potassium) in the bulk soil were measured. Dissolved organic carbon (DOC), dissolved organic nitrogen (DON) and dissolved organic phosphorus (DOP) as well as contents of carbon, nitrogen and phosphorus in the microbial biomass were also measured. The residual fractions of carbon, nitrogen, phosphorus and potassium were considered as the total values subtracted by the sum of the other analyzed (more mobile) fractions. Elemental contents of the microbial biomass, the dissolved organic fraction as well as labile phosphorus and potassium and dissolved inorganic nitrogen were considered as the biologically active fractions.

For each soil profile, a mixed sample of the foliar biomass of the according plant communities was analyzed for contents of total carbon, nitrogen, phosphorus and potassium. After air drying of the samples, all green leaves of vascular plants as well as the mosses were separated and homogenized. With respect to the sampling period at the end of the growing season, all of these leaves were considered as mature leaves.

Total carbon and nitrogen in the soil samples as well as in the vegetation samples have been measured using a C/N analyzer (Variomax CNMS, Elementar Analysensysteme GmbH, Germany). Total phosphorus and potassium also in the soil samples and in the vegetation samples were extracted with nitric acid using microwave application (1600 W, 200 °C, and 15 min). Subsequent to this extraction was a digestion with 5.5 M sulphuric acid (H_2SO_4) and ammonium persulfate ($(NH_4)_2S_2O_8$) at >150 °C(Hedley et al., 1982). Labile phosphorus and potassium were addressed as lactate-soluble phosphorus and potassium (VDLUFA, 1991). The content of phosphate in all extracts was determined using the colorimetric molybdenum blue reaction (Murphy and Riley, 1962). Potassium in the extracts was measured by an atomic absorption spectrometer (Varian 280FS AA, Agilent Technologies, USA).

3.2.2 Microbial Biomass Analyses

Microbial carbon, nitrogen and phosphorus were measured using the chloroform fumigation method (Brookes et al., 1985; Ivanoff et al., 1998). After fumigation under chloroform vapor in a desiccator for 24 h at 24 °C, the samples were extracted by 0.5 M K_2SO_4 (carbon and nitrogen) and 0.5 M H_2CO_3 (phosphorus), respectively. For each sample, a non-fumigated subsample was also extracted by K_2SO_4 and H_2CO_3. After shaking, all extracts were filtered (Macherey-Nagel 315; 4-12 μm). All K_2SO_4-extracts were measured using a TOC/TON analyzer (Shimadzu TNM-L, Shimadzu Corp, JPN) for carbon and nitrogen. The H_2CO_3 extracts were treated with sulphuric acid and ammonium persulfate as described before. Phosphorus in these extracts was measured photometrically using the colorimetric molybdenum blue reaction (Murphy and Riley, 1962). The differences in total extractable carbon, nitrogen and phosphorus between the non-fumigated and fumigated subsamples were calculated. To estimate elemental contents in the microbial biomass correction factors of 0.35 for carbon (Sparling et al., 1990), 0.54 for nitrogen (Brookes et al., 1985) and 0.37 for phosphorus (Hedley and Stewart, 1982) were applied. The content of carbon in the non-fumigated subsamples was considered as DOC. The differences between DIN and labile phosphorus, respectively and the contents of nitrogen and phosphorus in the non-fumigated subsamples were considered as DON and DOP (Jones and Willett, 2006).

3.2.3 Soil-Physical Analyses

Bulk densities were calculated by the dry mass of the samples and the sample volume (100 cm^3). The gravimetric water contents of the samples were calculated by the mass loss of the samples after drying at 105 °C for 24 h. Gravimetric water contents and bulk densities were used to calculate volumetric water contents. Particle densities were measured using a He-Pycnometer (AccuPyc II 1340, Micromeritics GmbH, Germany). Soil volume was calculated by the bulk density and the particle density. The remaining volume was considered as the total pore volume. The air-filled pore volume results from the difference between the total pore volume and the volumetric water content.

3.2.4 Incubation of Soil Samples

An incubation experiment was designed using the volumetric soil samples from the soil profile IND-3.4. After transport under frozen conditions to the laboratory of the University of Hamburg, three replicate samples from each horizon were placed in glass bottles under ambient air and incubated at either 5 °C or 15 °C for 42 days. This particular incubation time was selected to simulate the short period of warmer soil temperatures (above 3 °C; Fig. A.5b) in summer. The two temperature treatments were selected to simulate current soil temperatures in summer as well as soil temperatures in a substantially warmer summer climate. Concentrations of CO_2 and CH_4 in the headspace of these bottles were measured by a gas chromatography (Agilent Technologies, 7890A, USA) directly before and after thawing of the samples and subsequently once in a week. The amount of CO_2 and CH_4 in the bottles was calculated from the concentration of the gases in the headspace, headspace volume, water content, gas solubility in water, temperature and pressure using Henry´s law. Production rates of CO_2 and CH_4 were calculated on a daily base and expressed per volume of the soil (μg C d^{-1} cm^{-3}) .

3.3 Statistical Analyses

3.3.1 Nutrient Stoichiometry

Although it is common in ecological reports to express elemental stoichiometry as mass ratios (e.g. g N/g P) atomic ratios are used in this study (e.g. mol N/mol P) as they reflect the actual stoichiometry. The molar based N/P ratios are equal to 2.2 times the mass based N/P ratios. The N/K and K/P ratios in molar units are equal to 2.8 times and 0.8 times the ratios in mass units, respectively. All mass-based elemental ratios from the literature were recalculated by these factors to molar ratios. The mean N/P ratios of the two vegetation communities were compared by Student´s two-sample t-test. Differences in the N/K and K/P ratios of the vegetation communities were identified, due to missing homogeneity of variances, by Welch´s two sample t-tests. Differences in the chemical composition between the soils in the studied polygon and the soils in the surrounding study area were also analyzed by Welch´s two sample t-tests. To analyze relationships between microbial carbon and microbial nitrogen as well as relationships between microbial nitrogen and DIN, linear ordinary least squares regression was used. Nonlinear ordinary least squares regression was used to identify relationships between microbial carbon and total carbon as well as relations between microbial nitrogen and labile phosphorus. All statistical analyses were performed using the program *R* (R Core Team, 2013). A vegetation map was constructed using the software Qgis version 1.8.0 *Lisboa* and modified with drawing software. The 546 vegetation quadrates were classified into two communities using the function *isopam* from the *R* package *isopam* (Schmidtlein et al., 2010). Indicator values and significance levels of the indicator species for the dry and the wet community were calculated using the function *multipatt* from the *R* package *indicspecies* (De Cáceres and Legendre, 2009).

3.3.2 Elemental pools

Mean pools of carbon, nitrogen, ammonium and nitrate in the active layer and the permafrost were calculated for each of the eleven investigated permafrost soil profiles. The eight soil profiles from the study area in in the Kolyma River Delta were allocated to three groups (*Polygon ridges*, *Polygon centers*, *Floodplains*) and mean elemental pools were calculated for the three groups and significant differences between the active layer and the permafrost were investigated by Student´s two sample t-test. Mean annual nitrogen release was estimated by multiplying the mean pools of ammonium with the annual active layer thickness increase for the three groups from the Kolyma River Delta and also for the three soil profiles from the study areas in the Lena River Delta and the Indigirka Lowlands.

3.3.3 Incubation experiment

One-Way Analyses of Variance (ANOVA) were applied for each of the investigated soil parameters with the groups of the incubation (*Control*, *5 °C* and *15 °C*) as independent variables to identify changes within the elemental contents of the samples. To identify the contributions of the different soil horizons to the total carbon emissions of the soil, One-Way ANOVAS were also applied for the CO_2 production rates with the soil horizons (*Oi*, *Oe* and *Bg*) as independent variables. Furthermore, to describe the studied soil profile, One-Way ANOVAs were applied for each of the investigated soil parameters, including the physical soil characterization, with the soil horizons (*Oi*, *Oe* and *Bg*) as independent variables. After performing all ANOVAs, significantly differing groups were identified by means of Tukey´s HSD test. All statistical analyses were performed using the program *R* (R Core Team, 2013). Additionally, the package *agricolae* (de Meniburu, 2014) was used to perform Tukey's HSD test.

In all incubated samples, there was an initial flush of CO_2 (and partially of CH_4) after the first day of incubation, directly after thawing of the samples. Probably, this flush was only related to the thawing of the samples, and is not affected by the different temperature treatments (cf. Schimel and Clein, 1996). Thus, the initial gas concentrations in the bottles were ignored with respect to the statistical analyses. Linear models were fitted for each parallel sample with the duration of the incubation (in days) as predictor value and the gas concentration (CO_2 and CH_4) as response value. The slopes of the linear regression models were then considered as production rates of CO_2 and CH_4 of the samples, respectively. The mean production rates and the standard deviation of three parallels were used to present approximate production rates of CO_2 and CH_4 for each horizon and temperature treatment.

3.4 Modeling Active Layer Thickness

The evolution of the active layer thickness (ALT) was simulated at each site under different climate warming scenarios using the CryoGrid2 permafrost model (Westermann et al., 2012; Langer et al., 2013). CryoGrid2 is a 1D transient permafrost model that calculates ground temperatures according to conductive heat transfer with phase change in the soil and in the snow pack. The model is forced by time series of surface temperature and snow depth at the upper boundary of the model domain and with a geothermal heat flux at the lower boundary. The modeled soil domain extends to a depth of 600 m. The thermal properties of the soil domain were set according to the specific soil composition at each site, consisting of the volumetric contents of organic and mineral material and of ice and water. For the uppermost two meters, these information were directly inferred from cryolithological analyses of the soils, whereas the composition of the deeper soil was estimated according to field observations and geological maps (cf. Tab. A.2). The thermal properties of the snow cover were calculated according to snow density which was estimated using a scheme similar to the CMC snow cover reanalysis product (Brasnett, 1999).

The model was forced by air temperature, which is a good approximation of the surface temperature on timescales longer than the diurnal cycle. For the purpose of model spin-up and validation, the model was run from 1979 until 2013. A forcing dataset was generated for each site using ERA-INTERIM reanalysis data for air temperature (Dee et al., 2011) and the CMC snow reanalysis product for snow depth. The forcing dataset was found to be realistic in comparison with site meteorological data when available (cf. Langer et al., 2013). The model was initialized assuming thermal equilibrium based on the average air temperature from 1979 to 1989. After initialization, the model was brought into a dynamic equilibrium by running the model of 50 years using the same period. The following period from 1989 to 2012 was used for controlling the annual active layer dynamics. A reasonable agreement with differences of less than 5 cm between modeled and observed maximum active layer thickness was found at each site. For the simulation of active layer thicknesses from 2012 to 2100 a fully synthetic forcing dataset was generated for each site. Air temperature warming trends for each site were extracted from climate projections based on the CCSM4 coupled climate model (Meehl et al., 2012). Specifically, we made use of the Permafrost Carbon RCN forcing dataset obtained from Earth System Grid (Earth System Grid, 2015). The same product was used by Koven et al. (2015) for investigating permafrost carbon feedback processes. A moderate and a strong climate warming scenario was selected, following the Representative Concentration Pathway (RCP) 4.5 and 8.5. The temperature trends of the RCP scenarios were added to a synthetic air temperature time series, made up of randomly selected annual periods of the period from 1979 to 2012. The corresponding snow depth forcing was modified in order to avoid snow above 0 °C. In addition, the model was forced with a synthetic air temperature time series without trend as control run.

4 Geographical Characterization of the Study Areas in the Sakha Republic

4.1 The Sakha Republic

The Eastern Siberian Arctic is one of the largest tundra regions in the world. However, Eastern Siberia also remains a poorly studied region in terms of Northern circumpolar soil carbon stocks (Hugelius et al., 2013) and is also underrepresented in the database of Northern peatlands soil properties (Loisel et al., 2014). One half of the Far Eastern Federal District of the Russian Federation is represented by the Sakha Republic, also known as Yakutia. Covering 3,103,200 km^2, the of Sakha Republic is the largest sub-national governing body by area of the world. It covers 20 % of Russia and is larger than France, Austria, Germany, Italy, Switzerland, England, Finland and Greece put together (Chevychelov and Bosikov, 2010). With a population density of 0.31 km^{-2} these vast areas are barely inhabited and there are scarcely any traffic facilities (Rosstat, 2011). As extensive studies in remote areas require large financial and logistical efforts, there is currently a large imbalance between studies in the North-American Arctic and studies in the Eastern Siberian Arctic.

The presented study was conducted within three study areas in North-Eastern Siberia in the Sakha Republic, covering a distance of more than 1,000 km (Fig. 4.1). The first study area was located in the Lena River Delta (Samoylov Island, 72° 22´ N, 126° 30´ E). The second study area was located in the Lowlands of the Indigirka River (Kytalyk, 70° 53’ N; 147° 48’ E) and the third study area was located in the Kolyma River Delta at the eastern-most part of Yakutia (Pokhodsk, 69° 4’ N; 160° 57’ E). The three sites were characterized by a strongly continental climate, continuous permafrost and extended areas of polygonal tundra.

4.2 Lena River Delta - Samoylov Island

4.2.1 Study Area in the Lena River Delta

The first study area was located on Samoylov Island in the Lena River Delta (72°22´N, 126°30´E). The Lena River Delta is the largest delta in the Arctic (Walker, 1998). It consists of three main geomorphic terraces of different ages from the middle Pleistocene to the late Holocene and also a modern floodplain level (Grigoriev, 1993; Schwamborn

Figure 4.1 Map of the circumpolar arctic permafrost extent. The three permafrost zones (continuous, discontinuous and sporadic permafrost) are shown in grey colors. The location of the three study areas is marked by red circles. Modified after (Brown et al., 1998).

et al., 2002). The investigation in this study area focuses only on the youngest river terrace of Holocene age.

The expedition to Samoylov Island was conducted in August 2012. The nearest weather station is located in the village Tiksi (WMO 21824, 110 km southeast to the study location) and reports for the period from 1998 to 2012 a mean annual air temperature of -12.4 °C. Monthly mean air temperature of the warmest month (July) is +8.9 °C; mean air temperature of the coldest month (February) is -32.3 °C. The annual mean precipitation (period from 2000-2004) was approximately 300 mm (Fig. 4.2; Russia's Weather Server, 2013).

Samoylov Island is located in one of the main channels of the Lena River delta. The western part of this Island is formed by the modern floodplain level and the eastern part is formed by the youngest river terrace of Holocene age. The elevated river terrace is mainly shaped by polygonal tundra (Muster et al., 2012). Many previous studies have investigated Samoylov Island, including energy and carbon cycling (Kutzbach et al., 2004b; Knoblauch et al., 2008; Wille et al., 2008; Runkle et al., 2013), belowground carbon and nitrogen pools (Zubrzycki et al., 2013), microbial communities (Wagner et al., 2007) as well as soils and hydrological conditions (Fiedler et al., 2004; Helbig et al., 2013). A summary

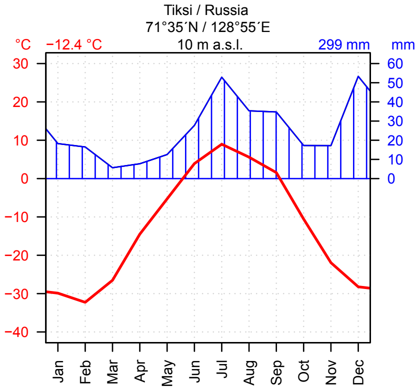

Figure 4.2 Climate diagram from the city Tiksi, near the study site in the Lena River Delta. Average monthly air temperature and precipitation is shown. Mean annual air temperature and total annual precipitation is shown above the diagram.

of previous research and the meteorological and land surface characteristics of Samoylov Island is presented by Boike et al. (2013).

4.2.2 Soils and Vegetation on Samoylov Island

Two soil types are typical for the river terrace on Samoylov Island: Following the US Soil Taxonomy (Soil Survey Staff, 2014), the soils on the polygon ridges are mainly characterized as *Typic* or *Glacic Aquiturbels*. The soils in the polygon centers are mainly characterized as *Typic Historthels* (Fig. 4.3; Boike et al., 2013). The vegetation of the wet tundra in the polygon centers and on collapsed polygon ridges consists of mosses and sedges and is dominated by a *Drepanocladus revolvens-Meesia trigueta-Carex chordorhizza* community. The dry tundra on polygon ridges is characterized by a *Hylocomium splendens-Dryas punctata* community (Boike et al., 2013). One low centered ice-wedge polygon has been investigated on Samoylov island by two soil profiles of approximately one meter depth; one on the polygon ridge and one in the polygon center. A detailed description of these two soil profiles, including different soil parameters, is given in table 4.1.

- LEN-1-R: The soil profile on the polygon ridge consisted of a small layer of peat (5 cm) above the mineral soil. The mineral material of this soil was characterized by sandy and loamy silt and was influenced by cryoturbation. Thus, this soil was classified as a *Typic Aquiturbel*.

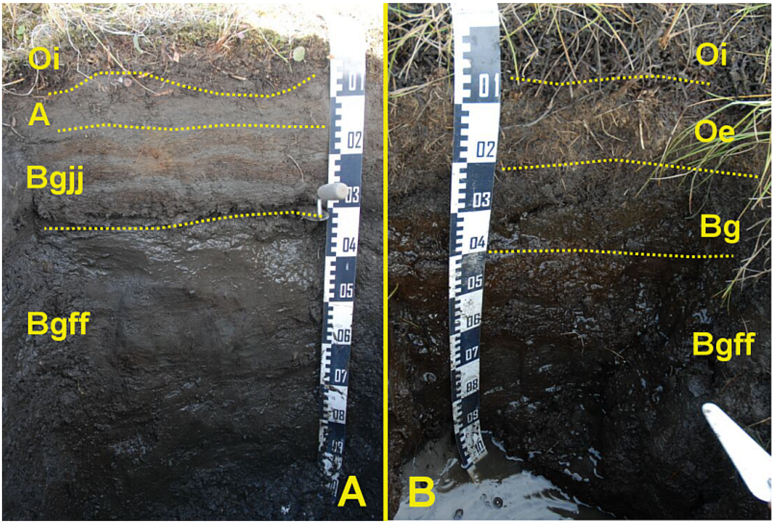

Figure 4.3 Two different soil profiles from Samoylov Island in the Lena River Delta. **A:** *Typic Aquiturbel* from a polygon ridge (LEN-1-R); thaw depth in August 2012 was 30 cm. **B:** *Typic Historthel* from a polygon center (LEN-1-C) with a thaw depth of 41 cm (August 2012). Photos by courtesy of Julia Boike, AWI Potsdam.

- LEN-1-C: The upper part of the soil in the polygon center consisted of two horizons of peat in different states of decomposition. The mineral soil below was characterized by sandy silt and showed no characteristics of cryoturbation. As this soil consisted mainly of mineral material below a substantial layer of peat it was characterized as *Typic Historthel*.

Table 4.1 Detailed description of two soil profiles from the polygonal tundra on Samoylov Island and selected soil properties.

Typic Aquiturbel, LEN-1-R, Polygon Ridge, Thaw Depth (August 2012): 30cm

Horizon	Depth (cm)	Texture	Roots	Watercontent (% by weight)	pH	EC μS cm^{-1}	Carbon (%)	C/N
Oi	0-5	Sandy Silt / Peat	frequent	42	6.0	48	6.5	23
A	5-15	Sandy Silt	frequent	31	5.8	19	3.1	18
Bjjg	15-32	Loamy Silt	few	42	5.7	15	5.3	18
Bgff	32-100	Sandy Silt	none	57	5.8	25	8.9	20

Typic Historthel, LEN-1-C, Polygon Center, Thaw Depth (August 2012): 41cm

Horizon	Depth (cm)	Texture	Roots	Watercontent (% by weight)	pH	EC μS cm^{-1}	Carbon (%)	C/N
Oi	0-5	Peat	frequent	NA	NA	NA	NA	NA
Oe	5-23	Peat / Sandy Silt	many	63	5.0	43	11	27
Bg	23-41	Sandy Silt	few	51	5.9	29	4.1	18
Bgff	41-89	Sandy Silt	none	60	6.0	23	6.7	24

4.3 Indigirka Lowlands - Kytalyk

4.3.1 Polygonal Tundra in the Indigirka Lowlands

This study area is located in the Indigirka Lowlands 28 km northwest of the village Chokurdakh near the World Wildlife Fund station Kytalyk in the Sakha Republic, Russian Federation (70°53‘ N, 147°48‘ E). The site is located at the Berelekh River, a tributary to the Indigirka River. The Berelekh River is known for the so-called Mammoth Graveyard at its upstream. Both a mammoth cemetery and an archaeological excavation site, the Mammoth Graveyard is investigated since the 1970s. It is one of the earliest archaeological sites found above the Arctic Circle and the earliest inhabitation of this area was between 14,000 yr B.P. and 19,000 yr B.P. (Pitulko, 2011).

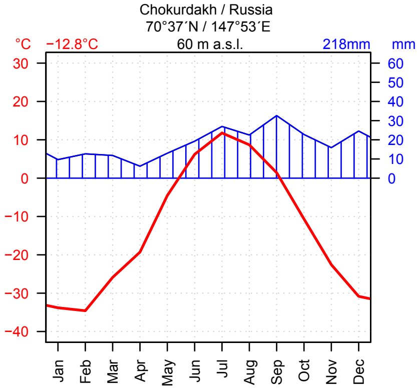

Figure 4.4 Climate diagram for the city Chokurdakh, near the study site in Kytalyk. Average monthly air temperature and precipitation is shown. Mean annual air temperature and total annual precipitation is shown above the diagram.

The expedition to Kytalyk was conducted in the late summer season in 2011 between the 14th July and the 28th August. The nearest weather station is located at Chokurdakh (WMO 21946, 30 km distant to the study location) and reports for the period from 2001 to 2011 a mean annual air temperature of -12.8 °C. Monthly mean air temperature of the warmest month (July) is +11.8 °C; mean air temperature of the coldest month (February) is -34.6 °C. The monthly mean air temperature is above 0 °C between June and September. The annual mean precipitation (period from 2001-2003) does not exceed 250 mm (Fig. 4.4 Russia’s Weather Server, 2013).

The study site is located at the bottom of a previous thermokarst lake which was intersected and drained by the Berelekh River (Fig. 4.6; cf. Tumskoy and Schirrmeister, 2012). The thermokarst depression has formed within the elevated and ice-rich permafrost deposits, the so called Yedoma. Remnants of the Yedoma are still present and border the south-eastern and south-western parts of the thermokarst depression. The thermokarst depression is characterized by two different ground-levels, indicating two former maximum extensions of the thermokarst lake before its drainage. The northern part of the thermokarst depression represents the second ground-level, in which the ground-level was approximately 50 cm below the ground-level of the first level. Thus, the second level of the thermokarst depression was overall much wetter than the first level. The microrelief in the whole thermokarst depression was formed by extended areas of polygonal tundra.

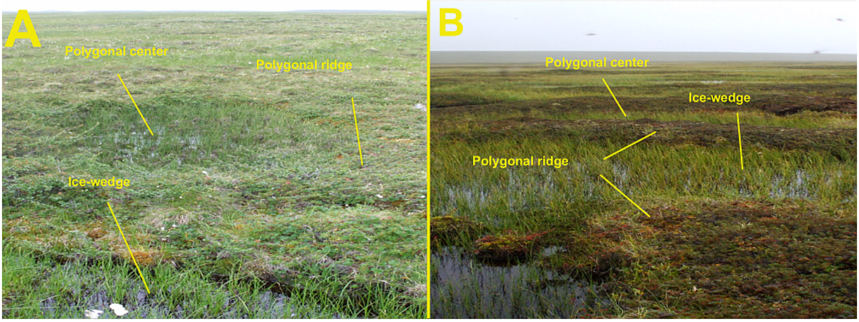

Figure 4.5 Polygonal tundra in the Indigirka Lowlands in Kytalyk. **A:** A thermal-contraction crack polygon with extended polygon ridges. **B:** A highly degraded thermal-contraction crack polygon. Locations of the polygonal center, the polygon ridge and the ice-cracks are indicated.

The polygonal tundra in this area was characterized on the one hand by extended polygon ridges (Fig. 4.5A) and on the other hand by highly degraded ice-wedge polygons (Fig. 4.5B). Probably, the polygon ridges extended due to the accumulation of segregation ice. Following this extension was a thawing of the ice-wedges, replacing the ice-cracks by extensive troughs (Teltewskoi et al., 2012). In the studied polygonal tundra, the wet polygon depressions are mainly characterized by sedges and also mosses. The lower soil water contents on the polygon ridges provide the conditions for the growth of lichens, mosses, herbs and dwarf shrubs (van Huissteden et al., 2005; van der Molen et al., 2007; Teltewskoi et al., 2012).

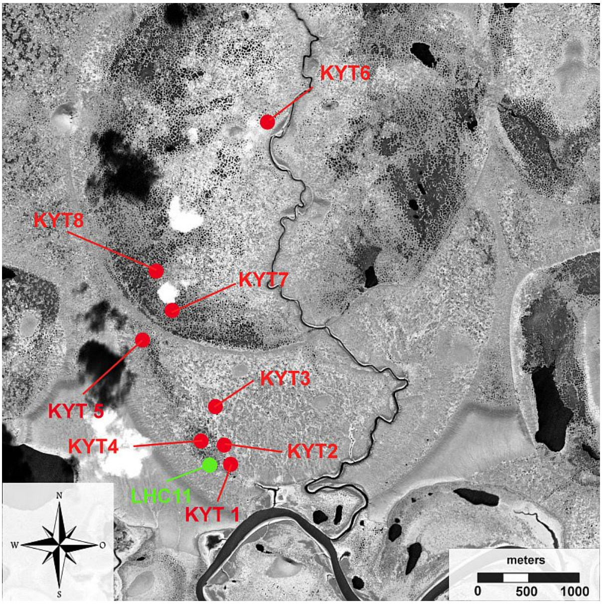

Figure 4.6 Aerial image of the study area Kytalyk in the Indigirka Lowlands. The location of the investigated polygon Lhc11 is marked by a green circle. Locations of the seven additionally investigated polygons (IND 1-8) are marked by red circles (GeoEye image from 2010, 0.5 m resolution, by courtesy of Jacobus van Huissteden, Vrije Universiteit, Faculty of Earth and Life Sciences, Amsterdam).

4.3.2 Soils in the Indigirka Lowlands

The soils in the study area in Kytalyk were generally characterized by thick layers of peat, ranging from 7 cm to more than 40 cm. Average peat-layer thickness on the polygon ridges was 13±3 cm. In the polygonal depression, average thickness of the peatlayers was 28±7 cm. A general soil profile in this area was build up by three horizons of peat in different states of decomposition (*Oi* > *Oe* > *Oa*) above the mineral *Bg* horizon. Following the US Soil Taxonomy (Soil Survey Staff, 2014), the soils then were either characterized as *Histels* (Fig. 4.7C) or as *Orthels* (Fig. 4.7D), dependent on the thickness of the peatlayer. One soil profile directly on an ice-wedge was characterized as *Hemic Glacistel* (Fig. 4.7A). Soils characterized by cryoturbation were found as well (*Typic Aquiturbel*; Fig. 4.7B).

One ice-wedge polygon (Lhc11) was investigated in detail by 24 soil profiles in a grid of 5*5 m. This polygon was subject to the study presented in chapter 5 - *Stoichiometric Analysis of Nutrient Availability (N, P, K) within the Polygonal Tundra* - and a detailed description of this polygon can be found there. Furthermore, eight ice-wedge polygons were investigated at this site by microtransects of four soil profiles, from the polygon ridge into the polygon center. In detail, these polygons were:

- **IND-1:** A typical low-centered ice-wedge polygon with dry and elevated ridges and a depressed center with high soil-water contents. The soil profiles on the polygon ridge were characterized as *Hemic Glacistel* (Fig. 4.7A) and *Typic Historthel*. The soils in the polygonal depression were both characterized as *Typic Historthel*. A detailed description of this polygon is given by Bobrov et al. (2013).
- **IND-2:** This polygon was in close distance and quite similar to the polygon IND-1. The soils on the polygon ridge as well as the soils in the polygon center were all characterized as *Typic Historthel*.
- **IND-3:** This polygon was characterized by the aforementioned extended polygon ridges. The center of this polygon was only approximately 2 m in diameter. In contrast, the ridges of this polygon were approximately 10 m wide and completely vegetated by dwarf-shrubs like *Betula nana* and *Salix spec.* All soil profiles in this polygon were characterized as *Typic Historthel*. One soil profile of this polygon was subject to the incubation study which is presented in chapter 7 - *Effects of Different Temperatures on Soil Microbial Biomass, Microbial Respiration and Nutrient Availability*.
- **IND-4:** This polygon was characterized by highly degraded ridges. On the western side, the polygon ridge was completely collapsed. On the opposite side, only the ice-wedge was thawed and replaced by a deep trough. The soil profiles on the remaining ridge were characterized as *Typic Historthel* and *Typic Hemistel*, respectively. The center of this polygon was completely filled by water with a water-depth of approximately 30 cm. No soil profiles were sampled in the polygon center as all soils in the polygonal center were submerged.
- **IND-5:** This polygon was located at the northern edge of the first level of the thermokarst depression. This low-centered polygon was characterized by a *Typic Historthel* and a *Tyic Haplorthel* on the polygon ridge and two *Typic Historthels* in the polygon center.

- **IND-6:** Located in the second level of the thermokarst depression (like IND-7 and IND-8), this polygon was a low-centered polygon at first sight. However, the ridges apparently started to expand into the center as sphagnum-mosses have started to elevate the ground-level above the water-table in the transition zone between the ridge and the center. The ice-crack was also deeper and wetter than in e.g. the polygons IND-1 and IND-2. Probably, this polygon is currently at the very start of its transition from a low-centered polygon to a high-centered polygon. The soils

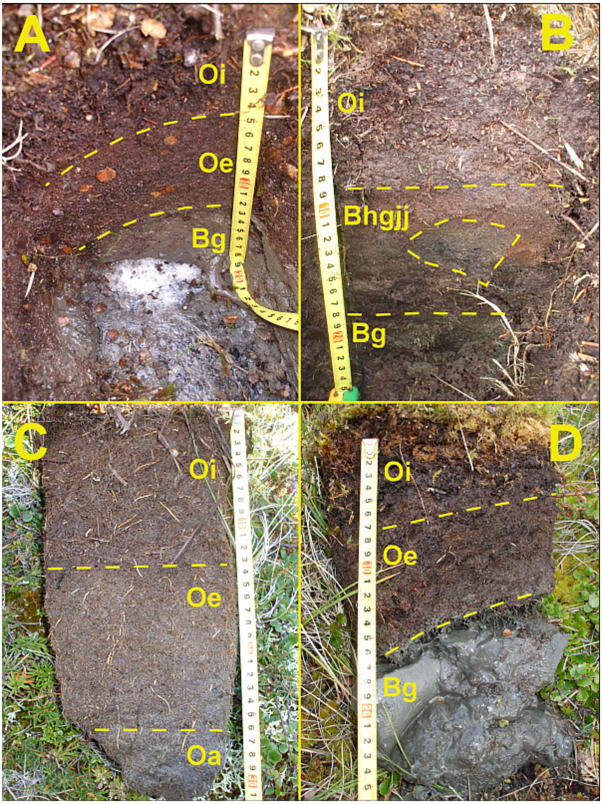

Figure 4.7 Four different soil profiles in the study area in Kytalyk are shown. **A:** *Hemic Glacistel*; **B:** *Typic Aquiturbel*; **C:** *Typic Fibristel*; **D:** *Typic Historthel*. Chemical and physical properties of these soils can be found in table 4.2

on the polygon ridge were characterized as *Typic Historthel* and *Typic Haplorthel*, respectively. The soil profile in the transition zone between the polygon ridge and the polygon center was characterized as *Sphagnic Fibristel*. The second soil profile in the polygon center was again characterized as *Typic Historthel*.

- **IND-7:** In this polygon, approximately half of the polygon ridges were collapsed and the underlying ice-wedges were thawed to some extent. In the polygon center, the water-level was approximately 20 cm high and thus the soils were submerged in the polygon center . Two soil profiles were sampled on the collapsed ridge, and two soil profiles were sampled on the intact ridge. The soil profiles on the intact ridge were characterized as *Glacic Haploturbel* and *Typic Historthel*, respectively. The soils on the collapsed ridge were both characterized as *Typic Historthel*.
- **IND-8:** This polygon was characterized by partially collapsed polygon ridges as well. On the other hand, though characterized by high soil-water contents, there was no open water surface in the polygon center. Soil profiles were sampled on the intact ridge and in the polygonal center. The soils on the polygon ridge were both characterized as *Typic Historthel*. The soils in the polygonal depression were both characterized as *Typic Fibristel*.

In summary, there were no clear differences in the soil types between the polygon ridges and the polygon centers. Although located in a peatland, the soils in this study mostly were not characterized as peaty permafrost soils (*Histel*). Following the US Soil Taxonomy (Soil Survey Staff, 2014), a permafrost soil is characterized as a *Histel* when it comprises 80 % organic material or more, by volume, "from the soil surface to a depth of 50 cm or to a glacic layer [...]". However, the peat layers were mostly below the criteria of 80 % organic material or more, by volume. Thus, the great majority of soils in this peatland were characterized as normal Gelisols (*Othels*) but not as peaty Gelisols (*Histels*). On the other hand, there are probably some false classifications included as not all soils were thawed as deep as 50 cm. Thus, when there is no mineral soil found to a given permafrost table at 30 cm, no statement can be made if the soil comprises 80 % organic material or more, by volume, "from the soil surface to a depth of 50 cm". The criteria for a *glacic layer* which would limit the soil profile is only met by ice, but not by frozen soils. In all of these critical cases, the soils were characterized as *Orthel* instead of *Histel*.

Table 4.2 Detailed description of soil properties from the polygonal tundra in the Indigirka Lowlands. Typical soils from the polygonridges and the polygonal centers across the thermokarst depression around the station Kytalyk are selected. Photos of the soil profiles are presented in Fig. 4.7.

Hemic Glacistel, IND-1, Polygon Ridge, Thaw Depth (August 2011): 19cm

Horizon	Depth (cm)	Texture	Roots	Watercontent (% by weight)	pH	EC μS cm^{-1}	Carbon (%)	C/N
Oi	0-5	Peat	Many	78	4.0	96	47	27
Oe	5-12	Peat	few	79	4.3	59	34	17
Bg	12-19	Sandy Silt	none	24	5.1	22	3.5	18

Typic Aquiturbel, Lhc11, Polygon Ridge, Thaw Depth (August 2011): 30cm

Horizon	Depth (cm)	Texture	Roots	Watercontent (% by weight)	pH	EC μS cm^{-1}	Carbon (%)	C/N
Oi	0-9	Peat	many	71	4.1	94	46	30
Bhgjj	9-18	Sandy Silt	common	61	4.9	27	25	19
Bg	18-25	Sandy Silt	few	63	5.2	19	22	15

Typic Hemistel, IND-5, Polygon Center, Thaw Depth (August 2011): 25cm

Horizon	Depth (cm)	Texture	Roots	Watercontent (% by weight)	pH	EC μS cm^{-1}	Carbon (%)	C/N
Oi	0-13	Peat	many	82	4.1	39	47	43
Oe	13-26	Peat	frequent	77	4.5	34	40	21
Oa	26 - ?	Peat	few	73	5.0	13	32	21

Typic Historthel, IND-8, Polygon Center, Thaw Depth (August 2011): 50cm

Horizon	Depth (cm)	Texture	Roots	Watercontent (% by weight)	pH	EC μS cm^{-1}	Carbon (%)	C/N
Oi	0-7	Peat	frequent	85	5.8	44	41	22
Oe	7-16	Peat	common	79	6.1	17	37	20
Oa	16 - ?	loamy silt	none	25	6.3	17	3.3	15

4.3.3 Vegetation in the Indigirka Lowlands

In contrast to the soils, there were obvious differences in the plant-species composition between the polygon ridges and the polygonal depression (Tab. 4.3). The polygon ridges were characterized by dwarf-shrubs like *Betula nana* and *Ledum palustre*, the herb *Rubus chamaemorus* and mosses like *Hylocomium splendens*. The polygonal centers were characterized by sedges like *Carex aquatilis* and *Eriophorum angustifolium*, by the herb *Potentilla palustris* and different moss-species. The willow species *Salix pulchra* was ubiquitously found on the polygon ridges and in the polygonal depressions.

Table 4.3 Plant communities in Kytalyk on the polygon ridges and the polygon centers are shown. Highly diagnostic species are marked in bold.

Polygon ridge	Polygon center
Betula nana	***Carex aquatilis***
Vaccinium vitis-ideae	***Eriophorum angustifolium***
Ledum palustre	***Potentilla palustris***
Rubus chamaeomorus	*Carex chordorrhiza*
Hylocomium splendens	*Sphagnum spec.*

4.4 Kolyma River Delta - Pokhodsk

4.4.1 Study Area in the Kolyma River Delta

The third study area was located in the Kolyma River Delta, 36 km northwest of the city Chersky in the easternmost part of the Sakha Republic. The studies were conducted in the vicinity around the village Pokhodsk (69° 04’ N; 160° 58’ E). Climatic parameters measured at the nearest weather station in Chersky (WMO 25123) show a mean annual air temperature of -9.7 °C, an average temperature of the warmest month (July) of 13.9 °C and that of the coldest month (February) of -33.5 °C. Annual precipitation is low with about 215 mm (Russia’s Weather Server, 2013, Fig. 4.8). The expedition to Pokhodsk was conducted in the summer season 2012 between the 13th July and the 14th August. This expedition was planned and conducted as a drilling campaign. Thus, instead of sampling a great number of soil profiles from the active layer only a small number of soils was investigated, but down to a depth of 1 m and also within the perennially frozen ground (see also Chapter3 - *Material and Methods*).

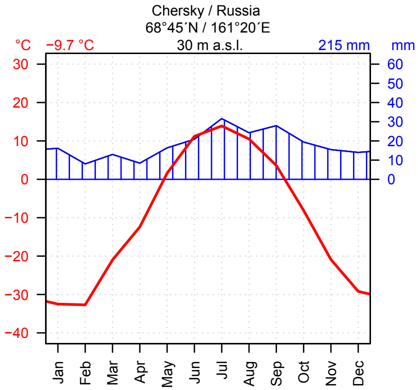

Figure 4.8 Climate diagram for the city Chersky, near the study area in Pokhodsk. Average monthly air temperature and precipitation is shown. Mean annual air temperature and total annual precipitation is shown above the diagram.

The area around the town Chersky is famous for the so-called Pleistocene Park, which is located 5 km south to Chersky. Five major herbivore species (bison, musk ox, moose, horses and reindeer) were established at this site to test the hypothesis that the Pleistocene mammoth-steppe ecosystem was replaced by wetlands only due to the absence of herbivore mammals but not by a changed climate in the Holocene (Zimov, 2005; Zimov et al., 2012). It was proposed that mosses get trampled down by these large mammals which would favor growth of grasses and thus, typical steppe vegetation would establish. Due to their higher transpiration rate, the grasses then would dry out the soil, causing lower methane emissions from these soils (Zimov, 2005; Zimov and Zimov, 2014). In the long-term, re-establishment of the Pleistocene steppe ecosystems possibly would lower methane emissions from Siberian soils.

This site was located directly at the timberline between tundra and taiga (Kuznetsova et al., 2010). Thus, small trees were found sporadically and also the dwarf-shrubs appeared to be larger than at the study area in the Indigirka Lowlands in Kytalyk. In contrast to the study area in Kytalyk, there were no Yedoma deposits in this area. However, large thermokarst lakes can be found all around the village Pokhodsk. The polygonal tundra in this area was highly variable and was found in different stages of the succession, ranging from just developing polygons to highly degraded polygons.

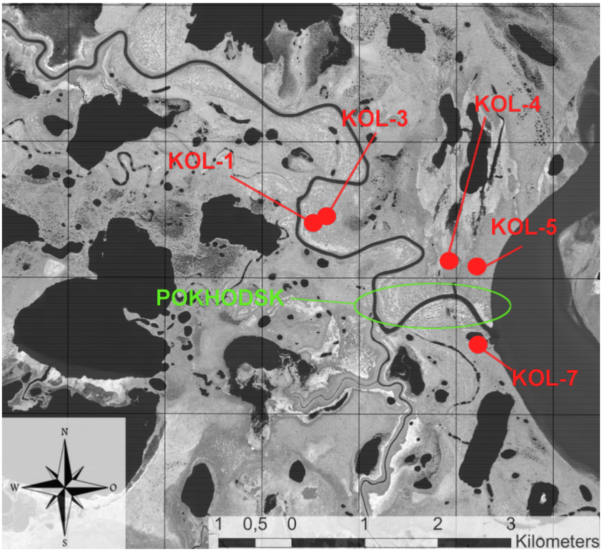

Figure 4.9 Aerial image of the study area in Pokhodsk in the Kolyma River Delta. Locations of the investigated polygons (KOL-1, KOL-3, KOL-4) and the locations of the cores on the floodplain (KOL-5, KOL-7) are marked by red circles. Location of the village Pokhodsk is indicated as well.

4.4.2 Soils and Vegetation in the Kolyma River Delta

The soils in this area were characterized as *Histels*, *Turbels* and *Orthels*. Frequent flooding in the whole study area and input of mineral material by the nearby Kolyma River is indicated by the results of the soil classification: A majority of the soils were classified by the prefix *Fluvaquentic*, which describes small layers of mineral material within a peat profile or irregular decreases in the organic carbon contents within the soil profile. The vegetation was characterized similar to the expedition to the Indigirka Lowlands (Section 3.1.3 - *Vegetation Sampling*). However, as the number of relevés were too small, no detailed classification of the vegetation in the Kolyma River Delta was conducted. Samples were taken in areas of polygonal tundra (KOL-1, KOL-3, KOL-4) and on the floodplains of the Kolyma River (KOL-5, KOL-7; Fig. 4.9):

- **KOL-1:** A 'typical' low-centered ice-wedge polygon with dry and elevated ridges and a depressed center, consisting of a small pond. The soil of the polygon ridge was characterized as a *Typic Aquiturbel*. At a depth of ~54 cm there was a shift from mineral to organic material (cf. Fig. 4.10a, Tab. 4.4). The organic material was ice-rich and showed cryoturbic inclusions of mineral material. The soil core in the polygon center was drilled within the small pond. The submerged soil above the permafrost table contained only peat and was characterized as a *Typic Fibristel*. The frozen soil contained also almost only peat and was characterized by very high ice-contents. The vegation on the polygonridge was dominated by the dwarf-shrubs *Betula nana, Ledum palustre* and *Vaccinium uliginosum*; the sedge *Eriophorum vaginatum* and the moss *Hylocomium splendens.* On the more shallow places, the vegetation of the polygon center was characterized by the moss *Drepranocladens revolvens* and the sedges *C. rotundata, C. chordorrhiza* and *Eriophorum angustifolium.*

- **KOL-3:** This site was located near the polygon KOL-1 in a very flat and wet area, approximately 50 cm below the ground-level of the are around KOL-1. The polygonal tundra in this area appeared to be developing polygonal tundra at the very first stage of the succession. Ice-cracks were visible around the polygonal center but there was no clear differentiation between the polygon ridge and the polygon center. The soil of this polygon center was a *Fluvaquentic Saprsitel.* Though containing mainly organic material there were two layers of mineral material at a depth of 53 cm and at a depth of 82 cm within the soil profile (cf. Fig. 4.10b, Tab. 4.4). The soil of the polygon ridge directly above the ice-wedge was characterized as a *Glacic Histoturbel.* The frozen soil was characterized by mineral material with inclusions of peat. Starting at a depth of 63 cm, there was only pure ice. At this site, the vegetation of the polygon ridge and the polygon center was characterized by sedges (*Carex aquatilis, Carex chordorrhiza Eriophorum angustifolium*), mosses (*Drepranocladens revolvens*) and herbs (*Potentilla palustris*).

- **KOL-4:** This low-centered polygon appeared to be in an advanced stage of degradation. The ice-cracks around this polygon were replaced by deep but dry troughs. Probably, the ice-wedges were partially thawed, forming large gullys around the polygon. However, as the polygon was located near the border to the floodplain of the Kolyma River, drainage was supported and these gullys were not filled with water. Due to frequent flooding by the adjacent Kolyma River, there were high amounts of mineral soil material within the soil profiles. The soils of the polygon ridge and the polygon center were classified as *Fluvaguentic Historthel* and *Fluvaquentic Sapristel*, respectively. The

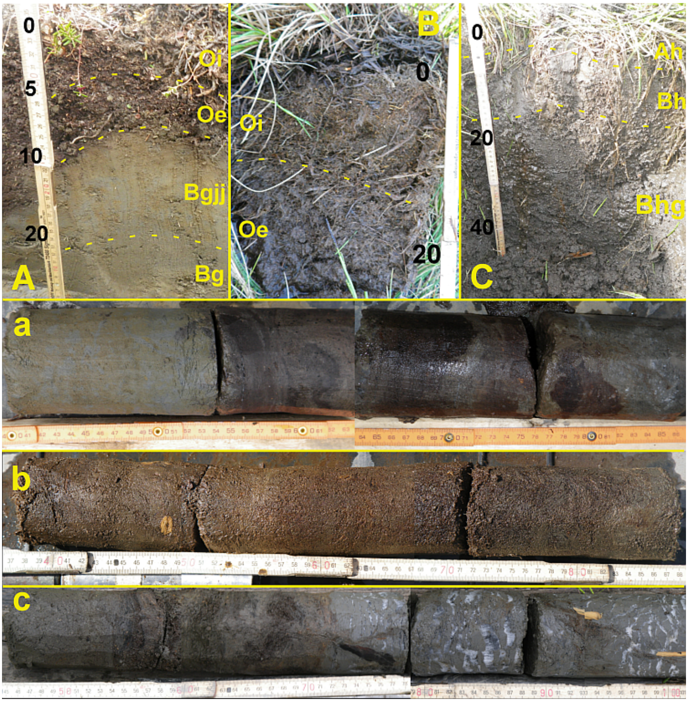

Figure 4.10 Three different soil profiles in the Kolyma River Delta. A-C show the topsoils from the thawed active layer. a-c show the according soil cores from the frozen ground. **A:** *Typic Aquiturbel* from a polygon ridge (KOL-1); thaw depth was 40 cm. **B:** *Fluvaquentic Sapristel* from a polygon center (KOL-3) with a thaw depth of 53 cm. **C:** *Fluvaquentic Aquorthel* from the Kolyma floodplains (KOL-7) with a thaw depth of 61 cm. Thaw depths were measured in August 2912

deeper and frozen parts of the polygon ridge were characterized by high contents of peat with inclusions of mineral material and by many ice-lenses between 48 cm and 100 cm. The frozen soil of the polygon center was characterized by high contents of peat with irregular inclusions of mineral material down to a depth of 1 m. The vegetation on the polygon ridge was dominated by the moss *Hylocomium splendens* and dwarf-shrubs like *Betula nana, Ledum palustre, Vaccinium vitis-idaea* and *Andromeda polifolia* but also willow and alder species like *Salix glauca, Salix pulchra* and *Alnus fruticosa* were found. In the polygonal center, the vegetation was characterized by the sedges *Carex aquatilis, Eriophorum angustifolium* and the herb *Potentilla palustris*

- **KOL-5:** This site was located on the floodplain of the Kolyma River, near to the site KOL-4. The ground-level of the floodplain was approximately 1.5 m below the ground-level of the area around KOL-4. Due to the nearby river, no ice-wedge polygons were developed. One soil core was drilled at this site. The soil was characterized by fluvial sediments with high amounts of iron oxides down to a depth of 65 cm Between 65 and 100 cm there were many inclusions of peat. This soil has been classified as a *Fluvaquentic Aquorthel.* Though located at a completely different location, the vegetation at this point was quite similar to the other polygonal centers: Dominant species were the sedges *Eriophorum angustifolium* and *Carex aquatilis* but also herbs and grasses like *Potentilla palustris* and *Arctagrostis latifolia* were found.

- **KOL-7:** This site was located on the floodplain of a small lake with connection to the Kolyma River. The mineral material of this soil down to a depth of 70 cm was characterized by high contents of peat. Between 70 and 100 cm there were many ice-lenses (cf. Fig. 4.10c, Tab. 4.4). Again, this soil was characterized as a *Fluvaquentic Aquorthel.* The vegetation at this site was dominated by the horse tail *Equisetum variegatum,* but also sedges and grasses like *Eriophorum scheuchzerii* and *Arctagrostis latifolia* were found.

Table 4.4 Detailed description of three soil profiles from the polygonal tundra in the Kolyma River Delta and selected soil properties. Typical soils from the polygon ridges, the polygon centers and the floodplains of the Kolyma River are shown. Photos of the soil profiles can be found in figure 4.10.

Typic Aquiturbel, KOL-1, Polygon Ridge, Thaw Depth (August 2012): 40cm

Horizon	Depth (cm)	Texture	Roots	Watercontent (% by weight)	pH	EC μS cm^{-1}	Carbon (%)	C/N
Oi	0-5	Peat	many	70	4.5	68	40	29
Oe	5-12	Peat	frequent	76	4.9	35	33	22
Bgjj	12-26	Sandy Silt	few	41	6.1	15	9.6	15
Bg	26-40	Sandy Silt	none	22	6.8	16	1.4	11
Bgff	40-54	Sandy Silt	none	26	6.8	21	0.9	10
Bhjjff	54-80	Sandy Silt / Peat	none	71	6.2	52	22	19

Fluvaquentic Sapristel, KOL-3, Polygon Center, Thaw Depth (August 2012): 53cm

Horizon	Depth (cm)	Texture	Roots	Watercontent (% by weight)	pH	EC μS cm^{-1}	Carbon (%)	C/N
Oi	0-12	Peat	many	85	5.9	83	36	25
Oe	12-30	Peat	frequent	77	5.7	62	31	22
Oa	20-53	Peat	few	78	5.7	35	31	18
Bhff	53-58	Sandy Silt / Peat	none	74	5.8	24	20	19
Oaff	58-82	Peat	none	80	5.9	23	25	23
Bhgjjff	82-100	NA	none	76	5.9	28	12	17

Fluvaquentic Aquorthel, KOL-7, Floodplain, Thaw Depth (August 2012): 61cm

Horizon	Depth (cm)	Texture	Roots	Watercontent (% by weight)	pH	EC μS cm^{-1}	Carbon (%)	C/N
Ah	0-5	Silty Clay	many	60	5.1	250	10	15
Bh	5-20	Silty Clay	frequent	55	5.3	76	7.3	12
Bhg	20-45	Silty Clay	few	55	5.6	49	7.0	13
Bhgjj	45-61	Silty Clay	none	59	5.6	49	15	16
Bhgjjff	61-72	Silty Clay	none	55	5.8	22	17	20
Bgff	72-100	Silty Clay	none	50	6.1	54	5.0	13

5 Stoichiometric Analysis of Nutrient Availability (N, P, K) within the Polygonal Tundra

5.1 Introduction

Plant growth in the arctic tundra is typically limited by nitrogen availability (Mack et al., 2004; Weintraub and Schimel, 2005a; Reich et al., 2006) or co-limited by nitrogen and phosphorus (Chapin et al., 1995; Giesler et al., 2012). The supply of bioavailable nutrients primarily depends on the rate of microbial decomposition. Along different ecosystems, nitrogen mineralization rates have been found to be lowest in the arctic tundra (Nadelhoffer et al., 1992). To assess a complete picture of the nutrient relations in the arctic tundra, it is crucial to integrate plant communities and microbial organisms within the analysis of the soil-vegetation system. In this study, the macronutrients carbon (C), nitrogen (N), phosphorus (P) and potassium (K) were partitioned in the soils into inorganic, microbial and residual fractions. Elemental contents of the foliar biomass of the according plant communities were studied as well.

Input of inorganic nitrogen into pristine ecosystems occurs on the one hand by decomposition and mineralization of soil organic matter and on the other hand by microbial fixation of atmospheric nitrogen (N_2, Aber and Melillo, 2001). In contrast to the nitrogen cycle, the phosphorus cycle lacks a major atmospheric component (Aber and Melillo, 2001). As weathering processes are very slow under low temperatures, there is little phosphorus input from geological parent materials in arctic soils (Hill and Tedrow, 1961). The pool of labile phosphorus is mainly filled by periodical crashes of microbial communities (Chapin et al. 1978). In contrast, the potassium cycle is quite different from the nitrogen and phosphorus cycles. It is negligibly bound to the organic matter (Scheffer and Schachtschabel 2002) and within dead plant tissues it is not bound to organic compounds but is mobile by diffusion in ionic form. Thus, it is released into the soil by leaching of dead organic matter (Titus and Malcolm 1992).

Increased temperatures in the course of climate change will have major impacts on arctic ecosystems. Higher soil temperatures will probably enhance microbial decomposition and mineralization rates in arctic soils (MacDonald et al., 1995; Rustad et al., 2001). Higher nutrient availability will influence the plant species diversity and composition of arctic ecosystems (Aerts, 2006; Eriksson et al., 2010). Experimental studies have found that increased nutrient availability in high latitudes can compensate higher soil CO_2 emissions by increased primary production (Natali et al., 2012). Mack and colleagues (2004) observed a doubling of primary production after 20 years of fertilization, but also net carbon losses from the ecosystem are possible. Therefore, changes of nutrient availability will indirectly control the carbon balance of arctic ecosystems by influencing changes in the plant community composition (Weintraub and Schimel, 2005a). Higher nitrogen availability can lead to higher CH_4 production in arctic peatlands (Eriksson et al., 2010) but can also depress microbial respiration in these soils (Schimel and Weintraub, 2003). However, higher decomposition rates could lead in the long-term also to phosphorus limitation of arctic ecosystems (Peñuelas et al., 2012). Thus, nutrient pools and their mobility in soils play a key role for the further development of arctic ecosystems.

Many Lowlands tundra landscapes are characterized by the formation of thermal-contraction-crack polygons (French, 2007). Worldwide, polygonal Lowlands tundra covers about 250.000 km^2 of earth's surface (Minke et al., 2007). In the last decade, these complex tundra wetlands have been in the focus of ecological and biogeochemical arctic research because they are able to accumulate considerable amounts of peat and are significant sources of atmospheric methane (Kutzbach et al., 2004b; Wille et al., 2008; Parmentier et al., 2011; de Klerk et al., 2011). However, it is unclear how sensitively the carbon and greenhouse budget of the polygonal tundra ecosystems will react to the ongoing climatic warming in the Arctic. The long-term net effect of warming on the carbon balance will critically depend on the relative magnitudes of the changes of soil respiration on the one hand, and vegetation productivity on the other hand in these heterogeneous and dynamic ecosystems.

The polygonal pattern results from thermal-contraction-cracks which fill with refreezing snow melt water in spring. Repetition of this process leads to the formation of ice-wedges and the development of a distinct polygonal pattern. As the soil between these ice-wedges extends during summer warming it gets pushed above the ice-wedges and thus forms the elevated polygon ridges above the ice wedges (Chernov and Matveyeva, 1997; Mackay, 2000). However, the single polygons are not isolated systems but are connected via subsurface hydrological windows (Minke et al., 2007). This subsurface hydrological connectivity is mainly controlled in the short-term by the extend of soil thaw during summer (Helbig et al., 2013). In the long-term, polygonal dynamics controlled by climatic changes regulate the hydrological connectivity and the whole microtopography of this ecosystem - for instance, increased melt water flows may induce rapid collapses of single ice-wedges (de Klerk et al., 2011).

In this study a stoichiometric approach was used to investigate nutrient limitation in different compartments of the soil-vegetation system in the polygonal tundra. Nitrogen and phosphorus, as most limiting macronutrients, can be found in different organisms in a relatively fixed stoichiometry (Redfield, 1958; Cleveland and Liptzin, 2007). Their ratios can be used - instead of fertilization studies - to identify ecosystem nutrient limitation (Koerselman and Meuleman, 1996; Sterner and Elser, 2002; Olde Venterink et al., 2003; Güsewell, 2004). Also N/K and K/P ratios are indicators for potential potassium limitation (Olde Venterink et al., 2003). Though different elements or factors can limit plant growth or microbial activity at the same time (Saito et al., 2008; Harpole et al., 2011), these elemental ratios are useful as first order approximation of the nutrient limitation in the soil-vegetation system (Ågren et al., 2012). 23 soil profiles of one ice-wedge polygon in the Indigirka Lowlands (Lhc11) and the according vegetation communities were investigated for this part of the present study (cf. section - 3.1 *Fieldwork*). The goal of this study was to identify mechanisms of nutrient limitation by comparing elemental nutrient ratios in the foliar biomass of plant communities, within the fractions of inorganic nutrient compounds as well as in the microbial biomass within different soils of polygonal tundra. The assumption was that phosphorus plays a key role in the nutrient limitation of the polygonal tundra, beyond the well-known role of nitrogen.

5.2 Results

5.2.1 Soil Profiles and Plant Communities

Following the US Soil taxonomy (Soil Survey Staff, 2014), most of the 23 soil profiles belonged either to the great groups of *Histels* or *Orthels* (cf. section 4.3 *Indigirka Lowlands - Kytalyk*). *Histels* are permafrost soils (Gelisols) that comprise 80%, by volume, of organic material to a depth of 50 cm. The second great group *Orthels* contains less organic material and shows no features of cryoturbation. Typical soil profiles in the studied polygon were built up by three organic horizons of different states of decomposition above a mineral horizon. The uppermost organic horizons were always least decomposed, thus characterized as *Oi* horizons. Highly decomposed peat was commonly found at the bottom of the accessible (thawed) soil profile and characterized as *Oa* horizons. Moderately decomposed horizons were commonly found between the *Oi* and *Oa* horizons and were characterized as *Oe* horizons. Soils on the polygon ridges generally had lower thaw depths (32 ± 11 cm) than soils in the polygonal depressions (47 ± 8 cm; Fig. 5.1).

Locations and horizons of the soil profiles within the microtopography of the investigated polygon are shown in figure 5.1. The microtopography of the polygon Lhc11 showed a clear distinction between the dry polygon ridges and the wet polygonal depres-

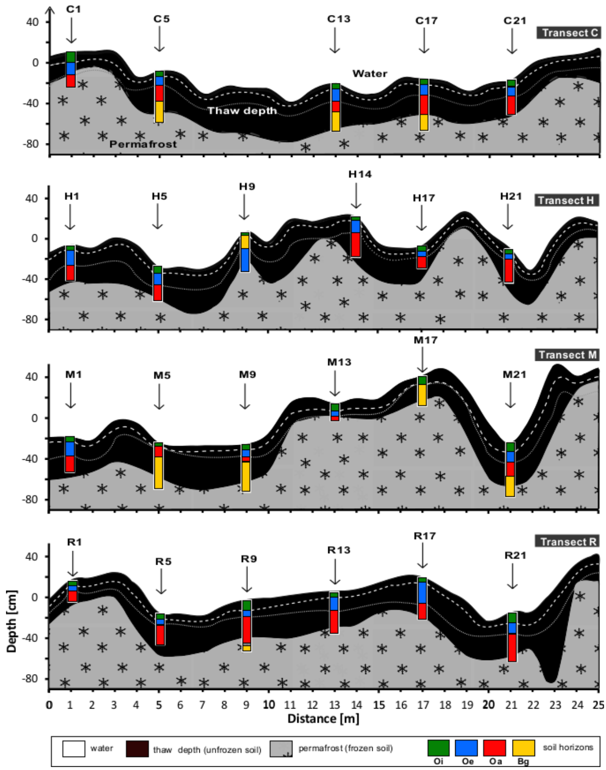

Figure 5.1 Investigated transects in the polygon Lhc11 in the Indigirka Lowlands. Thawed soil (measured between 26th July and 1st August 2011), frozen soil (stars) and water bodies (wavy lines) are indicated. Locations of the investigated soil profiles are marked and the different soil horizons are indicated by different colors (see legend). Soil profiles were investigated between 5th August and 7th August 2011. Extrapolated soil horizons are marked by dotted lines

sions. The polygon ridges were considered as the elevated parts of the polygon above the water table. The polygonal depressions were considered as the parts of the polygon below the water table. Thaw depths below the water body were generally greater than on the elevated polygon ridges.

Two vegetation types could be distinguished in the investigated polygon Lhc11: a wet vegetation type, located in the polygonal depressions and a dry vegetation type, located on the polygonal ridges (Fig. 5.2). Significant indicator species of the wet vegetation

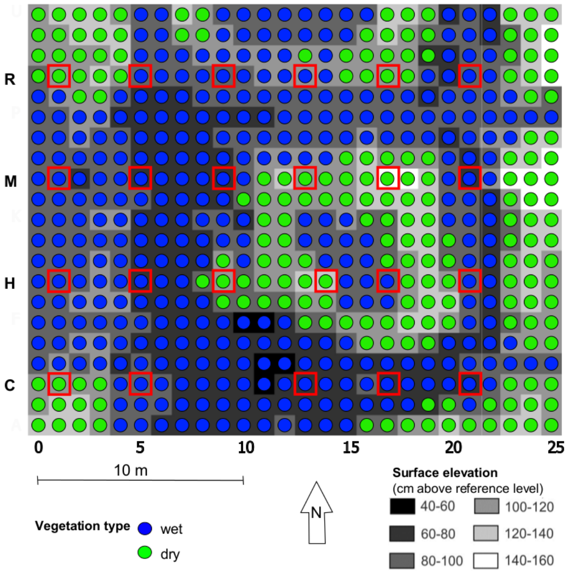

Figure 5.2 Distribution of the vegetation communities in the studied polygon. The grey colors indicate the elevation of the ground. The green and blue circles show the vegetation communities of the dry polygon ridges and the wet polygonal depressions, respectively. The investigated soil profiles are marked by red squares

type are *S. flexuosum*, *Utricularia ochroleuca* and *U. vulgaris*, *Carex chordorrhiza*, *Carex rotundata* and *Caltha palustris*. Significant indicator species of the dry vegetation type are *Ledum decumbens*, *Rubus chamaemorus*, *Vaccinium vitis-idaea*, *Betula exilis*, *Poaceae*, *Dicranum acutifolium*, *Aulacomnium palustre*, *Sphenolobus minutus*, *Ptilidium ciliare*, *Polytrichum swartzii*, *P. strictum* and several lichens taxa. The species *Carex concolor*, *Eriophorum angustifolium*, *Sphagnum squarrosum* as well as *Comarum palustris* occur on wet and dry spots but with a clear dominance in the wet depressions. *Salix spec.* is quite common in the transition between dry and wet spots.

5.2.2 Soil Chemistry and Nutrient Limitation

All soils had low pH-values between 4.0 and 6.0. The uppermost and lowermost *Oi* and *Oa* horizons on the polygon ridges were slightly more acidic than the horizons in the polygon depressions. However, there were no significant differences in the pH-values between the polygon ridges and the polygon depressions. Electrical conductivity was low with values between 9 and 60 μS cm^{-1} (Tab. 5.1).

Table 5.1 Chemical properties of the horizons of the soils on the polygon ridges and in the polygon depressions. Mean values and standard deviation of the pH-values, the electrical conductivity (EC) and the gravimetric water content are shown

	pH			EC (μS/cm)		
	Oi	Oe	Oa	Oi	Oe	Oa
Polygon center	5.5 ± 0.3	5.4 ± 0.3	5.7 ± 0.3	22 ± 9	22 ± 7	35 ± 20
Polygon ridge	5.1 ± 0.4	5.6 ± 0.3	5.1 ± 0.8	28 ± 15	18 ± 9	31 ± 30
p	>0.05	>0.05	>0.05	>0.05	>0.05	>0.05
	Water content (%)					
	Oi	Oe	Oa			
Polygon center	85 ± 16	80 ± 5	79 ± 7			
Polygon ridge	84 ± 4	80 ± 5	73 ± 5			
p	>0.05	>0.05	<0.05			

N/P ratios of the vegetation on the polygon ridges (25 ± 3) were slightly higher than in the polygon depressions (22 ± 4). N/P ratios of all samples were below 30 (Fig.5.3b). N/K ratios were mostly below 6 and K/P ratios of almost all samples were above 2 (Fig.5.3c-d). The results of the t-tests showed that there were only significant differences in the N/P ratios between the two vegetation communities (C/N ratio:, p=0.54; N/P ratio: p=0.05; N/K ratio: p=0.61, K/P ratio: p=0.25).

The analyses of macronutrients in the bulk soil materials showed that, overall, there were no significant differences between the soils on the polygon ridges and the soils in the polygon depressions. Only the content of nitrate (NO_3^-) was twice as high in the *Oi* horizons of the polygon ridge as in the *Oi* horizons of the polygon depressions ($NO_3^-{}_{\text{ridge}}$: 0.86 ± 0.96 mg kg^{-1}; $NO_3^-{}_{\text{depression}}$: 0.44 ± 0.38 mg kg^{-1}; p<0.05). Despite of larger variability in the *Oi* horizons of the polygonal depressions there were no significant differences in the water contents between the polygonal ridges and the polygonal depressions (Tab. 5.1). Dissolved inorganic nitrogen contents (DIN; NH_4^+ & NO_3^-) were generally low. There were no differences between DIN contents in the different horizons (Fig. 5.4b). In contrast, DON in the uppermost horizons was about 15 times higher than DIN and in the lower horizons on average seven times higher. Highest contents of labile phosphorus and potassium were found in the uppermost horizons (Fig. 5.4c-d).

Microbial carbon and nitrogen decreased with depth. However, there were no significant differences with depth in the contents of microbial phosphorus (Fig. 5.4a-c). An exponential relationship between total carbon and the microbial carbon over all soil hori-

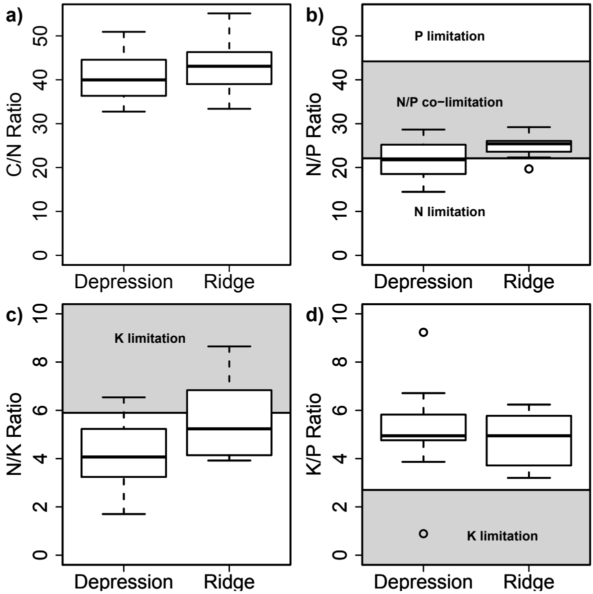

Figure 5.3 Molar-based elemental stoichiometry in the polygon depressions and on the polygon ridges of the aboveground foliar biomass of the plant communities. a) C/N ratio; b) N/P ratio; c) N/K ratio; d) K/P ratio; n=22. The thick line shows the median of the data. The boxes indicate the upper and lower quartiles. Outliers are marked by points. The grey colors indicate areas of N/P co-limitation and K limitation, respectively

zons was observed (R^2=0.54, Fig. 5.5a). Highest contents of total carbon and therefore of microbial carbon as well, were found in the uppermost *Oi* horizons. Microbial nitrogen content was related to the content of microbial carbon in a linear way (R^2=0.56; Fig. 5.5b). In contrast, microbial phosphorus was neither related to microbial carbon (R^2=0.09, data not shown) nor to microbial nitrogen (R^2=0.24; data not shown). Thus, highest contents of microbial biomass were found in the uppermost *Oi* horizons, with no differences with depth in the contents of microbial phosphorus.

The contents of the residual-fractions of carbon and nitrogen were orders of magnitudes higher than the contents of the residual-fractions of phosphorus and potassium. There were no significant differences between the different horizons in the contents of residual nitrogen and phosphorus. However, in contrast to decreasing contents of labile potassium, there was an increase with depth in the content of residual potassium (Fig. 5.4a-d).

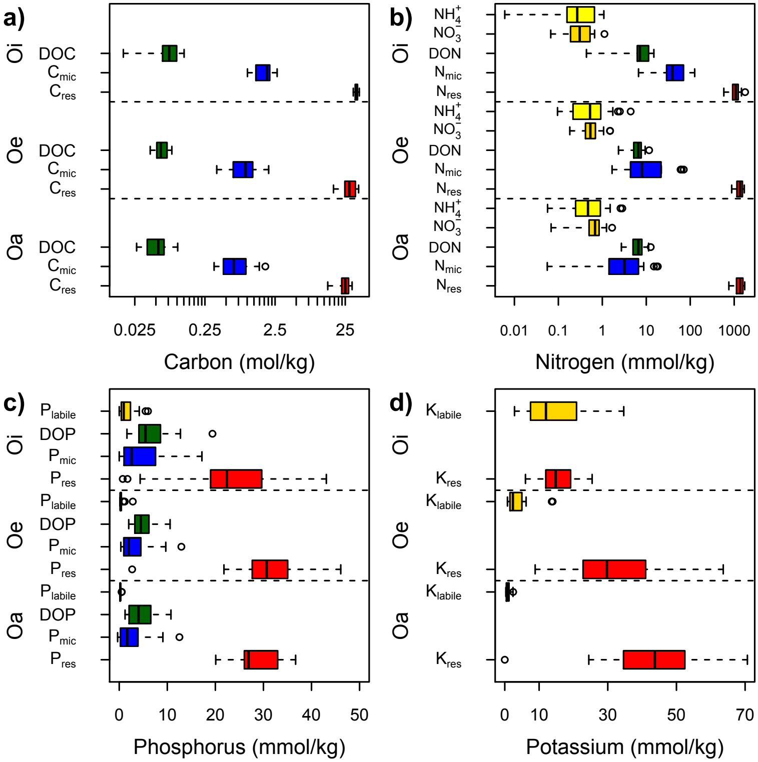

Figure 5.4 Nutrients of different compartments of the soil-vegetation system in all soil horizons. Inorganic fractions are shown in yellow, dissolved organic fractions are shown in green, microbial fractions are shown in blue and the residual fractions are shown in red. a) Carbon as DOC, microbial carbon (C_{mic}) and residual carbon (C_{res}). The X-Axis is scaled logarithmically. b) Nitrogen as DIN (NH_4^+-N + NO_3^--N), DON, microbial nitrogen (N_{mic}) and residual nitrogen (N_{res}). The X-Axis is scaled logarithmically. c) Phosphorus as labile phosphorus (P_{labile}), DOP, microbial phosphorus (P_{mic}) and residual phosphorus (C_{res}). d) Potassium as labile potassium (K_{labile}) and residual potassium (K_{res}). n=50

Regarding total phosphorus, labile phosphorus, ammonium, nitrate as well as the water contents there were no significant differences between the soils in the studied polygon (Lhc11) and the average properties of the soils in the surrounding study area (KYT). Total carbon and nitrogen as well as labile potassium differed only marginally between the studied polygon and the surrounding polygons. The studied polygonal depressions appeared to have significantly lower contents of total potassium than the polygon depressions of the surrounding area. The largest differences between the studied polygon Lhc11 and the polygons in the surrounding study area were found in the pH values. All horizons in the depressions as well as on the ridges of the study area were more acidic than the soils in the studied polygon (Tab. A.1). However, as these two groups of samples were measured at different times there is probably a methodological bias behind the investigated differences in the pH values.

In the uppermost Oi horizons, 6 % of the total nitrogen was found in the biologically active fractions on average. In the lower *Oe* and *Oa* horizons, this part was decreasing to 2 % and 1 %, respectively. In contrast, the amount of phosphorus in the biologically active fractions accounted for 40 % of the total phosphorus in the Oi horizons and for 24 % and 20 % in the *Oe* and *Oa* horizons, respectively. Labile potassium accounted even for 43 % of the total potassium in the *Oi* horizons. In the lower *Oe* and *Oa* horizons, labile potassium accounted for 13 % and 2 %, respectively (Tab. 5.2). Thus, only small percentages of the total contents of carbon and nitrogen were found in the biologically active fractions, whereas large percentages of the total phosphorus and potassium contents were found in the biologically active fractions.

Table 5.2 Percentages of the total contents of carbon, nitrogen, phosphorus and potassium that were found in the biologically active fractions (dissolved inorganic, dissolved organic and microbial)

Horizon	Carbon	Nitrogen	Phosphorus	Potassium	n
Oi	7.2 ± 9.4 %	5.6 ± 3.6 %	39.9 ± 32.2 %	43.0 ± 18.4 %	18
Oe	4.5 ± 4.0 %	2.0 ± 1.9 %	23.9 ± 19.2 %	13.2 ± 14.8 %	20
Oa	4.8 ± 5.0 %	1.0 ± 0.5 %	19.8 ± 13.6 %	2.2 ± 1.6 %	20

The lowest N/P ratios in the inorganic fractions were found in the uppermost horizons. On average, the N/P ratios in the inorganic fraction were in the uppermost horizons below 1 (0.9±0.6) and increased in the lower *Oe* and *Oa* horizons to 6.0±7.1 and 6.7±4.0, respectively (Fig. 5.6). The N/P ratios of the dissolved organic fractions had similar low values as the N/P ratios of the inorganic fraction in the *Oi* horizons (1.9±1.4). There was no significant increase in the lower *Oe* and *Oa* horizons within the N/P ratios of the dissolved organic fractions (*Oe*: 1.4±1.6; *Oa*: 2.0±1.3). There was a large variability of the microbial N/P ratios in the uppermost *Oi* Horizon (19.6±17.8). However, approximately half of the investigated samples had a microbial N/P ratio below 10 (median = 9.7; Fig. 5.6). In the *Oe* and *Oa* horizons the microbial N/P ratio was much lower than in the

Oi horizons (6.8 ±7.8 and 7.0 ±10.2). The residual fractions of nitrogen and phosphorus (which are shown in Fig. 5.4) showed a large excess in nitrogen, which was reflected by the high N/P ratios of approximately 40 and above (Fig. 5.6).

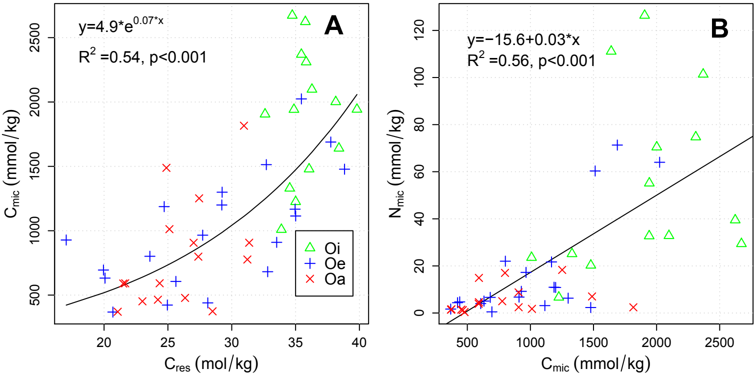

Figure 5.5 Relationships between microbial biomass carbon (C_{mic}), microbial biomass nitrogen (N_{mic}) and residual carbon (C_{res}) across all soil horizons are shown. **A**: Relationship between microbial carbon (C_{mic}) and residual carbon (C_{res}). **B**: Relationship between microbial nitrogen (N_{mic}) and microbial carbon (C_{mic}). n=50

There was an exponential dependence of labile phosphorus to microbial carbon and nitrogen, respectively. However, the exponential model relating microbial nitrogen and labile bound inorganic phosphorus (R^2=0.69; Fig. 5.7B) had much higher explanatory power than the exponential model relating microbial carbon content and labile phosphorus (R^2=0.43, Fig. 5.7A). However, no relationship has been found between DIN and microbial carbon or microbial nitrogen, respectively ($R^2{}_{C_{mic}\sim DIN=0.001}$; $R^2{}_{N_{mic}\sim DIN}=0.02$; data not shown).

5.3 Discussion

Based on the N/P ratios of the aboveground foliar biomass, solely phosphorus limitation of the vegetation in the study site can be excluded. Critical molar-based N/P ratios for sole nitrogen limitation of plant communities have been determined to be below 22 (mass-based N/P ratio of 10; Güsewell, 2004) or 31 (mass-based N/P ratio of 14 Koerselman and Meuleman, 1996; Olde Venterink et al., 2003). N/P ratios between 22 and 44 indicate co-limitation by nitrogen and phosphorus (mass-based N/P ratios of 10 and 20; Güsewell, 2004). The N/P ratios of the foliar biomass were all below 31 and in some cases also below 22. They were also much lower than N/P ratios reported for temperate or tropical forests (48 - 95; McGroddy et al., 2004) which are known to be limited by phosphorus, at least on highly weathered, old soils (Vitousek et al., 1997). Thus, the presented results indicate that the investigated plant communities are at least co-limited by nitrogen and phosphorus and in some cases only limited by nitrogen.

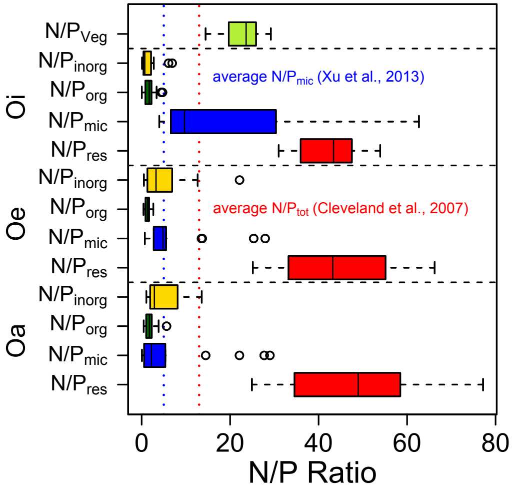

Figure 5.6 Molar-based N/P ratios in different fractions of the soil-vegetation system in all organic horizons (in mmol· kg^{-1} / mmol· kg^{-1}). N/P$_{veg}$veg shows the average N/P ratio of the overlying vegetation and is marked in light green. N/P$_{inorg}$ describes the ratio of dissolved inorganic nitrogen to plant-available phosphorus. N/P$_{org}$ shows the ratio of dissolved organic nitrogen (DON) to dissolved organic phosphorus (DOP) and is marked in dark green. The N/P ratio of the microbial organisms is marked in blue. The red boxplots show the total N/P ratios. Thick lines show the medians of the data. The boxes indicate the upper and lower quartiles. Outliers are marked by points. The dotted blue line indicates an average microbial N/P ratio in the arctic tundra (Xu et al., 2013), the dotted red line indicates the average N/P ratio of soil elements in the arctic tundra (Cleveland and Liptzin, 2007). n=50

The N/P ratios of the vegetation on the polygon ridges were slightly higher than in the polygon depressions, possibly indicating higher nitrogen limitation in the polygon depressions. However, woody plants - which occur mainly on the polygon ridges - have been shown to have higher N/P ratios than herbaceous plants (Sardans et al., 2012). Furthermore, ericoid mycorrhizae have been shown to have access to nitrogen bound in proteins of the soil organic matter (Bending and Read, 1996). Therefore, the plant-species composition could account for the different N/P ratios between the polygon depressions and the polygon ridges. Considering molar-based N/K ratios below 5.9 and molar-based K/P ratios above 2.7 in the foliar biomass, we can exclude potential potassium limitation of the vegetation (mass-based N/K and K/P ratios of 2.1 and 3.4 Olde Venterink et al., 2003). Considering also high contents of labile potassium our results indicate that potassium is not a limiting factor for plant growth in the polygonal tundra.

As plant-growth in the investigated polygon appears to be most or only limited by nitrogen, microbial nitrogen fixation and mineralization appear to be key processes for plant growth in the polygonal tundra. Microbial nitrogen mineralization rates have been shown to be lowest in the arctic tundra in comparison with other ecosystems (Nadelhoffer et al., 1992) but are expected to increase in the course of climate change (Rustad et al., 2001). On the other hand, microbial nitrogen fixation is already a major nitrogen input in arctic ecosystems (Hobara et al., 2006).

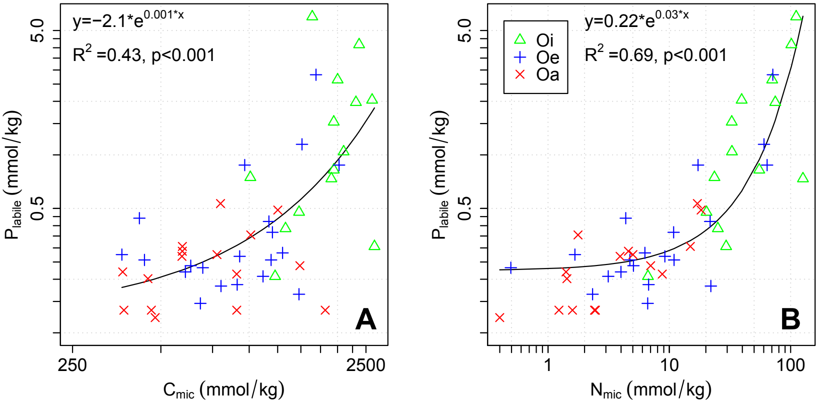

Figure 5.7 Relationships between inorganic phosphorus and the microbial biomass across all soil horizons. **A:**Relationship between labile bound inorganic phosphorus (P_{labile}) and microbial carbon (C_{mic}). **B:** Relationship between labile bound inorganic phosphorus (P_{labile}) and microbial nitrogen (N_{mic}). All axes are scaled logarithmically to achieve normality

Considering the present knowledge about nutrient limitation of arctic plant communities, these results are consistent with the common picture of arctic nutrient limitation. However, the detailed results on the distribution of macronutrients across pools of different availability allow some enhanced understanding of nutrient limitation and element cycle processes in the soil-vegetation system. The N/P ratios of the inorganic fraction in all samples were below the N/P ratios of the vegetation. This implies that plant growth is limited by nitrogen. There were only low contents of DIN and labile phosphorus. Only in the uppermost *Oi* horizons, there were higher contents of labile phosphorus. Considering the higher nitrogen demand of plants, lower contents of phosphorus than nitrogen in the *Oe* and *Oa* horizons do not imply phosphorus limitation. There is at least deficient input of inorganic nitrogen into the soils. Probably most of the mineralized nitrogen is immediately taken up by the vegetation. However, as the DON fraction dominates over the DIN fraction, it can be assumed that amino acids are used by plants rather than becoming mineralized to ammonium (Schimel and Bennett, 2004). Thus, the present plant communities may sufficiently be supplied by nitrogen, but there are little nutrient resources to support further productivity increases of the vegetation.

The contents of nitrate were twice as high in the *Oi* horizons of the polygon ridges as in the *Oi* horizons in the polygonal depressions. As aerobic conditions are required to oxidize ammonium to nitrate, lower water contents on the polygon ridges can be expected. Though there were no significant differences in the gravimetrical water contents between the polygon ridges and the polygonal depressions during the sampling period, the polygon ridges were clearly dryer on a volumetrical basis than the soils in the polygonal depression. As aerobic conditions are commonly found only on the polygon ridges (e.g. Fiedler et al., 2004), measurement of volumetric water contents or O_2 measurements probably could have shown differences between the polygon ridges and polygonal depressions. Therefore, the microtopography of the polygon probably accounts for the different nitrate contents on the polygon ridges and in the polygonal depressions.

The highest contents of microbial biomass (as measured as C_{mic} and N_{mic}) were found in the uppermost, organic-rich horizons. This reflects the results of previous studies (e.g. Fierer et al., 2003). In contrast to linear dependencies of microbial carbon to total organic carbon (Anderson and Domsch, 1989), there was an exponential relationship between microbial carbon and total carbon. The uppermost horizons of permafrost-affected soils provide the best hydrological and thermal conditions. So these horizons offer the best habitat for microbial activity. Also microbial nitrogen depended on the amount of microbial carbon. However, the amount of microbial phosphorus was neither related to microbial carbon nor to microbial nitrogen. N/P ratios of microbial communities are known to be relatively independent from the nutrient supply ratios which is known as metabolic homeostasis (Cleveland and Liptzin, 2007; Hartman and Richardson, 2013). By maintaining a homeostatic metabolism, the average N/P ratio of microbial organisms in soils is between

6 and 7 (Cleveland and Liptzin, 2007; Xu et al., 2013). Also in the lower horizons (*Oe*, *Oa*) of the investigation site, the average N/P ratio of the microbial biomass was in this range. Only in the *Oi* horizons it was significantly higher, and also the variability of the microbial N/P ratios was much greater.

As microbial biomass (carbon and nitrogen) - unlike microbial phosphorus - was decreasing with depth, these high N/P ratios could indicate phosphorus limitation of the microbial communities in the uppermost horizons. The uppermost soil horizon provides the interface between soils and atmosphere, and most nitrogen fixation might happen in this area. However, as was shown before, these horizons are the zone of the highest microbial activity and thus also for mineralization processes. According to the growth rate hypothesis (Elser et al., 1996; Sterner and Elser, 2002; Makino et al., 2003), organismal growth rate is dependent on the phosphorus content as a measure of ribosomal RNA. Hence, further development and growth of microbial populations in the polygonal tundra might be limited by phosphorus.

The mineralized labile phosphorus was most related to the content of nitrogen in the microbial biomass. Decomposition processes are mainly catalyzed by enzymes which are built of proteins. Hence, microbial nitrogen appears to be more important for nutrient mineralization than microbial carbon. However, there was no relationship between the content of DIN and the microbial biomass. Additionally and quite similar to microbial growth, phosphorus is most needed in the early phase of plant growth (Ågren et al., 2012). As the field campaign was conducted in the later vegetation period, some accumulation of labile phosphorus in the zone of highest microbial activity can be assumed. Also low contents of DIN are consistent with the sampling period: Though there is continuous nitrogen mineralization throughout the growing season (Chapin, 1996), there is large seasonal variability in the availability of inorganic nitrogen and phosphorus. Depletion of inorganic nitrogen is associated with plant growth in July (Weintraub and Schimel, 2005a).

Potassium contents were not related to the microbial biomass. It easily leaches from the litter without microbial decomposition (Titus and Malcolm, 1992). Since potassium is not limiting the plant growth in the polygonal tundra, there is a large accumulation of plant-available labile potassium in the uppermost horizons in comparison to phosphorus and nitrogen. Also in comparison to other ecosystems, labile potassium in our study was as high as total potassium in boreal peatlands (Wind-Mulder et al., 1996) and twice as high as in tropical peatlands (Sjögersten et al., 2010). Overall, there were no differences in the amount of total potassium between the different soil horizons. However, the ratio of bioavailable potassium to residual potassium was changing greatly with depth. The cation exchange capacity (CEC) of soil organic matter increases with decomposition (Scheffer and Schachtschabel, 2002; Oorts et al., 2003). Thus, in the lower horizons most of the potassium appears to be adsorbed to the surfaces of the organic matter.

Contrarily to the biologically active fractions (inorganic, dissolved organic and microbial nitrogen and phosphorus), the residual *passive fraction* showed a large excess in nitrogen. On average, the global ratio of nitrogen to phosphorus in the bulk soil is about 13 (Cleveland and Liptzin, 2007). In contrast, the average N/P ratio of the bulk soil in our samples was between 33 and 40. The amount of *passive* nitrogen, which is less accessible for microorganisms, was more than 20-fold higher than the amount of *passive* phosphorus. Up to 40 % of the total phosphorus is already part of the active cycling in the investigated tundra soils but only 5 % of the total nitrogen was found in the biologically active fractions. Thus, higher decomposition rates of the soil organic matter in the course of climate change (Weintraub and Schimel, 2003; Aerts, 2006) could eventually result in an excess of bioavailable nitrogen.

Additionally, hydrologic properties have large implications for the further progression of arctic peatlands. Under dry conditions, decomposition and CO_2 production is favored, while water-saturated conditions promote methane production (Tveit et al., 2013). Hydrologic properties following permafrost degradation show large spatial and small-scale variability (O'Donnell et al., 2011), but a large decrease of arctic wetlands is projected in the course of climate change (Avis et al., 2011). Thus, increased temperatures and enhanced mineralization rates could lead to a switchover from nitrogen limitation to phosphorus limitation as the pool of potentially mineralizable phosphorus is comparatively restricted.

Presently, nitrogen mineralization and fixation appear to be crucial for plant nutrition in the soil-vegetation system of the polygonal tundra. Possibly, nitrogen fixation and mineralization as key processes for plant nutrition could already be limited by phosphorus. The presented data suggest that higher mineralization rates can lead in the long term to strict phosphorus limitation of the plant-available nutrients in the polygonal tundra. However, data for the plant litter stoichiometry could not be presented in this study. The stoichiometry of the plant litter influences the stoichiometry of the microbial communities (Wang et al., 2014), controls soil organic matter decomposition rates (Güsewell and Freeman, 2005) and thus is important for the nutrient resorption efficiency. Detailed analyses of litter stoichiometry should be done in follow-up studies to show the whole stoichiometric cascade from foliar biomass over litter and microbial biomass to soil nutrients allowing to clearly define the nutrient limitation in this ecosystem. In addition, it remains unclear whether the residual fractions of phosphorus are potentially mineralizable or not. Thus, further analyses on the soil phosphorus are needed to distinguish the amount of phosphorus which is bound in more mobile forms (e.g. calcium phosphates) from the amount of phosphorus in stable forms (e.g. occluded Fe and Al phosphates, humic acids) and even the amount of phosphorus in resistant and inaccessible forms.

6 Nitrogen Pools and Permafrost Thaw in Soils of Polygonal Tundra in Eastern Siberia

6.1 Introduction

In the last decades, many studies have been conducted to quantify the belowground organic carbon (C) pool of arctic permafrost-affected soils (Post et al., 1982; Tarnocai et al., 2009; Strauss et al., 2013; Hugelius et al., 2013; Zubrzycki et al., 2014). Currently, the soils of these high-latitude ecosystems are estimated to contain approximately 1300 Pg C (Hugelius et al., 2014). The projected increase in air and ground temperatures will have major impacts on arctic ecosystems: Substantial portions of the permafrost will thaw in the coming decades which will lead to a mobilization of previously frozen organic matter and nutrients (Lawrence and Slater, 2005; Kuhry et al., 2010; Grosse et al., 2011a; Schuur et al., 2015). The formerly freeze-locked organic matter will become vulnerable to microbial decomposition, resulting in increased greenhouse gas emissions from arctic soils (Nadelhoffer et al., 1991; Johnson et al., 1996; Dutta et al., 2006; Schuur et al., 2009). Especially, large amounts of labile organic C in permafrost soils will be prone to rapid microbial decomposition when the permafrost thaws (Mueller et al., 2015; Strauss et al., 2015). The additional warming through the release of C from newly thawed permafrost will account for 0.03 °C to 0.23 °C by the end of the 21st century (Schneider Von Deimling et al., 2012, 2015)

Aside of increased C emissions from arctic soils, higher soil temperatures will also enhance decomposition rates and thus lead to increased nutrient availability (MacDonald et al., 1995; Rustad et al., 2001; Keuper et al., 2012; Schaeffer et al., 2013). As N is known to be a main limiting nutrient for plant growth in the arctic tundra (Mack et al., 2004; Reich et al., 2006; Beermann et al., 2015), increased N availability will influence the plant species diversity of arctic ecosystems (Aerts, 2006; Eriksson et al., 2010; Sistla et al., 2013). Changes in the plant species composition of arctic ecosystems will control different positive climate feedback mechanisms like reduction of the surface albedo and amplification of the regional greenhouse warming by increased evapotranspiration (Foley, 2005; Swann et al., 2010; Loranty et al., 2011). On the other hand, shrub expansion may also reduce permafrost thaw (Blok et al., 2010; Myers-Smith et al., 2011). Furthermore, increased nutrient availability and long-term warming in high latitudes can compensate for increased greenhouse gas emissions by increased primary production (Natali et al., 2012; Sistla et al., 2013). Thus, nutrient availability indirectly controls both different positive and negative feedback mechanisms to climate warming and is an important factor for the further progression of arctic ecosystems.

Similar to the quantification of the belowground organic C pool in arctic soils, there are also recent approaches to quantify the total N stock of arctic permafrost-affected soils (Zubrzycki et al., 2013). Northern peatland soils alone store 8 to 15 Pg N, which is approximately 10 % of the global N pool (Limpens et al., 2006; Loisel et al., 2014). However, as mineralization rates are low in arctic ecosystems only small proportions of this N are available for plant nutrition as dissolved inorganic nitrogen (DIN; Schimel and Bennett, 2004; Harms and Jones, 2012; Wild et al., 2013). Thus, total N is not an appropriate measure to characterize the current N balance of arctic permafrost-affected soils.

In spite of frequent studies investigating the availability of inorganic N in the active layer of permafrost soils (e.g. Nadelhoffer et al., 1992; Chapin, 1996; Rodionov et al., 2007; Chu and Grogan, 2010), there are only few studies which quantify inorganic N compounds in the perennially frozen ground. Recently, Keuper et al. (2012) found significant amounts of ammonium in the perennially frozen ground of Swedish peatlands. Furthermore, the release of large amounts of inorganic N from thawing permafrost of arctic and alpine permafrost environments was reported (Barnes et al., 2014; Harms et al., 2014), and increased uptake of N by plants following permafrost thaw was observed (Schuur et al., 2007). Although there is growing evidence of plant-available N stores in arctic and alpine permafrost-affected soils, uncertainties are high and data from Siberia - the largest tundra region of the world - are sparse.

The present study aims to quantify the potential release of inorganic N (Including NH_4^+ and NO_3^-) from thawing permafrost. Eleven soil profiles reaching up to 1 m depth below surface (b.s.) have been studied in all three study areas; (Fig. 4.1 - see also section 3.1.2). By modeling the potential active layer increase of the studied soils in the course of climate change, a rough estimate of the potential annual N mobilization in these ecosystems in the coming decades could be given. The thickness of the active layer is influenced by many factors, including surface temperature (Hinkel, 2003), thermal properties of the surface cover (Beringer et al., 2001), grain size distribution and organic matter content of the soil (Inaba, 1983; Hinzman et al., 1991; Lawrence et al., 2008; Koven et al., 2009), soil moisture and ice contents (Romanovsky and Osterkamp, 2000) and also thickness of the snow cover (Zhang, 2005). Therefore, detailed cryolithological analyses of the studied soil profiles were conducted, including ice contents and mineral composition, in order to provide reliable model results of the active layer thickness (ALT) evolution for the coming decades.

6.2 Results

6.2.1 Cryolithology

The soil profiles at Samoylov Island in the Lena River Delta were characterized by relatively high volumetric contents of mineral components of 20-60 m^3m^{-3} and low volumetric ice contents (30-60 m^3m^{-3}) compared to the other study sites. The profile of the polygon ridge (LEN-1-R) consisted of alternations between mineral components and organic material while the profile of the polygon center (LEN-1-C) was mainly composed of organic material. Thaw depth in August 2012 was 30 cm on the polygon ridge and 40 cm in the polygon center. The dominant texture in both soil profiles was *Sandy Silt*.

The profile IND-R consisted of peat with many inclusions of silt between 15 cm and 30 cm depth. Thaw depth in August 2011 was 42 cm. There was no visible cryostructure in the frozen part of this profile. The dominant texture of the mineral components in this profile was *Sandy Silt*.

The cores from the Kolyma River Delta were dominated by high volumetric contents of water and ice. Thaw depth (end of August 2012) was highest on the floodplains (60 ± 1 cm) and the in the polygon centers (56 ± 4 cm), and lowest on the polygon ridges (43 ± 5 cm). In the frozen parts, the cryostructure was horizontal reticulate with several horizontal ice belts and lenses (5 - 10 mm thick) and thin (<1 mm) vertical ice veins. The cores from the ridges contained several horizons with volumetric contents of mineral components of about 50 m^3m^{-3}. The floodplain cores contained approximately 30 m^3m^{-3} mineral components. The volumetric content of organic matter in the floodplain cores was lower than on the polygon ridges and in the polygon centers with contents between 0.3 and 6 m^3m^{-3}, besides of near-surface samples of compacted unfrozen peat (8-12 m^3m^{-3}). The mineral soil material was composed of clay, silt and fine-grained sand. The dominant texture on the polygon ridges and in the polygon centers was *Sandy Silt*, whereas the dominant texture of the floodplain cores was *Silty Clay*. A comprehensive presentation of all soil cores can be found in the figures A.1, A.2, A.3 and also in the table A.2.

6.2.2 Soil Chemistry

Overall, the total carbon (TC) contents showed a large variability from less than 20 kg m^{-3} up to almost 100 kg m^{-3} within and also between the different soil profiles (Fig. 6.1A). The contents of TC and also total nitrogen (TN) were highly variable, dependent on the

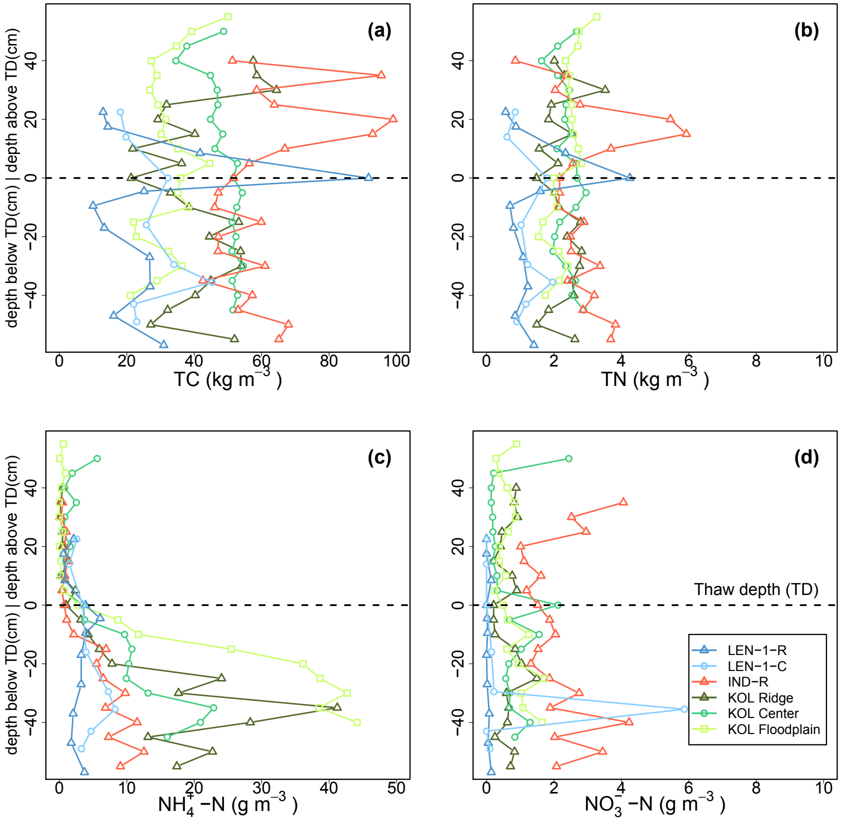

Figure 6.1 Pools of carbon, nitrogen ammonium and nitrate in soil cores from Eastern Siberia. Ammonium pools of two soil cores from the Lena River Delta (LEN-1-R, LEN-1-C), one soil core from the Indigirka Lowlands (IND-R) and means of three soil cores each from the polygonal tundra in the Kolyma River Delta (KOL Ridge, KOL Center) as well as means of two soil cores from floodplains of the Kolyma river (KOL Floodplain) are shown. Depth distribution of the elemental pools is adjusted to the respective permafrost table of each soil.

stratigraphy of the soil profiles. For instance, the soil profile KOL-1-R was characterized by a shift from organic material to mineral material at a depth of approximately 20 cm (Fig. A.2). Similar to this shift, there was a decrease in the contents of TC and TN at this depth. As there was an increase in the contents of organic matter between a depth of 50 cm and 60 cm, there was also an increase in the contents of TC and TN (Fig. A.4). The stratigraphy of the soil profiles from the polygon centers in the Kolyma River Delta was rather homogeneous, similar to the contents of TC in these soils (Fig. 6.1A). The contents of TN were less diverse than the contents of TC. All soil profiles from the study area in the Kolyma River Delta showed volumetric TN contents between 2 and 4 kg m^{-3}. The soils from the Lena River Delta showed overall the lowest contents of TN with values around 0.5 kg m^{-3}. Highest TN contents were found in the soil profile at the Indigirka Lowlands (IND-R), showing values up to 6 kg m^{-3} (Fig. 6.1B). A significant increase in the contents of TC and TN in the perennially frozen ground was only found in the soil profile LEN-1-R. On the other hand, there was a significant increase in the contents of ammonium in the frozen ground of all of the investigated soil cores; irrespective of the study area, the study site, the stratigraphy and the carbon contents of the respective soil core (Fig. 6.1C). Highest amounts of ammonium in the perennially frozen ground were found in the soil cores from the floodplains in the Kolyma River Delta, and the smallest increases in the ammonium pools were observed in the soil cores from the Lena River Delta. Highest amounts of ammonium in the active layer were found in the three soil cores of the polygonal centers in the Kolyma River Delta.

In contrast, the contents of nitrate were about ten times lower than the contents of ammonium and showed no overall increases towards the perennially frozen ground (Fig. 6.1D). Furthermore, there was no overall correlation between the contents of ammonium and the contents of TC as well as TN in all soil profiles (R_{TC}=0.01; R_{TN}=0.01). Only in the soil profile LEN-1-C, there was a strong positive relationship between the contents of ammonium and the contents of TC (R=0.86), whereas in the soil profile KOL-7, there was also a moderate negative relationship between the contents of ammonium and the contents of TC (R=-0.55). A comprehensive overview of the soil chemistry of all soil profiles from the three study areas is given in figure A.4.

There were no significant differences in the pools of TN and nitrate between the active layer and the perennially frozen ground in the polygon tundra and the floodplain of the Kolyma River Delta. The pool of TC was significantly increased only in the perennially frozen ground of the polygon centers in the Kolyma River Delta. On the other hand, significant differences between the ammonium pools in the active layer and the perennially frozen ground were observed in all investigated soil units: The ammonium pools in the perennially frozen ground were between two-fold (polygonal tundra, Lena River Delta) and 40-fold (floodplains, Kolyma River Delta) higher than the ammonium pools in the active layer (Tab. 6.1).

Table 6.1 Average volumetric contents of inorganic N compounds, total C and total N in the active layer (AL) and the perennially frozen ground (FG). Mean values of single soil profiles are presented for the study areas in the Lena River Delta (LEN) and the Indigirka Lowlands (IND). Mean values and standard deviations of three and two soil profiles, respectively, are presented for the study area in the Kolyma River Delta (KOL). Due to the lack of replicates in the other study areas, statistical analyses have only been conducted for the study area in the Kolyma Delta. Significant differences between the active layer and the perennially frozen ground are indicated by superscripted asterisks. Significance levels are at * $p<0.05$; ** $p<0.01$; *** $p<0.001$

			n	TC (kg m^{-3})	TN (kg m^{-3})	NH$_4^+$ (g m^{-3})	NO$_3^-$ (g m^{-3})
LEN	Polygon Ridge	AL	1	23.3	1.1	2.5	<0.01
		FG	1	30	1.3	5.5	1.3
	Polygon Center	AL	1	40.2	2	1.9	0.04
		FG	1	22.1	1.1	3.58	0.04
IND	Polygon Ridge	AL	1	68.3	3	0.8	2.0
		FG	1	54.7	2.9	7.8	2.3
KOL	Polygon Ridge	AL	3	47.2 ± 13.2	3.2 ± 1.5	0.6 ± 0.5	0.6 ± 0.1
		FG	3	41.3 ± 9.3	2.3 ± 0.2	$16.0 \pm 8.2^{*}$	0.7 ± 0.2
	Polygon Center	AL	3	45.7 ± 0.7	2.4 ± 0.2	2.3 ± 1.5	0.8 ± 0.5
		FG	3	$52.6 \pm 0.2^{**}$	2.4 ± 0.6	$13.2 \pm 4.4^{*}$	0.9 ± 0.2
	Floodplain	AL	2	36.6 ± 9.8	2.4 ± 0.9	0.6 ± 0.4	0.5 ± 0.2
		FG	2	36.4 ± 12.9	1.9 ± 0.5	$24.2 \pm 12.6^{*}$	1.4 ± 0.8

6.2.3 Soil Thermal and Hydrological Dynamics

The soil temperatures and volumetric water content profiles at the three sites show typical characteristics of the active layer in permafrost soils: (1) large seasonal temperature amplitudes of approximately -25 °C to +10 °C in the uppermost layers, (2) seasonal freeze-thaw as indicated by the decrease/increase of liquid water content and (3) liquid water contents in frozen soils up to 0.1 m^{3}m^{-3}.

The volumetric water contents of the polygon ridges range between 0.1 and 0.6 m^{3}m^{-3}, whereas the center of the polygon is always saturated with water contents up to 1 m^{3}m^{-3}. Differences in the water content indicate differences in the texture/porosity (peat with up to 100% of porosity) of the soil, as well as depth of the sensor (the surface sensors show drying and wetting due to response to rain events). At all sites, snow melt water infiltrates and warms the (frozen) soil during spring.

The soil temperatures at the study site in the Lena River Delta were recorded in the active layer between 6 cm b.s. and 38 cm b.s. Water contents in the same soil profile were recorded between 5 cm b.s. and 34 cm b.s. The soil was continuously frozen approximately between October 2011 and May 2012. Thawing and re-freezing of the soil occurred between May and June 2012. Minimum soil temperatures were ranging between approximately -27 °C at 6 cm b.s. and -24 °C at 38 cm b.s. Volumetric water contents of approximately 0.1 m^3m^{-3} were measured during the winter period in all soil layers. Water contents increased quickly after thawing of the soil. Highest volumetric water contents in the summer period of more than 0.6 m^3m^{-3} were measured at 22 cm b.s. whereas the uppermost soil layer at 5 cm b.s. showed values between 0.3 and 0.4 m^3m^{-3} (Fig. A.5B).

Monitoring of soil temperatures at the study site in the Indigirka Lowlands were conducted in depths between 6 cm b.s. and 20 cm b.s. and monitoring of water contents in the same soil profile was conducted between 12 cm b.s. and 30 cm b.s. Minimum soil temperatures in the winter period were ranging between -24 °C at 6 cm b.s. and -26 °C at 20 cm b.s. Volumetric water contents at the study site in Kytalyk were only measured in a short period between mid of July 2011 and mid of August 2011. Highest volumetric water contents between 0.4 and 0.5 m^3m^{-3} were measured at 27 cm b.s., and lowest water contents of approximately 0.1 m^3m^{-3} were measured at 12 cm b.s. (Fig. A.5A).

The soil temperatures at the study area in the Kolyma River Delta include continuous records from the active layer as well as from the underlying perennially frozen ground, down to 95 cm b.s. Highest temperature amplitude was observed in the uppermost soil layers down to 13 cm b.s. where minimum temperatures were below -20 °C. The soil temperatures in the deeper soil layers showed less variation and minimum soil temperatures were approximately between -18 °C at 25 cm b.s. and -14 °C at 95 cm b.s.

Below a depth of about 50 cm, soil temperatures remain perennially below 0 °C, which was also reflected by the maximum observed active layer thickness of 43 ± 5 cm for polygon ridges at this site. Soil moisture of the active layer is mainly affected by summer precipitation and soil thaw as well as by dry-out during rain-free periods. The highest volumetric moisture content of 0.5 m^3m^{-3} was recorded 14 cm below surface. The general pattern shows moister conditions in the middle part of the active layer at depths of 14 and 23 cm while the lowermost sensor, located directly above the perennially frozen ground at 28 cm, measured slightly lower volumetric water contents (Fig. A.5C).

6.2.4 Active Layer Thickness Evolution

The ALT evolution under RCP4.5 and RCP8.5 climate warming trends was simulated for all soil profiles at the three different field sites. The model was found to produce reasonable thaw depths under current climate conditions at all sites (Fig. 6.2). For displaying the active layer thickness (ALT) evolution a 5 year moving average filter was used in order to

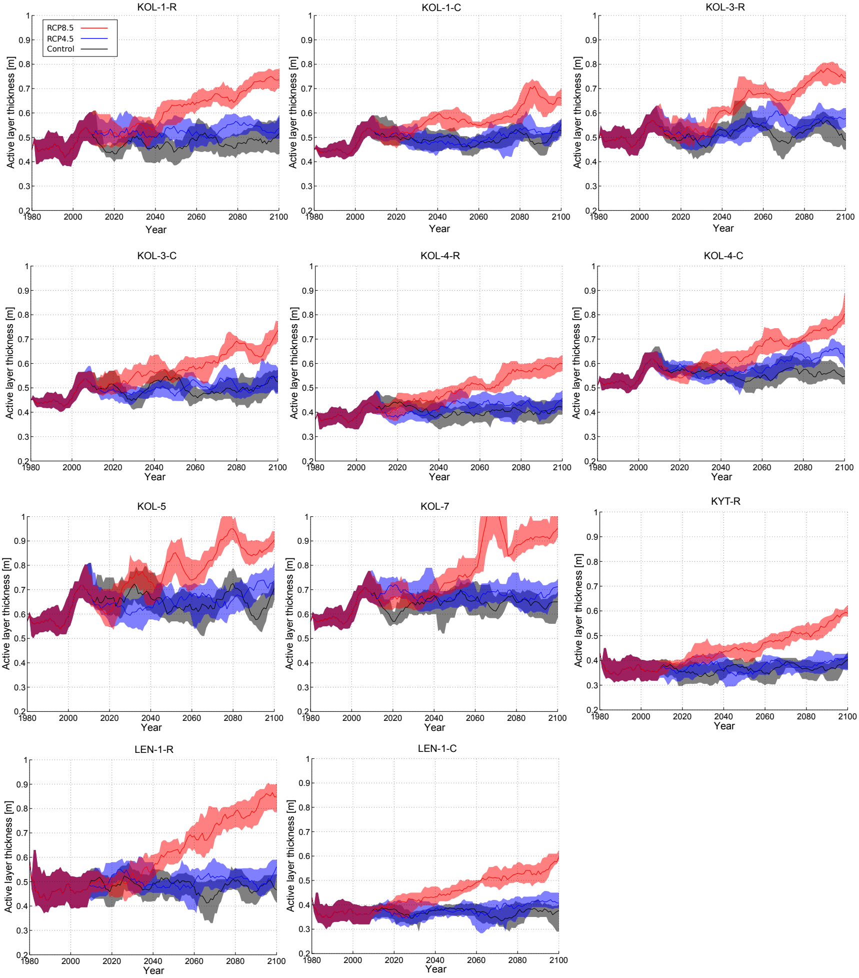

Figure 6.2 Modeled active layer thickness (ALT) for all soil profiles in the study areas in the Kolyma River Delta (KOL), the Indigirka Lowlands (IND) and the Lena River Delta (LEN). The ALT simulations were performed for two climate warming scenarios following the Representative Concentration Pathway RCP4.5 and RCP8.5. A control run without warming trend is shown for comparison. The shaded areas indicate the range of high frequency ALT variations within a five year averaging window.

smooth out high frequency ALT changes due to individual hot and cold years. The range of high frequency ALT changes is displayed as shaded area. These ranges can be considered an estimate of the ALT uncertainty resulting from the random composition of the forcing dataset. At all sites, the simulations reveal an almost stable ALT under the RCP4.5 scenario with only minor deviations to the control runs until 2100 (Fig. 6.2). In contrast, pronounced increases in ALT ranging between 14 ± 3 and 35 ± 6 cm were observed under the warming trend of the RCP8.5 scenario. Overall, highest ALT increases were observed for the polygon ridge in the Lena River Delta 35 ± 6 cm and the floodplain soils in the Kolyma River Delta 29 ± 5 cm. On the other hand, with average ALT increases between 19 cm and 22 cm, the polygon ridge in the Indigirka Lowlands, the polygon center in the Lena River Delta and the polygonal tundra soils in the Kolyma River Delta showed only minor differences (Tab. 6.2). A clearly increased ALT outside of the assumed uncertainties was simulated to occur as early as 2040 for most of the investigated soil profiles. The results of the ALT modeling show that local differences in ALT evolution can be expected despite a same climate forcing (Fig. 6.2).

Based on the performed ALT simulations and the measured N concentrations, the mean annual N release until the year 2100 for the RCP8.5 scenario was estimated (Tab. 6.2. Highest N release rates were estimated for the soils on the floodplains of the Kolyma River (81 ± 14 mg y^{-1} m^{-2}). The soils on the polygon ridges and in the polygon centers at the study area in the Kolyma River Delta showed mean annual N release rates between 41 and 34 mg y^{-1} m^{-2}. The annual N release rates for the soils in the Lena River Delta and the Indigirka Lowlands were substantially lower with values between 8 and 22 mg y^{-1} m^{-2}.

Table 6.2 Increase of active layer thickness in the three study areas until 2100 (RCP8.5) and annual release of NH_4^+-N in this period. The results from the Kolyma River Delta (KOL) are based on three and two soil profiles, respectively. The results from the study areas in the Lena River Delta (LEN) and in the Indigirka Lowlands (IND) are based on one soil profile each.

		n	ALT increase(cm)	N-release (mg yr^{-1} m^2)
LEN	Polygon ridge	1	35 ± 6	22 ± 4
	Polygon center	1	19 ± 6	8 ± 3
IND	Polygon ridge	1	19 ± 3	17 ± 3
KOL	Polygon ridge	3	22 ± 3	41 ± 6
	Polygon center	3	22 ± 5	34 ± 8
	Floodplain	2	29 ± 5	81 ± 14

6.3 Discussion

6.3.1 Nitrogen Pools

The present study shows for the first time significant stores of plant-available ammonium within the perennially frozen ground of Siberian permafrost-affected soils. Increased amounts of ammonium in eleven soil profiles from three different study sites in the Siberian Arctic, along a distance of more than 1,000 km were observed. The soil profiles were sampled on dry polygon ridges and wet polygon centers in the Lena River Delta, the Indigirka lowlands and the Kolyma River Delta as well as on the floodplain of the Kolyma River. By containing different lacustrine and fluvial sediments as well as peat and pure ice, the different sites represent typical features of arctic periglacial landscapes. Similar accumulations of ammonium were reported previously only for permafrost soils in Swedish peatlands (Keuper et al., 2012). As the diversity of soils and study sites represent a large geographical and geomorphological part of the Siberian lowland tundra, the accumulation of ammonium in the perennially frozen ground probably is a general feature of permafrsot affected soils in arctic tundra lowlands.

There is a large seasonal variability in nitrogen availability in arctic soils, with highest nitrogen availability directly after snowmelt (Hobbie and Chapin, 1996) and lowest nitrogen availability at the peak of the growing season in mid-July when competition is highest (Weintraub and Schimel, 2005b). However, due to mineralization throughout the growing season, the pool of available nitrogen re-fills towards the end of the growing season (Chapin, 1996; Weintraub and Schimel, 2005b). As the soil profiles in all study areas were sampled at the end of the growing season, seasonal dynamics in nitrogen availability cannot explain the different contents of ammonium in the active layer and the perennially frozen ground.

Microbial organisms in arctic soils are known to be adapted to cold temperatures and are active down to temperatures of -15 °C (Panikov, 2009; Mykytczuk et al., 2013; Jansson and Tas, 2014). Despite of the frozen state of the soil there is still unfrozen pore water in permafrost soils, which is essential for microbial activity (Ershov, 1998; Jessen et al., 2014) (Ershov 1998, Jessen et al. 2014). Though microbial organisms can be active at temperatures below 0 °C, their temperature optima in arctic soils are above 0 °C (Thamdrup and Fleischer, 1998; Mikan et al., 2002). However, on a timescale of 10^3 to 10^4 years, even low microbial activity under subzero conditions can have a substantial impact on the geochemical composition of arctic permafrost-affected soils (Panikov, 2009). In soil cores from the Lena River Delta, high amounts of methane were found in depths down to 400 cm b.s. as a result of Holocene methanogenesis within the frozen soil (Wagner et al., 2007). During the decomposition of soil organic material, organic N first becomes mineralized to ammonium and afterwards becomes oxidized to nitrite and finally to nitrate. However, under anoxic conditions - typical for water-logged permafrost soils in polygonal landscapes - further oxidation of the ammonium is impeded (Delwiche, 1970; Gebauer et al., 1996). Thus, the observed accumulation of ammonium in the perennially frozen ground probably is a result of microbial activity under low temperatures and anoxic conditions, similar to the accumulation of methane in permafrost soils that was observed by Wagner et al. (2007).

Measuring of thaw depths was conducted in all study areas between mid of August and end of August. Though re-freezing of the soils in all study areas started in September (as indicated by decreasing soil temperatures), the late summer thaw depths are a good approximation of the maximum annual thaw depths as the late-summer thaw rates in August and September are usually very low (Kutzbach et al., 2004a; Boike et al., 2013). The increase in the ammonium contents in the perennially frozen ground was highest in the soils from the Kolyma River Delta and smallest in the soils from the Lena River Delta. The soil temperatures and volumetric water content profiles at the three sites show the typical processes of permafrost soils, including a large seasonal temperature amplitude from up to -25 °C to approximately +10 °C in the surface layer and liquid water contents in the frozen soil up to 0.1 m^3 m^{-3}. However, there were strong differences in the minimum soil temperatures between the study site in the Kolyma River Delta and the two other study sites. The soil profile in the Kolyma River Delta showed minimum temperatures that were almost 10 °C higher than in the two other study sites. Furthermore, in 25 cm b.s. the temperatures were even higher and showed less variation, indicating reduced influence of the air temperature on the soil temperature. On the other hand, the soil temperatures in the Lena River Delta were nearly identical between 6 and 38 cm b.s., indicating less pronounced isolation of the soil. Probably, continuously warmer soil temperatures provided better conditions for the accumulation of ammonium. Furthermore, reduced isolation of the soil can also allow deeper thawing during warmer periods, mobilizing previously accumulated stores of ammonium. Thus, the site specific differences in the ammonium contents in the perennially frozen ground are probably a result of different soil temperatures during winter and differences in the inter-annual variability of active layer depths.

6.3.2 Active Layer Thickness Evolution

In general, the presented active layer thickness (ALT) model was able to realistically reproduce the ALT for all soil profiles under current climate conditions with the used climate forcing datasets. This gave confidence that for the future projections realistic magnitudes of ALT increases are calculated. For all soil profiles, a significant increase in ALT was only observed under the RCP8.5 scenario. This corresponds to findings of other permafrost sensitivity studies using different model approaches (Chadburn et al., 2015; Koven et al., 2015). However, permafrost modeling studies (including this study) usually do not take into account the full set of possible permafrost degradation processes like thermokarst and thermo-erosion (van Huissteden et al., 2012). As these processes are assumed to be highly sensitive to small warming rates (e.g. Grosse et al., 2011a), the presented permafrost degradation rates should be considered conservative estimates.

The presented results demonstrate that the future evolution of ALT strongly depends on the local soil composition (cf. Langer et al., 2013). In particular, the floodplain sites showed a high sensitivity to climate warming, which is most likely related to the lower contents of ice and higher mineral contents of the soils in comparison with the soils from the polygonal tundra.

6.3.3 Nitrogen Fluxes and Release

The results from the ALT model indicate significant permafrost thaw under the RCP8.5 scenario. Under this scenario, a mean increase in active layer thickness between 0.35 and 0.44 cm yr^{-1} was expected. Thawing of permafrost will lead to a mobilization of formerly frozen N stores. The calculated annual release of NH_4^+-N across all soil cores until the year 2100 is between 8 and 81 mg m^{-2}. A slightly higher amount of N release was projected from thawing permafrost soils in Swedish peatlands with 30 to 130 mg m^{-2} (Keuper et al., 2012). Furthermore, the estimated annual N release from thawing permafrost in this study is also only slightly lower than the annual N fixation rates in arctic surface soils, which is estimated to be between 80 to 130 mg m^{-2} (Hobara et al., 2006). N mineralization in arctic tundra ecosystems accounts for 50 to 500 mg m^{-2} yr^{-1} (Nadelhoffer et al., 1992; Schmidt et al., 1999; Schimel and Bennett, 2004). On the other hand, the annual N demand of arctic tundra plants was estimated to be between 500 and 2000 mg m^{-2} yr^{-1} (Chapin et al., 1988; Shaver and Chapin, 1991). Thus, N mineralization and fixation together hardly meet the annual N demand of the vegetation, illustrating the current N limitation of arctic ecosystems.

Considering the current N fluxes in the Arctic, the estimated annual N releases from thawing permafrost represent a significant and additional N source. By releasing a substantial part of the annual N demand of the vegetation, permafrost thaw most likely will cause a considerable change in the plant species composition of arctic ecosystems (Jonasson and Shaver, 1999; Eriksson et al., 2010). Particularly, deep-rooting plant species but also microbial organisms could benefit from simultaneously increasing N contents and active layer depths. Changes in the plant species composition could enhance the C storage function of the arctic tundra and potentially mitigate higher C emissions from the arctic tundra (Mack et al., 2004; Natali et al., 2012). Furthermore, a northward shift of the shrub line would be supported by higher N availability. Increased shrub growth would increase the snow-holding capacity of the arctic tundra, insulating the soil in winter and reducing summer thaw of the permafrost (Sturm et al., 2001; Blok et al., 2010). However, increased shrub growth will also reduce winter albedo and by altering the regional energy budget represents a positive climate feedback (Loranty et al., 2011; Pearson et al., 2013).

The presented data in this chapter show that permafrost thaw can lead to significant releases of inorganic N, probably mitigating N limitation of arctic terrestrial ecosystems. The projected annual release of N following permafrost thaw accounts for approximately half of the annual input of N by fixation of atmospheric N. Increased N availability will change the plant species composition of arctic ecosystems, causing different major positive and negative feedbacks on climate change. However, the permafrost in arctic riverine landscapes probably is less sensitive to climate change than currently expected; as temperature increases under the RCP4.5 scenario may not lead to significant changes in the active layer depth by the year 2100.

7 Effects of Different Temperatures on Soil Microbial Biomass, Microbial Respiration and Nutrient Availability

7.1 Introduction

Arctic permafrost-affected soils represent a significant global carbon reservoir, containing about 1300 Pg carbon (Hugelius et al., 2014). The projected increases in air and ground temperatures will have major impacts on arctic ecosystems: Substantial portions of permafrost will thaw in the coming decades which will lead to a mobilization of previously frozen resources like carbon (C) and nitrogen (N; Lawrence and Slater, 2005; Kuhry et al., 2010; Grosse et al., 2011a; Schuur et al., 2015). Microbial organisms in arctic soils are known to be adapted to cold temperatures and can be active even at temperatures below 0 °C (Mikan et al., 2002; Panikov, 2009). In the course of climate change, these cold-adapted microbial communities will experience substantially increased temperatures. Many studies have shown that higher temperatures in arctic ecosystems will lead to increased microbial carbon dioxide (CO_2) production, making permafrost-affected soils a potentially large C source (Nadelhoffer et al., 1991; Johnson et al., 1996; Dutta et al., 2006; Schuur et al., 2009). Changes in the soil-hydrological regime towards higher soil moisture levels can favor future methane (CH_4) effluxes from arctic ecosystems as well (Tveit et al., 2013; Nauta et al., 2015). Since CH_4 has a 34-fold higher global warming potential on a 100 year time-scale than CO_2 (Myhre et al., 2013), even low fluxes of CH_4 can turn greenhouse-gas sinks into greenhouse-gas sources in terms of CO_2 equivalents (Wille et al., 2008).

Aside of increased C emissions from arctic soils, higher soil temperatures will also enhance decomposition rates and thus lead to increased nutrient availability (MacDonald et al., 1995; Rustad et al., 2001; Keuper et al., 2012; Schaeffer et al., 2013). As N is known to be a main limiting nutrient for plant growth in the arctic tundra (Mack et al., 2004; Reich et al., 2006; Beermann et al., 2015), temperature induced increases in N availability will influence the plant species diversity and productivity of arctic ecosystems (Chapin et al., 1995; Natali et al., 2012). Changes in the plant-species composition of arctic ecosystems will control different positive climate feedback mechanisms like reducing of the surface albedo and amplification of the regional greenhouse-warming by increased evapotranspiration (Foley, 2005; Swann et al., 2010; Loranty et al., 2011). On the other hand, shrub expansion may also reduce permafrost thaw (Blok et al., 2010; Myers-Smith et al., 2011). Furthermore, increased nutrient availability and long-term warming in high latitudes can compensate for increased greenhouse-gas emissions by increased primary production (Natali et al., 2012; Sistla et al., 2013). Thus, nutrient availability indirectly controls different positive and negative feedback mechanisms to climate warming and is an important factor for the further progression of arctic ecosystems.

Microorganisms do not only release nutrients during organic matter degradation but also compete with plants for nutrients and represent a substantial sink capacity for N (Jonasson et al., 1996; Jonasson and Shaver, 1999; Schimel and Bennett, 2004; Churchland et al., 2010). Beside temperature, substrate quality and availability affect the decomposition rate of soil organic matter (Davidson and Janssens, 2006; Treat et al., 2014). Though a large proportion of the soil organic matter (SOM) in the arctic tundra is potentially mineralizable (Weintraub and Schimel, 2003), the SOM consists of various C pools with different recalcitrance to microbial decomposition (Dutta et al., 2006). However, if no other external factors (for example low temperatures) reduce microbial activity, microbial communities are able to get access to pools of more stable organic matter (Fierer et al., 2005; von Lützow and Kögel-Knabner, 2009).

This study was conducted to investigate the short-term effects of different temperatures on net microbial biomass growth, microbial respiration and nutrient availability in one permafrost-affected soil profile. The soil profile IND-3.4 from the Indigirka Lowlands was investigated in detail for this part of the present study (cf. section - 3.1 - *Fieldwork*). The coupled investigation of soil microbial respiration and net microbial biomass growth during this incubation study provides a detailed insight into the reactions of the soil-microbial communities to increased temperatures in this soil profile.

7.2 Results

7.2.1 Soil Chemistry

Highest volumetric amounts of total carbon (TC) in the control samples were found in the uppermost *Oi* horizon and the lowest amounts of TC were found in the *Oe* horizon. The *Oe* horizon provided also the lowest amounts total nitrogen (TN) while there were no differences between the *Oi* and the *Bg* horizons. There was a decrease in DOC contents from the *Oi* horizon to the *Bg* horizon while the highest amounts of DON (and also NH_4^+) were found in the *Bg* horizon. Highest amounts of C_{mic} were found in the *Oi* horizon and the lowest amounts of N_{mic} and also C_{mic} were found in the *Bg* horizon. NO_3^- was only detectable in the *Oi* horizon. Approximately 54 Vol.% of the samples from the *Bg* horizon were occupied by soil and additional 42 Vol.% of the samples were filled by water, indicating mostly anaerobic conditions in this horizon. Though absolute amounts of volumetric water contents were higher in the organic horizons, also the air-filled pore space was higher in these horizons due to the low volume of the organic material (Tab. 7.1).

Table 7.1 Chemical and physical properties of the control samples of the three different soil horizons of the soil profile IND-3.4. Significant differences between the different soil horizons are indicated by the by the F-value and the p-value of the respective ANOVA. Significantly differing horizons are indicated by superscripted letters (Tukey's HSD test)

	Oi	Oe	Bg	Statistics
C (mg cm^{-3})	74.5 ± 7.2^{a}	39.7 ± 0.3^{c}	61.2 ± 1.3^{b}	F(2,6)=45.1, p<0.001
N (mg cm^{-3})	4.3 ± 0.8^{a}	0.7 ± 0.1^{b}	3.7 ± 0.2^{a}	F(2,6)=47.3, p<0.001
DOC (μg cm^{-3})	186 ± 31^{a}	$159 \pm 25^{a}b$	112 ± 7^{b}	F(2,6)=8.0, p<0.05
DON (μg cm^{-3})	22.8 ± 3.2^{b}	12.3 ± 1.9^{c}	63.3 ± 5.2^{a}	F(2,6)=165, p<0.001
C_{mic} (mg cm^{-3})	0.9 ± 0.1^{a}	0.5 ± 0.0^{b}	0.5 ± 0.0^{b}	F(2,6)=32.8, p<0.001
N_{mic} (μg cm^{-3})	21.3 ± 3.8^{a}	28.4 ± 2.6^{a}	4.6 ± 5.8^{b}	F(2,6)=21.9, p<0.01
NH_4^+ (μg cm^{-3})	0.5 ± 0.1^{b}	0.5 ± 0.3^{b}	1.5 ± 0.4^{a}	F(2,6)=9.9, p<0.05
NO_3^- (μg cm^{-3})	1.0 ± 0.1^{a}	0 ± 0^{b}	0 ± 0^{b}	F(2,6)=480, p<0.001
Bulk density (g cm^{-3})	0.22 ± 0.05^{b}	0.08 ± 0.03^{c}	1.30 ± 0.08^{a}	F(2,6)=101, p<0.001
Water content (Vol.%)	76.8 ± 3.4^{a}	68.1 ± 6.6^{b}	41.8 ± 2.0^{c}	F(2,6)=52.1, p<0.0001
Air-filled pore space (Vol.%)	9.7 ± 3.4^{b}	25.9 ± 7.8^{a}	4.1 ± 4.8^{c}	F(2,6)=31, p<0.0001
Soil volume (Vol.%)	13.5 ± 3.5^{b}	6.0 ± 2.1^{c}	54.1 ± 3.3^{a}	F(2,6)=54.7, p<0.0001

After six weeks of incubation, we observed no significant differences in the amounts of TC and TN between the control samples and both temperature treatments (Tab.A.3). In contrast, temperature had a significant effect on the amount of microbial biomass (measured as C_{mic}) in the *Oi* horizon (F(2,6)=93.7, *p<0.0001*), in the *Oe* horizon (F(2,6)=37.5, *p<0.0001*) and in the *Bg* horizon (F(2,6)=38.7, *p<0.001*). There was an increase in C_{mic} in all soil horizons after six weeks of incubation at 5 °C. The samples of the organic horizons showed also an increase in microbial biomass after the incubation at 15 °C. However, increase of microbial biomass was stronger at 5 °C than at 15 °C (Fig. 7.1A-7.1B). In the *Bg* horizon, there was no net increase of microbial biomass after six weeks of incubation at 15 °C (Fig. 7.1C).

Despite the strong temperature effect on the increase of C_{mic} across all horizons, the temperature treatments had a significant effect on the amount of N_{mic} only in the uppermost *Oi* horizon (F(2,6)=20.7, *p<0.01*). We observed an increase in the content of N_{mic} after the incubation in this horizon. However, there were no significant differences between the two temperature treatments (Fig. 7.1D). A possible increase in the content of

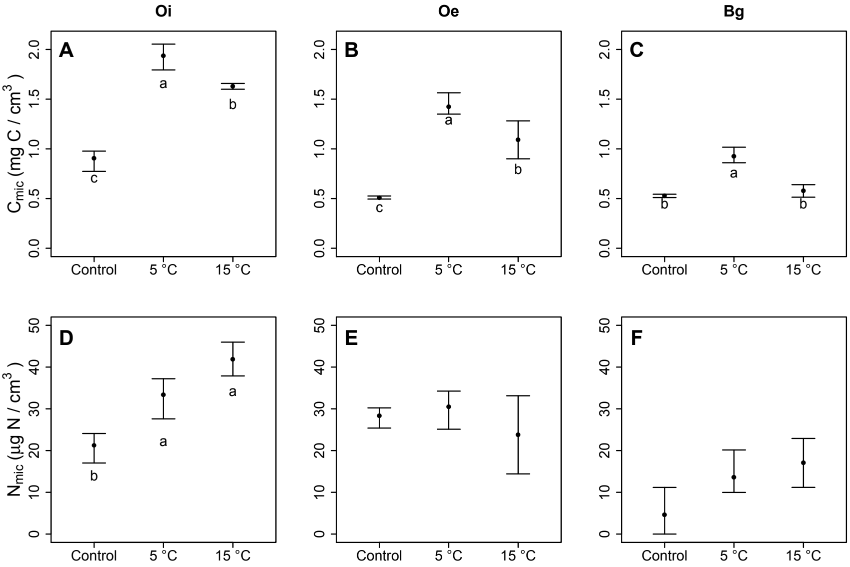

Figure 7.1 Microbial carbon (C_{mic}) and microbial nitrogen (N_{mic}) in the control samples as well as in the samples incubated at 5 °C and 15 °C, respectively, in all three investigated soil horizons. Average values as well as minimum and maximum values of three replicates are shown. The lowercase letters indicate significantly differing groups of the ANOVA.

N_{mic} during the incubation was also observed in the *Bg* horizon (Fig. 7.1F).

Significant effects of the two temperature treatments on the amount of DOC were observed in the *Oe* horizon (F(2,6)=13.7, *p<0.01*) and the *Bg* horizon (F(2,6)=24.4, *p<0.001*). In both of these horizons, there was a decrease in DOC which was not influenced by the different temperature treatments. However, the observed increases of C_{mic} in these horizons were about 10-fold higher than the decrease in the amount of DOC. Furthermore, in the samples of the *Oi* horizon there appeared to be a similar decrease in DOC (Fig.7.2A-C).

Similar to the decrease in the DOC contents, there was also a significant decrease in the DON contents in the samples of the *Bg* horizon after the incubation (F(2,6)=26.7, *p<0.001*). However, there were no differences between the two temperature treatments. In the samples of the organic *Oi* and *Oe* horizons, the contents of DON were overall lower than in the *Bg* horizon and were not significantly affected by the two temperature treatments (Fig. 7.2D-F).

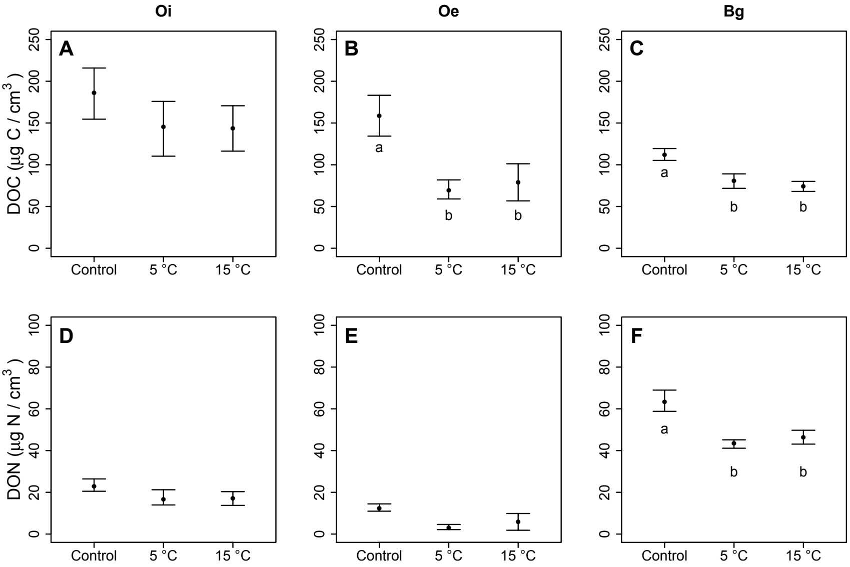

Figure 7.2 Dissolved organic carbon and dissolved organic nitrogen in the control samples as well as in the samples incubated at 5 °C and 15 °C, respectively, in all three investigated soil horizons. Average values as well as minimum and maximum values of three replicates are shown. The lowercase letters indicate significantly differing groups of the ANOVA.

The contents of nitrate were almost negligible in all of the investigated soil horizons and showed no significant differences after the incubation under both of the temperature treatments (Tab. A.3). The contents of ammonium (NH_4^+) were also almost negligible in the organic *Oi* and *Oe* horizons samples and were not affected by temperature. In contrast, in the *Bg* horizon, there was a significant twentyfold increase in ammonium after the incubation under the two temperature treatments (F(2,6)=66.9, $p<0.001$; Fig. 7.3C). Similar to the decrease of the DON contents in the *Bg* horizon, there were no differences between the two temperature treatments. Furthermore, the increase in ammonium was as high as the decrease in DON (Tab. A.3).

7.2.2 Gas Production Measurements

There were large differences in the volumetric production rates of CO_2 and CH_4 between the two temperature treatments and also between the different soil horizons at given tem-

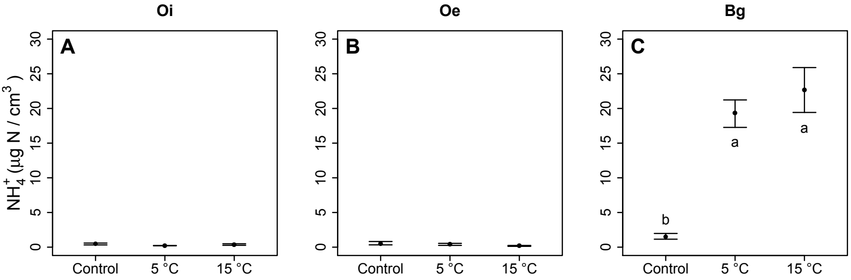

Figure 7.3 Contents of ammonium in the control samples as well as in the samples incubated at 5 °C and 15 °C, respectively, in all three investigated soil horizons. Average values as well as minimum and maximum values of three replicates are shown. The lowercase letters indicate significantly differing groups of the ANOVA.

peratures during the 42 days of incubation. Under the temperature of 5 °C, only one of three replicates showed significant increases in the CO_2 concentration in both organic horizons, probably due to a leakage of the bottles. Thus, statistical analyses between the two temperature treatments could only been conducted in the *Bg* horizon. Though temperature had no significant effect on the CO_2 production rates in the *Bg* horizon, the CO_2 production rates in both organic horizons were probably two to three times higher under the temperature treatment of 15 °C (Tab.7.2).

Release of CH_4 was detected under both temperature treatments in the samples of the *Bg* horizon and also in the samples of the *Oi* horizon under the temperature treatment of 15 °C. In contrast to the CO_2 production, the release rates of CH_4 in the *Bg* horizon

Table 7.2 Daily volumetric production rates of CO_2 and CH_4 in the three horizons under the two temperature treatments. Mean production rates and the standard deviation of the production rates of three parallels are shown. Significant differences between the two temperature treatments are indicated by a bold p-value. Differences in the CO_2 production between the soil horizons are indicated by the F-value and p-value of the respective ANOVA. Detected differences are indicated by bold numbers; significantly differing groups are marked by superscripted letters. *CH_4 production started after 14 days of incubation.

	CO_2-C (μg cm^{-3} d^{-1})			CH_4-C (μg cm^{-3} d^{-1})		
	5 °C	15 °C	*p*	5 °C	15 °C	*p*
Oi	2.2	$5.27^b \pm 1.10$	-	-	$> 0.003^*$	-
Oe	2.3	$7.47^b \pm 2.15$	-	-	-	-
Bg	1.65 ± 0.44	$1.74^a \pm 1.02$	*>0.05*	0.06 ± 0.02	0.02 ± 0.02	***<0.05***
		F(2,6)=11.0,				

were significantly higher at 5 °C than at 15 °C. The CH_4 production in the *Oi* horizon was detected only after 14 days of incubation, and the CH_4 production rates were a magnitude lower than in the *Bg* horizon (Tab. 7.2). During the incubation at 5 °C, between 0.05 % and 0.19 % of the initial C-pool were lost as CO_2 and CH_4 across all three horizons. The amount of C lost with respect to the initial C-pool was highest with 1.03 % at 15 °C in the *Oe* horizon (Tab. 7.3). A detailed graphical presentation of the CO_2 and CH_4 production in all horizons is given in Figure7.4.

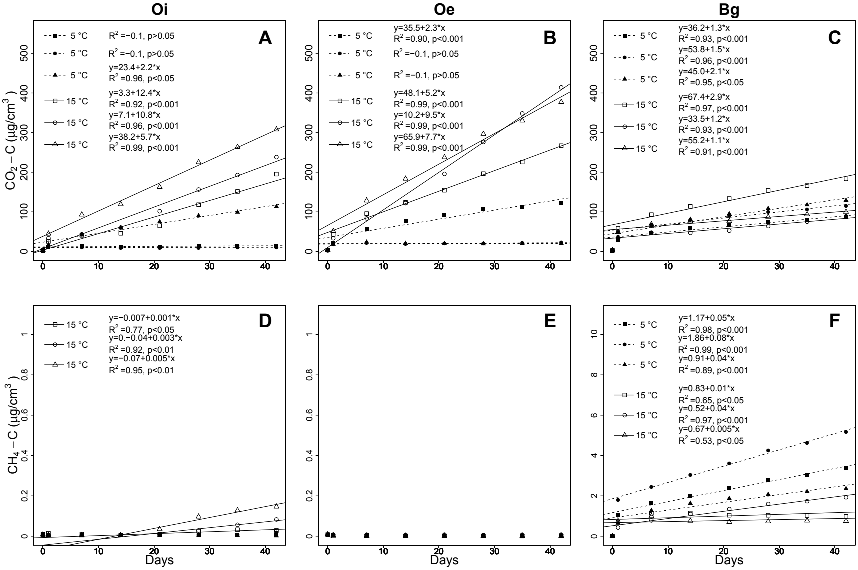

Figure 7.4 Cumulative release of CO_2 and CH_4 during the incubation of soil material of the three soil horizons. Temperature treatment at 5 °C is shown by open circles and a dotted line; temperature treatment at 15 °C is shown by closed circles and a continuous line. R^2 and p-values of linear regressions are shown.

7.3 Discussion

This part of the present study illustrates that temperature changes in arctic ecosystems can have large effects on carbon mineralization by heterotrophic respiration as well as on the growing conditions for microbial organisms. By the incubation of soil samples in intact stratification, we are able to show the reactions of a whole soil profile to experimental warming. Under current temperatures, there appeared to be no differences in the carbon emissions between the three horizons of this soil profile. In contrast, under the temperature treatment of 15 °C, the CO_2 production rates in both organic horizons were presumably two to three higher in comparison with the temperature treatment of 5 °C. This temperature-dependent increase in CO_2 production rates of arctic soil microbial communities was previously reported by many other studies, supporting the results of the present study (e.g. Nadelhoffer et al., 1991; Johnson et al., 1996; Rustad et al., 2001; Davidson and Janssens, 2006). However, there were no significant differences in the CO_2 production between the two temperature treatments in the lowest Bg horizon. Currently, the underlying mineral horizon may contribute to the carbon emissions of this soil profile in the same order of magnitudes than the organic soil horizons. Though in a warmer climate, most of the carbon emissions may originate from the organic horizons of this soil, which was also suggested by Schaedel et al. (2014).

Table 7.3 Percentages of TC which was respired as CO_2 and CH_4, respectively. Significant differences between the two temperature treatments are indicated by a bold p-value.

Horizon	5 °C	15 °C	p
Oi	0.05 ± 0.07 %	0.34 ± 0.10 %	***<0.05***
Oe	0.16 ± 0.22 %	1.03 ± 0.22 %	***<0.01***
Bg	0.18 ± 0.04 %	0.19 ± 0.08 %	*<0.05*

In contrast to the CO_2 production rates, the increase of microbial biomass in all soil horizons was much stronger after the incubation at 5 °C than after the incubation at 15 °C. In the lowermost *Bg* horizon, there was even no net increase in microbial biomass after the incubation at 15 °C. Microorganisms in permafrost-affected soils are adapted to cold temperatures and are often classified as psychrophiles (Jansson and Tas, 2014). Growth of these psychrophilic microorganisms is constrained to specific temperatures, typically ranging from -17 °C to +10 °C (Panikov et al., 2006; Larionova et al., 2007; Jansson and Tas, 2014). Otherwise, microbial respiration in permafrost-affected soils was observed at a much broader temperature range between -39 °C and +20 °C (Kato et al., 2005; Panikov et al., 2006). Like any other biochemical reaction, also decomposition of organic matter depends on the kinetics of enzyme reactions. Soil organic matter (SOM) pools of different recalcitrance mainly differ by the activation energies which are required for the specific enzymatic reactions. Thus, decomposition of SOM is most sensitive to increased temperature in cold regions (Davidson and Janssens, 2006; von Lützow and Kögel-Knabner, 2009). When available substrates are depleted, microbial communities can adapt under higher temperatures to decompose more recalcitrant pools of SOM (Waldrop and Firestone, 2004; von Lützow and Kögel-Knabner, 2009). On the other hand, increased temperatures favor also carbon losses by microbial respiration over carbon processed into new microbial biomass (Manzoni et al., 2012). Thus, decomposition rates increase under higher temperatures, but also decreases the proportion of C used for microbial growth, resulting in increased CO_2 production despite reduced microbial growth.

In addition to the increases in C_{mic}, there was a significant increase in N_{mic} in the *Oi* horizon. As the uppermost *Oi* horizon provides the interface between soils and the atmosphere, most of the N fixation might happen in this area (Hobara et al., 2006). Furthermore, there were no significant changes in the amounts of N_{mic} in the lower horizons. Thus, the increase of N_{mic} in the uppermost soil horizons could be related to the abundance of nitrogen fixing microbial communities in this horizon.

Substantial CH_4 emissions were only observed in the mineral *Bg* horizon which was sampled in the deeper zone of the active layer directly above the permafrost table. There were also significant emissions of CH_4 in the *Oi* horizon under the temperature treatment of 15 °C. However, the production of CH_4 started only after 14 days of incubation and the production rates were a magnitude lower than in the *Bg* horizon. In contrast to the CO_2 emissions, CH_4 emissions in the *Bg* horizon were significantly higher at 5 °C than at 15 °C. Unlike CO_2, which is produced by bacteria, CH_4 is also produced by methanogenic archaea (Garcia et al., 2000). Ganzert et al. (2007) found low temperature optima of methanogenic archaea near the permafrost table in Siberian soils. Thus, the incubation at 5 °C probably provided better conditions for CH_4 production than the incubation at 15 °C.

The aerobic incubation of samples in intact stratification most likely preserved more areas with anaerobic conditions than an incubation with mixed samples, resulting in substantial CH_4 emissions from the samples of the mineral *Bg* horizon. The missing CH_4 emissions in the samples of both organic horizons are probably a result of the balance between CH_4 production and oxidization to CO_2 due to more aerobic conditions in the organic horizons. Although significant CH_4 fluxes have been reported previously from this site, they were highly sensitive to hydrological conditions (van der Molen et al., 2007; Parmentier et al., 2011). The samples from this study were taken on a relatively dry polygonal ridge with significant amounts of air filled pore volume, providing the conditions to oxidize CH_4 to CO_2. Thus, due to small-scale differences in the abundance of methane oxidizing bacteria between the mineral and the organic soil horizons, the CH_4 produced in the *Bg* horizon probably would have been oxidized to CO_2 by its way through the soil column under in-situ conditions (cf. Liebner and Wagner, 2007).

During this incubation, there were no significant changes in the content of nitrate in all of the three horizons. During the decomposition of the soil organic material, N compounds become mineralized to ammonium prior to the oxidation to nitrite and nitrate (Delwiche, 1970). Thus, the supply of nitrate ultimately depends on the supply of ammonium. As there were no significant increases in the amount of ammonium in the organic horizons, there was no substrate which could become oxidized to nitrate in these horizons. Only in the mineral *Bg* horizon, there was a tenfold increase of ammonium after the incubation under both temperature treatments. This increase was as high as the decrease of DON in this horizon after the incubation and thus, approximately one third of the DON in this horizon was mineralized to inorganic ammonium during 42 days of incubation. Thus, as there was no effect of the different temperatures on the amount of extractable inorganic nitrogen, higher temperatures may not lead to increased nitrogen availability in the short-term.

The contents of DOC and DON mostly decreased during this incubation. However, the increases in C_{mic} and N_{mic} were orders of magnitudes higher than the decreases in DOC and DON. There is usually a very rapid turnover of DOC in arctic soils which is relatively insensitive to temperature (Boddy et al., 2008) and also the abundance of DON shows large seasonal variability (Farrell et al., 2011). Thus, the decreases of DOC and DON cannot be directly related to the increase in C_{mic} and N_{mic}, although concentration and composition of these low molecular carbon compounds drive microbial respiration (van Hees et al., 2005).

Microbial respiration and net microbial biomass growth in this arctic soil-incubation study show contrasting responses to increased temperatures. Probably, respiration rates were increased under higher temperatures, but net microbial biomass growth was reduced under these temperatures. Thus, higher temperatures probably result in increased microbial respiration rates at the expense of microbial growth, whereas nitrogen mineralization rates are not affected by temperature in the short-term. However, long-term warming may result in balanced microbial respiration rates due to microbial adaptation and depletion of easily decomposable substrate. The presented results demonstrate the importance of coupled observations of growth and respiration of microbial communities. Even similar respiration rates at different temperatures may not indicate similar responses of the microbial biomass to these temperatures, as microbial biomass growth is contrarily affected by temperature in arctic soils. Though the soils in this study area are quite homogeneous, the investigated soil profile may not be representative for the whole study area, and follow-up studies should investigate respiration rates and growth of microbial communities in arctic soils by a larger sample size.

8 Synthesis and Conclusions

The overall goal of this interdisciplinary thesis was to investigate nutrient availability and limitation in the arctic polygonal tundra. An integrated ecosystem approach was used by investigating nutrient availability in the soils and their amounts within the microbial biomass and the vegetation biomass as well. The arctic tundra ecosystem is highly sensitive to the projected changes in temperature. Increased temperatures will cause thawing of the permafrost and will also induce thermokarst (Grosse et al., 2011a; Morgenstern et al., 2013). Higher soil temperatures will affect microbial decomposition rates, and increased nutrient availability is expected (Wild et al., 2013). Increased nutrient availability will affect the whole ecosystem by controlling changes in the plant-species composition (Schuur et al., 2007). Thus, nutrient availability and limitation are important parameters to assess the future development of the arctic tundra. In detail, the focus of this study was on the following objectives:

1. **To identify limiting and available nutrients in the polygonal tundra by analyzing stoichiometric relationships in the vegetation biomass, in the microbial biomass, in the pools of dissolved inorganic and dissolved organic nitrogen and phosphorus as well as in the total elemental pools**

Limiting nutrients on the level of plant communities are traditionally identified by the factorial addition of different nutrients like nitrogen, phosphorus or potassium and a subsequent investigation of the growth response of the vegetation to the different additions (c.f. Chapin et al., 1986). As growth responses are slow, these experiments are time-consuming, expensive and thus, limited to only small amounts of samples. On the other hand, stoichiometric approaches can be used instead of fertilization experiment to identify limiting nutrients on a plant community level (Koerselman and Meuleman, 1996). This approach is based on Liebig´s law of the minimum which states that organismal growth is ultimately controlled by the scarcest resource (Liebig, 1840). However, during the last century, the concept of resource limitation has shifted to a concept of co-limitation by multiple resources (Saito et al., 2008; Harpole et al., 2011), and different fertilization studies from arctic ecosystems showed synergistic responses of plant growth to combined N and P additions as well (e.g. Giesler et al., 2012; Zamin and Grogan, 2012). Though fertilization experiments are the most certain way to identify limiting nutrients of plant communities, we are able to get a first order approximation of the nutrient limitation in an ecosystem by analyzing elemental ratios (Ågren et al., 2012). In this thesis, one of the first successful applications of stoichiometric nutrient analyses in arctic ecosystems is presented. The values of the N/P, N/K and K/P ratios in the vegetation were consistent with previous studies from other wetland ecosystems (c.f. Koerselman and Meuleman, 1996; Güsewell, 2004; Cleveland and Liptzin, 2007; Xu et al., 2013), and a coherent picture of the current situation of the nutrient limitation in this ecosystem could be presented.

Plant growth in the investigated polygonal tundra ecosystem was found to be simultaneously limited by nitrogen and phosphorus. Moreover, the integrated approach of this study allowed a more detailed insight into the nutrient balance of the investigated polygonal tundra: The present study proposes that the microbial activity may currently be limited by phosphorus. Thus, the supply of inorganic nitrogen by microbial decomposition and fixation of atmospheric nitrogen is probably limited by a low availability of phosphorus. In addition to the availability of inorganic nutrients, the amounts of potentially mineralizable nutrients are of high importance as higher microbial decomposition rates are expected in a warmer climate (MacDonald et al., 1995; Rustad et al., 2001). In contrast to the nitrogen cycle, the phosphorus cycle lacks a major atmospheric component and input of phosphorus into pristine ecosystems occurs only by weathering of primary minerals (Aber and Melillo, 2001). However, as chemical weathering is usually very slow in periglacial environments (Allen et al., 2001), decomposition of phosphorus compounds in the organic soils is the most important source of phosphorus for plant growth and microbial activity in arctic soils. This study shows that the amounts of total nitrogen are orders of magnitudes higher than the amounts of total phosphorus, reflected by a molar-based mean N/P ratio of 44 in the total elemental pools. On the other hand, the plant communities were characterized by molar based mean N/P ratios between 15 and 25, indicating an imbalance in favor of N between the stoichiometry of the current vegetation and the pool of potentially mineralizable nutrients. Furthermore, up to 40 % of the total phosphorus are already cycling through the biologically active fractions, including inorganic phosphorus, microbial biomass phosphorus and dissolved organic phosphorus, indicating that the amount of potentially available phosphorus is highly constrained. Thus, higher microbial activity in the course of climate change probably will shift nitrogen limitation of arctic plant communities to phosphorus limitation of these ecosystems.

Though the arctic tundra is traditionally known to be limited by nitrogen, phosphorus is already a limiting nutrient in this ecosystem (Giesler et al., 2012). In contrast to carbon and nitrogen, phosphorus is efficiently recycled during tissue senescence in northern peatlands (Wang et al., 2015). Thus, there is almost no phosphorus accumulation during peat formation in these soils (Wang et al., 2014). The present study highlights the current and future shortage of phosphorus in the arctic polygonal tundra by showing the stoichiometric nutrient balance of the soil-vegetation system in this ecosystem. Plant growth is currently co-limited by nitrogen and phosphorus. However, the supply of inorganic nitrogen by microbial mineralization and fixation of atmospheric nitrogen could already be caused by phosphorus limitation of the microbial biomass.

Stoichiometric nutrient analysis is an inexpensive but efficient tool to characterize an ecosystems nutrient balance. Extensive use of stoichiometric analyses could help to improve the knowledge about the current nutrient limitation in the arctic tundra. Follow-up studies should include the elemental stoichiometry of the plant litter as well. Recycling of nutrients from the dead organic matter is a major component in the trophic web of northern peatlands (Wang et al., 2015). Thus, the elemental contents of the plant litter are an important piece of information to define nutrient limitation in these ecosystems.

2. To assess pools of potentially available nitrogen within the perennially frozen ground of permafrost-affected soils

The first part of this study showed the importance of nitrogen availability for plant growth in the arctic polygonal tundra. Higher nitrogen mineralization rates under higher temperatures probably can mitigate the nitrogen limitation of arctic ecosystems (Wild et al., 2013). However, mineralization rates may increase only slowly in response to higher temperatures, resulting in a delay between increased temperatures and increased nutrient availability (Rinnan et al., 2007). On the other hand, thawing of the permafrost will release currently frozen and immediately available nutrient resources from the perennially frozen ground (Kuhry et al., 2010; Grosse et al., 2011b). Thus, nutrient stores in the perennially frozen ground of permafrost-affected soils are of major importance for plant nutrition in arctic ecosystems in the future. This study shows for the first time significantly increased amounts of inorganic ammonium in the perennially frozen ground of Siberian permafrost-affected soils. The amount of ammonium in the perennially frozen ground of all investigated soils was between ~2-fold and ~40-fold higher than in the active layer. Previously, similar results were only reported for permafrost soils in Swedish peatlands (Keuper et al., 2012).

As the soils of this study represent typical features of periglacial landscapes, these accumulations of ammonium could be a widespread phenomenon of arctic permafrost-affected soils. These accumulations of ammonium are probably a result of Holocene microbial activity within the perennially frozen ground. There are considerable amounts of unfrozen pore water in permafrost soils despite of the frozen state of the soil, which is the requirement for microbial activity (Ershov, 1998; Jessen et al., 2014). Arctic microorganisms have been shown to be active at temperatures down to -15 °C (Mykytczuk et al., 2013; Jansson and Tas, 2014). Thus, on long time-scales they can have a substantial impact on the geochemical composition of arctic permafrost-affected soils (Panikov, 2009). Previous studies already showed accumulations of methane in Siberian permafrost soils as a result of Holocene microbial activity (Wagner et al., 2007). Permafrost soils are traditionally partitioned into a seasonally thawed and a perennially frozen layer. However, as the extent of thawing may vary over the centuries with respect to climate fluctuations, some authors suggested an episodically thawed transient layer between the seasonally thawed active layer and the perennially frozen ground (Shur et al., 2005; Bockheim and Hinkel, 2005). This transient layer is ice-rich due to infiltration of snow-melt water over time (Hinkel et al., 2001), and migration of water can also cause enrichment of soluble cations in the permafrost (Kokelj and Burn, 2003). The transient layer is comparatively resistant to thawing as the latent heat storage of ice is considerably higher than the latent heat storage of mineral material (Halliwell and Rouse, 1987). By containing high amounts of ice and probably also considerable amounts of unfrozen water, the transient layer provides conditions to support ammonium accumulation due to microbial activity over long time scales. Thawing of the transient layer due to climate fluctuations would then deplete previously accumulated amounts of ammonium, and regional differences in the historical climate and weather as well as differences in the dynamics of the transient layer could account for regional differences in the ammonium accumulation.

By modeling the annual increase of the active layer under different climate scenarios, this study provides a first estimate of the potential annual release of inorganic nitrogen due to thawing of the permafrost. Two different climate scenarios were selected to model the potential active layer increase, using representative concentration pathway (RCP) 4.5 and 8.5 scenarios (van Vuuren et al., 2011). The first scenario, RCP4.5, is a stabilization pathway that reaches plateau atmospheric carbon concentrations early in the 21st century; the second, RCP8.5, is an unmitigated *business as usual* emission scenario with increasing carbon emissions. At all sites, the simulations revealed an almost stable active layer thickness under the moderate warming of the RCP4.5 scenario with only minor deviations to the control runs until 2100. In contrast, pronounced increases in active layer thickness ranging between 14 ± 3 and 35 ± 6 cm were observed under the warming trend of the

RCP8.5 scenario. However, the simulations of the active layer thicknesses only analyzed the effect of rising temperatures but did not include the full set of possible permafrost degradation processes like thermokarst and thermo-erosion (cf. van Huissteden and Dolman, 2012). As these processes are assumed to be highly sensitive to even small warming rates (Grosse et al., 2011a), the presented permafrost degradation rates should be considered conservative estimates.

Estimates of the annual release rate of nitrogen from thawing permafrost were only calculated for the RCP8.5 scenario as the active layer appeared to be stable under the RCP4.5 scenario. The annual release rate of ammonium under the RCP8.5 scenario was estimated to be nearly as high as as the annual fixation rates of atmospheric nitrogen by soil microorganisms in arctic soils. This released nitrogen will account for up to 10 % of the annual nitrogen demand of the vegetation. Thus, thawing of the permafrost in the arctic tundra will release substantial amounts of inorganic nitrogen, thereby changing the nutrient balance of the arctic polygonal tundra.

This study provides valuable data of the geochemical composition of Siberian permafrost-affected soils. Currently, eastern arctic Siberia is strongly underrepresented in the *Northern Circumpolar Soil Carbon Database* (Hugelius et al., 2013) and the *International Peatland Database* as well (Loisel et al., 2014). Values of total carbon and also total nitrogen can be shared within these international databases and thus can contribute to an improved understanding of the biogeochemistry of arctic peatlands. Follow-up studies should focus on the question, if accumulation of ammonium due to Holocene microbial activity is a general feature of arctic permafrost-affected soils. The present study already found this accumulation at three permafrost sites along a distance of more than 1,000 km in the Siberian Arctic and a general occurrence of this phenomenon would have major implication for the nutrient balance of arctic ecosystems in the future. Aside of this interesting phenomenon, potential phosphorus stores in the perennially frozen ground should also be investigated as phosphorus may become the main limiting nutrient in arctic ecosystems in the future. These analyses would also provide the data-basis for stoichiometric analyses of nutrient availability in the perennially frozen ground and contribute to an improved understanding of the future development of the arctic tundra.

3. To analyze microbial feedback to climate warming and to give an estimate how nitrogen availability may change under higher temperatures

By analyzing the ecological stoichiometry within the different fractions of the trophic web of the arctic polygonal tundra, the first part of this study showed the importance of nitrogen and phosphorus for plant nutrition and microbial activity in the arctic polygonal tundra. Subsequently, the second part of this study showed for the first time significant stores of inorganic ammonium within the perennially frozen ground of the arctic polygonal tundra. Furthermore, the importance of increased mineralization rates under higher temperatures and following changes of the ecosystems were highlighted previously in this study. As a complement to the first parts of this study, an incubation experiment was conducted to analyze the response of nitrogen availability, microbial growth and microbial respiration to increased temperatures.

Microbial mineralization rates are predicted to increase in the arctic tundra under higher temperatures (e.g. Aerts, 2006; Davidson and Janssens, 2006), probably resulting in increased nitrogen availability (Wild et al., 2013). However, this study showed that nitrogen mineralization rates may be not affected by rising temperatures in the short-term. Furthermore, the possible positive response of microbial respiration to higher temperatures was at the expense of the growth rates of the microbial communities. Thus, the microbial communities of arctic permafrost-affected soils may currently be not adapted to increased temperatures.

Carbon emissions from arctic permafrost-affected soils are predicted to increase in the course of climate change. However, different studies showed that the response of soil respiration to increased temperatures is only short-lived and elevated respiration rates return to pre-warming values within a few years (Oechel et al., 2000; Eliasson et al., 2005; Knoblauch et al., 2013). This could be a result of adaptation of the microbial communities to increased temperatures by adjusting of their respiration rates in order to maintain a positive carbon balance (Bradford et al., 2008; Malcolm et al., 2008). Thus, expecting microbial adaptation to increased temperatures, the expected strength of climate warming on soil respiration might be decreased in the long-term.

This study highlights that coupled observations of growth rates and respiration rates of microbial communities can substantially increase the information gained from incubation studies. As temperatures probably will rather increase gradually than by an abrupt rise, incubation experiments should focus on more than two different temperatures.

Soil horizons in thawing permafrost will probably experience the most drastic rise in temperatures. Thus, follow-up studies should investigate the response of nitrogen and phosphorus mineralization rates and their availability to increased temperatures in these soils, which were previously frozen for decades and centuries. Phosphorus availability should be included into future incubation studies as the availability of phosphorus may limit plant growth and microbial activity in the future.

The different parts of this study have investigated the nutrient stoichiometry of the soil-vegetation system of the polygonal tundra, nutrient availability within the perennially frozen ground of the polygonal tundra and also the short-term responses of microbial communities to increased temperatures in these soils. The presented results and discussions in this study led to the following main conclusions:

- Nitrogen mineralization and fixation are crucial for plant nutrition in the polygonal tundra. Increased mineralization under higher temperatures could lead to phosphorus limitation of the polygonal tundra.
- Thawing of the permafrost with increasing temperatures will release high amounts of readily available inorganic nitrogen, probably mitigating nitrogen limitation of the plant communities in the arctic tundra.
- In the short-term, there will be no increased nitrogen mineralization rates in response to increased temperatures. Adaptation of the microbial communities to a warmer climate may result in less increased microbial respiration rates than currently expected.

Arctic permafrost ecosystems are projected to experience substantial changes in the course of climate change. The seasonally thawed layer of permafrost soils is projected to increase (Grosse et al., 2011a; Koven et al., 2013), and permafrost thaw will induce thermokarst processes, drastically changing ground surface characteristics (Morgenstern et al., 2013). Thawing of the permafrost will allow drainage of near-surface water and a decrease of arctic wetlands is projected as well (Avis et al., 2011). Furthermore, increased growth of woody plants (Pearson et al., 2013) and increased primary production rates (Natali et al., 2012) in arctic permafrost ecosystems are expected. Specialized arctic species will be replaced by boreal species (Callaghan et al., 2004) and a shift to shrub-dominated plant communities is expected (Schuur et al., 2007).

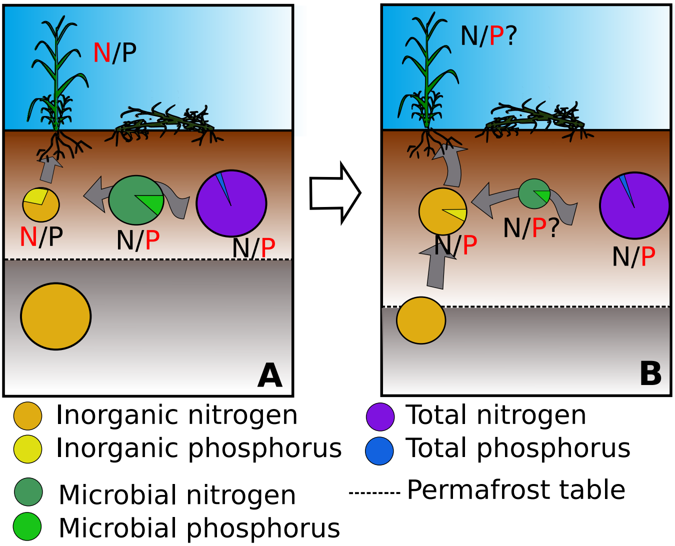

Figure 8.1 Nutrient availability and limitation in the soil vegetation system of arctic soils under current temperatures (A) and in a warmer climate (B) are shown. Inorganic nutrient pools are shown in yellow colors, total nutrient pools are shown in blue colors and the microbial biomass is shown in green colors. Element fluxes are shown by grey arrows. Limiting nutrients in the different soil fractions and the vegetation are marked red.

Arctic tundra plant communitites are currently limited by low availability of nitrogen (cf. chapter 5). However, increased temperatures may not cause increased nitrogen mineralization rates in the short-term (cf. chapter 7). On the other hand, permafrost thaw will release large amounts of inorganic nitrogen, probably mitigating nitrogen limitation of the arctic tundra (cf. chapter 6). Thus, the soil chemistry of arctic permafrost-affected soils will provide conditions to support shrub growth and increased primary production. Increased shrub growth is already observed (Tape et al., 2006) and probably will stabilize the permafrost by insulating the soils due to their higher snow-holding capacity and by increased shading in summer due to the higher leaf area in comparison with graminoid grasslands (Blok et al., 2010; Myers-Smith et al., 2011). Furthermore, increased snow accumulations will cause increased soil temperatures in winter, higher microbial activity and thus increased N mineralization in winter (Sturm et al., 2005). Increased shrub-growth will also amplify regional greenhouse-warming by increased evapotransiration (Swann et al., 2010) and strengthen regional warming by reducing the winter albedo of arctic ecosystems (Foley, 2005; Loranty et al., 2011). Thus, increased shrub-growth will significantly influence the energy budget of arctic permafrost landscapes.

There are large amounts of soil organic carbon stored in arctic permafrost-affected soils (Hugelius et al., 2014), which are vulnerable to microbial decomposition and will become released as CO_2 and CH_4 under higher temperatures (Schuur et al., 2015). Higher soil respiration due to higher temperatures will cause a significant positive climate feedback (Schneider Von Deimling et al., 2012). However, the large carbon stores of arctic permafrost-affected soils are not equally available to microbial decomposition (Schädel et al., 2014). Thus, the short-term response of microbial respiration in response to higher temperatures is different from long-term responses (Knoblauch et al., 2013), and microbial adaptation to higher temperatures probably will decrease microbial respiration rates (chapter 7; Bradford et al., 2008).

Long-term warming will cause a shift from heterotrophic to autotrophic respiration in arctic permafrost ecosystems (Hicks Pries et al., 2015). Hence, increased primary production can compensate higher CO_2 emission (Sistla et al., 2013). Furthermore, increased nutrient availability will increase the carbon-use efficiency of the microbial communities, resulting in decreased amounts of carbon respired as CO_2 and CH_4 (Manzoni et al., 2012). Thus, microbial adaptation, increased nutrient availability and increased primary production may prevent these ecosystems from becoming net carbon sources, mitigating the potential positive climate feedback from these soils.

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Appendix

Figures

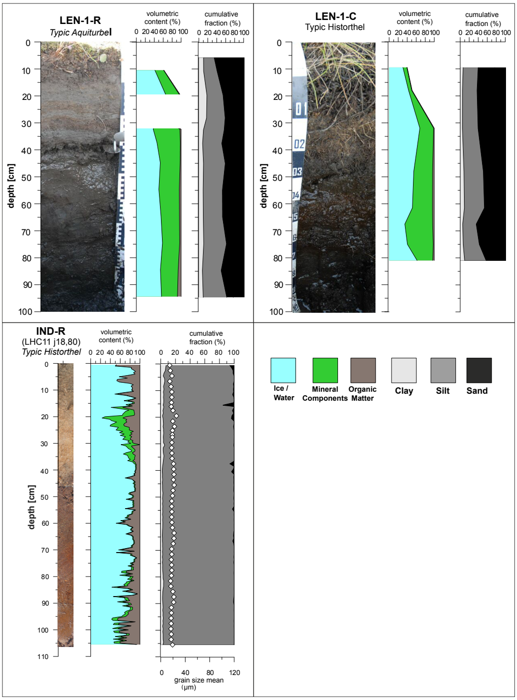

Figure A.1 Cryolithological data of soil cores from the Lena River Delta and the Indigirka Lowlands. Volumetric contents of water and ice, mineral components and organic matter are shown. Furthermore, grain size distribution is shown as the cumulative fractions of clay, silt and sand on the total amount of mineral components is presented Soil types are indicated, according to the US soil classification (Soil Survey Staff, 2014).

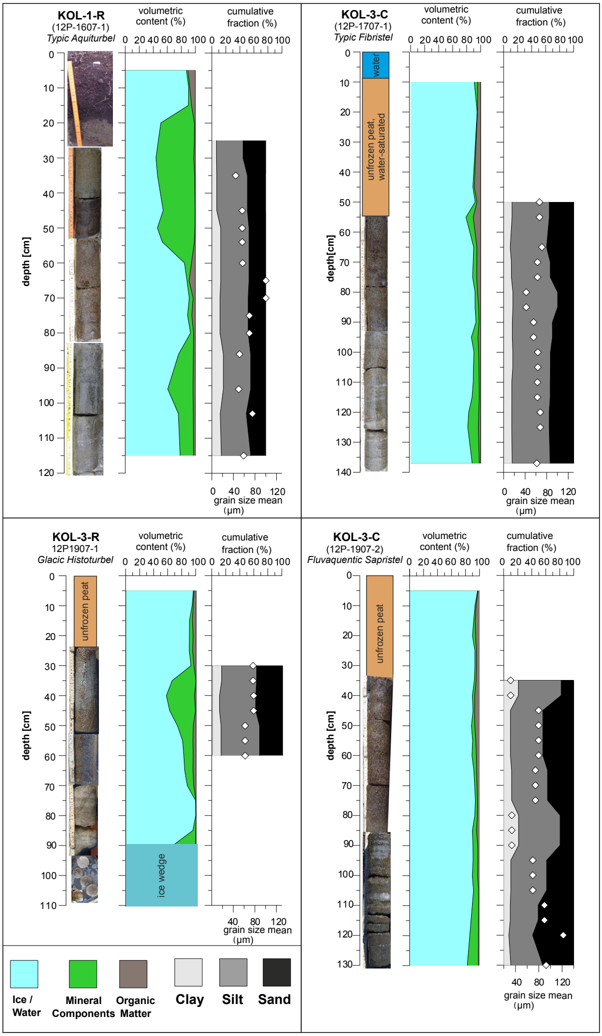

Figure A.2 Cryolithological data of soil cores from the Kolyma River Delta. Volumetric contents of water and ice, mineral components and organic matter are shown. Furthermore, grain size distribution is shown as the cumulative fractions of clay, silt and sand on the total amount of mineral components is presented Soil types are indicated, according to the US soil classification (Soil Survey Staff, 2014).

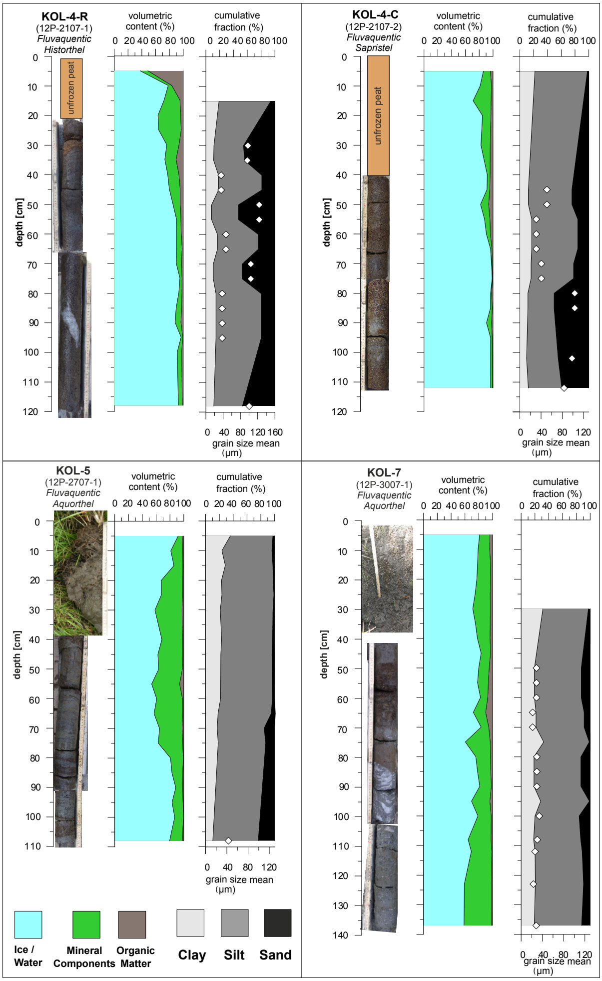

Figure A.3 Cryolithological data of soil cores from the Kolyma River Delta. Volumetric contents of water and ice, mineral components and organic matter are shown. Furthermore, grain size distribution is shown as the cumulative fractions of clay, silt and sand on the total amount of mineral components is presented Soil types are indicated, according to the US soil classification (Soil Survey Staff, 2014).

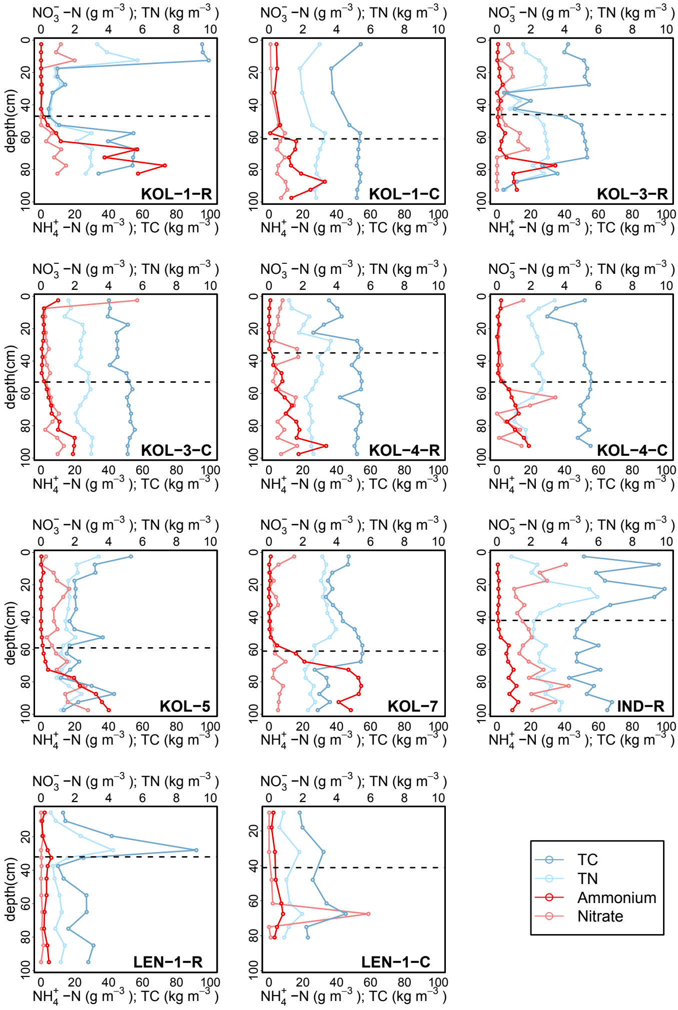

Figure A.4 Pools of total carbon (TC), total nitrogen (TN), ammonium and nitrate in eleven soil cores from the three study areas. The permafrost table of each soil core is indicated by a dotted line.

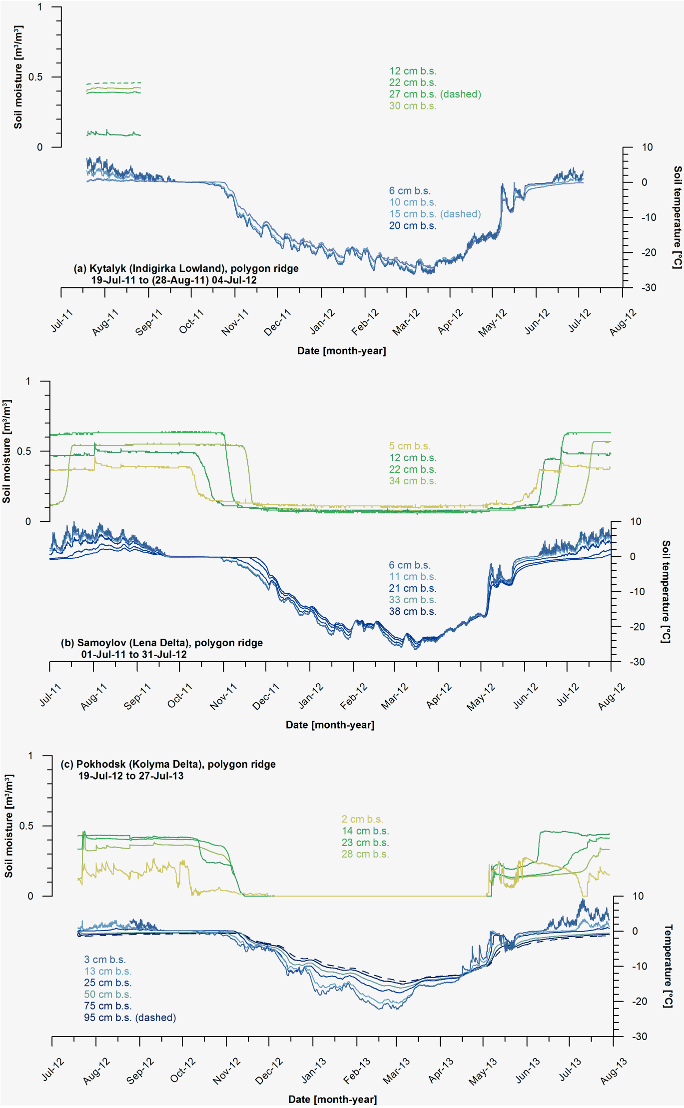

Figure A.5 Monitoring of soil temperatures and soil moisture of different soils in the Indigirka Lowlands (a), in the Lena River Delta (b), and in the Kolyma River Delta (c). Soil moisture for different depths is shown in green colors, soil temperatures for the different depths is shown in blue colors.

Tables

Table A.1 Comparison of the soils in the studied polygon (LHC) and the surrounding study area (KYT) in the Indigirka Lowlands. Mean values and standard deviations of the soil parameters in the different soil horizons are shown. Differences between the studied polygon and the surrounding area were investigated by Welch´s two sample t-tests. The p-values of these analyses are reported and significant differences are indicated by bold numbers

	Carbon$_{tot}$ (mol kg^{-1})			Nitrogen$_{tot}$ (mol kg^{-1})			Phosphorus$_{tot}$ (mmol kg^{-1})			Potassium$_{tot}$ (mmol kg^{-1})		
	KYT	**LHC**	***p***	**KYT**	**LHC**	***p***	**KYT**	**LHC**	***p***	**KYT**	**LHC**	***p***
Oi												
Center	35.7 ± 2.7	37.4 ± 1.0	*>0.05*	**1.35 ± 0.23**	**1.15 ± 0.20**	*>0.05*	48.3 ± 34.0	34.3 ± 7.8	*>0.05*	**36.9 ± 16.4**	**22.5 ± 7.9**	***<0.01***
Ridge	36.8 ± 3.5	38.2 ± 3.0	*>0.05*	1.06 ± 0.30	1.16 ± 0.39	*>0.05*	35.7 ± 10.6	37.4 ± 13.4	*>0.05*	41.3 ± 13.7	75.5 ± 87.7	*0.05*
Oe												
Center	32.9 ± 4.0	28.6 ± 7.9	*>0.05*	1.32 ± 0.48	1.30 ± 0.29	***<0.05***	36.4 ± 14.0	39.6 ± 6.6	*>0.05*	35.2 ± 13.1	41.1 ± 17.8	*>0.05*
Ridge	30.7 ± 4.1	31.5 ± 5.5	*>0.05*	1.29 ± 0.30	1.43 ± 0.17	*>0.05*	39.1 ± 8.5	38.9 ± 9.6	*>0.05*	39.0 ± 11.0	32.7 ± 6.6	*0.05*
Oa												
Center	26.6 ± 8.5	26.5 ± 5.0	*>0.05*	1.26 ± 0.38	1.29 ± 0.27	*>0.05*	34.8 ± 8.1	36.4 ± 6.9	*>0.05*	**69.3 ± 28.5**	**46.4 ± 14.2**	***<0.05***
Ridge	**30.7 ± 3.9**	**27.0 ± 2.1**	***<0.05***	1.38 ± 0.30	1.51 ± 0.14	*>0.05*	42.9 ± 9.2	35.7 ± 6.7	*>0.05*	39.5 ± 12.0	43.1 ± 8.1	*0.05*

	NH_4^+-N (mmol kg^{-1})			NO_3^--N(mmol kg^{-1})			PO_4^{3-}-P (mmol kg^{-1})			K^+ (mmol kg^{-1})		
	KYT	**LHC**	***p***	**KYT**	**LHC**	***p***	**KYT**	**LHC**	***p***	**KYT**	**LHC**	***p***
Oi												
Center	1.0 ± 0.6	0.5 ± 0.4	*>0.05*	0.4 ± 0.4	0.3 ± 0.1	*>0.05*	0.8 ± 0.5	1.0 ± 0.8	*>0.05*	8.4 ± 6.0	9.2 ± 5.9	*>0.05*
Ridge	1.3 ± 1.1	0.4 ± 0.3	*>0.05*	0.9 ± 1.0	0.5 ± 0.3	*>0.05*	3.2 ± 2.3	2.5 ± 2.2	*>0.05*	16.8 ± 5.8	20.4 ± 9.1	*>0.05*
Oe												
Center	1.1 ± 0.4	1.5 ± 1.4	*>0.05*	0.5 ± 0.2	0.7 ± 0.5	*>0.05*	0.4 ± 0.3	0.3 ± 0.2	*>0.05*	4.2 ± 3.5	2.6 ± 1.7	*>0.05*
Ridge	0.7 ± 0.5	0.4 ± 0.3	*>0.05*	0.8 ± 0.2	0.6 ± 0.2	*>0.05*	0.5 ± 0.3	0.7 ± 0.8	*>0.05*	3.4 ± 2.1	5.2 ± 5.1	*>0.05*
Oa												
Center	1.3 ± 0.5	0.9 ± 0.8	*>0.05*	1.0 ± 0.5	0.7 ± 0.4	*>0.05*	0.4 ± 0.3	0.2 ± 0.1	*>0.05*	1.8 ± 1.7	0.7 ± 0.4	*>0.05*
Ridge	0.5 ± 0.5	0.5 ± 0.5	*>0.05*	0.7 ± 0.3	0.7 ± 0.4	*>0.05*	0.6 ± 0.9	0.3 ± 0.2	*>0.05*	**4.3 ± 3.3**	**1.5 ± 0.9**	

Table A.2 Summary of the input data for the active layer thickness (ALT) modeling. Volumetric contents of mineral soil, water and ice, organic matter and air-filled pore space are shown for each soil core and the deeper underground of the respective study area. Furthermore, each soil horizon is characterized by a short description.

lower boundary (m)	**mineral soil (Vol.%)**	**water / ice (Vol.%)**	**organic matter (Vol. %)**	**pore space (Vol.%)**	**Further information on soil texture / composition**
KOL-1-R (12-P-1607-1), Kolyma River Delta / polygon ridge, ALT 0.37 m					
0.15	2	64.2	5.8	92.2	vegetation cover, peat, medium decomposed, brown, unfrozen
0.35	50.5	45.9	1.4	48.1	peaty silty fine-sand, brownish, unfrozen
0.54	48.2	50.9	0.9	50.9	silty fine-sand, frozen
0.8	5.8	89.1	5.1	89.1	grey silty fine sand, horizontal peat layers, frozen
1.15	24.4	72.7	2.9	72.7	grey silty fine sand, horizontal peat layers, frozen
KOL-1-C (12-P-1707-1), Kolyma River Delta / polygon center, ALT 0.45 m					
0.45	2.8	91.6	5.7	91.6	peat, water- saturated, brown, unfrozen
1.1	6.5	89.4	4.1	89.4	peaty silty fine-sand, frozen
1.37	12.8	85	2.1	85	silty fine-sand, frozen
KOL-3-R (12-P-1907-1), Kolyma River Delta / polygon ridge, ALT 0.3 m					
0.3	3.5	92.2	4.3	92.2	peat, vegetation, unfrozen
0.45	36.9	61.7	1.3	61.7	peaty silty fine-sand, frozen
0.7	14.4	81.4	4.3	81.4	peaty silty fine-sand, frozen
0.85	1.8	98	0.3	98	ice lens (band)
0.95	39.1	60.1	0.8	60.1	silty fine-sand
3	0	100	0	100	ice wedge
KOL-3-C (12-P-1907-2), Kolyma River Delta / polygon center, ALT 0.41 m					
0.05	0.65	97.27	2.08	97.27	vegetation cover, water saturated
0.35	2.4	88.6	4.9	92.8	peat, unfrozen
0.85	4.1	91.1	4.9	91.1	peat, frozen
1.05	7	90.6	2.2	90.9	peaty silty fine-sand
1.3	15.8	82.5	1.7	82.5	silty fine-sand
KOL-4-R (12-P-2107-1, Kolyma River Delta / polygon ridge, ALT 0.25 m					
0.1	5.5	39.1	23	71.5	peat not compacted, weakly decomposed, grey-brown
0.25	24	54.2	3.2	72.9	peat, brown
0.45	16.5	76.6	6.9	76.6	peaty sand, light-brown
0.7	7.4	83.9	2.9	89.7	peaty silty fine-sand, alternate bedded
1.18	5.5	92.5	2	92.5	silty peat, brown
KOL-4-C (12-P-2107-2), Kolyma River Delta / polygon center, ALT 0.43 m					
0.3	15.6	81.2	3.2	81.2	peat weakly decomposed, unfrozen
0.6	6.7	88.6	4.7	88.6	peat weakly decomposed,
0.8	1.2	97.3	1.4	97.3	silty peat, brownish grey

Continued on next page

ALT model input data - ***continued from previous page***

lower boundary (m)	**mineral soil (Vol.%)**	**water / ice (Vol.%)**	**organic matter (Vol. %)**	**pore space (Vol.%)**	**Further information on soil texture / composition**
1.12	3.7	95	1.4	95	silty peat, brownish grey
KOL-5 (12-P-2707-1), Kolyma River Delta / Floodplain / lowermost level, no polygon, ALT 0.45 m					
0.15	11.8	86.3	1.9	86.3	peaty clayish silty fine-sand, unfrozen, water saturated
0.75	35.2	62.4	2.4	62.4	peaty clayish silty fine-sand
1.08	15.1	83.6	1.4	83.6	alternate bedding of gray clayish silt and plant detritus layers
KOL-7 (12-P-3007-1), Kolyma River Delta / Lake shore near Pokhodsk / no polygon, ALT 0.45 m					
0.4	19.7	76.9	3.4	76.9	peaty silty sand, brown, unfrozen
0.7	14	80	6.1	80	peaty silty sand, brown
1.37	28.1	69.6	2.4	69.6	silty sand, gray, plant fragments, peat inclusions
deeper underground, Kolyma River Delta					
89	50	25	25	25	flood plain/deltaic deposits (Holocene)
399	48	10	2	40	Tertiary sands and gravels
500	99	1	0	0	bedrock
				-8	permafrost temperature (°C)
IND-R (LHC 11 j18,80), Indigirka Lowlands / Alas /polygon ridge, ALT 0.20 m					
0.16	1	75.4	23.6	75.4	peat, unfrozen
0.36	18.8	63.2	18	63.2	silty peat, frozen
105.5	4.2	76	19.9	76	peat, frozen
deeper underground, Indigirka Lowlands					
5	50	25	25	25	flood plain / thermokarst deposits
15	31.4	67.3	1.2	67.3	Yedoma
65	48	10	2	40	Tertiary sands and gravels
500	99	1	0	1	bedrock
				-10	permafrost temperature (°C)
LEN-1-R, Samoylov Island, Lena River Delta, polygon ridge, ALT 0.26 m					
0.3	25	53.4	1.2	73.9	
0.4	55.9	41.9	2.2	41.9	
1	40.8	54.6	4.6	54.6	
LEN-1-C, Samoylov Island, Lena River Delta, polygon center, ALT 0.23 m					
0.23	7.8	36.9	0.9	91.3	
0.81	45.1	48.2	3	48.2	
deeper underground, Lena River Delta					
15	30	60	10	60	deltaic deposits (Holocene)
1000	48	10	2	40	sandy to silty river deposits.
				-9	permafrost temperature (°C)

Table A.3 Effects of incubation at 5 °C and 15 °C on the elemental composition of samples of three horizons from the soil profile IND-3.4 in the Indigirka Lowlands. All soil properties are shown for the three groups (*Control*, *5 °C*, *15 °C*) and the three soil horizons (Oi, Oe, Bg) are shown. Test statistics for each ANOVA are indicated by the respective p-value. Detected differences are indicated by bold numbers; significantly differing groups are marked by superscripted letters.

	Oi				Oe			
	Control	5 °C	15 °C	Statistics	Control	5 °C	15 °C	Statistics
Water content (vol.%)	76.5 ± 1.6	74.3 ± 1.8	78.8 ± 4.2	*$p>0.01$*	91.3 ± 1.0	87.8 ± 3.6	90.6 ± 0.9	*$p>0.01$*
Carbon (mg/cm^3)	74.5 ± 7.2	78.3 ± 7.4	73.7 ± 13.1	*$p>0.01$*	39.7 ± 0.3	42.5 ± 15.3	34.9 ± 2.5	*$p>0.01$*
Nitrogen (mg/cm^3)	4.3 ± 0.8	4.5 ± 0.5	4.2 ± 1.2	*$p>0.01$*	0.7 ± 0.1	1.0 ± 0.4	0.9 ± 0.1	*$p>0.01$*
DOC (μg/cm^3)	186.0 ± 30.7	145.2 ± 33.0	143.5 ± 37.1	*$p>0.01$*	**158.8 ± 24.5**^{a}	**69.1 ± 11.6**^{b}	**79.0 ± 31.8**^{b}	*$p<0.01$*
DON (μg/cm^3)	22.8 ± 3.2	16.6 ± 4.0	17.0 ± 3.2	*$p>0.01$*	12.3 ± 1.9	3.1 ± 1.3	5.8 ± 6.3	*$p>0.01$*
C$_{mic}$ (mg/cm^3)	**0.9 ± 0.1**^{c}	**1.9 ± 0.1**^{a}	**1.6 ± 0.0**^{b}	*$p<0.001$*	**0.5 ± 0.0**^{c}	**1.4 ± 0.1**^{a}	**1.1 ± 0.1**^{b}	*$p<0.001$*
N$_{mic}$ (μg/cm^3)	**21.3 ± 3.8**^{b}	**33.4 ± 5.1**^{a}	**41.9 ± 3.8**^{a}	*$p<0.01$*	28.4 ± 2.6	30.5 ± 4.8	23.8 ± 11.0	*$p>0.01$*
NH_4^+-N (μg/cm^3)	0.5 ± 0.1	0.2 ± 0.0	0.4 ± 0.1	*$p>0.01$*	0.5 ± 0.3	0.4 ± 0.2	0.2 ± 0.1	*$p>0.01$*
NO_3^--N (μg/cm^3)	1.0 ± 0.1	0.3 ± 0.2	0.1 ± 0.1	*$p>0.01$*	0 ± 0	0.1 ± 0.1	0.1 ± 0.1	*$p>0.01$*
	Bg							
	Control	5 °C	15 °C	Statistics				
Water content (vol.%)	23.9 ± 1.3	24.5 ± 1.1	23.8 ± 0.7	*$p>0.01$*				
Carbon (mg/cm^3)	61.2 ± 1.3	62.6 ± 1.1	63.1 ± 2.0	*$p>0.01$*				
Nitrogen (mg/cm^3)	3.7 ± 0.2	3.8 ± 0.1	4.0 ± 0.1	*$p>0.01$*				
DOC (μg/cm^3)	**117.7 ± 7.2**^{a}	**80.9 ± 8.7**^{b}	**74.0 ± 6.6**^{b}	*$p<0.001$*				
DON (μg/cm^3)	**63.3 ± 5.2**^{a}	**43.3 ± 2.1**^{b}	**46.4 ± 2.9**^{b}	*$p<0.001$*				
C$_{mic}$ (mg/cm^3)	**0.5 ± 0.0**^{b}	**0.9 ± 0.1**^{a}	**0.6 ± 0.1**^{a}	*$p<0.001$*				
N$_{mic}$ (μg/cm^3)	4.6 ± 5.8	13.7 ± 5.6	17.0 ± 5.9	*$p>0.01$*				
NH_4^+-N (μg/cm^3)	**1.5 ± 0.4**^{b}	**19.4 ± 2.0**^{a}	**22.7 ± 3.6**^{a}	*$p<0.001$*				
NO_3^--N (μg/cm^3)	0 ± 0	0.3 ± 0.4	0 ± 0	*$p>0.01$*				