Microbial Properties and Habitats of Permafrost Soils on Taimyr Peninsula, Central Siberia

Mikrobiologische Eigenschaften und Habitate in Permafrostböden der Taimyr Halbinsel, Mittelsibirien

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In memoriam

Gerardus Wilhelmus Bosman
(1920-1995)

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Die vorliegende Arbeit ist die inhaltlich unveränderte Fassung einer Dissertation, die im Dezember 1998 der Mathematisch-Naturwissenschaftlichen Fakultät der Christian-Albrechts-Universität zu Kiel vorgelegt wurde.

Contents

Summary and conclusions

The poetry of earth is ceasing never.
John Keats

Within the scope of a joint Russian-German research project, pedological and botanical studies have been carried out in order to investigate carbon fluxes in tundra soils of Central Siberia. Turnover of soil organic matter, CO_2 and CH_4 efflux represent biologically mediated processes, in which the soil microbiota plays the major part. The goal of this study was the description of the microbial pool of the decomposer cycle as well as its spatial variability.
For this study, field procedures were carried out on Taimyr Peninsula, Central Siberia, during July and August 1995 and 1996. The experimental site at Lake Labaz (72°N, 100°E) is situated within the belt of the 'Southern Arctic Tundra'. The other site at Lake Levinson-Lessing (74.5°N, 98.5°E) is characterized by the vegetation of the 'Typical Arctic Tundra'. During the 1995 expedition at Lake Labaz, field procedures were carried out by the IfB (Hamburg) and the IPÖ (Kiel). Three tundra soils and two different types of brown earth had been sampled. In the following year at Lake Levinson-Lessing, soils were mapped by the author in co-operation with the IfB (Hamburg). The soil sampling technique by the author accounted for variability of soil-patterned ground and vegetation complexes and was further designed to capture presumed successional stages. Thus, three sites in a polygonal tundra, two at solifluction slopes and another two in fellfields were selected. All soil profiles were sampled at all depths of the active layer.

A modern technique of direct microscopy (epifluorescence microscopy equipped with computer based image analysis) was applied to determine fungal hyphal length and biovolume, of which fungal biomass was calculated (BLOEM et al., 1995). Quantification and characterisation of the microbial pool was supplemented by bacteriological data by PD Dr. M. Bölter (IPÖ, Kiel). Viable and active micro-organisms were investigated by activity dependent methods such as adenosine triphosphate (HOLM-HANSEN & BOOTH, 1966; GRAF, 1977; VOSJAN et al., 1987) and microcalorimetry (SPARLING, 1983). Basal and substrate-induced heat output provided further information on the microbial community structure, substrate requirements and inhibition (RAUBUCH & BEESE, 1995). Investigation of structural and chemical soil properties was aimed at further characterisation of microbial habitats.

The results showed high variability of microbial biomass and activity between sites. Differences were mainly restricted to topsoil horizons as the microbiota was. Microbial biomass generally decreased with depth. This decrease was more prominent for fungi than for bacteria. The latter also decreased with depth, but occurred throughout the soil profile and showed a relative increase above the permafrost table. The soils generally showed high fungi to bacteria ratios showing that the microbiota was clearly dominated by fungi. Image analysis had shown that bacterial biomass values were rather low because of very small mean cell volumes. Yet, in comparison to other arctic soils values of fungal hyphal length were also within the lower range. At a depth of 10 to 20 centimetres, profiles generally showed strong increases of fungi (and bacteria) due to a rhizosphere effect and soil moisture conditions.

Vegetation cover was found to account for differences in microbial properties between sites. In the soils of solifluction slopes and in fellfields, the microbiota reflected the presence or absence of vegetation. Whereas bacteria predominated in unvegetated soils, fungi were largely restricted to vegetated sites indicating their importance in soil organic matter decomposition. Bacteria were further inhibited by the presence of lichens in the vegetation cover. Soil moisture conditions accounted for further differences in microbial properties. In wet micro-sites, bacteria were generally more competitive when compared to fungi. The latter prevailed in the adjacent drier micro-sites. Although fungi are aerobic micro-organisms, they also showed considerable biomass values in wet micro-sites.

In accordance with low microbial biomass values, contents of adenosine triphosphate (ATP) in the soils were generally low compared to other biomes. It was further hypothesised that protista may be an important component in tundra soil ecology as indicated by extremely high values at the respective sites. Interference was also suggested from nutrient status and lichens. Lowest ATP to microbial biomass ratios were found in the rhizosphere reflecting lower fungal activity. The ATP to substrate-induced heat output (SIQ) successfully distinguished between viable micro-organisms and shifts in microbial community composition.

In accordance with the other microbial properties, values of heat output were within the lower range of data from soils of temperate regions. Within profiles, heat output generally decreased non-linearly with depth, which was more pronounced in unvegetated inorganic soils. In this study, it was concluded that substrate-induced methods were inappropriate to estimate micro-

bial biomass in tundra soils. This resulted in a misjudgement of the microbiota of the uppermost topsoil horizons and in anaerobic subsoils and showed different substrate requirements. In addition, the ratio of basal heat output to substrate-induced heat output (i.e., caloric quotient) further elucidated successional stages of the microbiota as well as exposure to environmental stress. Yet, the caloric quotient failed to distinguish between the two in the polygonal tundra soils and in transitionary horizons between top- and subsoil (i.e., 'frontier'). For subsoil horizons, it was concluded that the caloric quotient was not applicable.

Statistical analysis of pedological parameters and microbial properties allowed a generalised view of microbial habitats in tundra soils. Respectively, wet and dry topsoils, 'frontier' horizons and the subsoil were differentiated. Wet topsoils were characterized as aquatic habitats with a sponge-like structure of the peat, which allows organisms to float freely. Compared to their drier counterpart, wet topsoils showed higher contents of carbon and nitrogen, higher C/N-ratios and less acid soil pH. A significant proportion of the energy flux appeared to pass through protista and bacteria ('microbial loop'). Decomposers such as fungi occurred in wet topsoils but were restricted in activity due to water saturation and low temperatures. Dry topsoils showed stratification of both edaphic conditions and microbiological properties. Insulating organic mats create a stable environment with respect to temperature and moisture, in which highest active microbial biomass was determined. The latter showed high affinity to carbon and nitrogen contents indicating heterotrophic micro-organisms. The data further suggested microbial succession during soil organic matter decomposition. In transition to the subsoil at wet and dry micro-sites, microbial properties showed strong gradients leading to a conception of 'frontier' horizons. These gradients were explained by a combined effect of a redox potential discontinuity (RPD) and the rhizosphere. 'Frontier' horizons were marked by the interface of iron oxidation bands at the upper boundary and underlying reducing conditions. On the one hand, redox potentials temporally allowed aerobic respiration, methane and iron oxidation to occur. On the other hand, sulphate reduction and methanogenesis had also been determined in the namely horizons. Significant greater values of microbial biomass were attributed to a rhizosphere effect. Yet, this was accompanied with inhibition of microbial activity. High caloric quotients failed to distinguish between environmental stress and a changes in the microbial community structure. Subsoil horizons were characterized by anaerobic conditions and distinct increases in soil organic matter contents above the permafrost. The microbial community was predominated by anaerobic heterotrophic bacteria. It has been discussed that the re-

spective microbial habitats represent a generalised view. In the field, they are likely to vary temporally and spatially and may as well interlock.

In a changing climate, microbial communities showed a high potential for increasing mineralisation rates at a short-term scale. Evaluation of the long-term response, however, bears more uncertainties mainly because of the incalculable response of the vegetation canopy. Yet at present, the Taimyr Peninsula appears to be relatively stable to climate change.

Zusammenfassung und Schlußfolgerungen

Im Rahmen eines Russisch-Deutschen Verbundprojektes wurden bodenkundliche und botanische Untersuchungen zu den Kohlenstoffflüssen in Tundraböden Mittelsibiriens durchgeführt. Umsatz von organischer Bodensubstanz, CO_2- und CH_4-Austräge stellen hierbei biologisch induzierte Prozesse dar, in denen die bodenmikrobiellen Gemeinschaften Hauptmotor sind. Ziel dieser Arbeit war es, sowohl die Gesamtheit der an der Mineralisation beteiligten Mikroorganismen zu charakterisieren als auch ihre räumliche Variabilität zu beschreiben.
Die Geländearbeiten für diese Arbeit wurden im Juli und August 1995 und 1996 auf der Taimyr Halbinsel, Mittelsibirien durchgeführt. Das Untersuchungsgebiet am Labaz See (72°N, 100°O) befindet sich in der Zone der Südlichen Arktischen Tundra. Das andere Untersuchungsgebiet am Levinson-Lessing See ist von Typischer Arktischer Tundrenvegetation geprägt.

Am Labaz See wurden während der 1995er Expedition die Geländearbeiten vom IfB (Hamburg) und dem IPÖ (Kiel) durchgeführt. Drei Tundrastandorte und zwei verschiedene Braunerden waren beprobt worden. Im Folgejahr am Levinson-Lessing See, wurde die Bodenaufnahme von der Autorin in Zusammenarbeit mit dem IfB (Hamburg) durchgeführt. Die Bodenprobennahme orientierte sich an Boden-Frostmuster-Vegetationskomplexen und war darüber hinaus so anlegt, eventuelle Sukzessionsstadien zu erfassen. So wurden drei Standorte in der Polygontundra, zwei an den Solifluktionshängen und zwei weitere in den Frostschuttflächen ausgewählt. Sämtliche Bodenprofile wurden in gänzlicher Tiefe der sommerlichen Auftauschicht beprobt.

Eine moderne Methode der direkten Mikroskopie (Epifluoreszenzmikroskopie mit EDV gestützter Bildauswertung) wurde zur Bestimmung von Pilzhyphenlängen und -biovolumina eingesetzt. Die Pilzbiomasse wurde aus den entsprechenden Biovolumina berechnet (BLOEM et al., 1995). Die Quantifizierung und Charakterisierung der Gesamtheit der Mikroorganismen wurden durch Bakterienkennwerte von PD Dr. M. Bölter ergänzt. Zur Untersuchung der lebenden und aktiven Mikroorganismen wurden aktivitätsabhängige Methoden wie die Bestimmung des ATP-Gehalts (HOLM-HANSEN & BOOTH, 1966; GRAF, 1977; VOSJAN et al., 1987) und die Mikrokalorimetrie (SPARLING, 1983) eingesetzt. Die basale und substratinduzierte Wärmeproduktion geben darüber hinaus Auskunft über die Struktur der mikrobiellen Gemeinschaft, Substratansprüche und eine eventuelle Hemmung ihrer Aktivität

(RAUBUCH & BEESE, 1995). Der weiteren Beschreibung der mikrobiellen Habitate diente die Untersuchung von strukturellen und chemischen Bodeneigenschaften.

Die Ergebnisse zeigten eine große Variabilität in mikrobieller Biomasse und Aktivität zwischen einzelnen Standorten. Unterschiede waren in der Hauptsache ebenso wie die mikrobielle Biomasse auf den Oberboden beschränkt. Im allgemeinen nahm die mikrobielle Biomasse mit zunehmender Tiefe ab. Diese Abnahme war deutlicher bei den Pilzen als bei den Bakterien. Letztere waren für das gesamte Profil konstatierbar, wiesen jedoch einen relativen Anstieg oberhalb der Permafrosttafel auf. Die Böden zeigten gemeinhin hohe Pilz-Bakterien-Verhältnisse, was aufzeigt, daß die mikrobiellen Gemeinschaften deutlich von Pilzen dominiert wurden. Die bakterielle Biomasse hatte dagegen eher niedrige Werte aufgewiesen, was durch kleine Zellvolumina erklärt worden war. Im Vergleich mit anderen arktischen Böden wiesen die Pilzhyphenlängen jedoch ebenfalls niedrige Werte auf. Eine starke Zunahme an pilzlichlicher (und bakterieller) Biomasse wurde in einer Tiefe von 10 bis 20 cm aufgrund eines Rhizosphäreneffektes und der Bodenwasserverhältnisse festgestellt.

Die Vegetationsbedeckung stellt eine wesentliche Steuergröße für Unterschiede in den mikrobiellen Eigenschaften dar. In den Böden der Solifluktionshänge und Schuttflächen spiegelten die mikrobiellen Gemeinschaften An- oder Abwesenheit von Vegetation wider. Während Bakterien hierbei an unbewachsenen Standorten dominierten, waren Pilze zumeist auf bewachsene Standorte beschränkt, was deren Bedeutung in der Mineralisation organischer Bodensubstanz aufzeigt. Durch Flechtenbewuchs wurden Bakterien limitiert. Eine weitere Steuergröße stellen die Bodenwasserverhältnisse dar. An feuchten Kleinstandorten zeigten sich Bakterien im Vergleich zu Pilzen konkurrenzfähiger. Letztere herrschten in den benachbarten trockeneren Kleinstandorten vor. Trotz aerober Lebensweise erreichten Pilze an feuchten Kleinstandorten beachtliche Biomassewerte.

Im Einklang mit den niedrigen Werten an mikrobieller Biomasse, waren die Adenosintriphosphat (ATP)-Gehalte im Vergleich zu anderen Biomen ebenfalls gering. Des weiteren wurde die Hypothese aufgestellt, daß Protisten einen weiteren wichtigen Bestandteil in der Ökologie von Tundraböden darstellen könnten, wie äußerst hohe ATP-Gehalte an den entsprechenden Standorten aufzeigten. Der Nährstoffgehalt und Flechtenbewuchs stellten möglicherweise weitere Einflußgrößen dar. Die Rhizosphere wies die engsten Verhältnisse von ATP zu mikrobieller Biomasse auf, welches eine weniger aktive Pilzflora widerspiegelt. Das Verhältnis

von ATP-Gehalt zur substrat-induzierten Wärmeproduktion (*SIQ*) unterschied erfolgreich zwischen lebenden Mikroorganismen und Veränderungen in der Gemeinschaftzusammensetzung.

Entsprechend der übrigen mikrobiellen Eigenschaften, lagen die Werte der Wärmeproduktion im unteren Bereich derjenigen für gemäßigte Breiten. Innerhalb des Profils nahm die Wärmeproduktion gemeinhin nicht-linear mit der Tiefe ab, dies stärker in unbewachsenen mineralischen Böden. Ein Ergebnis dieser Arbeit ist es, daß substrate-induzierte Methoden zur Abschätzung mikrobieller Biomasse für Tundraböden ungeeignet sind. Dies führt in den obersten Zentimetern des Oberbodens sowie im anaeroben Unterboden zu einer Fehleinschätzung der mikrobielle Gemeinschaften und zeigte andere Substratansprüche auf. Das Verhältnis von basaler und substrat-induzierter Wärmeproduktion (d.h. der kalorische Quotient) fand eine weitere Anwendung in der Beschreibung von Sukzessionsstadien und physiologischem Streß. Die jeweilige Differenzierung war jedoch im Falle der Polygontundra sowie in den Übergangshorizonten zwischen Ober- und Unterboden ('Frontier') nicht möglich. Im anaeroben Unterboden erwies der kalorische Quotient mangelnde Anwendbarkeit.

Die statistische Analyse der pedologischen Parameter und mikrobiellen Eigenschaften ermöglichte eine generalisierte Darstellung von mikrobiellen Habitaten in Tundraböden. Entsprechend wurden jeweils staunasse und trockene Oberböden, 'Frontier'-Horizonte und Unterböden differenziert. Staunasse Oberböden wurden als aquatisches Habitat mit einer schwammartigen Struktur der Torfauflage beschrieben, das Organismen freies Schwimmen ermöglicht. Im Gegensatz zu den entsprechenden trockenen Oberböden, waren Kohlenstoff- und Stickstoffgehalte höher, C/N-Verhältnisse weiter und pH-Werte weniger sauer. Ein signifikanter Anteil des Energieflusses passiert möglicherweise Protisten und Bakterien ('Microbial Loop'). Zersetzer wie z.B. Pilze wurden in geringerer Biomasse festgestellt, deren Aktivität durch Wassersättigung und niedrige Temperaturen gehemmt wurde. Trockene Oberböden wiesen eine Stratifizierung sowohl der edaphischen als auch mikrobiellen Eigenschaften auf. Die isolierende Wirkung der organischen Auflagen schafft ein temperatur- und feuchtestabiles Habitat, für das Höchstwerte an aktiver mikrobieller Biomasse ermittelt wurden. Diese wies eine hohe Affinität zu den Kohlenstoff- und Stickstoffgehalten auf, was ihre heterotrophe Natur aufzeigt. Darüber hinaus ließ die Datengrundlage auf mikrobielle Sukzession während der Mineralisierung von organischer Bodensubstanz schließen. Sowohl an staunassen als auch an trockenen Kleinstandorten wiesen die mikrobiellen Parameter im Übergang zum Unterbo-

den starke Gradienten auf, welches zur Auffassung von 'Frontier'-Horizonten führte. Diese Gradienten wurden mit der gekoppelten Wirkung einer Redoxsprungschicht (RPD) und der Rhizosphäre erklärt. 'Frontier'-Horizonte stellen die Grenzschicht zwischen Eisenoxidbändern an der oberen Grenze und den unmittelbar darunter befindlichen anaerob geprägten Horizonten dar. Temporär sind einerseits aerobe Atmung, Methan- und Eisenoxidation möglich sowie andererseits temporär auch Sulfatreduktion und Methanbildung nachgewiesen worden waren. Signifikant höhere Werte mikrobieller Biomasse resultierten aus einem Rhizosphäreneffekt, der jedoch von geringer mikrobieller Aktivität begleitet war. Hohe kalorische Quotienten konnten hierbei jedoch nicht zwischen physiologischem Streß oder Veränderungen in der Gemeinschaftszusammensetzung unterscheiden. Der Unterboden war durch anaerobe Verhältnisse und einen deutlichen Anstieg an organischer Bodensubstanz über der Permafrosttafel gekennzeichnet. Die mikrobiellen Gemeinschaften wurden hier in der Regel von anaeroben heterotrophen Bakterien dominiert. In der Diskussion wurde darauf hingewiesen, daß es sich bei den namentlichen Habitaten lediglich um eine generalisierte Darstellung handelt. Unter natürlichen Bedingungen variieren diese in zeitlicher und räumlicher Hinsicht und können sich darüber hinaus überlagern.

Im Hinblick auf globale Klimaveränderungen, weisen die mikrobiellen Gemeinschaften kurzfristig ein hohes Potential für eine erhöhte Umsetzung an organischer Bodensubstanz auf. Eine Einschätzung des langfristigen Wandels birgt hohe Unsicherheiten, da die Resonanz der Vegetation schwer zu ermessen ist. Dennoch gilt die Taimyr Halbinsel gegenwärtig als verhältnismäßig stabil gegenüber globalen Klimaveränderungen.

Abbreviations

a.s.l.	altitude **a**bove **s**ea **l**evel
AEC	**a**denylate **e**nergy **c**harge is the adenine nucleotide pool made up of adenosine triphosphate, adenosine diphosphate and adenosine monophosphate and characterizes the metabolic status
AMP	adenosine monophosphate
AO	acridine orange is a fluorescent stain and used for epifluorescence microscopy
ATP	adenosine triphosphate
BP	before present
cf.	confer (compare); used for quotations
CO_2	chemical sum formula of carbon dioxide
d.wt.	dry weight
DIN	German Institute for Standardization (Deutsches Institut für Normung)
e.g.	example given
EFM	**Epi**fluorescence **m**icroscopy
FDA	**F**luorescein **di**acetate is enzymatically hydrolyzed by metabolically active fungi
HT	hummock tundra
i.e.	id est (Latin: that is to say)
ibid.	ibidem (Latin: in the same place); used for quotations
IfB	Dpt. of Soil Science, University of Hamburg, Germany
IPÖ	Institute for Polar Ecology, University of Kiel, Germany
Mg	chemical symbol of **mag**nesium
NH_4^+	chemical sum formula of ammonia
O	chemical symbol of **o**xygen
P	chemical symbol of **p**hosphorus
PC	**p**oly**c**arbonate; the material of membrane filters used for microscopy
PT	polygonal tundra
Q_{10}	temperature quotient
RPD	redox potential discontinuity

RLU	**r**elative light **u**nit of a bioluminometer is the integrated light emission over a period of 10s for estimation of ATP
S.T.	Soil Taxonomy, American soil classification by the United States Department of Agriculture (SOIL SURVEY STAFF, 1994, 1998)
suppl.	supplement, used for quotations
TT	tussock tundra
w.w.	wet weight
WRB	**W**orld **R**eference **B**ase for Soil Ressources, Soil classification of the Food and Agricultural Organization (FAO) of the United Nations (SPAARGAREN, 1998)
WST	wet sedge tundra

Glossary

active layer	topsoil of permafrost soils that thaws during summer
Arctic	the term refers to the area north of the arctic treeline
hummock	earth mound formed by frost heave
Karginsk	interstadial of the Valdai Glaciation (50-25,000 BP)
Kazantsev	interglacial (= Eemian interglacial N-Europe)
mycorrhiza	symbiotic association between a fungus and plant
rhizobia	symbiotic association between a nitrogen fixing bacterium and plant
Sartan	Late-Glacial of the Valdai Glaciation (25-10,000 BP)
supra-permafrost layer	subsoil horizon above the permafrost table, often water-saturated
tussock	growth form of certain grass species
Valdai Glaciation	Last glacial of the Pleistocene in Eurasia (=Weichsel Glaciation, N-Europe), 75,000-10,000 BP
Zyryank	Early period of the Valdai Glaciation (75-50,000 BP)

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1. Introduction and approach

> And if I have prophetic powers, and understand all the mysteries, and all the knowledge, and if I have all faith, so as to remove mountains, but do not have love, I am nothing.
>
> 1 Cor 13, 2

Tundra is commonly referred to as the treeless landscape north of the arctic treeline. The geographic region is further defined as an area with permafrost, which include tree-covered areas called 'forest tundra' in Russian terminology. Tundra covers $7.34*10^6$ km^2 world-wide and represents some 10 % of the land-cover (MATTHEWS, 1983). Its importance is based on its functioning as a carbon sink in the global carbon cycle. Soil carbon stocks and turnover time are related to mean annual air temperature by negative exponential functions (SCHIMEL et al., 1994). As a result decomposition in the Arctic is slow and arctic soils contain 12 to 33 % of the total world soil carbon pool within the active layer and the permafrost (OECHEL & VOURLITIS, 1995; 1997). Within terrestrial systems, 90 to 98 % of the primary production passes through the decomposer cycle of the soil microbiota (BLISS, 1997; GOKSØYR, 1975), which therefore link to trace gas effluxes from soil to the atmosphere. Retarded decomposition is usually indicative for low biological productivity. Yet, PARINKINA (1974) has already suggested that relative microbial productivity must be greater in tundra than in temperate regions because of the short growing season. It is therefore assumed that tundra soils have a great potential for enhanced soil organic matter mineralisation. In a changing climate, they may therefore become a carbon source.

In the early 1970s, microbial studies in tundra soils have been carried out during the comprehensive tundra biome studies of the International Biological Programme (IBP). The IBP data are the most extensive available, but since then, little new information has been gained and techniques in soil microbiology have progressed. The present study is part of the Joint Russian-German Research Project 'Late Quaternary Environmental Development of Central Siberia' (German Federal Ministry of Science and Technology (BMBF) grant 03PLO14B), involving the Arctic and Antarctic Research Institute (St. Petersburg), the Alfred Wegener Institute of Polar and Marine Research (Potsdam), the Department of Soil Science (University of Hamburg) and the Institute for Polar Ecology (Kiel). This investigation was embedded in the research fields investigating actual processes in soil organic matter turnover, CO_2 and CH_4 effluxes in two different study areas on Taimyr Peninsula. The experimental site at Lake La-

baz (72°N, 100°E) is situated within the belt of the 'Southern Arctic Tundra'. The other site at Lake Levinson-Lessing (74.5°N, 98.5°E) is characterized by the vegetation of the 'Typical Arctic Tundra'.

The overall objective of this study was to characterize the microbial pool of the decomposer cycle in the context of site variability. Further emphasis was given to the microbial fitness for the environment. The following questions formed the background of this study:

- What is the order of magnitude and the microbial community structure, and what are the differences between sites?
- To which extent is microbial activity inhibited, and what are the controlling factors in micro-sites?
- What is the potential for enhanced mineralisation at these sites?
- Does a generalised view of microbial habitats contribute to future research in tundra soils?

At Lake Labaz, three tundra soils and two different types brown earth were sampled. At Levinson-Lessing three polygonal tundra soils, two sites at the solifluction slopes and another two in fellfields were sampled. Profile description provides the data base on both abiotic and biological properties of the microbial habitats. Within profiles, sampling techniques were designed to capture small spatial differences.

Direct observation methods quantify fungal and bacterial biomass. The fungi to bacterial ratio varies between different ecosystems and is used as an index for the microbial community structure. Studies at the IBP Tundra Biome sites of the 1970s draw different conclusions with respect to importance of fungal or bacterial components of the microbiota. Activity dependent indirect methods provide further estimates of microbial biomass and thus verify data by direct observation methods. Quotients of microbial parameters further elucidate the community structure and environmental stress. Analyses of soil structural and chemical properties aimed at the abiotic characterisation of the habitat.

I wish to end this introduction with a personal remark:
Within this joint co-operation many papers, Ph.D. and M.Sc. theses were written. The plethora of research interests becomes evident by the reports on the three expeditions to Taimyr

Peninsula (MELLES et al., 1997; BOLSHIYANOV & HUBBERTEN, 1996; SIEGERT & BOLSHIYANOV, 1995). Scientific exchange by joint publications as well as during conferences, workshops and the expeditions themselves make this interdisciplinary approach so fruitful. After all, science is meant to be about the exchange of knowledge.

The study of microbial habitats and properties, as any ecosystematical approach, ideally includes any information available on both abiotic and biotic factors. One advantage of research projects of this magnitude is the availability of many data sets. The present study attempted to make full use of external data in order to enhance the synergistic effect. Hence, external data were included in a separate Section 4.4 and only in full appreciation of my colleagues' work. For readability, some external data were partly cited in the result chapter, where the reader would expect to find the respective information. These, in particular, comprise bacterial biomass data as well as data on the experimental site at Lake Labaz, of the expedition in which I did not participate.

Quotations have been indicated as usual. However, some of these data, have not been published yet or publication is in preparation. In these cases the source has been stated as clear as possible. Furthermore, many valuable references and a lot of research by Russian scientists is naturally published in Russian, only part of which was available in English or German. Due to my extremely restricted knowledge of the Russian language, I often relied on translations by colleagues having command of the language. These sources generally have been indicated as personal communication and, if applicable the source of reference has been added.

2. Study area and experimental sites

> Wenn der Mensch mit regsamem Sinne die Natur durchforscht oder in seiner Phantasie die weiten Räume der organischen Schöpfung mißt, so wirkt unter den vielfachen Eindrücken, die er empfängt, keiner so tief und mächtig als der, welchen die allverbreitete Fülle des Lebens erzeugt. Überall, selbst nahe an den beeisten Polen, ertönt die Luft von dem Gesang der Vögel wie von dem Summen schwirrender Insekten.
>
> Alexander v. Humboldt

2.1 Taimyr Peninsula

2.1.1 Location

Taimyr Peninsula is located in northern Central Siberia and stretches from the Putorana Plateau (70°N) to the Arctic Ocean (Cape Chelyuskin, approximately 77°N). The peninsula is bordered by the river Jennesej (86°E) in the west and by the river Khatanga (115°E) in the east. FRANZ (1973) even defined the river Olenjok as the eastern border (115°E). Taimyr Peninsula thus comprises a total area of about 400,000 km^2 and equals thus Great Britain in size.

Taimyr may further be subdivided into three geomorphological units: the northern coastal plain, the Byrranga Mountains and the North Siberian Lowland in the south (FRANZ, 1973). The coastal plain in the North stretches into the Kara Sea on the western and the Laptev Sea on the eastern side. The Byrranga Mountains stretch approximately 1000 km from SW to NE with a width of 50-180 km. East of the Jenessej Gulf in the western part of the range, mountains start with low elevations of 300 to 400 m a.s.l. and gradually rise reaching heights up to 1100 m a.s.l. in the eastern part. Partly enclosed by the Byrranga and partly adjacent to the southern flanks, Lake Taimyr covers an area of 6000 km², thus representing the largest arctic fresh water lake. 50% of the total area, however, are the North Siberian Lowland in the South. These represent a gently rolling homogenous plain with an elevation exceeding rarely 150 m a.s.l.. The landscape is characterized by numerous shallow lakes, thermokarst lakes, meandering rivers and polygonal tundra soils.

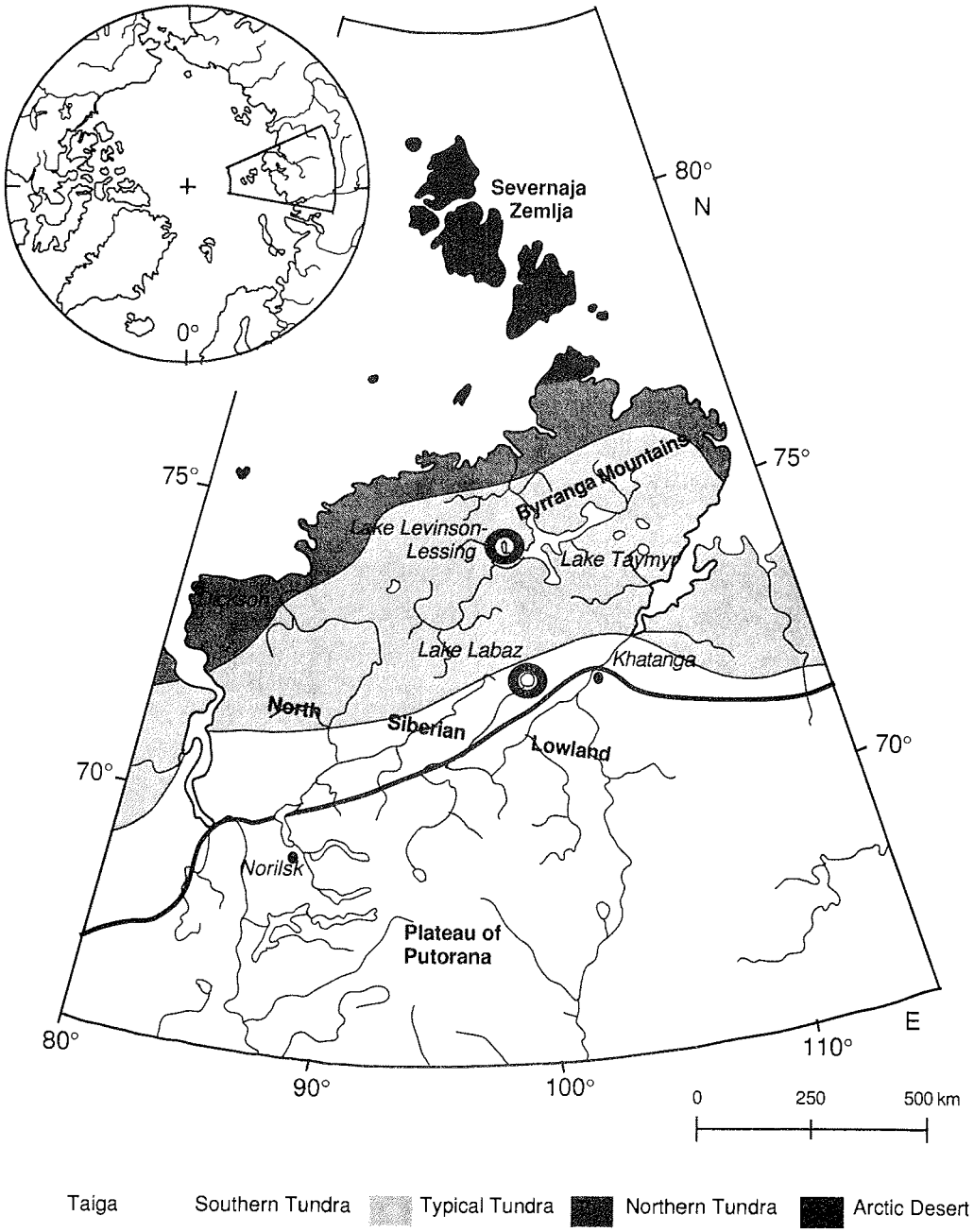


Fig. 2.1.1: **Map of Taimyr Peninsula showing geographical and geobotanical units. The study areas at Lake Levinson-Lessing and Labaz are encircled. Borders of geobotanical units refer to ALEKSANDROVA (1980), see Section 1.4 for details (modified from SOMMERKORN, 1998)**

2.1.2 Climate

The climate of Taimyr Peninsula represents a cold dry-continental regime. Continentality increases from north to south. The main characteristics are the lack of heat, low temperatures, short frost free periods, low precipitation and a high relative air humidity (CHERNOV & MATVEYEVA, 1997; WALTER & BRECKLE, 1986).

Solar radiation

On average the total annual solar radiation is approximately 70 kcal cm^{-2} yr^{-1}. It shows a seasonal peak from May to July, when 25 to 30% of the total radiation is received (CHERNOV & MATVEYEVA, 1997). Insolation increases in summer due to longer day length (up to 24 hours = polar day). Yet, a low radiation angle results in low heating. In addition, the albedo is generally very high. 80 to 95% of the solar radiation are reflected in snow-covered areas. The highest amount of radiation is absorbed in July. Thus, solar radiation already declines, when it can be used by organisms.

Temperature

As a result of low solar radiation, the frost-free period in the tundra may range between 55 and 118 days (WALTER & BRECKLE, 1986). Yet, on Taimyr Peninsula at Agapa, longest frost free period is 65 days at the border of southern tundra to forest tundra (VASSILJEVSKAYA et al., 1975). Thus, the growing season, which is marked by the frost free period, is 1.5 months in the polar desert increasing to 2.5 months the southern tundra. The mean air annual temperature ranges between -14.1°C at Cape Chelyuskin in the north and -13.5°C at Khatanga in the south (WALTER & BRECKLE, 1986). Along this sequence, climate varies particularly in mean July temperatures reflecting increasing continentality. Mean January temperatures are only 4°C higher in the north (-29.6°C at Cape Chelyuskin) than in the south (-33.8°C at Khatanga), whereas mean July temperatures vary more than 10°C (1.5°C at Cape Chelyuskin, 13°C at Khatanga) (ibid.). The July isotherm is the main criterion for further subdivision of the vegetation zones (see below). Furthermore, winter is accompanied by high wind speeds (8-8.6 m s^{-1}) compared to 5.3-5.6 m s^{-1} in summer (BARRY et al., 1981).

Precipitation

The annual amount of precipitation range from 150-200 mm in the arctic desert to 300-350 mm in the typical and southern tundra (see Sect. 2.1.3 and 2.1.5 for nomenclature). The Byrranga Mountains with 450-500 mm yr^{-1} clearly show an orographic effect. A third of the annual precipitation falls as rain during July and August of which 30% is lost by evapotranspiration. The snow cover ranges between 10 and 50 cm in thickness but is usually

20 to 30 cm. Massive snow-drifts are common because of strong winds.

Taimyr Peninsula is characterized by high relative air humidity typically 80%, which is a common feature in the Arctic. In the summer relative air humidity is some 20% lower in the southern tundra reflecting higher temperatures. Yet, this hardly represents a decrease in absolute humidity since there is abundant melt water (BARRY et al., 1981).

2.1.3 Tundra vegetation

World-wide the Taimyr Peninsula is unique in that respect that it shows the whole geobotanical sequence from the arctic desert to the taiga. As can be seen from Figure 2.1.1 vast areas are covered by tundra vegetation. Tundra conventionally represents the vegetation zone north of the arctic treeline and south of the arctic desert. By definition, its borders coincide with the 12°C July isotherm in the south and the 2°C July isotherm in the north. Yet, a unique subdivision of the vegetation zone is somewhat lacking and depends very much on the underlying criteria and individual points of view (ALEKSANDROVA, 1980; ANDREEV & ALEKSANDROVA, 1981; WALTER & BRECKLE, 1986; BLISS & MATVEYEVA, 1992, MATVEYEVA, 1994; CHERNOV & MATVEYEVA, 1997). Subzones were distinguished either along the July isotherm or floristic elements (presence of characteristic species; coverage). In this study, the geobotanical zonation of the Taimyr Peninsula by ALEKSANDROVA (1980) and the terminology of WALTER & BRECKLE (1986) will be adopted, the latter because of the significance of the ecological factors (SOMMERKORN, 1998).

Within subzones, abiotic factors vary leading to further differences in the composition and the structure of the vegetation cover. Hence, ALEKSANDROVA (1980) assigned the 'plakor' concept to the zonal type of vegetation. The zonal vegetation fully reflects the climatic conditions of the respective zone. 'Plakor' vegetation species inhabit mesic habitats on level to gently sloping grounds that are neither too wet nor too dry and show average snow accumulation. Riverbank terraces, wet depressions at hillocky and polygonal tundra sites, fell fields or southfacing drier slopes represent intrazonal or azonal vegetation stands (CHERNOV & MATVEYEVA, 1997). Thus, tundra vegetation patterns may also be described along an ecohydrological gradient (DE MOLENAAR, 1987). Intrazonal or azonal stands 'smooth out' climatic factors and are therefore of great ecological significance. Furthermore, their spatial proportion may also be important.

Southern tundra

The southern tundra represents a narrow belt of 100 to 150 km width in the North Siberian Lowland. Its limits coincide with the 10 and 12°C July isotherms. 'Plakor' vegetation consists of bushes like *Alnus fructiosa* and *Salix lanata* reaching heights of 1 to 2 m and 0.5 to 0.8 m respectively. The lower layer of the vegetation is characterized by subarctic dwarf shrubs, namely *Vaccinium spp., Ledum decumbens, Empetrum nigrum, Arctostaphylos alpinus*. The vegetation cover shows a mosaic structure enhanced by a hummocky ground. In wet depressions non-'plakor' species like *Eriophorum spp.* and *Carex spp.* occur. Trees (e.g., *Larix sibirica*) only occur extrazonally on river terraces. Boreal species still represent 20% of the vegetation whereas typical tundra species represent 10%.

Typical tundra

Typical tundra dominates the Taimyr Peninsula. Its belt is 300-350 km wide and coincides approximately with 10°C July isotherm in the south and the 5°C July isotherm in the north. This subzone covers a vast area of the North Siberian Lowland as well as the shores of Lake Taimyr and the valleys of the Byrranga Mountains.

The typical tundra is characterized by the absence of trees, tall bushes and close bush thickets. The latter comprise *Salix spp.* reaching heights of 20 cm, many develop semiprostate growth forms (*Betula nana, Salix pulchra*). These inhabit intrazonal habitats like river valleys and lake depressions. The 'plakor' vegetation is dominated by mosses (*Aulacomnium turgidum, Hylocomium alaskanum, Tormenthypnum nitens* and *Ptilium ciliare*). Thus, the typical tundra truly is a 'kingdom of mosses' (CHERNOV & MATVEYEVA, 1997). Yet, these occur associated with sedges (*Carex ensifolia* spp. *arctosibirica*, *Carex globularis* and *Carex lugens*).

Northern tundra

The northern tundra only covers a narrow belt along the northern coastal belt of the peninsula. Its southern border coincides with the 5°C July isotherm. In the north, it is either limited by shores of the Arctic Ocean or by the 2°C July isotherm at Cape Chelyuskin.

For the vegetation, the adverse climatic conditions show its main impact on the coverage. Bare ground may thus represent more than 50%. Plants are restricted to favourable micro-sites formed mainly by cryogenic processes. The vegetation furthermore impoverishes in diversity within and between sites. Growth forms change to tufted grasses and herbs, cushions and mats. Sedges and cotton grass are replaced by grasses (e.g., *Dupontia fisheri*) and forbs

(*Cardamine pratensis, Cerastium regelii, Saxifraga cernua)*. Dwarf shrubs are represented by *Salix polaris. Dryas* spp. only inhabit extrazonal habitats as for example fell fields. Mosses are still very abundant (*Aulacomnium turgidum, Hylocomium alaskanum, Tormenthypnum nitens*). Yet, moss covers can only be found adjacent to brooks.

2.1.4 Geology and geomorpholgy

2.1.4.1 Geologic history

Central Siberia is located between the West Siberian megasyncline in the west and the Lena-Anabar-Trough and Anabar-Saddle (anticline) in the east. The area is further subdivided into the southern craton of the Central Siberian Plateau, the Jenessej-Khatanga-Trough further north and the Taimyr-Severnaja Zemlja-Fold. Taimyr Peninsula tectonically belongs to the Taimyr-Severnaja Zemlja-Fold changing into and Jenessej-Khatanga-Trough in the south.
The Byrranga Mountains belong to the Taimyr-Severnaja Zemlja-Fold and were formed during the Pliocene (KHAIN, 1985). The rock massif embodies Triassic basalt, Carboniferous carbonates and Permian sandstone (Greywacke). These resulted from a sedimentation trough during the Carboniferous to Triassic. The thickness of these sediments is 5000 to 8000 metres. Flows of Pre-Cambrian schist and gneiss are also common. The glacial and interglacial periods of the Pleistocene were important to further landscape formation. Thus, glacial till of at least two glaciations has been suggested. Yet, glacial history is subject of dispute and object within the present research project (e.g., MØLLER et al., 1997; SIEGERT et al., 1996; SIEGERT et al., 1995; FRENZEL, 1992; FLINT, 1971). In the interglacial periods, marine transgressions formed marine-built terraces of sand and gravel at altitudes of 200 m and abrasion platforms are found as high as 300 m a.s.l.. A comparison of these terraces with those at Severnaja Zemlja suggests that the Byrranga Mountains are still being uplifted. The last transgression occurred during the Kazantsev interglacial period (= Eemian (NW-Europe)) (BOLSHIYANOV & ANISIMOV, 1995; FRANZ, 1973). Since the Pleistocene, the geomorphology of the Byrranga Mountains is further being formed by periglacial processes.

The North Siberian Lowland south of the Byrranga Mountains belongs to the Jenessej-Khatanga-Trough and is separated from the southern Altaides (= Variscan (Central Europe)) of the Central Siberian Plateau by fault lines. The depression was filled with 4000 to 5000 metres thick Mesozoic and Cainozoic sediments. These consist of mixed layers of sandy-clayey shallow water sediments and continental-sandy deposits. During the Quaternary washed-up moraines and littoral sand, silt and gravel deposits were added, partly by marine

transgression, partly by glaciation (SUSLOV, 1961). The ice-sheets of the Pleistocene in the area are believed to have been thin (FLINT, 1971). The North Siberian Lowland was presumably ice-free during the Sartan-Glaciation, the last stage of the Valdai-Glaciation (= Weichsel (N-Europe)).

The overall ice-sheet in Siberia diminished from West to East supposingly reflecting the strong continental climate. The only areas capable of supporting glaciers were the maritime Arctic and mountains of the interior. At maximum glaciation (Saale glacial in N-Europe) a single ice-sheet is believed to have covered the mountain areas (Putorana Plateau, Byrranga Mountains) as well as the intervening Lowland. Yet, the sheet was nowhere thick enough to bury the mountain summits. Furthermore, it moved little and thawed slowly having little till on its bed and leaving no boulders behind (SUSLOV, 1961). At the last glacial maximum (i.e., Valdai) the ice-sheet was less extent and disconnected. As a consequence the glaciation history of the Taimyr Peninsula particularly during the Sartan phase (last maximum of the Valdai glacial) is still object of scientific research and discussion. GROSSWALD (1989) and ARKHIPOV (1997) support the hypothesis that the entire peninsula was glaciated. On the contrary, VELICHKO et al. (1997a, b) argue that ice-caps were restricted to the mountain areas and the North Siberian Lowland were ice-free because of lacking moraines and the supposed aridity. The North Siberian Lowland had thus been a periglacial area subjected to deposition of glaciofluvial material, formation of glacial lakes and spillways (SUSLOV, 1961).

2.1.4.2 Periglacial processes

The geomorphology is characterized by periglacial freeze-thaw processes in the active layer. These result in solifluction and formation of patterned ground which is mainly a function of texture, slope position, drainage and temperature (WILLIAMS & SMITH, 1989; WEISE, 1983).

Freeze-thaw processes

Driving force of all freeze-thaw processes is the particular property of water inasmuch that it expands during freezing. Because of its dipole character, water furthermore is attracted by other water or ice molecules. The enlargement of 9% during freezing applies a prying force (frost wedging) which is complemented by the directional growth of ice crystals (TABER, 1929 cf. WASHBURN, 1979). This growth may be horizontal (e.g., ice lenses) or vertical (ice veins). Thus, physical weathering of rocks and rock forming minerals is mainly induced by frost wedging (frost shattering). Frost shattering not only depends on temperature and moisture

variations but also on the susceptibility of the rock (LAUTRIDOU, 1988; DOUGLAS et al., 1983). In unconsolidated material such as soils or fell-fields, frost wedging induces frost heave which is to say the upfreezing of objects (e.g., stones) or soil (frost stirring). Frost heave thus directly relates to the amount of water in the freezing zone (SCHENK, 1955). At subfreezing temperatures thermal contraction of ice is fracturing at the surface (frost-cracking). The initial crack is filled by summer meltwater and grows to form ice-wedges which are the shape of polygons.

Repeated freezing and thawing has a size sorting effect on soil due to the migration of water and the freezing front. This is accompanied by upfreezing of stones, mass displacement, cryostatic pressure and gravity movement of stones into polygonal cracks (WASHBURN, 1979). The movement of particles also shows involutions and turbulent patterns (cryoturbation). Thus, the rate of movement of particles also depends on the rate and direction of freezing (TEDROW, 1977). Sorting and cryoturbation are the main underlying processes of the formation of patterned ground (see below).

In the Arctic, solifluction is also a major geomorphological process. The seasonally thawed topsoil is often water saturated above the permafrost and instable in sloping positions. Gravitational forces cause the soil to flow from higher to lower ground with the permafrost table underneath as a 'glide plane' (gelifluction).

Some forms of patterned ground

A great amount of patterned ground features (some 1500) were described by TROLL (1944). WASHBURN (1956 cf. WASHBURN, 1979) classified the forms of patterned ground based upon the geometric shape (circles, polygons, nets, steps, and stripes) and presence or absence of sorting.

Ice-wedge polygons (Taimyr Polygons)

Frost cracking (see above) is supposed to be initial stage of ice-wedge polygon formation. The border of the polygons coincides with the ice-wedge. This may be elevated or depressed with respect to its centre. Raised borders characterize low-centred polygons and often have ponds in their centre during the thawing period. High-centred polygons show a higher centre and depressed borders in which they often hold water (WASHBURN, 1979). Ice-wedge polygons are common in level or undulating areas being largest in old landscapes such as northern Alaska and Siberia (FITZPATRICK, 1997).

Circles, frost boils, mud pits, Gährlehmbeulen (e.g., HÖGBOM 1905 cf. TROLL, 1944)

Circles are formed by an upward mass displacement in disruption of the vegetation cover. They are common in centres of polygons. As a result of upfreezing stones tend to accumulate at the surface. Due to the lacking vegetation they have a different thermal regime than the surrounding.

Hummocks (thufur)

Earth hummocks are mounds formed by cryoturbation (squeezing-up effect) of fine textured and (nearly) stone-free soil material. They occur in level or undulating areas that have an imperfect drainage. The initiation of hummock formation is unknown and has been discussed in detail by SCHUNKE & ZOLTAI (1988).

Steps

In sloping areas, cryoturbation and sorting is super-imposed by a downslope mass displacement (solifluction). Fine-textured soils form terrace-like forms consisting of lobes or steps. Because of higher movement in the upper steeper part, this process also results in overturning and involution of topsoil material. The downslope vegetation border encompasses bare ground upslope. Non-sorted steps are common on slopes with 5-15° inclination.

Stripes and nets

Nets are comparable to circles and polygons but are less distinct in their symmetrical form. At slopes with an inclination of 6° nets turn into stripes.

Further description of the inter-relationship of patterned ground and soil formation is found in FITZPATRICK (1997), RIEGER (1983), TEDROW (1977), SCHENK (1955).

2.1.5 Soils and pedogenetic processes

There is no unique concept of the geography of arctic soils. In addition, the terminology not only differs but is also somewhat confusing (see Tab. 2.1-1). The conventional geographical conception of the Arctic comprises the area within the Arctic Circle (66°32'N). Since the early times of Dokuchaev at the end of last century, the Russian conception of soil zonation is very much linked to the soil genesis and the vegetation zones. Thus, in the concept by IVANOVA et al. (1969) arctic soils only represent the soils of the arctic desert. On the contrary, GORYACHKIN et al. (1998) and TEDROW (1977) define the arctic treeline as the southern demarcation of the arctic soil zone, which stretches as far to the south as 55°N at Hudson Bay (Canada). This definition thus includes the soils of the tundra and arctic desert vegetation zone (i.e., geobotanical units by ALEKSANDROVA, 1980; WALTER & BRECKLE, 1986). BREBURDA (1987) stated that the presence of permafrost was the most important feature of the respective

soils. He thus suggested the term 'permafrost soils'. In the northern hemisphere, these would include soils from the taiga to the arctic desert and would stretch as far to the south as 52°N near Irkutsk in Siberia (WEISE, 1983). A further subdivision of arctic soils was generally tackled according to the predominating soil forming processes. Again this has led to differing classification systems.

Tab. 2.1-1: Zonation of arctic soils and important pedogenetic processes by IVANOVA et al. (1969); TEDROW (1977) and GORYACHKIN et al. (1998).

	South				North
Geobotanical units	Forest tundra	Southern tundra	Typical tundra	Northern tundra	Arctic desert
IVANOVA et al. (1969)	**Frozen taiga soils**		**Tundra soils**		**Arctic soils**
		Accumulation of soil organic matter			Physical weathering
		Acidification			Upward movement of solutes:
		Decalcification			Calcification
		Desalinisation			Salinisation
		Mobilisation and accumulation of sesquioxides			Accumulation of sesquioxides
		Gleying			
		Little mineral weathering (feldspars)			
TEDROW (1977)	**Tundra soils**		**Subpolar desert soils**		**Polar desert soils**
			← decreasing —		Physical weathering
	Accumulation of soil organic matter		— decreasing →		
	Acidification		←→		Upward movement of solutes:
	Decalcification		←→		Calcification
	Desalinisation		←→		Salinisation
	Podzolisation		— decreasing →		
	Gleying		— decreasing →		
GORYACHKIN et al. (1998)	**Subarctic tundra soils**		**Northern tundra soils**		**High arctic soils**
	——— decreasing accumulation of soil organic matter ——— →				
	——— decreasing gleying ——— →				
	——— decreasing acidification ——— →				
		Decalcification			Calcification
		Desalinisation			Salinisation
		Podzolisation			
	Clay formation				

One explanation for this ambiguity is that according to GORYACHKIN et al. (1998) almost any soil forming process in the Arctic may occur in any subzone, which is also the reason for their objection to current nomenclature in soil zonation.

Humus accumulation

The presence of vegetation results in humus accumulation. The humus form depends on the composition of the plant canopy and rates of decomposition. Peat formation occurs under water-logged conditions. At well-drained site mull-moder organic horizons may be formed. Mull to moder is found in the humid Arctic as well as in the more southern tundra areas of the continental Arctic (ibid.). On Taimyr Peninsula peat formation was observed up to Cape Chelyskin. In the mountain tundra soils the annual phytomass production was lower than the lowland tundra (GUNDELWEIN, 1998). Yet, according to BAZILEVICH (1995), little difference was found with respect to the net phytomass input (phytomass annual production, dead plant matter and its degradation rate).

Acidification

In the presence of decomposing organic matter, roots, microbial activity, acidification occurs as a result of the formation of carbonic and organic acids. These lead to a depletion of basic cations. Acidification thus decreases from the southern tundra towards the arctic deserts.

Calcification - decalcification and salinisation - desalinisation

The movement of solutes is determined by soil moisture and the orientation of the soil water movement. Leaching (i.e., downward movement) thus diminishes northward the soils sequence as precipitation decreases. Low soil moisture accompanied with high base saturation results in precipitation of carbonates and an accumulation of salts. Often precipitation can be observed macroscopically as calcareous pendings under stones and thin salt coatings. Calcification and salinisation are therefore characteristic for the arctic desert soils but may also be found locally in southern tundra soils at drier vegetation-free sites (see also Sect. 5.1.2.2). It may further be a temporal phenomenon where puddles (in lower micro-sites) periodically dry out.

Weathering and secondary minerals

In the Arctic biogenic weathering is probably more important than in most other parts of the world (FITZPATRICK, 1997). Biogenic weathering here is understood as biogeochemical

weathering brought about by lichens and mosses. Lichens are known to exude organic acids (particularly oxalic acid) and lichen compounds that release cations from rock forming minerals (SCHMIDT, 1993; ISKANDAR & SYERS, 1972; JONES & WILSON, 1986).

Sesquioxides are being formed as a result of geochemical weathering. At well-drained sites brunification ('Verbraunung') occurs. Under wet conditions iron stays in a reduced state (ferrous iron) and gives soils grey or bluish colour (i.e., gleying). Sesquioxides rarely crystallise but remain in hydrosol phase (IVANOVA et al, 1969). Yet, findings by ALEKSEEV et al. (submitted) also suggest that Fe^{2+} migrates downwards and crystallises as lepidocrocite above the permafrost table where it was found to accumulate.

Clay contents, however, tend to be rather low in Arctic soils. Generally, the clay fraction mainly consists of clay size rock forming minerals such as quartz and feldspar (EVERETT et al., 1981). In the valley of the river Pyasina (Taimyr Peninsula), GRADUSOV & IVANOV (1974) found high proportions of smectites and illite in the clay fraction (i.e., 70-80%), which decreased towards the Byrranga foot slopes (30-40%). This suggested that the smectites originated from parent material that were presumably sediments from the Putorana Plateau (IVANOV, pers. communication). Thus, there is only little evidence for pedogenic clay formation (IVANOVA et al., 1969; GORYACHKIN et al., 1998)

Gleying

Gleying is a prevailing and prominent feature of soil formation in the Arctic and a principal process in the tundra (RIEGER, 1974). The underlying permafrost represents a barrier above which soil water stagnates. Iron mottling is only formed in the active layer under partially dry conditions. During prolonged dry summer periods or in the freezing front during the refreezing period, ferrous compounds are converted to hydrated ferric oxides (ibid.). Gleying markedly decreases northward the soil sequence (TEDROW, 1977). According to GORYACHKIN et al. (1998) this is rather explained by coarse textured and stony substrates than by climatic conditions. At Cape Chelyuskin gleying occurs on fine textured, decalcified parent material.

Podzolisation

Arctic soils frequently show podzolisation features. Here, podzolisation is understood as the mobilisation of iron and aluminium by organic acids and transportation into the B horizon

which results in the formation of the diagnostic spodic horizon (WRB). Yet, there is controversy about podzolisation in Arctic soils. Although TEDROW (1977) reported the formation of podzols on well-drained and coarse textured material in the southern tundra, he only refers to iron and manganese transportation. SOKOLOV & GRADUSOV (1978) described the formation of an eluvial horizon at a micro-scale with lacking precipitation of organo-metallic chelates ('ochristye bodbury'). Often it is being argued that podzolisation properties (as defined above) represent relic features (LIVEROVSKII, 1974 cf. GORYCHAKIN et al., 1998). Yet, moisture was found to be sufficient for podzolisation under present climatic conditions (STONER et al., 1983, UGOLINI et al., 1987). In Antarctica, BLUME et al. (1998; 1996) have also shown that podzolisation takes place with mean annual precipitation as low as 180 mm. Bleached eluvial horizons of 1 to 3 cm thickness had formed in soils at ancient penguin rookeries (ibid) as well as under lichen-moss vegetation cover (BÖLTER et al., 1995). A preceding review (BOCKHEIM & UGOLINI, 1990), however, has concluded that podzolisation was unlikely to occur in Antarctica. Summing up, there appears to be little doubt about sufficient acidity for eluviation of sesquioxides under present Arctic (or Antarctic) climatic conditions (GORYACHKIN et al., 1998). Illuvial horizons of organo-metallic complex on the contrary are subject of dispute.

2.1.6 Human history and impact

2.1.6.1 Human history

In Siberia, human history dates back as early as to the Palaeolithic or early Neolithic Periods. 7,000 to 8,000 years BP, man (which naturally comprises men, women and children) is believed to have colonised Taimyr Peninsula (CHERNOV, 1985; ANDREEV, 1981). During the TAYMYR 1996 expedition, archaeological findings represented ceramic fragments, worked and fragmented bones from a reindeer hunting site at the brook Oleny in the upper Taimyr river area (PITUL'KO, 1997). These were approximately 1,800 to 2,000 years old (ibid.). The name of the brook (i.e., Oleny) translates to reindeer brook and probably suggests rich grounds of the respective mammal. Reindeer represented the main food resource although fish and birds were also part of the diet.

Historical records on the Siberia started with the European development after annexation of the *khanate sibir* in the 16th century (POSSELT, 1990). In the following period, all efforts were committed to the implementation of the Tsarian power, the collection of taxes in kind (i.e., a sable fur tax called *Jasak*) and trading. Administrative outposts became necessary and

settlements of Europeans came into being. Khatanga for instance was also founded in that period (1626). Bondage in the European part of the Russian empire made poor farmers move to the East. First reports on Siberia were written by trading travellers. Thus, the reports by the Dutch trader Nicolaas Witsen, who travelled through Siberia to China from 1697-1701, delivered important maps for scientific expeditions later on.

The indigenous people of Taimyr Peninsula comprise some 3,000 'Dolgans', 1,000 'Ngasans' as well as descendants of 'Nentsens' and 'Evenkens'. These peoples were nomads following the migrating reindeer herds. In the 1930s the indigenous people were settled in settlements and organised in Sowchos leading a modern Soviet life with some remaining elements of their original culture (such as hunting and fishing). With certain reservations to modern life style, reindeer and fish still represents the main food resource as well as a source of income.

Taimyr Peninsula has some 350,000 inhabitants, most of which (i.e., 300,000) live in the mining town Norilsk. The smelters of Norilsk represent a major source of pollutants.

2.1.6.2 Scientific history

Scientific interest in Siberia arose in the period of Enlightenment during the tsardom of Peter I. (POSSELT, 1990). Peter I. had founded the Russian Academy of Sciences in St. Petersburg which was fully established in 1725 and happened to guide many of the Siberian expeditions later on. The new Academy attracted many scientists from Germany since it offered many opportunities (and jobs) that were not found back home due to the German particularism. Thus, it was the German medical scientist Daniel Gottlieb Messerschmidt who guided the first scientific expedition to Siberia by appointment of Tsar Peter I. (1720-1727). Many expeditions followed. In 1724, the Dane Vitus Bering was put in charge of the First Kamchatka Expedition to explore the supposed land-bridge between Asia and America. The Second Kamchatka Expedition also by Bering was aimed at the exploration of further sea-routes to America and Japan. This expedition furthermore intended the description of the Arctic Sea, the natural history and ethnological studies. It was thus the biggest Russian scientific project until 1917 (ibid.). The material of above mentioned Messerschmidt was the basis for this expedition. The Germans Johann Georg Gmelin (natural scientist and botanist) and Georg Wilhelm Steller (medical and natural scientist) were part of the Pacific and Siberian group (ibid.). Gmelin and Steller described Eurasian peoples, flora

(e.g., *Larix gmelinii*) and fauna (the legendary Steller's sea-cow, *Hydroamalis gigas*). In 19th century more systematical ecological studies in a modern sense started with the works by SCHRENK (1848; 1854 cf. CHERNOV & MATVEYEVA, 1997) and MIDDENDORF (1869; ibid.). Alexander v. Middendorf was the first known European who travelled to Taimyr Peninsula. His botanical studies introduced previously unknown plant species, which was also appreciated by their names (e.g., *Betula middendorfii*, *Oxytropis middendorfii*). He already had recognised High tundra (mountain tundra) and Low tundra (wet plains) (TEDROW, 1977). This was followed by the Russian Polar expedition of Toll from 1900-1903. Scientific expeditions naturally ceased during the restless times of the Revolutions and World War I and II. In the 1950s ecological studies on Taimyr were reinstated. The botanical studies of ALEKSANDROVA (1951; 1956; 1959; 1960; cf. CHERNOV & MATVEYEVA, 1997) fall in this period. Her description of the Siberian flora and her assignation of the 'plakor' concept to the tundra is still essential to any ecologist working in the Siberian tundra. In the early 1970s four research sites on Taimyr Peninsula were included of the International Biological Programme IBP (ROSSWALL & HEAL, 1974). The fall of the Iron Curtain in 1989 was a stimulus for further expeditions with western participation. Several expeditions were carried out in co-operation with the World Wildlife Fund for Nature with the aim at a better protection of the vast breeding grounds of migrating birds (PROKOSCH & HÖTKER, 1995). The present joint Russian-German research project to study Quaternary Environmental Development of Middle Siberia was launched in 1993. Between 1993 and 1997 a total number of four joint Russian-German expeditions were carried out to investigate the permafrost-soil-hydrosphere-biosphere system (MELLES, 1994; SIEGERT & BOLSHIYANOV, 1995; BOLSHIYANOV & HUBBERTEN, 1996; MELLES et al., 1997).

2.1.6.3 Anthropogenic impact

Anthropogenic impact on the tundra ecosystems was mainly reported as induced changes in the vegetational but also in soil microfloral composition (CHERNOV & MATVEYEVA ,1997; ANDREEV, 1981, KIRTSIDELY et al., 1994). This may be caused by utilisation of biological resources, physical disruption of the vegetation cover or input of substances.

After mechanical disturbance by vehicles, aircrafts and/or trampling (the latter particularly around settlements) the vegetation cover may restore slowly depending on the degree of destruction. Yet, the species composition and the structure will be completely different

(CHERNOV & MATVEYEVA 1997). Particularly in the vicinity of settlements the invasion of new plant species brought into the system (for example as a food source) leads to the formation of a different vegetation cover. Unless the upper soil is affected by disruptive processes this may cause the formation of meadows. Another consequence of the presence of people in both historical and present times was the input of substances. This comprises the dumping of domestic refuse and burial of the deceased. In modern times, garbage certainly differs in quality and quantity. Furthermore, soil pollution by coal heaps and oil spillage is a more recent phenomenon, which mainly occurs around settlements. Oil spillage also occurs locally everywhere in the tundra due to refuelling of vehicles and aircrafts.

Despite its remote location, Taimyr Peninsula is also affected by air pollution as for example acid deposition and heavy metal pollution (WOODIN, 1997; KIRTSIDELY et al., 1994; 1995). Although inputs of pollutants may be comparably low, there is evidence that the tolerance of arctic ecosystems is exceeded. As elsewhere, soils are sensitive to acidification where acid, shallow and poor in bases, which makes tundra soils particularly vulnerable. Some Arctic rivers, as for example the river Jenessej, are significant pathways for contaminants such as suspended solids of DDT or PCB. These enter the food web by birds of prey or fish (AMAP, 1998). Due to their high sensitivity, the 'tolerance' of Arctic ecosystems is exceeded in the sense that severe disturbances of functioning were observed (WOODIN, 1997). In contrast to ubiquitous air pollution, the above mentioned smelters of Norilsk represent a located source of pollutants (i.e., heavy metals) for the Taimyr Peninsula. Yet, these also contribute severely to Arctic pollution in general (AMAP, 1998).

2.2 Sites at Lake Levinson-Lessing

Lake Levinson-Lessing is situated within the typical tundra zone in the western part of the Byrranga Mountains at 40 m a.s.l. (Fig. A2.1-1). The lake is 15 km long in its north-south axis with 2 km in width and measures maximum depth of 108 m (BOLSHIYANOV & ANISIMOV, 1995). The main tributary represents the river Krasnaya at its northern shore. Its outflow, the river Protochny at the southern shore connects Lake Levinson-Lessing to Lake Taimyr in the southwest. The surrounding mountains reach altitudes of 300 to 500 m a.s.l..

The study area is situated at the northern shore of the lake (74.5°N, 98.5°E) and encompasses a total area of 43.5 km². There is no meteorological station at or near Lake Levinson-Lessing. Thus, local climatic conditions can only be described approximately using data from the Lake Taimyr Station, about 70 km to the east (see Tab. 2.2-1 DICKSON REGIONAL ADMINISTRATION, 1993). The climate is governed by cold-dry continental conditions. Mean annual temperature is -15°C with a mean January temperature of -33°C and a mean July temperature of 6.5°C. Annual precipition is 281 mm of which 26% fall as rain in the growing season. The frost-free period lasts 35-40 days. Short-term recordings of climatic data during the expedition, however, differed inasmuch that mean July and August temperature was 8°C.

Table 2.2 -1 Climatic data for Lake Taimyr Staion (from DICKSON REGIONAL ADMINISTRATION, 1993) and Khatanga Station (from NORIN & IGNATENKO, 1975).

Station	Temperature [°C]			Days	Precipitation
	Mean annual	January mean	July mean	(t > 0°C)	[mm yr^{-1}]
Lake Taimyr (1962-1992)	-15	-33	+6.5	35-40	281
Khatanga (25-year mean)	-13	-34	+13	35-45	243

In the valleys, the vegetation is characterized by typical tundra plants. 'Plakor' species represent dwarf shrubs (*Salix reptans*, *Dryas punctata* and *Cassiope tetragona*) which are associated with *Carex* spp. and mosses. The latter form dense moss carpets and are dominated by *Tormentypnum nitens*. At wetter micro-sites *Carex stans*, *Eriophorum vaginatum* and *E. angustifolium* predominate. At the slopes of the surrounding mountains the composition of the vegetation changes and plant coverage rarely exceeds 60%. The vegetation community

comprises *Dryas punctata*, *Carex arctosibirica*, *Novosiviersia glacialis* and mosses. On the mountain tops, plant coverage further decreases (< 10%). Typical plants were *Salix arctica*, *Novosiviersia glacialis, Minnuartia arctica, Papaver polare, Dryas punctata*. (SOMMERKORN, 1998; BECKER, 1997)

The Krasnaya valley is filled with fluvial silty loamy to sandy sediments but are presumably mixed with aeolian and solifluidal sediments from solifluction slopes. In the level area of the valley polygonal patterned ground with high or low centred forms and thermokarst lakes have developed. The diameter of the polygons ranges from 6 to 12 m. At the out banks of the river the edges are eroded by thermokarst. The morphology at the slopes of the surrounding mountains is formed by solifluction and intensive frost-shattering. The solid rock consists of greywacke, gneiss and schist. Soils developing here show little or no pedogenic differentiation in sesquioxide, silt or clay content (MÜLLER-LUPP, 1997). Smectite and illite are the principal clay minerals. Particularly, in fine-textured soils kaolinite, chlorite and interstratified minerals are also common. Yet, very little clay is thought to have formed by pedogenesis (HAGEDORN, pers. comm.). Geochemical investigations have shown that feldspar and montmorillonite may further dissolved under present thermodynamic conditions (HAGEDORN et al., SUBMITTED).

2.3 Sites at Lake Labaz

The experimental sites are at the northern shore of Lake Labaz (72°2'N, 99°4'E) which is situated within the southern tundra zone in the North Siberian Lowland at 47.5 m a.s.l. (Fig. A2.1-2). The lake is 30 km in its diameter and measures a shallow depth of less than 5 m. The landscape shows a uniform character of a low hill country with polygonal and tussock tundra as well as numerous thermokarst lakes and watercourses. Elevations rarely exceed 150 m a.s.l. and the watershed is irregular because of the low relief intensity. Consequently, the direction of flow of the main two watercourses of the study area strongly divert. They both finally represent tributaries to the river Khatanga but some 350 km apart.

The study area encompasses a total area of 8 km². As was the case for the study area at Lake Levinson-Lessing, there was no meteorological station at or near Lake Labaz. Thus, local climatic conditions were described using data of the nearest station at Khatanga (72°N, 102°E) (Tab. 2.2-1 modified from NORIN & IGANTENKO, 1975) in the forest tundra zone. Mean July temperature and the duration of the growing season may differ. In addition precipitation is likely to be higher at Lake Labaz (Sects. 1.2 and 1.3). The study area is characterized by a cold-dry continental climate. Mean annual temperature is -13°C with a mean January temperature of -34°C and a mean July temperature of +13°C. Annual precipitation is 243 mm of which 31% fall as rain in growing season. The frost-free period lasts 35-45 days. During the 1994 and 1995 expeditions short-term recordings did not deliver differing climatic data (SOMMERKORN, 1995; 1997).

The vegetation is characterized by typical plants of the southern tundra. 'Plakor' vegetation comprises bush thickets of *Salix* spp., *Betula* spp. and *Larix* spp.. *Salix* spp. in particular reaches heights of 0.8 metres. Dwarf shrubs (*Vaccinium vitis-idea*, *Cassiope tetragona*, *Betula nana*) and lichens (*Cetraria cucullata*, *Thamnolia vermicularis*) are a further 'plakor' plants. At wetter sites, sedges (*Carex* spp.), cotton grass (*Eriophorum* spp.) and mosses (*Tormentypnum nitens*, *Drepanocladus uncinatus*) predominate (SOMMERKORN, 1998; 1995). The mountain tops represent well aerated dry ruderal habitats where the plant coverage decreases (< 80%). The vegetation is dominated by chinophobous (e.g., *Certraria nivalis*) and ruderal species (*Carex rupestris*).

During the last glaciation maximum, a glacial lake had formed a Pre-Labaz lake of which the

present and neighbouring lakes developed as relicts (SIEGERT & BOLSHIYANOV, 1995; ISAYEVA, 1984). The northern shore of Lake Labaz consists of marine terraces (Sect. 1.4.1) and deposits of the Kazantsev interglacial (= Eemian interglacial N-Europe) and the Karginsk interstadial (FISHER et al., 1990). These deposits generally show silty-loamy texture. Peat lenses with thickness of up to 2 m occurred in mixed layers and were dated to the Karginsk interstadial as well as to the Holocene (SIEGERT, pers. comm.).

3. State of the art

Wohin der Blick des Naturforschers dringt, ist Leben oder Keim zum Leben verbreitet.
Alexander v. Humboldt

3.1 Microbiota in arctic soils

Soil microbial ecology is concerned with the structure and function of soil micro-organisms. Microbial communities are considered to inhabit microhabitats in soil. Yet, the terminology is rather ambiguous and invariably subject of dispute (HARRIS, 1994). At its simplest, 'microbial community' is regarded as the coincident occurrence of micro-organisms. As such the term is used in this study, aware of insufficient information on interactions between components of the community. 'Microbial habitat' is also poorly defined but suggests a spatial and even time dimension. It is therefore a question of scale, which will be elucidated in a separate section of this chapter.

3.1.1 Community structure

In the Arctic, comprehensive studies of the soil microbiota were carried out at the experimental sites of the IBP Tundra Biome Programme (HOLDING et al., 1974, ROSSWALL & HEAL, 1975; BLISS et al., 1981). Since then very little new information on the community structure has been gained (ROBINSON & WOOKEY, 1997). Within terrestrial ecosystems, soil microbiota represents the main component of the decomposer cycle through which between 90 to 98% of the primary production passes (BLISS, 1997; GOKSØYR, 1975). Soil micro-organisms not only govern decomposition processes but they furthermore participate in primary production processes (COLEMAN & CROSSLEY, 1996).

Primary production

Symbiotic associations between micro-organisms and plants enhance the nutrient acquisition of the host. In exchange the involved micro-organism receives assimilates. In tundra basidiomycetes for instance form ectomycorrhizal associations with *Betula* and *Salix* spp. but are also reported with ericaceous shrubs and *Dryas* spp.. The diversity of mycorrhizae is interwoven with the vegetation cover but is generally lower than in other biomes (MILLER & LAURSEN, 1978). In the Arctic, ectomycorrhizal enzyme systems appear to be adapted to cold (TIBBETT et al., 1998a) and nutrient deficiency (TIBBETT et al., 1998b). Endomycorrhizae (i.e., vesicular-arbuscular mycorrhizae) are also common and found in association with *Ranunculus* spp., *Saxifraga* spp. and Graminae (MILLER & LAURSEN, 1978). At drier sites mycorrhizal forming fungi are as common as saprophytic (decomposing) fungi (BUNNELL et al., 1975).

Furthermore nitrogen fixing bacteria are also known to form symbiotic associations with plants. The latter occurs as nodules at root hairs, which develop after infection of the host's roots by the bacterium *Rhizobium* (KILLHAM, 1994). In the Arctic, rhizobia were occasionally observed in association with *Alnus*, *Dryas spp.*, *Astragalus alpinus*, *Lotus croniculatus* and two species of *Oxytropis* but may also be absent (WALTER & BRECKLE, 1986; GRANHALL & LID-TORSVIK., 1975; CHAPIN & BLEDSOE, 1992) and is subject to seasonal variation (NOSKO et al., 1994). Although nitrogen fixation by rhizobia may be locally important, it is generally of subordinate significance in tundra (HOLDING, 1981). Detailed description of symbiotic microbial-plant associations are given e.g., by TATE (1995), GILLER & DAY (1985), READ et al. (1985), and BULL & SLATER (1982).

However, in tundra soils cyanobacteria (former blue-green algae) are by far the more important taxonomic group of micro-organisms with respect to nitrogen fixation (ALEXANDER, 1974a,b; ALEXANDER & BILLINGTON, 1986; CHAPIN & BLEDSOE, 1992). The nitrogen input by fixation may be fourfold greater (CHAPIN & BLEDSOE, 1992) than from other sources (as for instance from precipitation). The predominant genera (i.e., *Nostoc*, *Anabaena*) occur in wet depressions and melt ponds (ALEXANDER et al., 1978) as well as associated with fungi and soil algae in crusts (GRANHALL & LID-TORSVIK, 1975) or with plants (HENRIKSON et al., 1987; SOLHEIM et al., 1996). Other nitrogen fixing bacteria are less important (DUNICAN & ROSSWALL, 1974) or not found in tundra (e.g., MATVEYEVA et al., 1975). In addition cyanobacteria, along with green algae and diatoms also release other nutrients into the soil not only upon the decay of dead cells but also as metabolites (e.g., polysaccharides, polypeptides (CAMERON et al., 1978). Because of their ability of photosynthesis, they formerly had been summarised as soil algae. Consequently cyanobacteria and soil algae take up and release CO_2 by photosynthesis and respiration respectively. Some groups are even known to be 'fertilised' by CO_2 supplied by live and decaying roots (ibid.). Photoautotrophs are largely restricted to the upper few centimetres of soils and decrease logarithmically with depth. In the Arctic, they are practically found in all habitats although their biomass, species composition and productivity largely depends on moisture (BUNNELL et al., 1975). At wetter sites, the species composition was found to approximate that of aquatic environments (ibid.) but was also reported to be generally less diverse and more specialised in arctic terrestrial systems (ELSTER et al., 1994). Depending on the author and the methodology, green algae are thought to prevail over diatoms or cyanobacteria (BUNNELL et al., 1975). The latter, however, are more difficult to culture. Therefore, the relationship was also reported to be inverse (CAMERON et al., 1978).

The ecological significance in the Arctic is particularly high because cyanobacteria and soil algae represent the first organisms in primary succession on land. In the high Arctic, they may even represent the only life forms. In association with bacteria, they from crusts on bare rock and soil surfaces. During the last decade, intense studies were carried out on these cryptobiotic crusts in high alpine (BELNAP & GARDNER, 1993; BELNAP et al.,1993; BELNAP, 1992; ST. CLAIR & JOHANSEN, 1993) and polar desert systems (PARINKINA & PIIN, 1992; WYNN-WILLIAMS, 1985; 1994; BOCKHEIM & WILSON, 1992, FRIEDMANN, 1982). On the contrary, algal biocenoses of moist terrestrial ecosystems are largely unknown (SVOBODA & FREEDMANN, 1994; ELSTER et al., 1994).

Symbiotic microbe-plant relationships as well as cyanobacteria and soil algae represent primary producers. Microbial aid of nutrient uptake by plants as well as microbial C and N_2 fixation are pathways of nutrient input in soils from above- and belowground and thus primary production processes (COLEMAN & CROSSELY, 1996).

Decomposer cycle

As mentioned above, particular importance of the soil microbiota lies in its predominance in the decomposer cycle. Yet, the microbiota is greatly reduced in the Arctic. In wetter habitats bacteria are more numerous than fungi, and fungi are more abundant in mesic habitats (BLISS, 1997; SYZOVA & PANIKOV, 1995; BUNNELL et al., 1975). FEDOROV-DAVYDOV (1998) reckons about 32% of the microbiota tundra among micro-organisms decomposing fresh plant remains, another 15% among decomposers of organic substances in peat and 52% among the microbial population living on decaying roots and root exudates.

In drier and warmer (mesic) arctic soils, fungi have been reported to predominate in the decomposition of organic matter because of the acid reaction of the humus layer. Bacteria have been considered to be of secondary importance (BUNNELL, et al., 1975; WALTER & BRECKLE, 1986). In wetter habitats, fungi have been observed to play a subordinate role and have only been found as sterile mycelia (SYZOVA & PANIKOV, 1995; MATVEYEVA et al., 1975; CHERNOV et al., 1975). Yet, fungal productivity (i.e., production of fungal biomass per unit area and time) is greater than the productivity determined for bacteria (ROSSWALL, 1975). Fungi convert between 50-60% of the carbon in litter to CO_2 (HOLDING, 1981). They may be subdivided into three groups according to their carbon source. Sugar fungi utilise simple sugars, proteins and organic acids as their carbon source. Cellulolytic fungi are able to utilise

cellulose in addition. Last but not least, xylolytic fungi are capable of decomposing complex polymers such as lignin and lignified cellulose. In tundra, cellulose decomposition is mainly carried out by fungi (HOLDING, 1981). Fungi are very competitive in (GOKSØYR, 1975) utilising structurally intact plant material. Thus, standing dead plant material as well as litter and roots are heavily invaded by fungi and by bacteria only to a lesser degree (ibid.). In tundra soils, fungi are less divers than in other biomes (BUNNELL et al., 1975; BAB'YEVA & CHERNOV, 1982). Species composition is also different and furthermore varies between sites. *Cladosporium*, *Mortierella* and *Penicillium* are the most widespread genera. At Tareya (W.-Taimyr), cellulolytic species such as *Phoma eupirena*, *Aspergillus versicolor*, *Penicillium* spp. (CHERNOV et al., 1975) were isolated. Estimates of yeasts represent up to 17% of the fungal biomass (BAB'YEVA & CHERNOV, 1982) but may vary dramatically between years (BUNNELL et al., 1975). They seem to be largely restricted to the uppermost centimetres of drier soils (ibid.; HOLDING, 1981). Data provide conflicting evidence with respect to the significance of sterile mycelia. Many authors (HOLDING, 1981; ROSSWALL, et al., 1975) consider sterile mycelia as very widespread fungi. Yet, FLANAGAN & SCARBOROUGH (1974) rarely found sterile mycelia in litter or soil. Abundance and diversity also change between tundra types and within profiles. Thus, fungal species that were observed to colonise standing plant material differed from the rhizosphere with respect to species composition (CHERNOV et al., 1975) and physiology (FLANAGAN & SCARBOROUGH, 1974).

Bacteria become more competitive once the plant material has mechanically been disintegrated for example by passing through the gut of an invertebrate (GOKSØYR, 1975). Fungi are very much confined to the presence of plant material. Therefore they predominate in the upper few centimetres of soil and decrease with depth. Bacteria also predominate in the upper horizons and decrease with depth (PARINKINA, 1974). Yet, in contrast to fungi, they occur throughout the soil profile down to the permafrost table or even within the permafrost (MATVEYEVA et al., 1975; LYSAK & DOBROVOL'SKAYA, 1982, GILICHINSKY et al., 1995). Tundra soils are generally marked by moist to very wet conditions. Under these conditions, fungi are less competitive and bacteria may represent up to 75% of the microbiota (BUNNELL et al., 1975). Nevertheless, compared to dry sites, the bacterial productivity is much smaller at wet sites (PARINKINA, 1974). Also, aerobic bacteria are manifold more numerous than anaerobic or facultative anaerobic groups (DUNICAN & ROSSWALL, 1974). Among the physiological groups, those involved in nitrogen cycling predominate: utilisers of organic and inorganic nitrogen as well as aerobic and anaerobic ammonifying bacteria. Yet, nitrifying and

denitrifying bacteria are either rare or absent (MATVEYEVA et al., 1975; BUNNELL et al., 1975). Some physiological groups of bacteria participate in carbon cycling. Despite the fact that cellulolytic bacteria are generally less common in tundra (DUNICAN & ROSSWALL, 1974), bacteria were found to be responsible for anaerobic cellulolytic activity (ROSSWALL et al., 1975). Under anaerobic conditions in wet habitats, methanogenic bacteria are present (ibid.). Methane produced in subsoil horizons may further be oxidised by bacteria in better aerated upper or adjacent horizons (e.g., SLOBODKIN et al., 1992; SCHIMEL et al., 1993; WHALEN, et al., 1996). Despite the fact that methane oxidation appears to be an obligatory aerobic process (SCHIMEL et al., 1993), methanotrophs were also determined in water saturated soils (VECHERSKAYA et al., 1993). Methane may further be oxidised by nitrifiers due to similar shape and size (i.e., tetrahedral molecule and Van der Waals radii) of CH_4 and NH_3 and low specificity of the responsible monooxygenase enzymes (SCHIMEL et al., 1993). Yet in tundra, this process is presumably of minor importance since nitrifiers were reported to be less abundant. In addition to the just mentioned chemoautrophic bacteria, sulphate oxidising and reducing bacteria as well as iron oxidising and few reducing bacteria have been isolated (ibid., BUNNELL et al., 1975; DUNICAN & ROSSWALL, 1974; VAINSHTEIN & GOGOTOVA, 1992).
DUNICAN & ROSSWALL (1974) have concluded that the bacteria present in soils at the IBP sites are not specific for tundra (tundraphilic). Yet, the biome provides environmental conditions suitable for autotrophs that are less common in other environments (ibid.).

3.1.2 Microbial ecology

In the Arctic, as elsewhere, soil microbiota is controlled by both abiotic and biotic factors. Synoptic descriptions are given for instance by COLEMAN & CROSSLEY (1996), TATE (1995), KILLHAM (1994) or PAUL & CLARK (1989).

3.1.2.1 Abiotic factors

The microbiota is influenced by soil temperature and moisture, redox potential, pH and nutrients. In the Arctic, the most important and most evident controlling factors represent soil temperature and moisture. They both show independent and interactive effects (NADELHOFFER et al., 1997). Having a pergelic soil temperature regime with hard or dry, loose permafrost within the soil profile (S.T.), arctic soils insinuate a psycrophilic microbiota although it is rather cold tolerant than cold adapted. True psycrophilic micro-organisms represent the minor proportion (e.g., 10-20% fungi) (BLISS, 1975; FLANAGAN & SCARBOROUGH, 1974). For bacteria, this proportion increases in wetter and colder habitats (VASSILYEVSKAYA et al., 1975). Also fungi are more affected by moisture than bacteria (BUNNELL et al., 1975).

Microbiological and enzyme activities show many temperature optima (FLANAGAN & SCARBOROUGH, 1974). Furthermore, micro-organisms may also compensate for lower enzyme activities at low temperature by an increase of enzyme production (TIBBETT et al., 1998c). Thus, a complex of functional differences in both microbial community structure and physiology influence decomposition processes. At any scale, decomposition is generally slow and incomplete with increasing moisture and decreasing temperature (NADELHOFFER et al., 1992). On the other hand. lacking moisture inhibits decomposition independently of temperature. Microbiota is influenced by the litter quality and nutrients, particularly nitrogen (WALKER; 1996). Nutrient availability influences microbial growth. Although fungal growth is limited by nitrogen (KJØLLER & STRUWE, 1982), fungi are less influenced by nitrogen contents than bacteria (HOLDING, 1981). The microbial carbon source may be subdivided into two groups: substrates with low molecular weight that are soluble in water (i.e., simple sugars, organic acids) and complex polymer compounds such as starch, cellulose, hemicellulose, lignin and pectin (BLISS, 1997). Decomposition of the latter is slow particularly in the Arctic. Differences are enhanced by difference in substrate quality and different combination of soil moisture and temperature regime (NADELHOFFER et al., 1992). Soil pH influences the microbial community composition. Most fungi predominate in acid habitats (FLANAGAN & SCARBOROUGH, 1974). Actinomycetes occur in soils with neutral to alkaline soil reaction. This requirement along with their heterotrophic nature may explain their lower abundance in tundra (DUNICAN & ROSSWALL, 1974). Bacteria inhabit soils with more neutral reaction. Yet, they predominate in soils with acid pH when the site is water-logged (CLARHOLM et al., 1975) which suggests that bacteria are less competitive when fungi are present. In addition to community structure, soil pH influences microbial processes as for example methanogenesis (DUNFIELD et al., 1993; SCHIMEL et al., 1993). During the last decade, the general interest in soil structure and microbiota interrelationships increased (e.g., SMILES, 1988; BRUSSAARD & KOOISTRA, 1993; MONREAL & KODAMA, 1997). Soil physical properties influence for instance substrate location and accessibility, enzyme activity (PAGLIAI & DENOBILI, 1993; KANDELER & MURER, 1993) and grazing pressure (HASSINK et al., 1993). Yet, to date there are only few investigation of these relationships in arctic soils (e.g., GEBAUER et al., 1996).

3.1.2.2 Biotic factors

The composition of the plant canopy, roots and fauna are among the biotic controls of the microbiota. Detailed descriptions are given for example by FITTER et al. (1985) and COLEMAN & CROSSLEY (1996).

Symbiotic relationship between micro-organisms of plants have been described above. Furthermore, certain fungi and yeasts occur in association with particular plants (CHERNOV et al., 1975; BAB'YEVA & CHERNOV, 1982). This relationship is partly symbiotic (BLISS, 1997; BUNNELL et al., 1975; MILLER & LAURSEN, 1974) and partly not well understood. Ammensalism that is to say inhibition by toxins, is known for lichens. They exude antibiotics that particularly suppress bacteria. Plant-microbe relationships may partly be explained by a plant specific rhizosphere (see below). Roots exudates (e.g., soluble carbohydrates) enhance microbial proliferation (BARBER & LYNCH, 1977). In the Arctic, roots have developed specific interactions to exploit the resources of the soil (SCHIMEL et al., 1996).

Despite the importance of trophic interactions between fauna and microbiota for soil function (COUTEAUX & BOTTNER, 1994; LAVELLE et al., 1996), in the Arctic these relationships are only partially investigated (BLISS, 1997). Protozoa and invertebrates directly influence the microbiota by grazing, inhibition, faeces addition and dispersal (WHITTAKER, 1974). Faunal impact is not restricted to soil animals. As such cyanobacteria on the soil surface for instance, are being grazed by herbivore geese (SOLHEIM et al., 1996). An indirect effect results from the input of nutrients (e.g., ammonium, nitrate, phosphate) by animal faeces of birds and lemmings (CHERNOV & MATVEYEVA, 1997; WÜTHRICH, 1994).

3.1.2.3 Microbial habitats

The functioning of the microbial community is interwoven with space, time and food resource. These represent the three dimensions of the original 'niche' concept that define the role of an organism in a community (LOESCHKE, 1987). Thus, space, or habitat, where functioning takes place, represents one dimension. The concept was largely applied to the understanding of population and its linkage to competition. Its limitation lies in the separation of organisms and environmental factors as well as in neglecting scale (ibid.). The microbial loop concept elucidated the role of protozoa and bacteria in the oceanic food web (POMEROY, 1974). Its applicability to soil is subject of discussion (CLARHOLM, 1994). In order to determine the function of the microbial loop in soil, the investigation of the environmental controls led to the formulation of a hierarchical concept of 'spheres' of influence (COLEMAN, 1994; BEARE et al., 1995). This concept was already beyond the microbial loop concept

inasmuch that it included soil biota in general. It aims at the explanation of the spatial heterogeneity of biotic communities and functioning, one hierarchical level influencing another. The 'spheres' of influence include the rhizosphere and detritusphere as well as the drilosphere (the region of faunal activity), the porosphere (the zone of aerated or water-filled pores), and the aggregatussphere of macro- and micro-aggregates. In this study, the conception of 'spheres' of influence is adopted. Furthermore, 'microbial habitat' is used as a more general term in awareness of its hierarchical and interlocking nature. The respective habitats are investigated to different degrees and so is the evaluation of the significance for biodiversity and biogeochemical cycling (e.g., COUTEAUX & BOTTNER, 1994; BOLTON et al., 1993). The hierarchical concept narrows the problem of spatial dimension. Yet, as for example experienced for the rhizosphere, definition of spatial profiles show experimental constraints that may consequently be tackled by mathematical models (e.g., SMITH, 1982, p. 37). In addition to the hierarchical approach, ZVYAGINTSEV et al. (1994) and ZVYAGINTSEV (1994) suggest a stratigraphic concept that describes changes in microbial communities between layers of vegetation and soil. According to the authors, temporal and spatial differences elucidate ecosystem functioning at ecosystem level and even between vegetation zones as suggested by MISHUSTIN (1975). Further implications of the microbial scale for the ecosystem level are discussed by SCHIMEL (1995).

3.2 Methodology

In early studies on soil micro-organisms, culture plates and direct microscopy were common tools to characterize the microbial pool. As a consequence, these direct methods were also applied for the analysis of the microflora at the IBP sites (HOLDING, 1981). Quantitative estimates of the microbial pool by culture methods are 10^2 to 10^3 smaller than by direct microscopy (PARINKINA, 1974). This is explained by the fact that only a small proportion of soil micro-organisms may be cultured. The inaccuracy of culture methods is even more dramatic as recent application of molecular techniques has revealed. Thus, the phylogeny of bacteria from a wide variety of habitats differs substantially from characterized bacteria cultured from those same environments (DELONG, 1996). The problem of culturability is irrelevant to direct microscopy (bright field or fluorescence microscopy). More recently, computer based image analysis has facilitated enumeration and biovolume determination (BÖLTER et al., 1993). Methods differ depending on the target group of micro-organisms and with respect to staining. Procedure protocols are given for instance by BLOEM et al. (1995), TROLLDENIER (1993), ALEF (1991), or FÆGRI et al. (1977). A constraint of direct microscopy represents lacking differentiation between dead cells or 'ghost' hyphae (JENKINSON & LADD, 1981; PARINKINA, 1974). The use of specific stains as acridine orange and fluorescein diacetate (SÖDERSTRÖM, 1979) partially overcame this constraint. Further sources of inaccuracy are sample homogenisation, dilution factors, magnification and conversion factors (BLOEM et al., 1995; RICHAUME et al., 1993).

As mentioned before, DNA extraction (SÅÅNO & LINDSTRÖM, 1995; TORSVIK et al., 1994; PIETRAMELLARA et al., 1997) along with determination of specific biomarkers (ZELLES & ALEF, 1995) elucidate microbial community structure partially down to the species level. However, to date many aspects of specific functions remain unknown despite this increasing knowledge about structure.

In studies on mineral cycling and energy flow, the microbial pool has often been considered as an undifferentiated whole (NANNIPIERI et al., 1994). Indirect methods provided tools for the estimation of microbial biomass. The use of chloroform fumigation methods (JENKINSON & LADD, 1981; JOERGENSEN, 1995; VANCE et al., 1987; HORWARTH, et al., 1996), substrate induced respiration (ANDERSON & DOMSCH, 1978; SPARLING, 1995) and heat output (SPARLING, 1983) enabled indirect determination of microbial biomass. As an example given, SPARLING

(1983) calculated the relationship between heat output at 22°C and microbial biomass of soil amended with glucose to a saturated level. Heat evolution is measured by means of microcalorimetry, which is based on the principles of thermodynamics of irreversible processes (GUSTAFSSON, 1991). These are described in classical textbooks about bioenergetics or in reviews on microcalorimetry (e.g., GNAIGER, 1989; FORREST, 1972). This calculation of microbial biomass only applies to the heat production immediately after substrate amendment and before cell proliferation (SPARLING, 1983). The latter is always accompanied with a much greater heat production (BELAICH, 1980; LAMPRECHT, 1980). Accordingly, calculation of microbial biomass may not always be done accurately. Furthermore, it has to be borne in mind that only the active microbial biomass is measured and the proportion of dormant micro-organisms may be significant. As it is known for substrate induced respiration (SIR), only particular micro-organisms are stimulated by substrate amendment whereas others are not (e.g., anaerobic micro-organisms). Microbial biomass may thus be underestimated in for instance forest soils or waterlogged soils (HEILMANN, 1993). Since heat output also (with or without substrate amendment) represents biological activity, the tool has proved to be a sensitive method to investigate the overall microbiological activity in soils (MORTENSEN et al., 1973; LJUNGHOLM et al., 1979a,b; ZELLES et al., 1990; RAUBUCH & BEESE, 1995). ZELLES et al. (1987a;b) even consider heat production (along with ATP analysis and respiration) a better parameter for these purposes than specific activity measurements. Heat output is associated with respiration (SPARLING, 1981b; BÖLTER, 1994) and shows good correlation with enzyme activity analyses (ALEF et al., 1988). Equipped with a perfusion system, microcalorimetry may also be designed to investigate anaerobic processes only (ALBERS et al., 1995). High costs of microcalorimeters limit the use as a routine analysis. Thus, data for comparability are not widely spread. Furthermore, data from the bibliography have to be read cautiously because standardisation of the method is still in its infancy.

Other methods to determine the microbial pool are based on the extraction of specific cell components such as adenosine-triphosphate (ATP). The use of ATP as an index of microbial biomass (OADES & JENKINSON, 1979; BROOKES & OCIO, 1989) is based on the assumption that ATP is a constant component of diverse microbial cells. ATP is extracted from soil using either acid extractants such as trichloracetic acid (JENKINSON & OADES, 1979), sulphuric acid (EILAND, 1983), phosphoric acid (CIARDI & NANNIPIERI, 1990) or DMSO (BAI et al., 1988) or alkaline extractants such as Tris-EDTA (VAN DE WERF & VERSTRAETE, 1979) or boiling Tris-

buffer (HOLM-HANSEN & BOOTH, 1966, GRAF, 1977). The assays differ with respect to extraction efficiency, recovery of an internal standard, and quenching effects during measurement. Comparative studies of different extraction methods are given for example by CONTIN et al. (1995), FRIEDEL (1991), ZELLES et al. (1985), VERSTRAETEN et al. (1983) or EILAND (1983; 1979). SPARLING & EILAND (1983) therefore consider the extraction method as most important factor causing differences in ATP measurements. The most appropriate method also depends on the soil material under investigation since soil properties influence the quality of the assay (VERSTRAETEN et al., 1983). Thus, most studies have been carried out on agricultural soils whereas ARNEBRANDT & BÅÅTH (1991) encountered strong quenching effects when measuring ATP-contents of forest humus. Since ATP-contents in soil were found to fluctuate under field conditions (e.g., BARDGETT & LEEMANS, 1995; WANNER et al., 1994; INUBUSHI et al., 1989) as well as due to storage and sample treatment (e.g., SPARLING et al., 1986; AHMED et al., 1982), it is being argued that the ATP-contents of soils rather reflect the physiological state of the soil micro-organisms (NANNIPIERI et al., in press). Estimation of microbial biomass is recommended under standardized conditions prior to extraction (i.e., preincubation, adjustment of water content).

Indirect determination methods only provide an estimate and the risk of error is higher than in direct methods (NANNIPIERI et al., 1994). Comparative studies or reviews on methods to estimate the microbial pool are given for instance by BECK et al. (1997), ALEF (1993), OCIO & BROOKES (1990), JENKINSON & LADD (1981) or ANDERSON & JOERGENSEN (1997).

In addition to determination of the microbial pool, its ecophysiological characterisation gains importance in understanding ecosystem functioning (ANDERSON, 1994; INSAM & ÖHLINGER, 1993). Relationships between microbial and/or soil parameters describe for instance the state of equilibrium of soil organic matter (C_{mic}:C_{org}-ratio; ANDERSON & DOMSCH, 1989). The metabolic (ANDERSON & DOMSCH, 1993) or caloric quotient (RAUBUCH & BEESE, 1995) characterizes the energetic state of soil micro-organisms.

General books on methods in soil microbiology have been published by ALEF & NANNIPIERI (1995); WEAVER et al. (1994), ALEF (1991) and SCHINNER et al. (1993). Synoptic reviews are given by NANNIPIERI et al. (in press), NANNIPIERI (1990), SPARLING (1985) or JENKINSON & LADD (1981).

4. Materials and Methods

> Denn da der Beobachter nie das reine Phänomen mit Augen sieht, sondern vieles von seiner Geistesstimmung, von der Stimmung des Organs im Augenblick, von Licht, Luft, Witterung, Körpern, Behandlung und tausend andern Umständen abhängt, so ist ein Meer auszutrinken, wenn man sich an die Individualität des Phänomens halten und diese beobachten, messen, wägen und beschreiben will.
>
> J.W. v. Goethe

4.1 Field procedures

4.1.1 Soil survey and selection of sites

Levinson-Lessing

Soil survey had been started during the expedition TAYMYR 1995 (BECKER, 1997; PFEIFFER et al., 1996) and was completed in the subsequent year during the expedition TAYMYR 1996 in co-operation with my colleagues H. Becker, A. Gundelwein and Th. Müller-Lupp (GUNDELWEIN et al., 1997). The procedure followed the soil mapping at Labaz (GUNDELWEIN, 1998, PFEIFFER et al., 1996) and is summarised in Section 4.4.1.1.

For this study, three predominant groups of soil-patterned ground-vegetation complexes were selected according to their spatial proportion: polygonal tundra, solifluction slope with non-sorted steps, and soils of mountain tops with non-sorted stripes. Each of these compound mapping units was represented with either two or three profiles.

4.1.2 Profile description

Levinson-Lessing

Profile description followed the procedure as described for the soils at Labaz (Sect. 5.4.1.1). As mentioned before a peculiarity of arctic soils represents the presence of patterned ground due to freeze-thaw processes. The micro-relief was accounted for by separate profile descriptions with affixes to the profile number (e.g., profile 11.1 and 11.2). In addition to the assessment of soil drainage according to the Soil Taxonomy (S.T.), site specific soil moisture conditions were further described (depth of water table, slope water, supra-permafrost water). In this study soil profiles clearly represented the active layer of a particular soil since no drillings of the underlying permafrost were carried out. Besides soil classification according to the S.T. (SOIL SURVEY STAFF, 1994; 1998), soil types were additionally classified according to the WRB (SPAARGAREN, 1998).

Labaz

Profile description was carried out by my colleague A. Gundelwein (IfB) and is described in Section 4.4.1.1. Micro-sites were described separately and differentiated with affixed letters to the profile numbers (e.g., 2a and 2b). On the basis of the profile description, soil classification was supplemented by soil types according to the S.T. (SOIL SURVEY STAFF, 1998) and WRB (SPAARGAREN, 1998).

4.1.3 Soil sampling

Levinson-Lessing

Soil sampling procedure was described in the expedition report (BÖLTER & SCHMIDT, 1997) Sampling generally followed the horizon notations and ensured mixed bulk samples. When topsoil horizons were thicker than 5 cm subsamples were taken. The top 0.5 cm were sampled in unvegetated soils. In addition, special features like roots, ferruginated fabric, soil around roots and water veins were also sampled. These samples were taken in order to investigate whether these spots showed other microbial properties than the ambient soil horizon.

As far climatic conditions allowed soil samples for pedological analyses were air dried in aluminium dishes. Mineral horizons were then sieved through a 2 mm mesh size sieve. Fresh samples for microbial analyses were stored in a permafrost pit which served as a refrigerator. During transportation it was ensured that these samples were kept at cool places. In the home laboratory they were stored deep-frozen at -20°C until analysis.

For determination of bulk density and pore size distribution core samples of the top 4 cm were taken with 100 cm^3 cores, where feasible (see appendices for details). The cores had been driven into the soil by means of a percussion tool that ensured even placement. The core samples were stored in special sample cases in the permafrost pit. During transport (by helicopter, aircraft, car and on foot) maximum care was taken to minimalize exposure to vibrations.

4.1.4 Statistical considerations

Due to methodical restrictions, limited time and financial resources as well as restricted transportation capacities neither a DIN standardised sampling procedure (HARTGE & HORN, 1989) nor a randomised plot design were applied. Spatial representativity of a particular soil

was decided upon the basis of the soil map (with a grid of 20 to 250 m) and its relative proportion of the whole study area. As mentioned before, at Levinson-Lessing two to three profiles per unit of soil-patterned ground-vegetation complex were sampled to account for the variability within units. For the soils at Labaz, an according selection of sites was not feasible because of restricted labour. Yet, the most characteristic and dominant soils were sampled as is described in Sections 4.1.1 and 4.1.2. All soils were sampled over the period of the respective expeditions during which the vegetation changed from early spring to late autumnal aspect. Because of the short vegetation period temporal variability could not be accounted for.

4.2 Pedological parameters

4.2.1 Total and organic carbon (C_t and C_{org}) and total nitrogen content

Total carbon and total nitrogen contents were analysed by a CNS-Analyser. Aluminium cups with 5-10 mg of air-dried and ground soil (2 replicates) were combusted at 1050°C (flash combustion). The combustion products (CO_2 and N_2) were measured by thermal conductivity using helium as a carrier gas and metallic copper in the reduction reactor.

At both experimental sites inorganic carbon content (C_{inorg}) of the soils was not detectable (GUNDELWEIN, 1998), further analysis of organic carbon (C_{org}) thus was neglected. The only exception represented the dry uphill soil (profile Lb1/95), where a mean C_{inorg} content of 0.2% w.w. had been measured in the mineral horizons (ibid.). In the following C_{org} is considered as being equal to C_t.

4.2.2 Determination of soil pH

Field analyses

During the 1996 expedition at Levinson-Lessing, determination of soil pH was carried out in the field. Fresh soil was measured in a 0.01 M $CaCl_2$ (soil/solution-ratio was 1:2.5). Soil pH was determined potentiometrically in the supernatant solution after automatic equilibration of the pH meter.

Laboratory analyses

The pH of the Labaz 1995 soil samples was measured in the laboratory according to SCHLICHTING et al. (1995). Approximately 10 g of air-dried soil was suspended in 25 ml H_2O and 0.01 M $CaCl_2$ respectively. Soil pH was determined potentiometrically in the supernatant solution after 30 min. of equilibration.

4.2.3 Bulk density and carbon inventory (*CI*)

Levinson-Lessing

After determination of the pore size distribution (see below), bulk density was determined according to SCHLICHTING et al. (1995). Dried (at 105°C) core samples (100 cm^3) were weighed (*DW*). Bulk density (D_b) was calculated by the ratio between the mass (*DW*) and the total volume (V_t):

$$D_b = \frac{DW\,[g]}{V_t\,[cm^3]} \qquad (4.2.3.1)$$

Since only the top 4 cm of the soils at Levinson-Lessing were sampled. The carbon inventory (*CI*) was calculated for the top 4 cm using the equation:

$$CI = D_b * depth\,[cm] * C\text{–}content\,[g\ C * g^{-1} d.wt.] * 10 \qquad (4.2.3.2)^1$$

where

CI is the carbon inventory [kg m^{-2}]

D_b = bulk density (Equation (2.3.1))

depth is either the depth of horizon or core (max. 4 cm)

C-content [g C*g^{-1} d.wt.]

In cryogenic soils, carbon contents can only be extrapolated to an area if attention is paid to ratio of the micro-relief to the total area (GUNDELWEIN, 1998). However, the carbon inventory *CI* is expressed in kg m^{-2}.

When the soils contained gravel, the *CI* values were corrected for volumetric gravel content (V_g). The volume of the fine earth (V_f) was calculated by deducting V_g from the total volume of the solid phase (V_s):

$$V_f = V_s - \left(\frac{V_s}{100} * V_g \right) \qquad (4.2.3.3)$$

The bulk density of the fine fraction (D_{bf}) was calculated by the ratio of its weight (DW_f)

$$D_b * V_f = DW_f \qquad (4.2.3.4)$$

to the total volume (100 cm^3)

$$\frac{DW_f}{100\,cm^3} = D_{bf} \qquad (4.2.3.5)$$

The carbon inventory was then calculated using Equation (4.2.3.2) and the corrected bulk density (D_{bf}) from Equation (4.2.3.5).

Labaz

For the Labaz samples, bulk density and carbon inventory were measured accordingly by my colleagues of the Dpt. Soil Science of the University of Hamburg. By courtesy I used their data (published by GUNDELWEIN, 1998) and modified (according to Equation (4.2.3.2)) them for comparison (see Section 4.4.2).

[1] factor was derived from 10,000 cm^2/1,000 cm^2

4.2.4 Pore size distribution

Pore size distribution in soil was determined by drainage at successive suctions applied (SCHLICHTING et al., 1995). The method is based on the relationship of volumetric water content at a given suction and the neck diameter of pores (Tab. 4.2.4-1).

Tab. 4.2.4-1: Relationship between suction [matric suction; kPa] and classes of pore size and their biological significance

Suction		Pore size class		Biological significance
Matric suction [m]	pF	Neck diameter of pores [µm]	Classes	
10^5	7			Hygroscopic water
150	4.2	<0.2	< micro-pores	Permanent wilting point
3	2.5	10	meso-pores	Available water
0.6	1.8	50	macro pores <	Field capacity
0.04	0.6	1000		Gravitational water

The water saturated core samples (100 cm^3) were drained on a sand bed at a constant water table of 2 cm below surface (0.04 m suction). This suction drains pores with a neck diameter greater than 1000 µm. The cores were than placed on to porous ceramic plates at which a suction of 0.6 m and then 3 m was applied. The water loss corresponds to the pore volume with a neck diameter of 1000-50 µm and 50-10 µm respectively.

A suction of 150 m can only be applied in closed high pressure chambers. For practical reasons, 0.5 cm subsamples were placed on to the suction plate in the high pressure chamber. At constant weight the sampled were weighed and dried at 105°C. The water loss corresponds to the pore volume with a neck diameter 10 - 0.2 µm.

The water content [%] at each suction was calculated as follows:

$$water\ content\,[\%] = \frac{water\ content\,[g]}{d.wt.\,[g]} * 100 \qquad (4.2.4.1.)$$

The volumetric water content [vol.%] was calculated with the water content [%] from Equation (4.2.4.1) multiplied with the bulk density D_b from Equation (4.2.3.1). The pore volume of the above given pore size classes was derived by deduction of the respective volumetric water content from the porosity (Equation (4.2.4.2)). The total pore volume or porosity (Vp) is obtained from the volumetric water content after water saturation:

$$V_p\,[\%] = \left(1 - \frac{D_b}{D_p}\right) * 100 \qquad (4.2.4.2)$$

where: D_b is the bulk density (Equation (4.2.3.1.))

D_p is the particle density

i.e., 2.65 g cm^{-3} for mineral horizons, 1.30 g cm^{-3} for organic horizons

The proportion of the freely draining pores (>50 µm) is defined as the air capacity of the soil. The proportion of the pore sizes between 0.2 and 50 µm is the available field capacity. The air capacity and the available field capacity were evaluated according to the German Soil Classification (AG BODEN, 1994).

4.3 Microbial parameters

4.3.1 Total hyphal length and fungal biovolume

Total hyphal length and fungal biovolume were determined by epifluorescence microscopy and image analysis. The method was described by BLOEM et al. (1995). The procedure was modified as follows (SCHMIDT & BÖLTER, unpubl. data):
The soil suspension (100 mg soil per ml H_2O) was resuspended for 1 min. with a blender and a vortex respectively. 100-500 µl of the soil suspension were added to 5 ml of a acridine orange (AO) stain (1:10,000 solution). After 3 min. staining in the dark, the suspension was filtered through a 3 µm pore size polycarbonate (PC) filter. The filter was then mounted on a slide with immersion oil (Cargille™ type A). The slides were analysed by epifluorescence microscopy with blue light at a 400X magnification. Total hyphal length and biovolume were measured by image analysis (LEITZ™ Aristoplan and Quantimed 500™).

Hyphal length L [m g^{-1}] was calculated from the mean hyphal length per grid and the hyphal length per filter as is described for fungal biovolume in the following.

Based on the assumption that fungal hyphae resemble ideal cylinders, the mean fungal biovolume per grid was calculated from the length and width using the equation:

$$V_g = \frac{\frac{\pi}{4} * W^2 * L}{n_g} \qquad (4.3.1.1)$$

where V_g the mean fungal biovolume per grid
L the total hyphal length [µm]
W total fungal width [µm]
n_g number of grids counted

The volume per filter was then calculated as follows:

$$V_f = V_g * M_f \qquad (4.3.1.2)$$

where V_f fungal biovolume per filter
V_g mean fungal biovolume per grid (Equation (4.3.1.1))
M_f microscope factor
$M_f = A_f/A_g$
A_f area of filter (here: 19,231.0 µm)
A_g area of grid (here: 4,940.8 µm)

The fungal biovolume V per gram soil (d.wt.) was calculated by

$$V = \frac{V_f * f_d}{V_s * DW} \qquad (4.3.1.3)$$

where V fungal biovolume [$\mu m^3\ g^{-1}$][1]
V_f fungal biovolume per filter (Equation (4.3.1.2))
f_d dilution (here: 10 ml)
V_S volume of suspension (e.g. 0.5 ml)
DW dry weight of the soil sample

Accordingly hyphal length L [m g^{-1}] was calculated from the mean hyphal length per grid and the hyphal length per filter.

The fungal biomass [$\mu g\ C_f\ g^{-1}$] was estimated using a specific carbon content of $1.3*10^{-13}$ g C μm^{-3} (BLOEM et al., 1995).

4.3.2 Microcalorimetry

Physiological processes are accompanied by production of heat (Q) which can be measured by means of a microcalorimeter. Heat output of soils is used to characterize the overall microbial activity (LJUNGHOLM et al., 1979a; SPARLING, 1981a,b; ALBERS ET AL., 1995) as well as to estimate microbial biomass after glucose amendment (SPARLING, 1983). The evolved heat (Q) comprises the heat produced by catabolic (Q_{cat}) and anabolic (Q_{an}) reactions (BELAICH, 1980).

$$Q = Q_{cat} + Q_{an} \qquad (4.3.2.1)$$

The contribution of anabolic processes accounts for 1.5 and 8% of the overall change in heat evolved (Q) under aerobic and anaerobic conditions, respectively. Anabolic processes may thus be neglected (BELAICH, 1980). Since the heat production due to abiotic reactions is not greater than 10% of the Q value (MORTENSEN et al., 1973), it can be concluded that the measured heat production mainly represents the catabolic heat production (Q_{cat}).

[1] In the result section, the fungal biovolume was given in mm^3. The result from Equation (3.1.3) [μm^3] was devided by 10^9.

Microcalorimeter

The apparatus is arranged as a two channel twin calorimeter (BÖLTER, 1994; FORREST, 1972; WADSÖ, 1980) with a closed chamber system. The reaction of the studied sample takes place in one chamber whereas the other serves as a reference. The heat produced in the reaction vessel is transferred to a surrounding heat sink, i.e. metal block. By means of a thermopile between the reaction vessel and the heat sink, the heat flow is recorded as a voltage signal of the thermopile. The device is equipped with two reaction and two reference vessels. The voltage (V) signal is continuously recorded by one nanovoltmeter for each reaction vessel (DMM181 and DMM190, Keithley, Germany). V is proportional to the heat flow (dQ/dt):

$$\frac{dQ}{dt} = \varepsilon^* V \qquad (4.3.2.2)$$

where ε is a electrical calibration constant (here: 7.4 and 8.31 $\mu W \mu V^{-1}$ respectively)

Thus, the microcalorimeter acts a Watt-meter (MORTENSEN et al. 1973). Good thermal equilibrium is reached after 2 to 3 hours after introduction of the soil sample into the reaction chambers (LJUNGHOLM et al., 1979a,b). The voltage signal V of the soil sample [after 3 h] is corrected for the baseline and converted into Watt [μW] using Equation (4.3.2.2) and given in microwatt per gram dry soil [$\mu W\ g^{-1}$ d.wt.].

4.3.2.1 Basal heat output

Basal heat output is the heat output without substrate amendment. Sample preparation and measurement procedure have been described in detail (ALEF, 1991; 1995; ALBERS et al., 1995b; MORTENSEN et al., 1973). The following alterations were made:

Defrosting soil samples causes a flush of activity due to decomposing dead cells (e.g. VAN GESTEL et al., 1993). Preliminary tests on the present soil material showed that after defrosting, the samples had become stabilised after four days at 4°C. As a consequence soil samples were loosely capped and defrosted at these conditions. Prior to measurement the soils were preincubated at measurement temperature for 24 h to enable heat output and respiration rates to stabilise (SPARLING, 1983). The water content was adjusted by percolating an excess amount of water through the soil samples. Two replicates of approximately 5 g were put into an aluminium envelop and placed in the reaction vessel.

4.3.2.2 Substrate induced heat output

Sample preparation followed the procedure as described for the basal heat output (Equation (4.3.2.1)). Glucose was added shortly before measurement.

SPARLING (1983) calculated the relationship between heat production at 22°C and microbial biomass of soil amended with glucose at saturated level:

$$1\,g\,C_{mic} = 180\,mW \qquad (4.3.2.3)$$

At the time, the addition of 5% w.w. or 0.5% w.w. of glucose for organic horizons or mineral horizons respectively had been considered as the saturated level. Although more recently prior investigation of the best glucose:soil-ratio has been recommended (ALEF, 1995), SPARLING (1983) also emphasised that the relationship of Equation (4.3.2.3) only applies to the given laboratory conditions.

For the above stated reasons, 5% w.w. glucose (30 vol.% glucose solution) were added to organic horizons (S.T. > 12% C_{org} depending on clay content). 0.5% w.w. glucose (3 vol.% glucose solution) were added to the mineral horizons.

Calculation of results

The heat output of the soil sample in Watt [μW] obtained from Equation (4.3.2.2) was given in microwatt per gram dry soil [μW g^{-1} d.wt.]. Since the microcalorimeter used in this study does not provide a temperature control, the actual temperature (T) during measurement was therefore recorded. For comparability reasons the actual heat output (Q_a) was then extrapolated to a theoretical heat output at 22°C (Q_e) using an Arrhenius correction. The Arrhenius Equation (4.3.2.4) calculates the influence of temperature on rate constants for chemical reactions (SPARKS, 1988).

$$k = Se^{-E/RT} \qquad (4.3.2.4)$$

where k is the rate constant
S is a frequency factor
R is the universal gas constant
T is the temperature [K]
E is the activation energy

The frequency factor S was calculated as follows:

$$S = \frac{Q_a}{e^{-E_0/T-T_0}} \qquad (4.3.2.5)$$

where S is the frequency factor

Q_a is the actual heat output

T is the temperature during measurement [K]

E_0 and T_0 are regression parameters

with E_0 = 308.56 K and T_0 = 227.13 K from LLOYD & TAYLOR (1994). The heat output at 22°C (Q_e) was then calculated using the Arrhenius Equation (4.3.2.4):

$$Q_e = S * e^{-E_0/T_{22}-T_0} \qquad (4.3.2.6)$$

where Q_e is the heat output at 22°C

S is the frequency factor as obtained from Equation (4.3.2.5)

T_{22} is temperature T=295 °K

E_0 and T_0 are the regression parameters as in Equation (4.3.2.5)

Microbial biomass

In anaerobic soils substrate induced methods for the determination of microbial biomass are troublesome. During measurements this also turned out to be the case for the soils in this study. Therefore, further calculation of microbial biomass from the substrate induced heat output (Equation (4.3.2.3) by SPARLING, 1983) was neglected. SIQ values were given in μW g^{-1} d.wt.. It is left to the reader to use the *SIQ* values as an indicator of microbial biomass (for this purpose Equation (3.2.3) may be expressed as 5.6 μg C_{mic} per μW).

4.3.3 Adenosine triphosphate

The estimation of adenosine triphosphate (ATP) is based on the luciferine-luciferase bioluminscence assay by means of a bioluminometer (e.g., JENKINSON & LADD, 1981). Light is emitted during the oxidation of luciferine by ATP, which is catalysed by luciferase in the presence of Mg^{2+}. During this reaction (Equation (3.4.1)), luciferine is first adenylated. In the presence of O_2, it then further breaks down to form adenosine monophosphate (AMP), inorganic phosphorus (P_i) and light. Hence, the emitted light correlates to the ATP content (translated from ALEF, 1991):

$$ATP + luciferine + O_2 \xrightarrow{luciferase+Mg^{2+}} AMP + P_iP_i + CO_2 + oxyluciferine + light \qquad (4.3.4.1)$$

ATP extraction

ATP was extracted from soil using boiling Tris buffer solution (HOLM-HANSEN, 1966; GRAF, 1977; VOSJAN et al., 1987).

One gram of triplicate samples of fresh soil were extracted with 50 ml of boiling 0.02 M Tris buffer solution (pH 7.8) for one minute. For determination of the recovery rate, 50 µl of standard solution (equivalent of 1 µg ATP) were added to two more replicates and extracted accordingly. Extracts were kept frozen until analysis.

Assay

Prior to analysis, extracts were defrosted and kept at room temperature. 100 µl of the extract were pipetted into a cuvette containing 150 µl of assay solution (0.02 M Tris-7.5 mM $MgSO_4$-solution). Inside the bioluminometer (Lumac BV), 100 µl crude luciferine-luciferase enzyme solution (firefly lantern extract, Sigma FLE 50™) were added to the diluted soil extract. The light emission is integrated over a period of 10 s. The relative light units (RLU) are converted into ATP contents against a calibration curve. In this manner, three replicated cuvettes were measured. For determination of the inhibition rate, an internal standard of 0.5 ng ATP was added to another three replicated cuvettes of the diluted soil extract and measured accordingly.

Calculation of results

The ATP contents of the soil extract (A-value), the soil extract with standard in the extract (C-value) and the soil extract with standard during measurement (B-value) were read from the standard curve. A- and C-values were corrected for inhibition (obtained from B-value). The measured ATP content of the soil (A-value) was given in micrograms per gram dry weight of soil and corrected for recovery of added ATP (obtained from C-value). See appendices (A1.1-A1.5) for equations.

4.4 External data

4.4.1 Field procedure at Labaz

4.4.1.1 Soil survey and profile description

Soil survey had been started during the expedition TAYMYR 1994 (PFEIFFER & HARTMANN, 1995) and was completed in the subsequent year during the expedition TAYMYR 1995 (PFEIFFER et al., 1996). The procedure was described in detail by GUNDELWEIN (1998) and is summarised here as follows:

The study area comprised a total area of 6 km². Prior to mapping and site selection the area was walked thoroughly to achieve an overview. First, units of patterned ground and vegetation complexes were marked off since these reflect the edaphic conditions particularly well (THANNHEISER, 1989). Soils and soil boundaries were confirmed by control diggings. Depending on site specific properties (morphology, patterned ground) distance between two controls ranged from 20 to 250 m. Thus, compound mapping units of soil- patterned ground and vegetation complexes were established in accordance with the topography. For each mapping unit representative soil pits were selected and profiles described in detail. Soil profiles were dug up to the permafrost table.

Profile description was carried out using the US Soil Taxonomy, 6th edition (SOIL SURVEY STAFF, 1994). Supplementary characteristics (texture, gravel content, structure, rooting intensity) were described according to the German Soil Survey Manual (Bodenkundliche Kartieranleitung, 4th edition, AG BODEN, 1994). Soil colour was given in hue and chroma values by the MUNSELL SOIL COLOR CHART (1988).

Finally, the soils were classified according to the soil taxonomy (S.T.) to the subgroup level. The S.T. represents the most commonly used classification system for arctic soils.

4.4.1.2 Soil sampling

During the expedition TAYMYR 1995 (BOLSHIYANOV & HUBBERTEN, 1996), soil sampling was carried out by my colleague M. Sommerkorn (IPÖ) at Labaz in July 1995 (SOMMERKORN, 1998). Soils were sampled in steps of several centimetres. Topsoils were sampled in steps of 2, 3 and 5 centimetres, whereas subsoil horizons were sampled in steps of 10 centimetres. Samples were air-dried immediately after sampling. At the laboratory in Kiel, subsamples for microbiological analyses were kept frozen at -20°C. Bulk soil samples were sieved through 2 mm mesh size sieve and stored under dry and cool conditions.

4.4.2 Bulk density and carbon inventory

For the Labaz samples, bulk density and carbon inventory were determined by my colleagues of the Dpt. Soil Science of the University of Hamburg. The procedure was the same as was described for the Levinson-Lessing samples in Section 4.4.2.3. Data were used for carbon inventory (Section 5.2.3) and microbial inventory (Section 5.4.3).

4.4.3 Total bacterial number and bacterial biovolume

Total bacterial number and bacterial biovolume were determined by means of epifluorescence and image analysis by M. Bölter, IPÖ Kiel (BÖLTER, 1998, SCHMIDT & BÖLTER, unpubl. data). Sample preparation and analysis followed the procedure as described for determination of fungal biomass in Section 4.3.1 with the following alteration:

The soil suspension was resuspended for 1 min with a vortex and filtered through a 0.2 µm pore size PC filter after AO staining. The slides were analysed by epifluorescence microscopy with blue light at a 800X magnification. Cells were counted and biovolume was measured by image analysis (LEITZ™ Aristoplan and Quantimed 500™) and calculated according BÖLTER et al. (1993).

4.5 Statistics

4.5.1 Regression analyses

The relationship between microbiological data sets (i.e., parameters of microbial biomass, basal and substrate induced heat output, ATP content) was tested by linear regression analysis. In these pairs of observation of y and x, y was assumed to depend on x, the independent variable. A relationship was accepted when $r^2 \geq 0.70$.

4.5.2 Testing of equality of two populations

In the soils of this study, populations showed non-normal distribution (difference of variance $s_1^2 \neq s_2^2$). For the comparison of two data sets, equality of means (μ_1, μ_2) was thus tested using a computer package (Statview™) based significance Mann-Whitney U-test when random sample size n_1, $n_2 \geq 7$. Difference of means (μ_1, μ_2) was accepted as significantly different at the following significance level p: $p \leq 0.01$, $p \leq 0.05$, $p \leq 0.10$ and $p \leq 0.15$. Difference was rejected at significance level $p > 0.15$.

4.5.3. Correlation between parameters

For investigation of the general relationship between parameters, the degree of association was investigated by calculating the sample spearman correlation coefficient ρ (Systat™). Correlation was accepted when $\rho \leq -0.6$ or $\rho \geq 0.6$. Positive values show that variables are positively associated, the slope of the line being positive. Accordingly values are negatively associated when ρ values and thus the slope of the line are negative.

5. Results

> "The Answer to the Great Question (...) Of Life, the Universe and Everything (...) Is (...) Forty-Two," said Deep Thought, with infinite majesty and calm. (...) "So once you do know what the question actually is, you'll know what the answer means."
>
> D. Adams, The Hitchhiker's Guide to the Galaxy

5.1 Soils

5.1.1 Soil survey

Levinson-Lessing

The distribution of soils in the study area at Lake Levinson-Lessing can be seen in Figure A2.1-1. The soil map covers an area of 24 km². At Levinson-Lessing the soils were generally characterized by very little or no profile differentiation and water-logging. Accumulation of organic matter generally occurred where vegetation was present.

About a quarter of the total area represented the valley of the river Krasnaya where polygonal tundra soils formed. These soils developed on alluvial loamy-sandy sediments and were characterized by accumulation of organic matter and gleying due to wet conditions. Thus the vegetation was adapted to wet environments. Accordingly, these were classified as Typic Aquorthels, Typic or Ruptic Historthel (Histic Cryosol, WRB) depending on the thickness of the organic horizons. At the end of the field season 1996, maximum thickness of the active layer was 48 centimetres (ANISIMOV & PANASENKOVA, 1997).

At steeper slopes east and west of the river Krasnaya, non-sorted steps and mud pits developed. These were formed in silty-loamy colluvial sediments of Greywacke. The thickness of the active layer was ± 50 cm and showed thixotropic properties. Due to slope water at a depth of ± 40 cm, these soils were rather wet. Yet, gleying features were not discernible (e.g., iron mottling) although reduced iron (Fe^{2+}) was determined in subsoil horizons. As was described before, non-sorted steps and mud pits here also represented pits of bare and raw earthy material surrounded by vegetation rings. Mud pits were also partially overgrown from the vegetation ring at further stages of successional development. Due to solifluction, profiles also showed involution of topsoil organic matter. Thus, the soils of the solifluction slopes were weakly developed though physically highly dynamic. Accumulation of organic matter and occasional gleying were the only pedogenic processes. Accordingly, these soils were classified as Ruptic-Histic Aquiturbel (Turbic/Histic Cryosol, WRB). The respective soils were associated with drainage ditches, where no patterned ground was formed. Further downhill, organic matter content increased. The soils of the solifluction slopes covered about 12% of the total area.

In valleys on top of the 300 to 500 m (a.s.l.) high surrounding mountains, weakly developed soils were found. These soils developed on frost-shattered rock debris of Greywacke and generally showed high contents of gravel and coarser fragments. Sorted and non-sorted forms of stripes and nets developed. The soils were comparably dry and showed maximum thaw depths of > 70 cm (MÜLLER-LUPP, 1997). The water table was at ± 30 cm below surface. Vegetation cover was sparse (usually 10-20%). When vegetation was present, mats of weakly decomposed organic matter and roots covered the rock debris. Accordingly, these soils were classified as Typic Aquorthel (Leptic Cryosol, WRB) and covered approximately 8.8 km² of the area.

A peculiarity of the study area represented a lime-stone ridge with a length of 2.5 km that stretches north-east from Lake Levinson-Lessing. On top and at upper slopes, shallow soils developed on frost-shattered rock debris. These soils thawed to a depth of > 80 cm and water table was found at a depth ±80 cm (GUNDELWEIN, 1998). Patterned ground did not develop although features of solifluction processes were found. As for the soils of other mountain tops, vegetation coverage was < 20% and accumulation of organic matter only occurred in vegetated soils. These soils were classified as Carbonatic Pergelic Cryorthents (S.T. 6th Ed.) (Cryic Leptosols, WRB). At the footslope of this ridge, vegetation cover increased (80% coverage) and humus rich A-horizons developed in carbonatic colluvial sediments. These soils were classified as Pergelic Cryoboroll (Gelic Cambisol, WRB) but only represented 0.6% of the study area.
The soils of this lime-stone ridge were not included in this soil microbiological study because of their small proportion of the total study area.

Labaz
At Labaz the soil map covers approximately 8 km² (see Fig. A2.1-2). The study area was subdivided into six landscape compartments according to the meso-relief and was described in detail by GUNDELWEIN (1998). 90% of the study area were covered with clayey-loamy sediments resulting in poor drainage. Thus, typical tundra soils developed showing weak profile differentiation, gleying properties and accumulation of organic matter. Thaw depths were < 50 cm and shallow. Accordingly, the soils were classified as Typic Haplorthel, Ruptic-Histic/Typic Aquorthel or Typic Historthel (S.T.) and Typic, Haplic, Histic or Gleyic Cryosol (WRB).
Differences were due to the meso-relief, the form of patterned ground, and the vegetation cover. At sloping sites, non-sorted circles (hummocks) were formed (profile Lb2/95). The vegetation of the wetter micro-site was dominated by mosses whereas at the drier elevated micro-site lichen species gained in significance. The hummock tundra also showed features of cryoturbation (i.e., mudboils). The presence of tussock forming sedges and grasses resulted in a micro-relief at an even smaller scale. Tussocks also occurred superimposed on the

hummocks (Lb3/95). These tundra soils were associated with drainage ditches where any form of patterned ground was lacking. The loamy substrate was covered with distinct mats of organic matter (Lb4/95).
A minor part of the study area at Labaz (i.e., 10%), represented the dry soils of the exposed tops of mountains or spurs. These showed generally high contents of gravel and coarser fragments. Thaw depths reached maximum values of 80-110 cm. Patterned ground was less common. At these sites, more advanced pedogenetic processes occurred and profile differentiation was more discernible. For instance, the formation of cambic horizons and podzolisation was observed. Gleying features occasionally occurred in subsoil horizons. Thus, Aquic Umbriturbel (Turbic Cryosol, WRB) and Typic Haploturbel (Turbic Cryosol, WRB) developed. However, soils with very less or no profile differentiation were associated with those just described.

5.1.2 Soil profile description

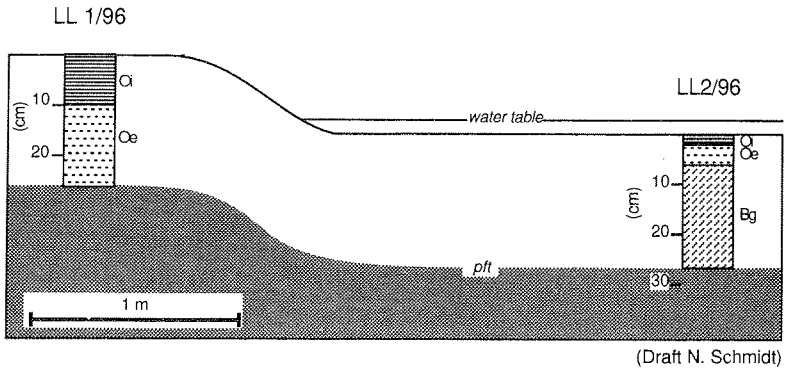
5.1.2.1 Soils at Levinson-Lessing

Polygonal tundra
The valley of the river Krasnaya was covered with polygonal tundra soils. These comprised low centred polygons (profiles LL1/96 and LL2/96), high centred polygons (profiles LL3/96 and LL4/96) as well as transitionary forms (profiles LL5/96, LL6/96 and LL7/96). Along the banks of the river and its affluents, degraded forms due to thermokarst were also found.

Figure 5.1.1 shows a transect of a typical low centred polygon and profiles (LL1/96 and LL2/96). The diameter of the polygon was approximately 10 m. The depression of the lower centre (LL2/96) covered two thirds of the area whereas the apices (LL1/96) only one third.
The apex was some 15 cm higher than the wet depression and in comparison relatively dry. Profile LL1/96 showed exceptionally thick organic horizons with sandy loam deposits up to the permafrost table. Usually organic topsoil horizons were 6 to 12 centimetres (GUNDELWEIN, 1998). The whole profile was very densely to densely rooted and was streaked with water bearing veins. The subsoil showed gleying features (i.e., Fe^{3+}-mottling).
In contrast to the drier apex, profile LL2/96 of the wet centre was usually below the water surface. Thaw depth was greater than in the apex. The soil was characterized by thinner organic horizons overlying the mineral subsoil. The subsoil did not show any gleying features although reduced iron (Fe^{2+}) was determined. The weakly silty sand of the subsoil was intensely interwoven with weakly decomposed plant debris.

Low centred polygon

Profile LL1/96:	Ruptic Historthel (Pergelic Cryofibrist) (S.T.) Histic Cryosol (WRB)
Profile LL2/96:	Typic Aquorthel (Histic Pergelic Cryaquept) (S.T.) Histic Cryosol (WRB)
Relief:	Valley floor of river Krasnaya
Altitude:	50 m a.s.l.
Vegetation:	Arctic and arctic-alpine vegetation: Apex: dwarf shrubs (*Dryas punctata, Salix pulchra*), mosses (*Hylocolomium splendens, Tormenthypnum nitens*), sedges (*Carex arctosibirica*), lichens (*Cetraria cucullata, Thamnolia vermicularis, Dactylina arctica*) Trough: segdes (*Carex stans, Dupontia fisheri*), mosses (*Drepanocladus revolvens, Calliergon sarmentosum, Plagomnium elatum,*) (100% coverage)
Substrate:	fluviatile sands
Drainage.	Apex: moderately drained, centre: very poorly drained



Profile LL1/96 (apex):

Depth (cm)	Horizon	Description
-26 - 16	Oi	Weakly decomposed plant debris, < 1 vol.% gravel, sandy deposits, very densely rooted, pH ($CaCl_2$] 6.1
16 - 0	Oe	Moderately decomposed plant debris, reddish black (2.5 Y 2.5/1), sandy loam deposits, < 1 vol.% gravel, brown mottling (7.5 YR 4/4), dipyridyl [+], coherent structure, densely rooted, pH [$CaCl_2$] 6.0
> 0	pft	Permafrost table

Profile LL2/96 (centre):

Depth (cm)	Horizon	Description
-6 - 4	Oi	Weakly decomposed plant debris, sandy deposits, < 1 vol.% gravel, weakly rooted, pH [$CaCl_2$] 5.2
4 - 0	Oe	Decomposed plant material, sandy deposits, < 1 vol.% gravel, moderately rooted, pH [$CaCl_2$] 5.5
0 - 20	Bg	Black (10YR2/1) weakly silty sand, decomposed organic matter, < 1 vol.% gravel, weakly rooted, dipyridyl [+], pH [$CaCl_2$] 5.2
> 20	pft	Permafrost table

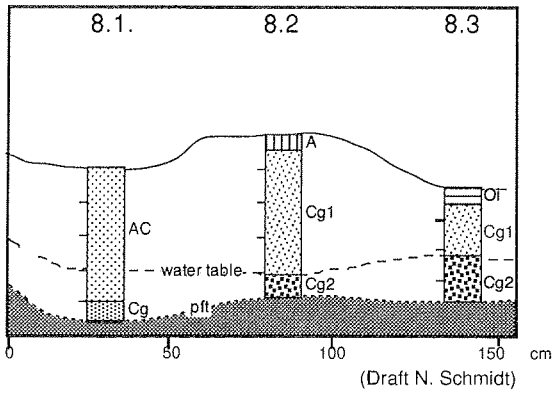
Fig. 5.1.1: Profile description low centred polygon (Profile LL1/96 and LL2/96), Levinson-Lessing.

The high centred polygon showed an inverse relationship (see Tab. A2.2-1) for profile description). The centre (Profile LL3/96) was some 40 to 50 centimetres higher than the adjacent frost crack (LL4/96). The diameter was 16 m. The soils of the apex covered 87.5% of the total area whereas the wet frost cracks covered 12.5%. As was described for the low centred polygon, profile 3 and 4 showed organic horizons (6 to 8 cm thickness) over a mineral subsoil. In the subsoils reduced iron (Fe^{2+}) was determined whereas only in the drier centre iron mottling could be found. Profile 3 showed water bearing veins as well as thick (< 5 cm) ice veins and oriented stones. Profile 4 was below the water table. Thaw depth was some 2 cm greater in the wet frost crack.

The polygonal tundra soils of profiles LL5/96, LL6/96 and LL7/96 took an intermediate position (see Tab. A2.2-2 for profile description). The centre of the polygon (LL5/96) was clearly elevated in comparison to the frost crack (LL7/96). Yet, the apex (LL8/96) represented the most elevated micro-site. A peculiarity in the subsoil of the intermediate polygon was the presence of silty loamy band (< 6 cm thick) overlying a buried organic horizon. Water in the upper horizons was found to stagnate due to this loamy band. Roots did not penetrate this barrier. The diameter of this intermediate polygon was 13 m. Soils of profile 5 covered 40%, soils of profile 6 covered 54% and soils of profile 7 covered 6% of the total area of this polygon.

Non-sorted steps

Profile LL8/96:	Ruptic-Histic Aquiturbel (Pergelic Cryaquept) (S.T.) Turbic Cryosol (WRB)
Relief:	Upper slope, moderately steeply sloping (15°), east exposition
Altitude:	90 m a.s.l.
Vegetation.	Arctic and arctic-alpine vegetation (100% coverage) around bare mud pits: dwarf shrubs (*Dryas punctata, Salix polaris, Salix reticula*), *Astragalus* spp., *Polygonium vivparum*, sedges (*Carex* spp.), mosses, lichens (*Thamnolia vermicularis*)
Substrate:	Kolluvium of fine-grained greywacke
Drainage:	Imperfectly to poorly drained, slope water above permafrost



Profile LL8.1/96 (mud pit):

Depth (cm)	Horizon	Description
0-40	AC	Sandy loam, 2-10 vol.% gravel, very dark grey (2.5Y 3/1), no humus, no roots, pH [$CaCl_2$] 5.5, dipyridyl [-]
40-46	Cg	Sandy loam, 2-10 vol.% gravel, black (5Y 2.5/1), no humus, no roots, pH [$CaCl_2$] 5.3 , dipyridyl [-]
>46	pft	Permafrost table

Profile LL8.2/96 (dry vegetation ring):

Depth (cm)	Horizon	Description
0- 5	A	Loamy sand, 50-75 vol.% gravel, very dark grey (7.5YR 3/1), weakly humic, pH [$CaCl_2$] 5.7
5-42	Cg1	Loamy sand, 10-25 vol.% gravel, very dark grey (2.5Y 3/1), no humus, weakly rooted, pH [$CaCl_2$] 5.3, Fe^{3+}-oxides, dipyridyl [-]
42-46	Cg2	Loamy sand, 2-10 vol.% gravel, black (5Y 2/1), no humus, no roots, pH [$CaCl_2$] 5.3, dipyridyl [+]
>46	pft	Permafrost table

Profile LL8.3 /96 (wet vegetation ring):

Depth (cm)	Horizon	Description
-5 - 0	Oi	Weakly decomposed plant debris, densely rooted, pH [$CaCl_2$] 4.6
0 -22	Cg1	Loamy sand, 10-25 vol.% gravel, very dark grey (2.5Y 3/1), no humus, weakly rooted, pH [$CaCl_2$] 5.3, Fe^{3+}-oxides, dipyridyl [-]
22-30	Cg2	Loamy sand, 2-10 vol.% gravel, black (5Y 2/1), no humus, no roots, pH [$CaCl_2$] 5.3, dipyridyl [+]
>30	pft	Permafrost table

Fig. 5.1.2: Profile description non-sorted step at the solifluction slope (Profile LL8.1/96 and LL8.2/96), Levinson-Lessing (modified from BÖLTER & SCHMIDT, 1997).

Non-sorted steps

As can be seen from Figure 5.1.2 the soils of the non-sorted steps only showed weak profile differentiation. The mud pit (profile LL8.1) showed lower gravel contents than the adjacent vegetated soils. The soils showed slope water above the permafrost table. Yet, reduced iron could only be determined in the subsoils of the vegetation ring. Accumulation of organic matter occurred when vegetation was present, though in the drier soil (LL8.2) a thin A-horizon developed. On the contrary, weakly decomposed organic matter accumulated at the wetter micro-site (LL8.3) of the vegetation ring. In the wetter micro-site thaw depth was lower than in the adjacent soils.

Profile LL11/96 (see Tab. A2.2-3 for profile description) differed from profile LL8/96 in that respect that the mud pit was partially overgrown by the surrounding vegetation. An AC-horizon weakly developed. The organic horizons of the vegetation ring were thicker than those fond in profile LL8.3.

Non-sorted stripes

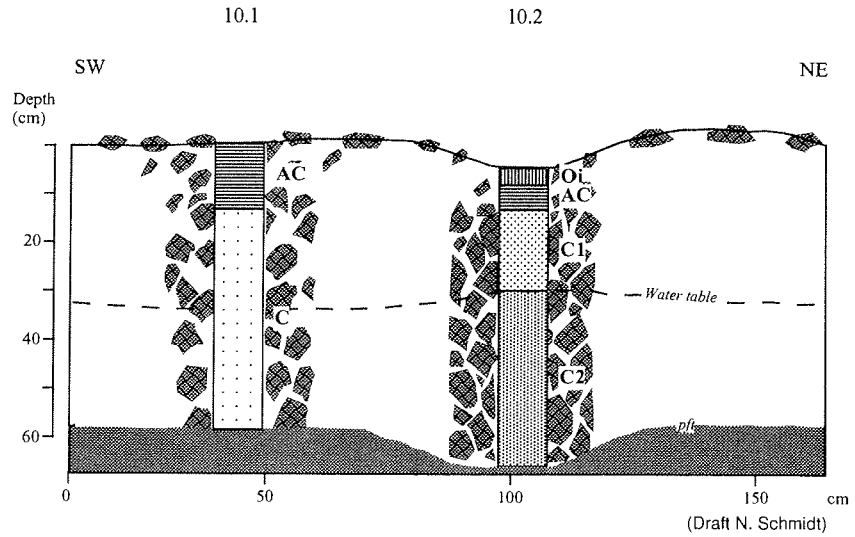
Figure 5.1.3 shows exemplarily the soils of the valley on top of mountains. They developed on frost-shattered rock debris and contained 50 to 90% gravel or coarser fragments. Vegetation coverage was very low (10-20%). Organic matter accumulated at these micro-sites. Yet, in unvegetated topsoils (LL10.1/96) AC-horizons could develop. In the respective horizons roots were found because of horizontal rooting strategies of the surrounding vegetation in the vegetation stripe (LL10.2).

Profile 9 (see Tab. A2.2-4 for profile description) differed from the latter in that respect that it was situated further downhill at a more steeply sloping site. Thus, non-sorted stripes developed whereas at profile 10 these were transitionary to nets. Generally the vegetation coverage was greater (i.e., 60%). The downslope position led to higher slope water contents in the soils of profile 9 which was at surface in the vegetation stripes (LL9.2). Thus, the organic mat was slightly thicker (i.e., 4 cm) and an A- or AC-horizon was lacking. Thaw depths were also lower than in profile LL10.

Non-sorted transitional nets

Profile LL10/96: Typic Aquorthel (Pergelic Cryorthent) (S.T.)
Leptic Cryosol (WRB)

Relief:	Middle slope at mountain top plateau, moderately steeply sloping (15°)
Altitude:	280 m a.s.l.
Vegetation.	Arctic and arctic-alpine vegetation (10-20% coverage): *Salix polaris, Papaver* spp., *Novosiviersia glacialis*, mosses, lichens (*Cetraria cucuiata, Thamnolia vermicularis*)
Substrate:	Frost shattered rock debris
Drainage:	Imperfectly drained, slope water



Profile LL10.1/96 (unvegetated stripe):

Depth (cm)	Horizon	Description
0 - 11	AC	Reddish brown (2.5Y 3/1) silty-loamy sand, 50 vol.% gravel, very weakly humic, moderately rooted, pH [$CaCl_2$] 6.2
11 - 60	C	Very dark grey (10YR 3/1) moderately sandy loam, 60-80 vol.% gravel, no humus, very weakly rooted, pH [$CaCl_2$] 6.6, dipyridyl [-], slope water at 36 cm
>60	Cf	Permafrost table

Profile LL10.2/96 (vegetation stripe):

Depth (cm)	Horizon	Description
-3 - 0	Oi	Weakly decomposed plant debris, pH [$CaCl_2$] 6.2
0 - 5	AC	Very dark grey (10YR 3/1) sandy silt, 10 vol.% gravel, very weakly humic, moderately rooted, pH [$CaCl_2$] 6.2
5 - 23	C1	Very dark brown (10YR 2/2) silty-loamy sand, 90 vol.% gravel, no humus, very weakly rooted, pH [$CaCl_2$] 6.4, dipyridyl [-]
23 - 60	C2	Moderately sandy loam, dipyridyl [-], Fe^{3+}-coating on stones, slope water
>60	Cf	Permafrost table

Fig. 5.1.3: Profile description non-sorted stripes (Profile LL10.1/96 and LL10.2/96), Levinson-Lessing.

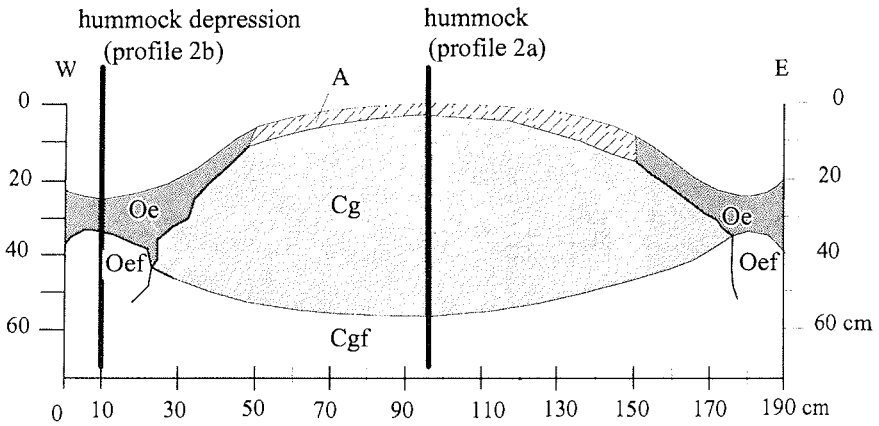
5.1.2.2 Soils at Labaz

In this study three typical tundra soils and two dry soils of top of mountains and spurs were investigated. Profile descriptions were translated from GUNDELWEIN (1998).

The soil showed distinct gleying properties. In the wet depressions between earth hummocks, the water table was predominantly at soil surface. They represented a proportion of 10 to 15% of the hummock tundra. Layers of organic matter were formed here, partly of great thickness with high organic carbon contents. Litter of the exposed hummocks (profile 2a/95) accumulated in these wet depressions. The hummocks, on the contrary, were lacking O-horizons. They thawed more rapidly and to greater depth.

Profile Lb2/95: **Hummock tundra**
Typic Haplorthel (Pergelic Cryaquept) (S.T.)
Histic Cryosol/Haplic Cryosol (WRB)

Landform:	Level footslope
Altitude:	65 m a.s.l.
Vegetation:	Subarctic vegetation adapted to wet habitats: *Cassiope*, *Ledum*, *Rubus*, *Vaccinium*, *Ledum* spp., mosses, lichens (100% coverage)
Substrate:	Sandy loam



Profile 2 a / Hummock

Depth (cm)	Horizon	Description
00 - 01	A	Reddish brown (5YR3/2) loamy sand, weakly decomposed plant debris, very densely rooted, < 1 vol.% gravel, Fe^{2+}, very acid
01 - 55	Cg	Brown (10YR4/3) very loamy sand, moderately rooted 1-20 vol.% gravel, coherent structure, Fe^{2+}, band of humified organic matter, neutral to acid (above permafrost table)
> 55	Cgf	Brown (10YR4/3) very loamy sand, no roots, 1 vol.% gravel, ice lenses, permafrost

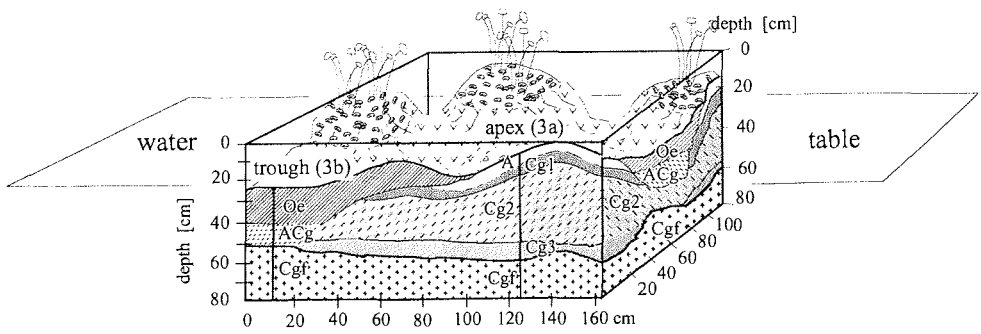
Profile 2 b / Depression

Depth (cm)	Horizon	Description
00 - 10	Oe	Very dark brown (10YR2/2) moderately decomposed plant debris, < 1 vol.% gravel, very acid
> 10	Of	Very dark brown (10YR2/2) moderately decomposed plant debris, < 1 vol.% gravel, very acid, permafrost

Fig. 5.1.4: Profile description profile Lb2/95 (earth hummock tundra site), Labaz (modified from GUNDELWEIN, 1998).

Profile Lb3/95: **Tussock tundra**
Ruptic-Histic Aquorthel / Typic Historthel
(Pergelic Cryaquept / Histic Pergelic Cryaquept) (S.T.)
Gleyic Cryosol / Histic Cryosol (WRB)

Landform: Level middle slope
Altitude: 60 m a.s.l.
Vegetation: Subarctic vegetation adapted to wet habitats: *Betula nana, Salix pulchra, Vaccinium vitis-idea, Eriophorum vaginatum, Carex bigelowii ssp. arctosibirica, Tomentypnum nitens, Drepanocladus uncinatus, Kiaeria starkii, Cetraria cucullata, Cladina arbuscula* (100% coverage)
Substrate: Weakly clayey loam



Profile 3 a / Tussock

Depth (cm)	Horizon	Description
00 - 05	A	Dark greyish brown (10YR4/2), weakly clayey loam, humified organic matter, very densely rooted, coherent structure, < 1 vol.% gravel, Fe^{2+}, very acid
05 - 08	Cg1	Dark grey (5Y4/1), weakly clayey loam, moderately rooted. < 1 vol.% gravel, coherent structure, Fe^{2+}, acid
08 - 44	Cg2	Dark yellowish brown (10YR4/4), weakly clayey loam, moderately rooted. < 1 vol.% gravel, coherent structure, Fe^{2+}, acid
44 - 50	Cg3	Dark olive grey (5Y3,5/1), weakly clayey loam, moderately rooted. < 1 vol.% gravel, coherent structure, Fe^{2+}, band of humified organic matter above permafrost, acid
> 50	Cgf	Clayey loam, no roots, ice lenses, permafrost

Profile 3 b / Depression

Depth (cm)	Horizon	Description
-17 - 00	Oe	Black (5YR2.5/1) moderately decomposed plant debris, < 1 vol.% gravel, acid
00 - 10	ACg	Very dark grey (5YR3/1) weakly clayey loam, < 1 vol.% gravel, moderately-weakly rooted, coherent structure, Fe^{2+}, acid
> 10	Cgf	Very dark grey moderately decomposed plant debris, < 1 vol.% gravel, ice lenses, permafrost

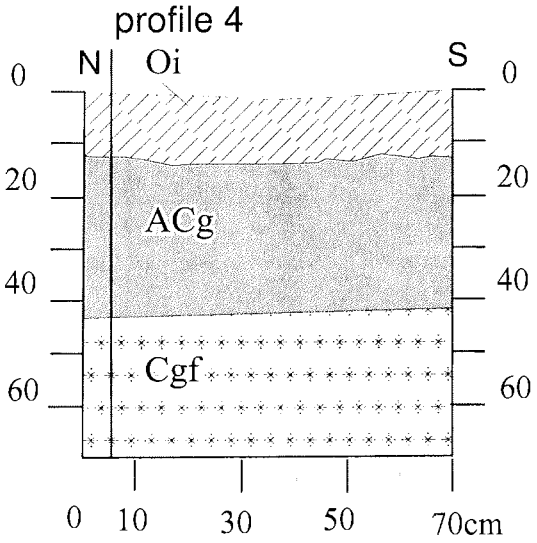
Fig. 5.1.5: Profile description profile Lb3/95 (wet tussock tundra site), Labaz modified from GUNDELWEIN, 1998).

The micro-relief was characterized by small non-sorted circles (earth hummocks) overgrown with tussock forming grasses (*Carex bigelowii* (suppl. by the author), *Eriophorum vaginatum*). Tussocks covered some 45%, depressions approximately 55% of the total area. At the sides tussocks enlarged due to accumulation of organic matter. Litter of the exposed tussocks (profile Lb3a/95) accumulated in the wet depressions (profile Lb3b/95) and formed (occasionally thick) organic layers. The tussocks, on the contrary, were lacking O-horizons. In the exposed tussocks, the soil moisture and temperature regime were drier and warmer than in the adjacent depressions.(...)

The soils showed distinct gleying features. In the wet depressions between tussocks, the water table was predominantly at soil surface. Soil texture consisted at equal proportions of sand, silt and clay. The clay content was clearly higher than in the hummock tundra of profile Lb2/95.

Profile Lb4/95: **Wet sedge tundra**
Typic Aquorthel (Pergelic Cryaquept) (S.T.)
Histic Cryosol (WRB)

Landform: Drainage ditch at level middle slope (profile Lb3/95)
Altitude: 57 m a.s.l.
Vegetation: Subarctic vegetation adapted to extremely wet habitats: *Salix pulchra, Carex stans, Eriophorum angustifolium, Drepanocladus uncinatus, Tomentypnum nitens, Plagomnium elatum* (100% coverage)
Substrate: Weakly clayey loam



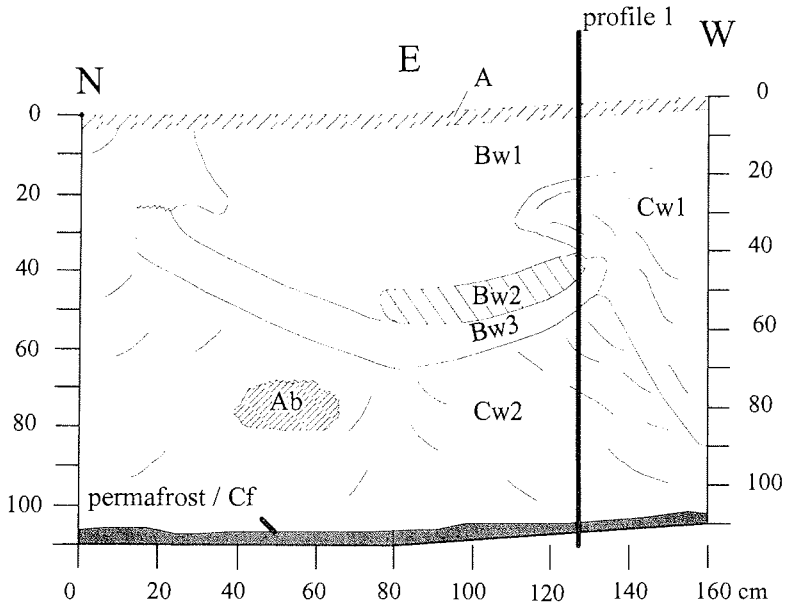
Depth (cm)	Horizon	Description
-12 - 00	Oi	Black to very dark brown (10YR2/1-2) weakly decomposed plant debris, very densely rooted, very acid
00 - 42	ACg	Dark yellowish brown (10YR4/6) and very dark grey (5Y3/1) weakly clayey loam, moderately rooted, < 1 vol.% gravel, coherent structure, Fe^{2+}, acid
> 42	Cgf	Very dark grey (5Y3/1) weakly clayey loam, no roots, weakly acid, permafrost

Fig. 5.1.6: Profile description profile Lb4/95 (wet sedge tundra site), Labaz (modified from GUNDELWEIN, 1998).

The site was very wet. The water table was permanently above soil surface. The ditch drained the surrounding polygonal and tussock tundra to the brook Tolton-Pastach. A micro-relief was lacking. The predominant plant (*Eriophorum angustifolium*) does not form tussocks. The open space and the deeper position of the ditch formed a relatively warm and protected habitat. The gleyed subsoil was covered by a thick layer.

Profile Lb1/95: **Dry exposed mountain top**
Typic Haploturbel (Pergelic Cryorthent) (S.T.)
Typic Cryosol (WRB)

Landform:	Top slope underneath the mountain top plateau, east exposition
Altitude:	110 m a.s.l.
Vegetation:	Subarctic vegetation adapted to dry habitats with little snow cover: *Salix*, *Dryas*, *Ledum* spp., Lichens (80% coverage)
Substrate:	Sand with coarse gravel (20-63 mm) over medium sand with little gravel content



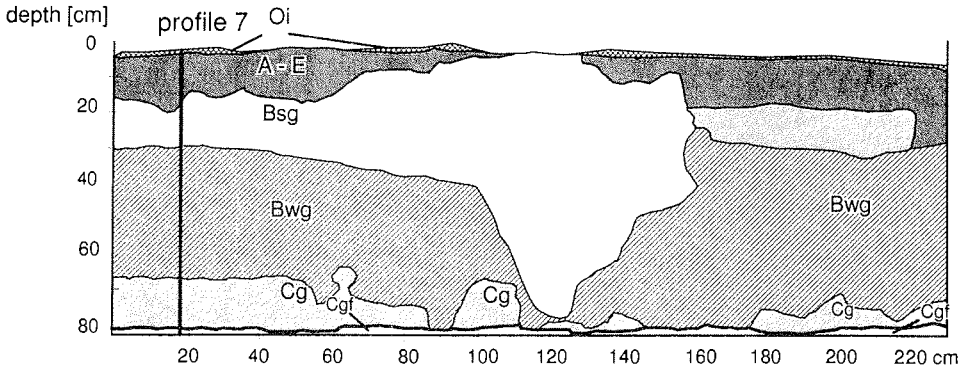
Depth (cm)	Horizon	Description
00 - 01	A	Very dark greyish brown (10YR3/2) medium sand with weakly decomposed plant debris, densely rooted, weakly acid, deflation crust
01 - 23	Bw1	Very dark brown (10YR2/2) medium sand, humified organic matter, 60-90 vol.% gravel, granular to subangular blocky structure, moderately rooted, neutral
23 - 35	2Cw1	Brownish yellow (10YR6/6) medium sand, 1 vol.% gravel, granular structure, weakly rooted, weakly alkaline
35 - 52	Bw2	Yellowish red (5YR5/8) medium sand, 60-90 vol.% gravel, granular to subangular blocky structure, moderately rooted, weakly alkaline
52 - 60	3Bw3	Yellowish red (5YR 5/8) medium sand, 1-10% vol.% gravel, subangular blocky structure, moderately rooted, weakly alkaline
60 - 110	3Cw2	Brownish yellow (10YR 6/6) medium sand, 1-10 vol.% gravel, granular structure, no roots, weakly alkaline
> 110	3Cf	Medium sand, granular structure, 1-10 vol.% gravel, ice lenses, weakly alkaline, permafrost

Fig. 5.1.7: Profile description profile Lb1/95 (dry exposed mountain top), Labaz (modified from GUNDELWEIN, 1998).

The soil clearly showed interwoven horizons, which indicated cryoturbation. The latter is unusual for coarse textured soils under the present well-drained conditions. These discontinuities were reflected by the C-contents of the respective horizons. Yet, soil pH increased steadily with depth. Gravel and coarser fragments consisted partly of limestone, carbonate coatings under stones indicate an upward movement of soil water. At the dry site, differences between horizons in C-contents were preserved. Soil pH, however, was characterized by recent processes of upward movement of soil water and precipitation of calcium carbonate. These properties indicate that cryoturbation represented a relic process.
Because of the dryness of the soil vegetation coverage was 80%. Carbon accumulated in the thin A-horizon. The transition to the underlying horizon was discrete, mixing of soil material was not discernible. The transition from the B- to C-horizons was striking and was accompanied by a decrease of gravel content from 60% to 10%.

Profile Lb7/95: **Dry spur**
Aquic Umbriturbel (Pergelic Cryaquept) (S.T.)
Turbic Cryosol (WRB)

Landform:	Spur above brook valley
Altitude:	50 m a.s.l.
Vegetation:	Subarctic spotty vegetation adapted to dry habitats: *Betula* spp., *Cassiope* spp., grasses, mosses and lichens (90% coverage)
Substrate:	Alternating layers of sand and loam



Depth (cm)	Horizon	Description
-1 - 00	Oi	Weakly decomposed plant debris, predominantly lichens and mosses, discrete horizon formation
00 - 10	AE	Dark yellowish brown (10YR 3/4) weakly humified, weakly clayey sand, < 1 vol.% gravel, densely rooted, granular structure, very acid
10 - 25	Bhs	Brown (7.5YR 4/4) sand , very weakly humified, < 1 vol.% gravel, densely rooted, granular structure, cemented illuviation zone, very acid
25 - 60	Bwg	Dark yellowish brown (10YR 4/4) sand, < 1 vol.% gravel, no roots, granular structure, gleying features, acid
60 - 80	Cg	Olive grey (5Y 5/2) sand, < 1 vol.% gravel, no roots, gleying features, weakly acid
> 80	Cgf	Olive grey (5Y 5/2) sand, < 1 vol.% gravel, no roots, gleying features, weakly acid, permafrost, little ice-enrichment

Fig. 5.1.8: Profile description profile Lb7/95 (dry spur), Labaz (modified from GUNDELWEIN, 1998).

Profile 7 represented a dry habitat. The exposed spur position and the sandy texture favoured good drainage and deep thaw depths. In the topsoil the proportion of the sand fraction was 87% and increased up to 96% above the permafrost table. Porosity was 47-49% in the topsoil as well as above the permafrost table. At a depth of 40 cm, the soil showed strong compaction. Porosity was 39% and bulk density was extremely high (1.9 g cm^{-3}).

According to the dryness vegetation cover was sparse, in particular higher plants occurred only sporadically. Pronounced and continuous O-horizons as well as any form of patterned ground were lacking.(...) The topsoil clearly showed podzolisation properties (bleaching, accumulation of sesquioxides). The upper boundary of the Cg-horizon was very irregular and indicated cryoturbation. The latter is unusual for sandy, dry soils and was probably a relic property. Features of cryoturbation were lacking in the topsoil. Despite good drainage and a high proportion of coarse pores, the subsoil showed iron mottling and precipitates indicating temporary anaerobic conditions. The soil was thus classified as Pergelic Cryaquept (S.T., 6^{th} ed.).

In the WRB system, soil properties of the topsoil (thickness, colour, low base saturation, organic C content, pH) qualified for an umbric horizon whereas gleying properties were not sufficient. However, the soil was classified as Aquic Umbriturbel and (Turbic Cryosol; S.T., 8^{th} edn. and WRB suppl. by the author).

5.2 Pedological Parameters

5.2.1 Organic carbon (C_{org}) and total nitrogen (N_t) content

Levinson-Lessing

Figures 5.2.1 - 5.2.7 show the contents of organic carbon (C_{org}) and total nitrogen (N_t) of the soils at Levinson-Lessing (see appendices for analytical data). The comparison of the soils of the polygonal tundra, solifluction steps and non-sorted stripes shows greatest C_{org} and N_t contents in the soils of the polygonal tundra (profiles LL1/96 - LL7/96). C_{org} and N_t contents of the solifluction steps and the non-sorted stripes were lower. C_{org} contents generally decreased with depth marked by distinct changes from organic to mineral horizon. This holds also true in case of the buried Oe-horizons in the transitional polygon soils. The overall C/N-ratio was wide and narrowed with increasing depth. Apart from greater C_{org} and N_t contents, the polygonal tundra soils also showed wider C/N-ratios.

In addition, C_{org} and N_t contents changed remarkably with the micro-relief. In the polygonal tundra (e.g., LL1/96 and LL2/96) the C_{org} and N_t contents were some 20% greater in the wet depression than in the elevated apex. The C/N-ratios were narrower in the elevated apices than

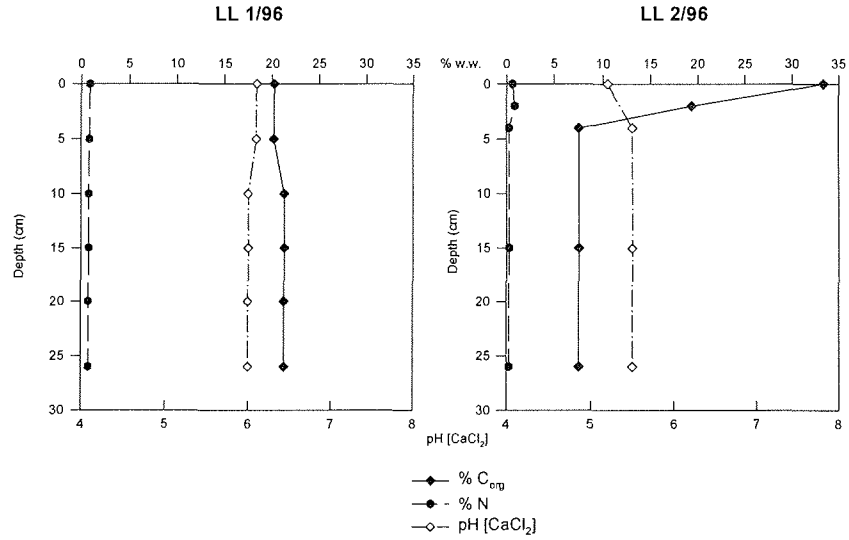


Fig. 5.2.1: Pedological parameters in the apex (LL1/96) and the centre (LL2/96) of the low centred polygon at Levinson-Lessing (where C_{org} organic carbon content [% w.w.], N total nitrogen content [% w.w.] and soil pH [$CaCl_2$].

in the depressions. In the soils of the solifluction steps (profiles LL8/96; LL11/96) and the non-sorted steps (profiles LL8/96; LL11/96), the C_{org} and N_t contents followed the patterned ground of alternate vegetation (i.e., stripes or rings) and mineral material. In the vegetated soils of the solifluction steps, the C_{org} and N_t contents were some 60% greater than in the bare soils. In the non-sorted stripes these differences were even more pronounced (80-90% increase). The C/N-ratios were similar.

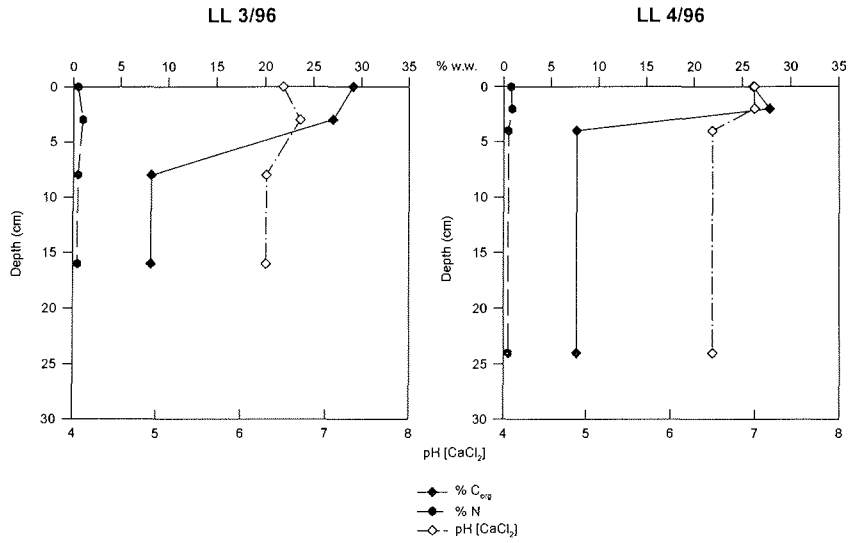


Fig. 5.2.2: Contents of organic carbon (% C_{org}), total nitrogen (% N) and pH [$CaCl_2$] in the apex (profile LL 3/96) and the depression (profile LL 4/96) of the high centred polygonal tundra at Levinson-Lessing.

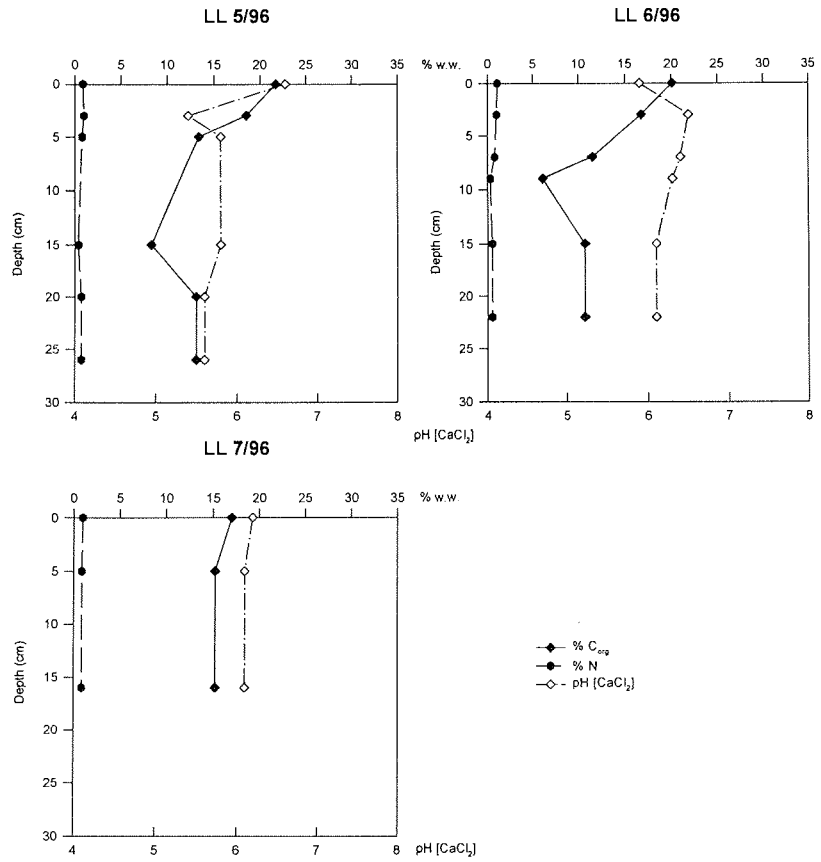


Fig. 5.2.3: **Content of organic carbon (% C_{org}), total nitrogen (% N) and pH [$CaCl_2$] in the apices (profiles LL 5/96 and LL 6/96) and the depression (LL7/96) of the intermediate polygonal tundra at Levinson-Lessing.**

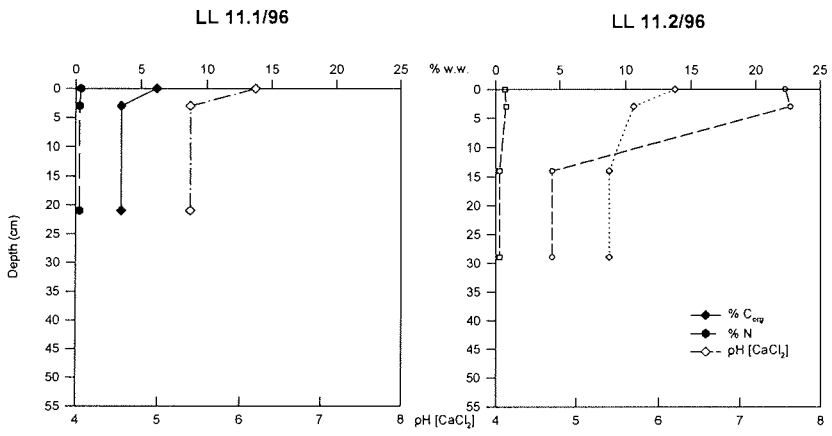


Fig. 5.2.4: **Contents of organic carbon (% C_{org}), total nitrogen (% N) and pH [$CaCl_2$] in the vegetated mud boil (LL 11.1/96) and the vegetation ring (LL 11.2/96) of the solifluction steps at Levinson-Lessing.**

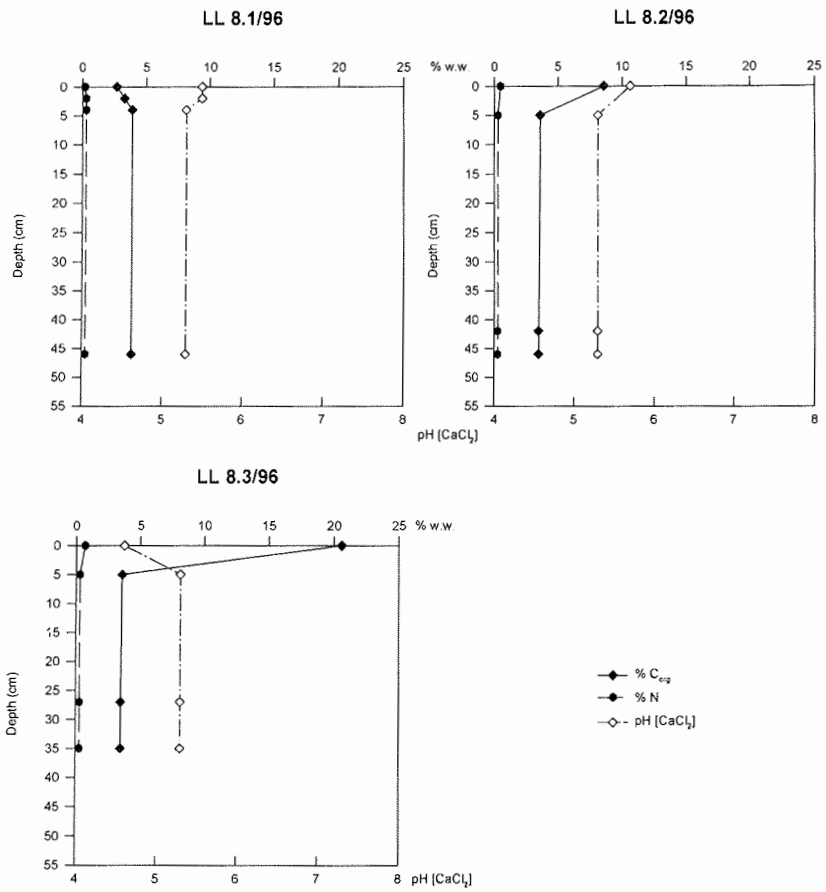


Fig. 5.2.5: Contents of organic carbon (% C_{org}), total nitrogen (% N) and pH [$CaCl_2$] in the unvegetated mud boil (LL 8.1/96) and the vegetation ring (LL 8.2/96 and LL 8.3) of the solifluction steps at Levinson-Lessing.

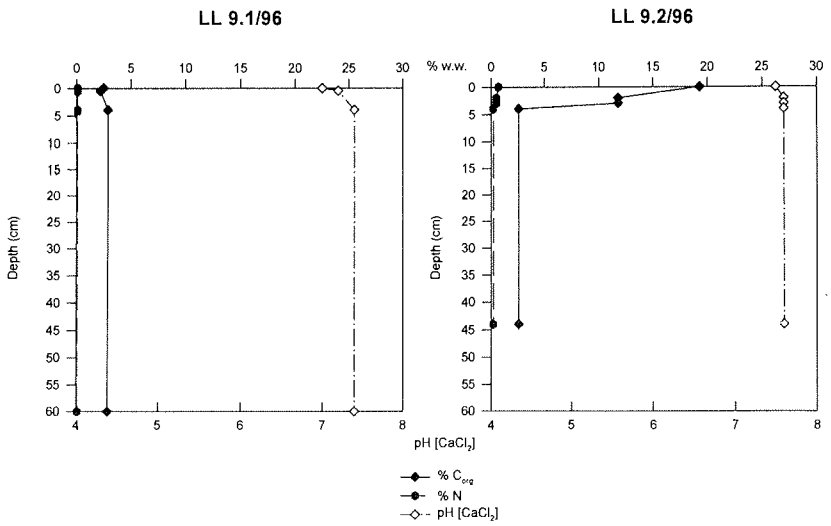


Fig. 5.2.6: Content of organic carbon (% C_{org}), total nitrogen (% N) and pH [$CaCl_2$] in the unvegetated mound (LL9.1/96) and the vegetation stripes (LL 9.2/96) of the non-sorted stripes at Levinson-Lessing.

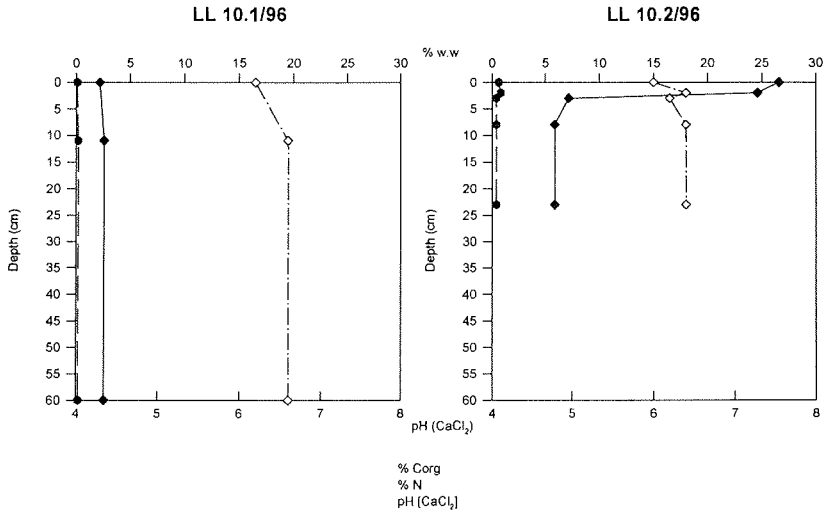


Fig. 5.2.7: Content of organic carbon (% C_{org}), total nitrogen (% N) and pH [$CaCl_2$] in the unvegetated mound (LL 10.1/96) and the stripes of vegetation (LL 10.2/96) of the non-sorted stripes.

Labaz

Figures 5.2.8 - 5.2.12 show the C_{org} and N_t contents of the soils at Lake Labaz (see appendices for analytical data).

C_{org} and N_t contents were generally lower and C/N-ratios narrower than at Levinson-Lessing. The C_{org} and N_t contents were largely confined to the organic horizons and decreased with depth. In case of the lowland soils (profiles Lb2/95 to Lb4/95), C_{org} and N_t increased remarkably in the supra-permafrost layers and at a depth 10-20 cm of the hummock and tussock tundra.

Greatest C_{org} and N_t contents were found in the wet sedge tundra soil in a drainage ditch (profile Lb4/95). The C/N-ratio here was also the widest. The most abundant soils of the hummock (profile Lb2/95) and the tussock tundra (Lb3/95) showed slightly lower C_{org} and N_t contents. In addition these values varied along with the micro-relief. C_{org} and N_t contents were 25-45% greater in the depression than in the corresponding elevated micro-site (i.e., hummock, tussock). Accordingly, the C/N-ratios were wider in the depressions. Lowest C_{org} and N_t contents were found in the dry soils (Lb1/95 and Lb7/95).

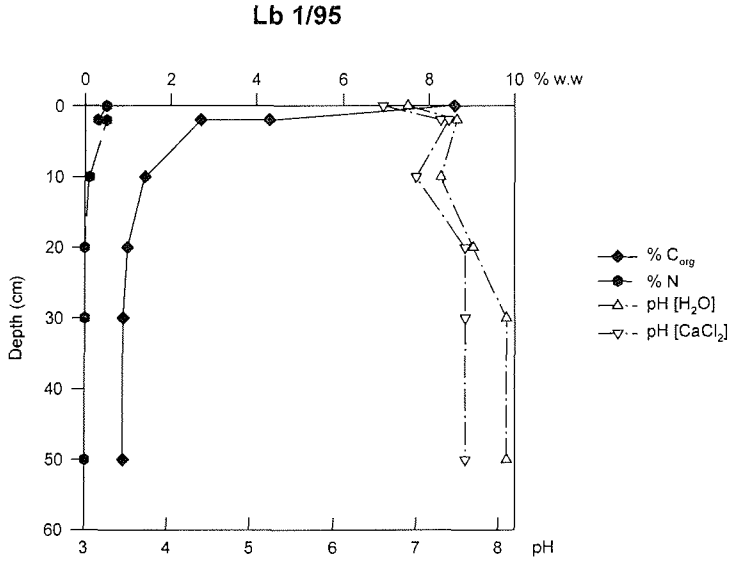


Fig. 5.2.8: Content of organic carbon (% C_{org}), total nitrogen (% N), pH [H_2O] and pH [$CaCl_2$] in dry brown earth (Lb 1/95) at Labaz.

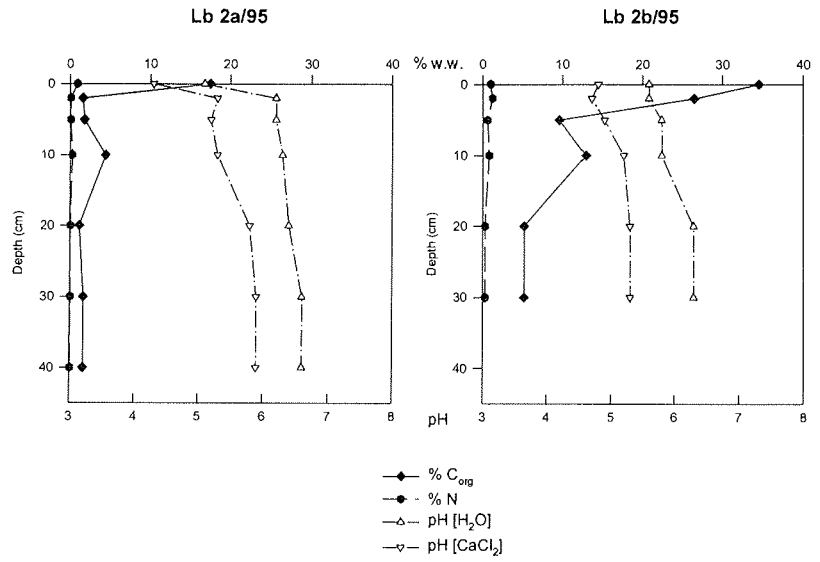


Fig. 5.2.9: Content of organic carbon (% C_{org}), total nitrogen (% N), pH [H_2O] and pH [$CaCl_2$] in the hummock (Lb 2a/95) and the frost crack (Lb 2b/95) of the hummock tundra, Labaz.

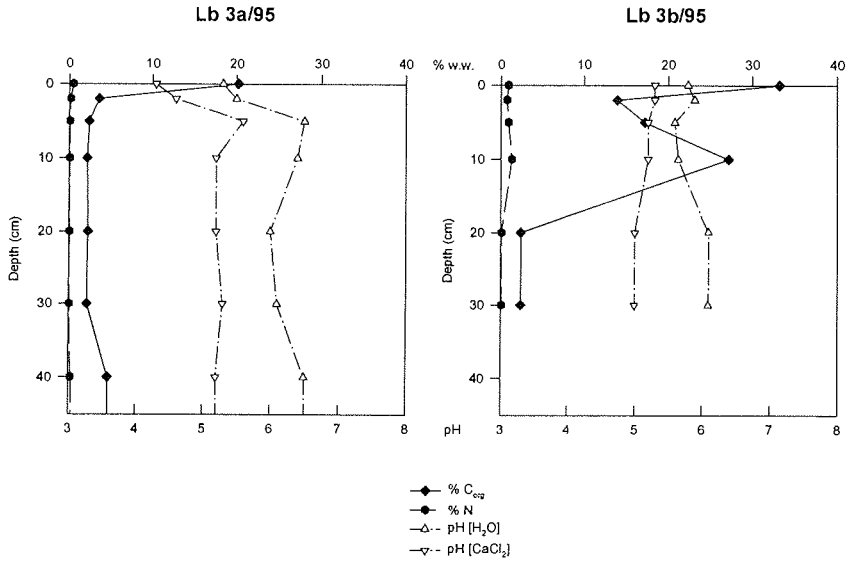


Fig. 5.2.10: Content of organic carbon (% C_{org}), total nitrogen (% N), pH [H_2O] and pH [$CaCl_2$] in the tussock (Lb 3a/95) and the frost crack (Lb 3b/95) of the tussock tundra, Labaz.

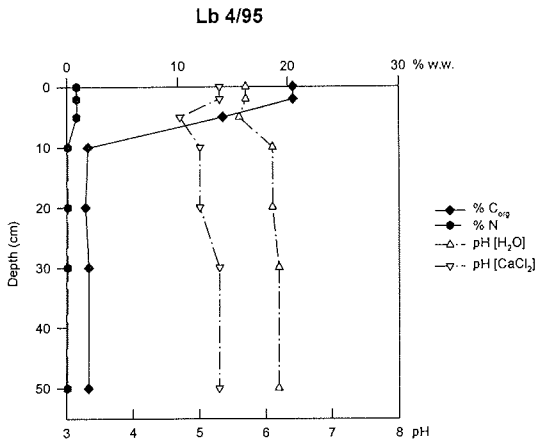


Fig. 5.2.11: Content of organic carbon (% C_{org}), total nitrogen (% N), pH [H_2O] and pH [$CaCl_2$] in the wet sedge tundra in the drainage ditch (Lb 4/95), Labaz.

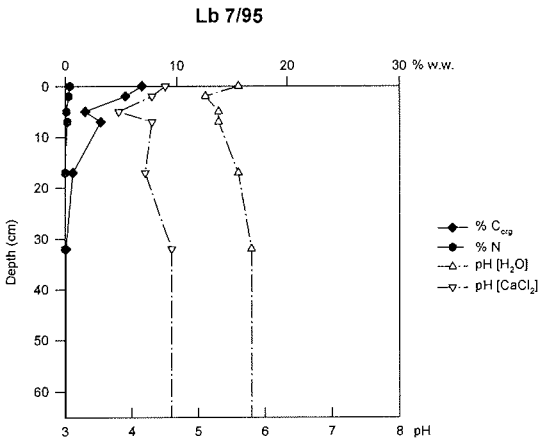


Fig. 5.2.12: Content of organic carbon (% C_{org}), total nitrogen (% N), pH [H_2O] and pH [$CaCl_2$] in dry podzolised brown earth (Lb 7/95), Labaz.

5.2.2. Soil pH

Levinson-Lessing

Mean soil pH [$CaCl_2$] of the fresh topsoils (0-10 cm) of the polygonal tundra was 6.2. In case of the soils of solifluction steps mean pH [$CaCl_2$] was 5.7. In the soils of the non-sorted stripes mean pH [$CaCl_2$] was 6.7.

In the soils of the solifluction steps, along with the vegetation cover, the pH [$CaCl_2$] was lower than in the neighbouring unvegetated mudboils. On the contrary, there was no distinct difference in pH [$CaCl_2$] with respect to the micro-relief in the soils of the polygonal tundra nor in the soils of the non-sorted stripes.

Labaz

Mean pH [$CaCl_2$] of the upper horizons (0-10 cm) of the tundra soils (profiles Lb2/95 - Lb4/95) was 5.2. Mean pH [$CaCl_2$] of the dry sites was 7.0 in case of the carbonatic uphill soil (Lb1/95) and 4.3 in case of the podzolic soil (Lb7/95).

The pH values [$CaCl_2$] of the tundra soils varied along with the micro-relief. Thus, in the depression of the hummock tundra the pH was more acid than in the hummock. On the contrary, in the elevated micro-site of the tussock tundra (Lb3/95) was more acid than in the corresponding depression.

Mean pH [H_2O] of the upper horizons (0-10 cm) of the tundra soils (profiles Lb2/95 - Lb4/95) was 5.8. Mean pH [H_2O] of the dry sites was 7.3 in case of the uphill soil and 5.3 in case of the podzolic soil (Lb7/95). Thus, the overall exchange acidity was high (mean ΔpH 0.9) being highest in the podzolic soil (mean ΔpH 1.1). The lowest exchange acidity was found in the dry uphill soil (mean ΔpH 0.2).

5.2.3 Bulk density and carbon inventory

Levinson-Lessing

Table 5.2.3-1 shows the carbon inventories (*CI*) in the soils at Levinson-Lessing calculated for the uppermost 4 centimetres. The carbon inventory of the soils showed high spatial variability along with the micro-relief. The values ranged between 0.3 and 4.8 kg C m^{-2}.

Tab. 5.2.3-1: Carbon inventories (*CI*) in the top soil (4 cm) at Levinson-Lessing

Profile	horizon/depth	% gravel	D_b [g cm^{-3}]	% C_{org}	CI [kg m^{-2}]	sum *CI* (0-4 cm)
Polygon tundra						
low centred (LL1/96)	Oi (0-4 cm)		0.48	20.19	3.9	**3.9**
high centred						
LL3/96 (centre)	Oi (8-5 cm)		0.34	29.09	3.0	**3.9**
	Oe (5-4 cm)			26.95	0.9	
mud boil	0-4 cm		1.09	5.20	2.3	**2.3**
LL4/96 (frost crack)	Oi (6-4 cm)		0.09	26.14	0.5	**0.9**
	Oe (4-2 cm)			27.83	0.5	
intermediate						
LL5/96 (centre)	Oi (15-12 cm)		0.34	21.70	2.2	**2.8**
	Oe1 (12-11 cm)			18.49	0.6	
LL6/96 (apex)	Oa1 (9-6 cm)		0.38	20.10	2.3	**2.9**
	Oa2 (6-5 cm)			16.75	0.6	
Non-sorted steps						
LL8.1/96 (mud boil)	AC (0-2 cm)	6.0	0.59	2.72	0.3	**0.7**
	AC (2-4 cm)	6.0	0.59	3.34	0.4	
LL8.2/96 (vegetated ring)	A (0-4 cm)	62.5	0.08	8.62	0.3	**0.3**
Non-sorted stripes						
LL9.1/96 (unvegetated)	AC (0-0.5 cm)	37.5	0.52	2.53	0.1	**0.5**
	AC (0.5-4 cm)	37.5	0.52	2.24	0.4	
LL9.2 (vegetated)	Oi (4-2 cm)		0.57	19.31	2.2	**3.6**
	Oie (2-0 cm)			11.83	1.3	
LL10.2/96 (vegetated)	Oi (3-1 cm)		0.57	26.55	3.0	**4.8**
	Oi (1-0 cm)			24.61	1.4	
	A (0-1 cm)			7.17	0.4	

In the polygon tundra, greater carbon inventories (2.3 -3.9 kg C m^{-2}) were calculated for the apices. Despite high carbon content (% w.w.) in the frost cracks, the carbon inventory was remarkably lower (0.9 kg C m^{-2}) due to a low bulk density. On the contrary, this relationship was inverse in the mud boil (LL3/96). The carbon inventory was high although the carbon content was low.

The carbon inventories in the non-sorted step (LL8/96) were lower than in the polygon tundra. In the mud boil, the carbon inventory (0.7 kg C m^{-2}) was twice as high as in the adjacent vegetation ring (0.3 g C cm^{-2}), where the gravel content was very high.
The widest range of carbon inventory (0.5 - 4.8 kg C m^{-2}) was found in the non-sorted stripes. Compared to the unvegetated mound (LL9.1/96), the greater inventories were determined in the vegetated soils (LL9.2/96 and 10.2/96). The gravel content in the mound was high.

Labaz

Table 5.2.3-2 shows the carbon inventories (*CI*) in the soils at Labaz calculated for the uppermost 4 cm using data by GUNDELWEIN (1998). As the soils at Levinson-Lessing, the carbon inventory of the soils at Labaz also showed a great heterogeneity. Along with the micro-relief, the values ranged between 0.8 and 11.0 kg C m^{-2}.

Tab. 5.3.2-2: Carbon inventories (*CI*) in the top soil (4 cm) at Lake Labaz (modified data from GUNDELWEIN, 1998)

Profile	horizon/depth	D_b [g cm^{-3}]	% C_{org}	CI [kg m^{-2}]	sum *CI* (0-4 cm)
Hummock tundra					
Lb2a/95 (hummock)	A (0-1 cm)	0.9	10.3	0.9	**1.5**
	Cg (1-3 cm)	1.3	1.5	0.6	
Lb2b/95 (frost crack)	Oe (10-6 cm)	0.3-0.6	46.0	5.5-11.0	**5.5-11.0**
Tussock tundra					
Lb3a/95 (tussock)	A (0-4 cm)	0.6	4.8	1.2	**1.2**
Lb3b/95 (depression)	Oe (17-13 cm)	0.2-0.5	33.6	2.7-6.7	**2.7-6.7**
Wet sedge tundra					
Lb4/95	Oi (12-8 cm)	0.5	16.8	3.4	**3.4**
Dry podzolized soil					
Lb7/95	AE (0-4 cm)	1.1	1.7	0.8	**0.8**

In the soils of the hummock and tussock tundra (Lb2/95 and Lb3/95) the carbon inventory (*CI*) ranged from 1.2 to 11.0 kg C m^{-2}. The lower *CI*s (1.2 and 1.5 kg C m^{-2}) were found in the relatively elevated hummocks (Lb2a/95) and tussocks (Lb3a/95). In the adjacent depression, these values were between 55 and 88 % higher. This increase was stronger in the hummock tundra. In the wet sedge tundra soil of the drainage ditch (Lb4/95), the *CI* was 3.4 kg C m^{-2}. This value is in the same order of magnitude as the polygonal tundra at Levinson-Lessing. The lowest *CI* (0.8 kg C m^{-2}) was found in the dry podzolized soil (Lb7/95). At Labaz the trend of the carbon inventory is according to the carbon content (% w.w.).

5.2.4 Pore size distribution

Levinson-Lessing

Figures 5.2.13 to 5.2.15 show the pore size distribution of the uppermost 4 cm in the soils at Levinson-Lessing. For profiles LL1/96 and 3/96, pore size distribution of the underlying horizon was also determined.

Within these 4 cm, the porosity was generally greater than 60 % and thus very high. An exception were the unvegetated soils or micro-sites, where porosity was lower (LL3/96, LL8.1/96 and LL9.1/96). The air (AC) and available field capacity (FC_a) were usually very high (AC >18 % and FC_a 20-30 %).

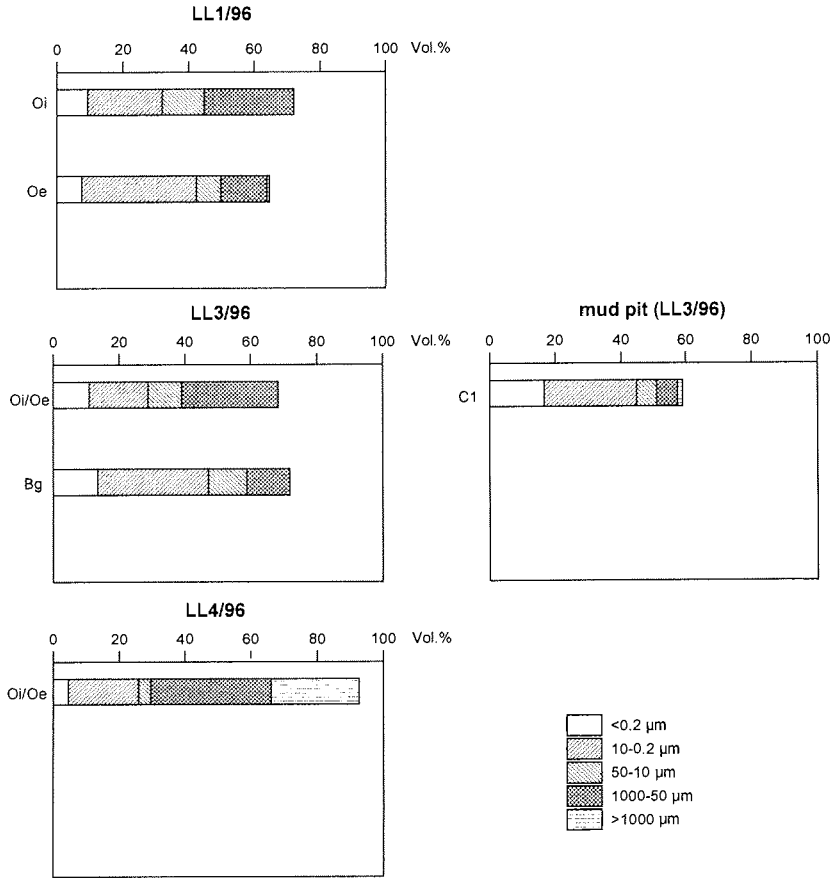


Fig. 5.2.13: Pore size distribution in the polygonal tundra at Levinson-Lessing.

In the polygonal tundra, the porosity and the pore size distribution were similar in the apices (LL1/96 and LL3/96). The air capacity was high and decreased with depth. The available field capacity was extremely high (>30 %) and increased with depth. On the contrary, porosity and air capacity was lower in the mud pit. Yet, the available field capacity was also extremely high. Maximum porosity was determined in the frost crack of the high centred polygon (LL4/96). Profile LL4/96 showed a sponge-like structure with a porosity of greater 80 % and an air capacity greater 60 %.

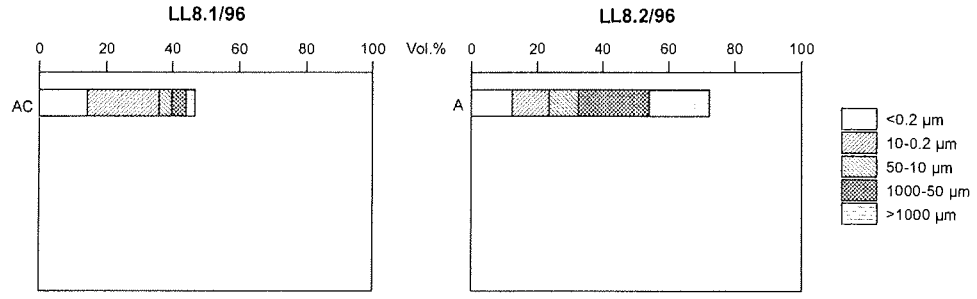


Fig. 5.2.14: Pore size distribution in the non-sorted step (profile LL8/96) at Levinson-Lessing.

In the soils of the non-sorted step, porosity and pore size distribution varied strongly along with the micro-relief. Porosity was 35 % lower in the unvegetated mud boil than in the vegetation ring. Compared to the mud pit of the polygon tundra, the porosity was some 20 % lower. The air capacity also decreased remarkably. In addition, the habitable pore space (> 0.2 µm) was half as big in the mud boil as in the surrounding vegetation ring. For both micro-sites, the available field capacity was very high (> 20 %). Yet, it was lower than in the polygon tundra.

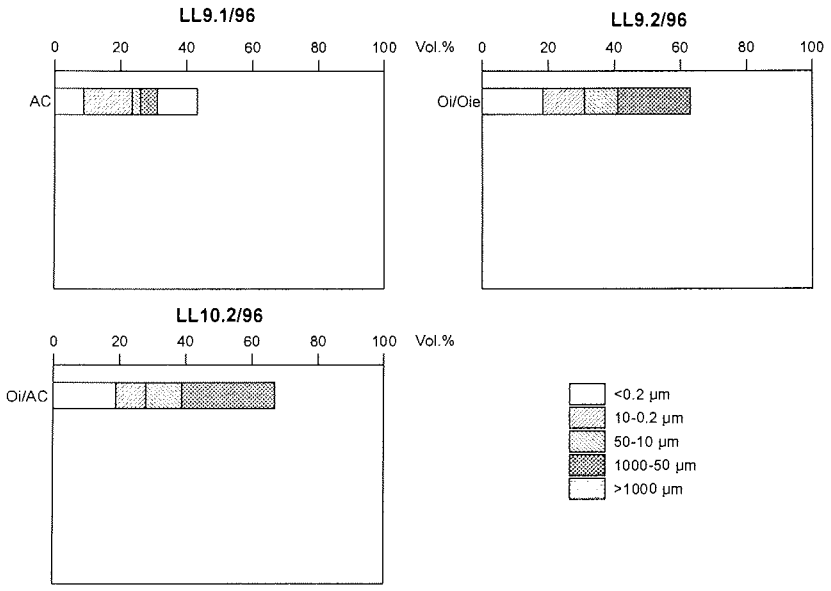


Fig. 5.2.15: Pore size distribution in the non-sorted stripes at Levinson-Lessing.

In the soils of the non-sorted stripes porosity and pore size distribution also varied along with the micro-relief. The soils of the vegetation stripe/ring (LL9.2/96 and LL10.2/96) showed similar properties. The porosity was > 60 %. The air capacity was high very high. The available field capacity was high but lower than for the soils of the polygon tundra. On the contrary, porosity, air capacity and available field capacity decreased some 25 % in the unvegetated mound (LL9.1/96). The habitable pore space decreased accordingly. Compared to the other unvegetated soils (mud pit LL3/96 and LL8.1/96), the air capacity was higher and the available field capacity was lower.

5.3 Microbial parameters

5.3.1 Fungi

Levinson-Lessing

In the soils at Levinson-Lessing, hyphal length of up to 393 m g^{-1} d.wt. (median 21 m g^{-1} d.wt.) and fungal biovolume of up to 3.5 mm^3 g^{-1} d.wt. (median 0.19 mm^3 g^{-1} d.wt.) were measured (see Tab. A4.1-1). Fungal biomass was up to 455.3 µg C g^{-1} d.wt. (median 24.3 µg C g^{-1} d.wt.). Fungi generally decrease with depth. Maximum values were measured in Oe-horizons. No or very little fungi were found in unvegetated soils (e.g., LL8/96; 9/96) and in horizons above the permafrost table (supra-permafrost layer).

Maximum values were found in the polygon tundra soils (Tab. 5.3.1-1). Median values of hyphal length (27 m g^{-1} d.wt.), biovolume (0.29 mm^3 g^{-1} d.wt.) and fungal biomass (37.5 µg C g^{-1} d.wt.) were also greater. The fungal distribution showed a complex and uneven pattern within profiles and with respect to micro-relief. In the high centred and intermediate polygon (LL3/96-LL7/96), fungal biomass was greater in the higher centre or apex than in the wet frost crack. On the contrary, in the low centred polygon (LL1/96; LL2/96), this relationship was inverse. However, the trend was similar when comparing hyphal length alone. At wet sites (LL2/96, 4/96 and 7/96) fungal biomass increased with depth. An exception represented the supra-permafrost layer, where fungi were usually lacking.

In the solifluction soils of the non-sorted steps, median hyphal length of 18.5 m g^{-1} d.wt. and biovolume of 0.15 mm^3 g^{-1} d.wt. were measured. The fungal biomass was 19.2 µg C g^{-1} d.wt.. These median values were lower than in the polygonal tundra soils. Hyphal length, fungal biovolume and biomass varied along with micro-sites. In the unvegetated mud boil (LL8.1/96), values were more than 90% lower than in the surrounding vegetated micro-sites. In the A-horizons of the drier sites (LL8.2/96; LL 11.1/96) values were 40 to 55% greater than in the O-horizons at wetter sites (LL8.3/96;11.2/96). Within profiles fungi generally decreased with depth. A peak was observed in the Oe-horizon of profile LL11.2/96. Worthwhile mentioning is the remarkable decrease of fungi within the first few centimetres of the unvegetated mud boil (LL8.1/96).

Tab. 5.3.1-1: Fungal parameters in the polygonal tundra at Levinson-Lessing.

Profile		Horizon/depth	L [m/g]	V [mm^3/g]	[µg C_f/g d.wt.]
Low centred polygon					
1/96	vegetated mound	Oi (0-5)	38.8	0.31	40.7
		Oi (5-10)	37.0	0.38	49.2
		Oe	5.0	0.09	11.5
2/96	centre	Oi	6.9	0.09	11.6
		Oe1	28.4	1.19	155.1
		Oe2	22.3	1.06	138.1
Special features:					
1/96	Carex roots	Oi	ND	ND	ND
	Fe-mottling	Bg	30.6	0.47	60.9
2/96	surface Fe-Ox.		0.8	0.01	1.4
High centred polygon					
3/96	vegetated mound	Oi	3.8	0.02	2.9
		Oe	41.2	0.26	34.2
		Bg	81.8	0.96	125.3
	frost boil	0-0.5	9.3	0.08	10.8
		0-4	7.5	0.07	9.5
4/96	frost crack	Oi	3.6	0.03	4.1
		Oe	34.7	0.41	53.7
		Bg	0	0	0
Special features:					
3/96	saprophytic fungi	Oe	7.9	0.11	13.8
4/96	transition Oe/Bg	Bg	53.9	0.63	82.0
Transitionary polygon					
5/96	centre	Oi	53.6	0.62	80.6
		Oe1	27.0	0.26	34.2
		Oe2	12.4	0.13	16.2
		Bg	5.3	0.25	32.4
		II Oe	0	0	0
6/96	mound	Oa1	101.4	0.93	120.3
		Oa2	85.3	0.74	96.5
		Oa3	49.4	0.43	55.8
		Bg	3.3	0.01	1.6
		II Oe	0	0	0
7/96	frost crack	Oe1	41.2	0.38	49.3
		Oe2	31.5	0.45	58.7
Special features:					
5/96	Fe-oxidation		ND	ND	ND
6/96	roots	Oe3	393.0	3.50	455.3
7/96	roots	Oe1	44.0	0.62	80.7
		x (min)	**0**	**0**	**0**
		x (max)	**393.0**	**3.50**	**455.3**
		mean	**39.4**	**0.45**	**59.0**
		median	**27.7**	**0.29**	**37.5**

Tab. 5.3.1-2: Fungal parameters in the non-sorted steps at Levinson-Lessing.

Profile		Horizon/depth	L [m/g]	V [mm^3/g]	[µg C_f/g d.wt.]
8/96	unvegetated mound	AC (0-0.5)	4.4	0.04	5.2
		AC (0-2)	2.0	0.02	2.2
		AC (2-4)	1.3	0.01	1.7
		Cg	4.6	0.09	11.6
	peat ring	Oi	82.8	0.56	72.9
		A	110.3	0.94	121.5
		Bg (5-9)	58.5	0.61	79.6
		Bg (>9)	18.5	0.15	19.2
11/96	vegetated mound	A	77.6	0.52	67.7
		Bg	1.8	0.03	4.1
	peat ring	Oi	47.7	0.56	72.6
		Oe	224.4	1.76	229.2
		Bg	3.5	0.03	4.2
		x (min)	**1.3**	**0.01**	**1.7**
		x (max)	**224.4**	**1.76**	**229.2**
		mean	**49.0**	**0.41**	**53.2**
		median	**18.5**	**0.15**	**19.2**

In the soils of the non-sorted and transitionary stripes (Tab. 5.3.1-3), median hyphal length of 14.5 m g^{-1} d.wt. and biovolume 0.11 mm^3 g^{-1} d.wt. were measured. Accordingly, median fungal biomass was 14.1 µg C g^{-1} d.wt.. As has been stated earlier for other soils, these values generally decreased with depth. In the transitionary stripes (LL10/96) values were greater than in the soil of the non-sorted stripes (LL9/96). In the latter, differences along with the micro-relief could also be established. Namely, no fungi were found in the unvegetated mound of profile LL9/96.

Summing up soils of the non-sorted steps and non-sorted stripes were below the overall median being most variable in the non-sorted steps. However, these differences were only significant between non-sorted stripes and polygon tundra ($p < 0.10$) or solifluction steps ($p < 0.05$) respectively. A relationship between fungi and plants that form mycorrhizal associations with fungi could not be established.

Tab. 5.3.1-3: Fungal parameters in the non-sorted (transitionary) stripes at Levinson-Lessing.

Profile		Horizon/depth	L [m/g]	V [mm³/g]	µg C_f/g d.wt.
Non-sorted stripes					
9/96	unvegetated mound	AC1 (0-0.5)	0	0	0
		AC1 (0-4)	0	0	0
		C2	0	0	0
	peat ring	Oi	6.8	0.03	3.7
		Oie (2-3)	24.3	0.18	23.9
		Oie (3-4)	17.1	0.12	16.1
Transtionary stripes					
10/96	unvegetated mound	A (0-0.5)	0	0	0
		A (0-11)	21.0	0.19	24.3
		C	45.8	0.53	68.4
	peat ring	Oi (0-2)	9.4	0.06	7.6
		Oi (2-3)	40.6	0.35	45.6
		A	64.2	0.49	63.9
		C	51.1	0.51	66.0
Special features:					
	peat	Oi (0-2)	12.0	0.09	12.1
	roots		ND	ND	ND
		x (min)	**0**	**0**	**0**
		x (max)	**64.2**	**0.53**	**68.4**
		mean	**20.9**	**0.18**	**23.7**
		median	**14.5**	**0.11**	**14.1**

Labaz

In the soils at Labaz, hyphal length up to 920 m g^{-1} d.wt. (median 4.07 m g^{-1} d.wt.) and fungal biovolume up to 9.6 mm^3 g^{-1} d.wt. (median 0.03 mm^3 g^{-1} d.wt.) were measured (see Tab. A4.1-2). Fungal biomass was up to 1248 µg C_f g^{-1} d.wt. (median 3.3 µg C_f g^{-1} d.wt.). Thus, despite a wider range of values less fungi (length, biovolume and biomass) were found in the Labaz soils compared to the soils at Levinson-Lessing.

Between sites at Labaz, hyphal length, fungal biovolume and biomass decreased in the order: wet sedge tundra (Lb4/95) > tussock tundra (Lb3/95) > hummock tundra (Lb2/95) > dry brown earth (Lb1/95) > dry podzolised brown earth (Lb7/95). The decrease of fungal biovolume and biomass was stronger than the decrease of hyphal length. In the tussock and hummock tundra soils values varied along with the micro-relief. Within profiles, fungi usually decreased with depth and were absent in supra-permafrost layer. Yet, many soils showed a distinct peak of fungi at a depth of 10-20 cm. This peak was found in organic as well as in mineral horizons.

As can be seen from Table 5.3.1-4, maximum values were found in the wet sedge tundra in the drainage ditch (Lb4/95). Median hyphal length was 59.7 m g^{-1} d.wt.. Median fungal biovolume of 0.58 mm^3 g^{-1} d.wt. and median fungal biomass of 75.5 µg C_f g^{-1} d.wt. were

determined. Within the profile, maximum values were found in the lower 5 centimetres of the Oi-horizon and otherwise decreased with depth.

Tab. 5.3.1-4: Fungal parameters in the wet sedge tundra at Labaz.

Profile		Horizon/depth	L [m/g]	V [mm³/g]	µg C_f/g d.wt.
Wet sedge tundra					
4/95	drainage ditch	Oi (0-2)	79.0	0.80	104.0
		Oi (2-5)	246.9	2.36	306.7
		ACg (5-10)	919.5	9.60	1247.7
		ACg (10-20)	40.3	0.36	46.9
		ACg (20-30)	2.7	0.01	1.3
		ACg (30-50)	0	0	0
		x (min)	**0**	**0**	**0**
		x (max)	**919.5**	**9.60**	**1247.7**
		mean	**214.7**	**2.19**	**284.4**
		median	**59.7**	**0.58**	**75.5**

Tab. 5.3.1-5: Fungal parameters at the hummock and tundra sites at Labaz.

Profile		Horizon/depth	L [m/g]	V [mm³/g]	µg C_f/g d.wt.
Hummock tundra					
2/95	hummock	A (0-2)	3.8	0.05	6.5
		Cg (2-5)	8.9	0.07	8.6
		Cg (5-10)	11.4	0.07	9.2
		Cg (10-20)	12.9	0.12	15.1
		Cg (20-30)	0.6	0.00	0.2
		Cg (30-40)	0	0	0
	frost crack	Oe (0-2)	16.9	0.13	17.5
		Oe (2-5)	2.0	0.03	3.6
		Oe (5-10)	43.1	0.38	48.9
		Of (10-20)	16.2	0.16	21.3
		Of (20-30)	0	0	0
Tussock tundra					
3/95	tussock	A (0-2)	ND	ND	ND
		A (2-5)	0	0	0
		Cg1 (5-10)	4.4	0.02	2.8
		Cg2 (10-20)	48.2	0.37	48.5
		Cg2 (20-30)	2.0	0.02	2.1
		Cg2 (30-40)	0	0	0
		Cg3 (40-50)	2.3	0.02	2.6
	depression	Oe (0-2)	64.9	0.53	69.2
		Oe (2-5)	77.7	0.60	78.4
		Oe (5-10)	124.9	0.75	97.9
		Oe (10-20)	82.4	0.45	57.8
		ACg (20-30)	0	0	0
		x (min)	**0**	**0**	**0**
		x (max)	**124.9**	**0.75**	**97.9**
		mean	**23.8**	**0.17**	**22.3**
		median	**6.6**	**0.06**	**7.6**

In the soils of the tussock (Lb3/95) and hummock tundra (Lb2/95), hyphal length, fungal biovolume and biomass were some 90% lower. As can be seen from Table 5.3.1-5, hyphal length up to 125 m g^{-1} d.wt. (median 6.6 m g^{-1} d.wt.) and fungal biovolume up to 0.75 mm^3 g^{-1} d.wt. (median 0.06 mm^3 g^{-1} d.wt.) were measured. Fungal biomass was up to 97.9 µg C_f g^{-1} d.wt. (median 7.6 µg C_f g^{-1} d.wt.). Furthermore, the variability depending on the micro-relief was high. Thus, hyphal length and fungal biomass was 50 to 97% greater in the depression than in the adjacent tussock or hummock. This increase was stronger in the tussock tundra. Whereas in the depressions fungi were confined to organic horizons, in the tussocks or hummocks maximum values were observed in the upper 15 cm of the Cg-horizon. No fungi were found in the supra-permafrost layer.

Tab. 5.3.1-6: Fungal parameters in the dry brown earth soils at Labaz.

Profile	Horizon/depth	L [m/g]	V [mm^3/g]	µg C_f/g d.wt.
Dry brown earth				
1/95	A (0-2)	14.8	0.08	10.7
	Bw1 (2-5)	13.9	0.11	14.6
	Bw1 (5-10)	17.3	0.08	10.5
	Bw1 (10-20)	4.7	0.02	3.0
	2Cw1 (20-30)	3.3	0.02	2.0
	Bw2 (30-50)	1.8	0.01	1.0
Dry podzolised brown earth				
7/95	Oi (0-2)	0.8	0.01	1.5
	Oi (2-5)	1.1	0.00	0.5
	Oi (5-7)	1.4	0.01	0.8
	AE (0-10)	0.5	0.00	0.4
	Bhs (10-25)	2.8	0.02	2.2
	Bwg (25-60)	0	0	0
	x (min)	**0**	**0**	**0**
	x (max)	**17.3**	**0.11**	**14.6**
	mean	**5.2**	**0.03**	**3.9**
	median	**2.3**	**0.01**	**1.7**

As can be seen from Table 5.3.1-6, fungal values were lowest in the dry soils at Labaz (Lb1/95 and Lb7/95). Yet, these two sites differed in the order of magnitude and the distribution pattern of fungi within the profile. In the dry brown earth (Lb1/95), median hyphal length of 9.3 m g^{-1} d.wt. and fungal biovolume of 0.05 mm^3 g^{-1} d.wt. were measured. Median fungal biomass was 6.73 µg C_f g^{-1} d.wt.. These values are comparable to those determined for the elevated tussocks and hummocks (Tab. 5.3.1-5). In the dry brown earth (Lb1/95), fungi clustered in the upper 10 centimetres of the profile.

On the contrary, in the dry podzolised brown earth (Lb7/95), fungi were some 90% lower than in the first brown earth. Median hyphal length of 0.98 m g^{-1} d.wt. and fungal biovolume of 0.01 mm^3 g^{-1} d.wt. were measured. Median fungal biomass was 0.63 µg C_f g^{-1} d.wt.. The distribution pattern within the profile also differed. Higher values were found in the Oi-horizon. The maximum value, however, was found in the Bhs-horizon.

At Labaz, the distribution of fungi in the drier soils (Lb1/95, Lb7/95, Lb2a/95 and Lb3a/95) was significantly ($p < 0.15$) different from the wetter soils (Lb4/95, Lb2b/95 and Lb3b/95). This relationship could not be established at Levinson-Lessing.

5.3.2 Bacteria

Levinson-Lessing

Data of total bacterial number, bacterial biovolume and bacterial biomass were determined by M. Bölter, IPÖ Kiel (publication SCHMIDT & BÖLTER, unpubl. data) and can be seen in Table A4.2-1.

At Levinson-Lessing, total bacterial number (TBN) up to $7.38*10^9$ g^{-1} d.wt. (median $1.16*10^9$ g^{-1} d.wt) and bacterial cellvolume (MCV) up to 0.056 μm^3 g^{-1} d.wt. (median 0.039 μm^3 g^{-1} d.wt.) were measured. Bacterial biomass (BBM) was 20.4 µg C g^{-1} d.wt. (median 4.7 µg C g^{-1} d.wt.). The distribution pattern of bacteria was different from what could be established for fungi. TBN was highest in the polygonal tundra whereas it was of the same order of magnitude in the soils of the non-sorted steps and stripes. On the contrary, BBM along with MCV decreased in the following order: polygonal tundra > non-sorted stripes > non-sorted steps. Between micro-sites and within profiles, distribution pattern also differed.

In the soils of the polygonal tundra, TBN, MVC and BBM generally decreased with depth at both micro-sites: frost cracks and apices/high centres. In the transitionary polygon (LL5-7/96), maximum values could be established in the supra-permafrost layer, where no fungi were found. Along with fungi, a relative increase in bacteria was found in the Oe-horizons of the apices of the high and low centred polygon (LL1 and 3/96).

In the soils of the non-sorted steps, TBN, MVC and BBM values were some 50% lower than in the polygonal tundra. This decrease was stronger for BBM and MCV. Within profiles these

values decrease with depth. A relative increase could be observed in the anaerobic C- or Bg-horizons. Between micro-sites, values were greater underneath vegetation (LL8.3/96, L11.2/96) compared to unvegetated soils (LL8.1/96). Hence, values were also greater in the overgrown step (LL11/96).

Despite comparable TBN in the non-sorted stripes (LL9 and LL10/96), BBM and MCV were some 10% greater. As has been stated for fungi, in the unvegetated mound values were lower than in the adjacent vegetation ring. However, this decrease was stronger in the soil of the transitionary stripes (LL10/96). Thus, the difference between micro-sites was more pronounced when looking at bacterial population.

Labaz

Data of total bacterial number, bacterial biovolume and bacterial biomass were determined by BÖLTER (1998) and can be seen in Table A4.2-2.

At Labaz, total bacterial number (TBN) up to $6.81*10^9$ g^{-1} d.wt. (median $0.37*10^9$ g^{-1} d.wt.) and bacterial cellvolume (MCV) up to 0.073 μm^3 g^{-1} d.wt. (0.047 μm^3 g^{-1} d.wt.) were measured. Bacterial biomass (BBM) was 33.1 μg C g^{-1} d.wt. (median 1.5 μg C g^{-1} d.wt.). Thus, TBN and BBM were lower than in the soils at Levinson-Lessing. The distribution pattern between sites generally resembled the pattern described for the fungal population. Thus, TBN, MCV and BBM decreased in the following order: wet sedge tundra > tussock tundra > hummock tundra > dry brown earth > dry podzolised soil. Yet, the differences were less pronounced.

In general bacteria clustered in the top few centimetres of the profile and decreased with depth which was particularly distinct between O-/A-horizons and mineral horizons. Furthermore, in the tussock and hummock tundra (Lb2/95 and 3/95) a relative increase or peak of TBN and BBM was observed at a depth of approximately 10 cm. This increase has already been described for fungi.

The micro-relief affected bacterial population at the hummock and tussock tundra sites. In the wet depressions (Lb2b/95 and Lb3b/95), TBN, MCV and BBM were greater than in the more elevated micro-site. This increase was more stronger in the tussock tundra.

At Labaz, the distribution of bacteria in the drier soils (Lb1/95, Lb7/95, Lb2a/95 and Lb3a/95) was significantly ($p < 0.05$) different from the wetter soils (Lb4/95, Lb2b/95 and Lb3b/95).

5.3.3 Microcalorimetry

5.3.3.1 Basal heat output (Q)

Levinson-Lessing

Basal heat output Q in the soils at Levinson-Lessing was up to 988.6 µW g^{-1} d.wt. (median 60.6 µW g^{-1} d.wt.). Between sites, Q values decreased in the order polygonal tundra, non-sorted steps and non-sorted stripes/nets. Within profiles Q values usually decreased with depth. Exceptions represented the unvegetated soils where Q values increased with depth.

In the soils of the polygonal tundra Q values varied along with the micro-site. In the topsoils of the drier elevated site (apex and centre) activities were greater than in the corresponding depression. Activities decreased with depth but in more pronounced manner at the drier elevated sites. In the frost boil of profile LL3/96 activities were half of the order of magnitude measured in the surrounding vegetated soil. The low centred polygon (LL1 and 2/96) differed from the high centred polygon (LL3 and 4/96) in that respect that the low centred polygon soils showed predominating microbial activity in the subsoil whereas in the high centred polygon higher activities were found in the topsoil.

Micro-sites and vegetation cover also affected the heat output in the soils of the non-sorted steps as well as of the non-sorted stripes/nets. In the respective topsoils without vegetation cover heat output was more than 70 % lower than in the adjacent vegetated soil. Also the activities in the subsoil differed. Thus, in the unvegetated soils (LL8.1/96; LL9.1/96) Q values were greater in the subsoil than in the topsoil whereas values decreased with depth in the vegetated soils.

Labaz

Basal heat output Q in the soils at Labaz was up to 1516.2 µW g^{-1} d.wt. (median 20.4 µW g^{-1} d.wt.). Thus, despite a wider range the median microbial activity was lower than in the soils at Levinson-Lessing. Between sites, Q values were greater in the hummock and tussock tundra than in the wet sedge tundra.

In the tussock tundra soil basal heat output was greater than in the soil. Also Q values varied along with the micro-relief although the two sites differed. Whereas at the tussock tundra site greater activities were measured in the depression compared to the drier tussock, at the hummock tundra site activities were lower in the frost crack. Activities generally decreased with depth. A relative peak at a depth of approximately 10 centimetres was observed in the hummock tundra. In the wet sedge tundra heat output was only determined in the upper 20 centimetres. In the subsoils values tended to zero. Maximum activity was found at a depth of 5 to 10 centimetres.

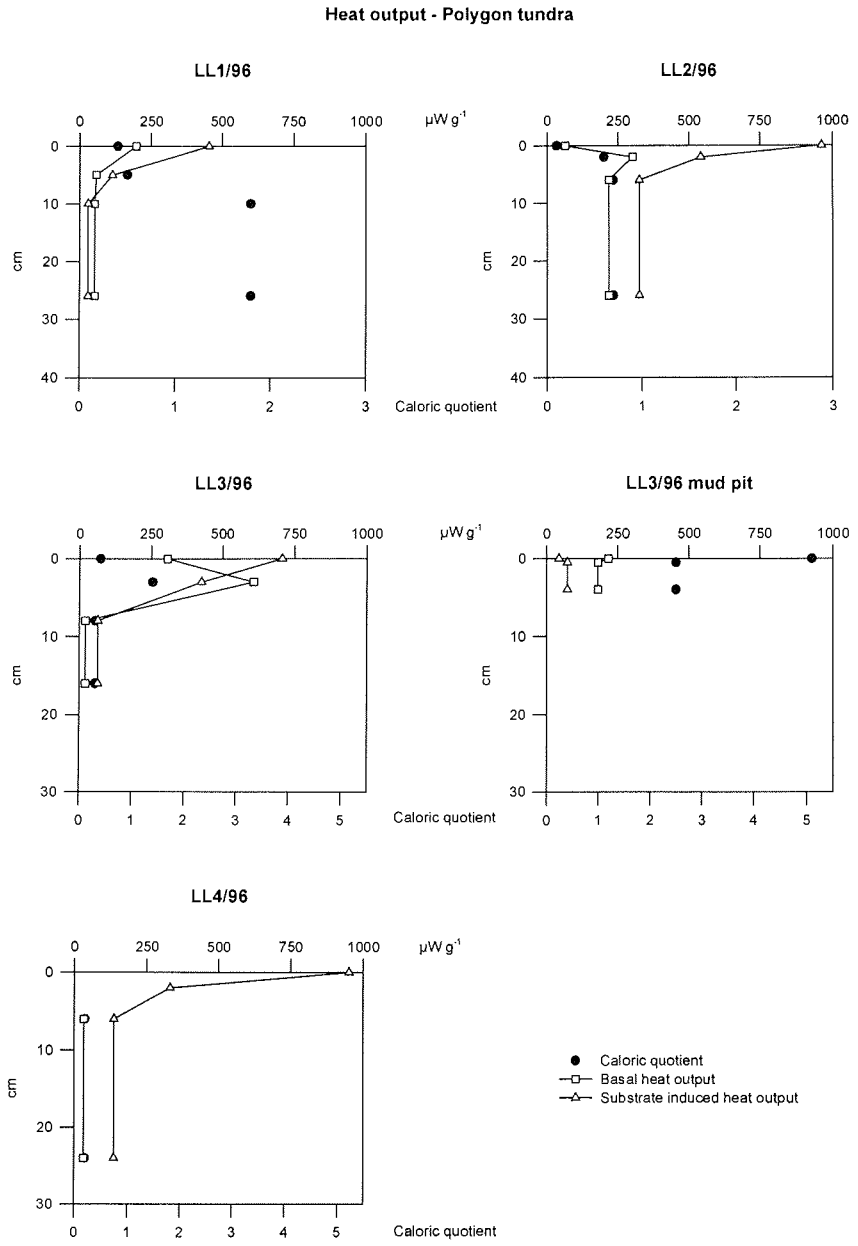


Fig 5.3.1: Basal and substrate induced heat output and caloric quotient in the soils of the low centred polygon (apex LL1/96; centre LL2/96) and the high centred polygon (centre LL3/96, unvegetated mud pit of the centre LL3/96 and frost crack LL4/96). Missing values were not determined. Note the different scales of the y-axes.

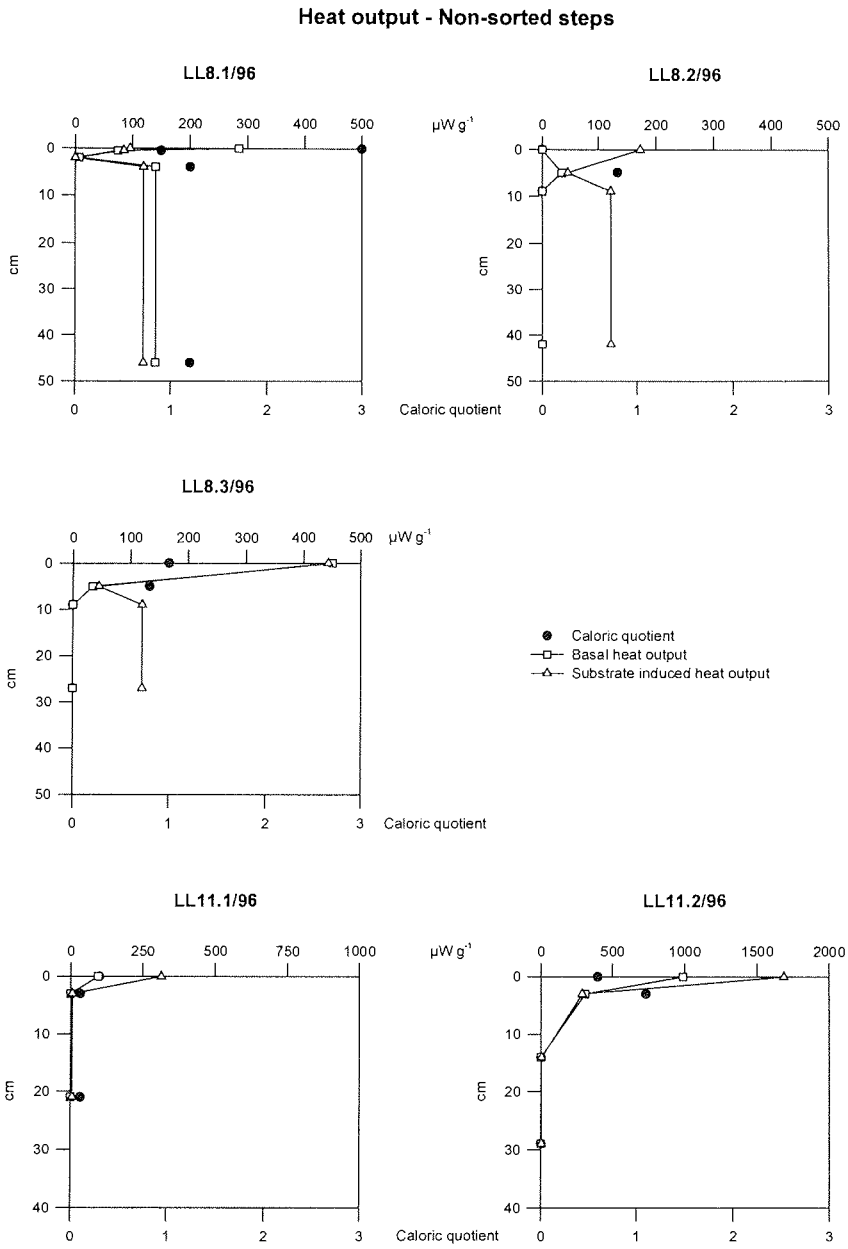


Fig. 5.3.2: Basal and substrate induced heat output and caloric quotient in the soil of the non-sorted step (LL8.1/96 bare mud pit, LL8.2/96 dry vegetation ring and LL8.3/96 wet vegetation ring) and the partially ovegrown non-sorted step (LL11.1 vegetated mud pit; LL11.2/96 vegetation ring). Missing values were not determined. Note the different scales of the x- and y-axes.

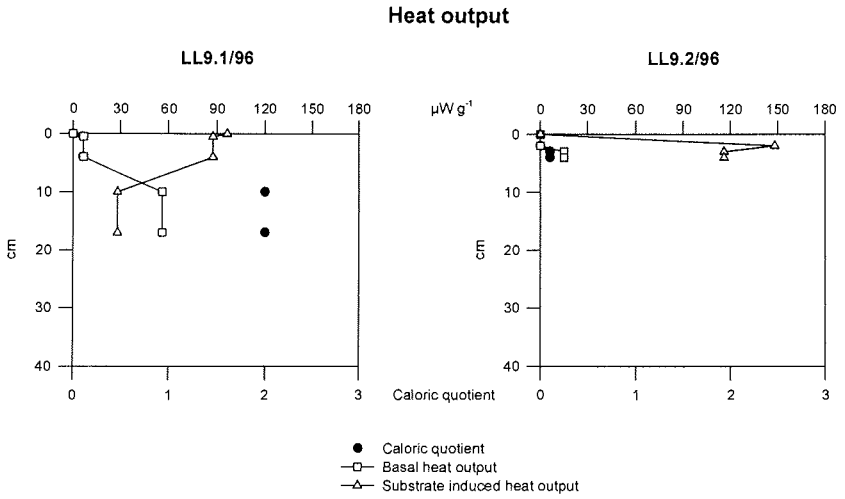


Fig 5.3.3: **Basal and substrate induced heat output and caloric quotient in the soils of the non-sorted stripes (9.1/96 unvegetated mound; 9.2/96 vegetation stripe). Missing values were not determined.**

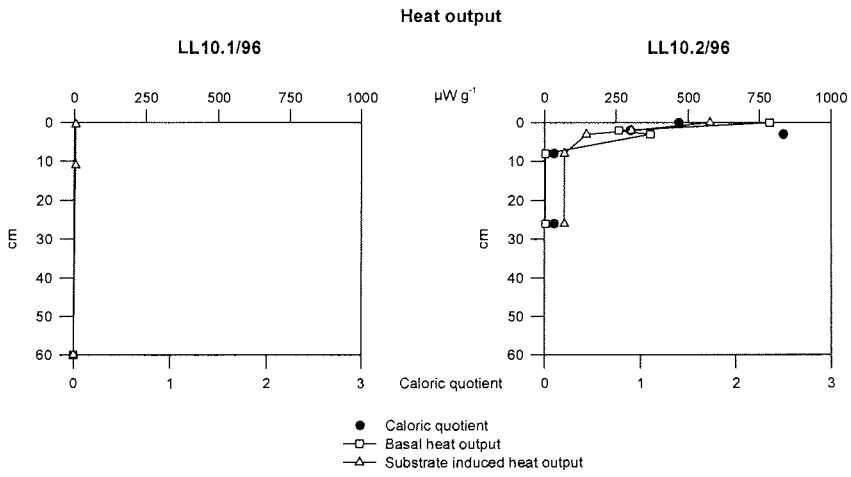


Fig. 5.3.4: **Basal and substrate induced heat output and caloric quotient in the soils of the transitionary stripes (10.1/96 unvegetated mound; 10.2/96 vegetation stripe). Missing values were not determined.**

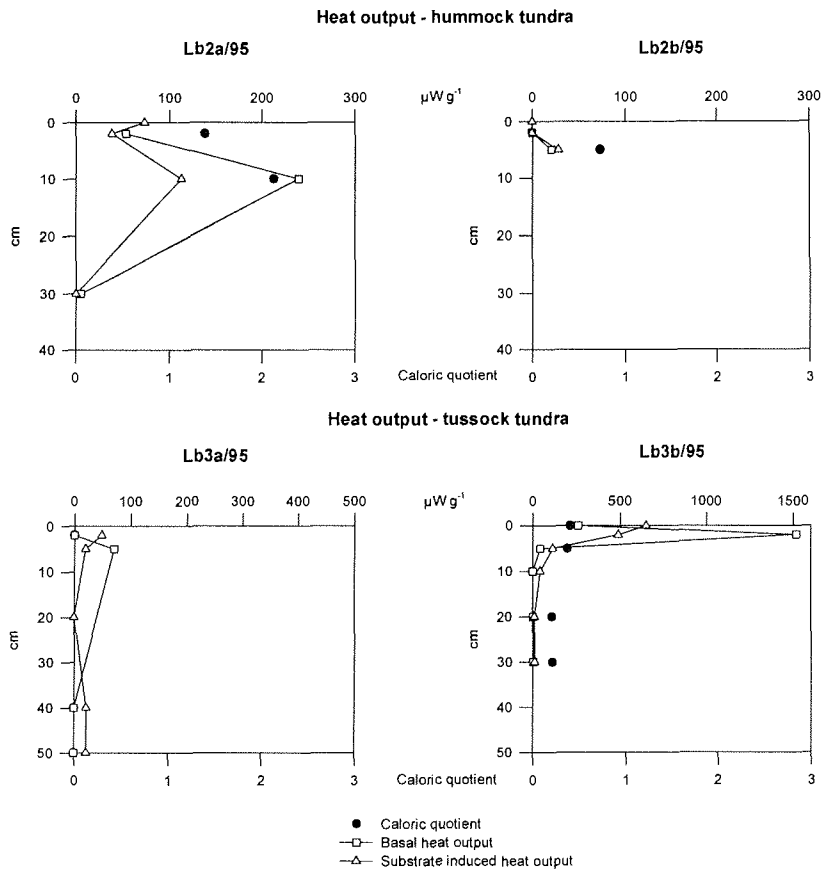


Fig. 5.3.5: Basal and substrate induced heat output and caloric quotient in the hummock tundra (hummock Lb2a/95, frost crack Lb2b/95) and the tussock tundra (tussock Lb3a/95, depression Lb3b/95) at Labaz. Missing values were not determined. Note the different scales of the x- and y-axes.

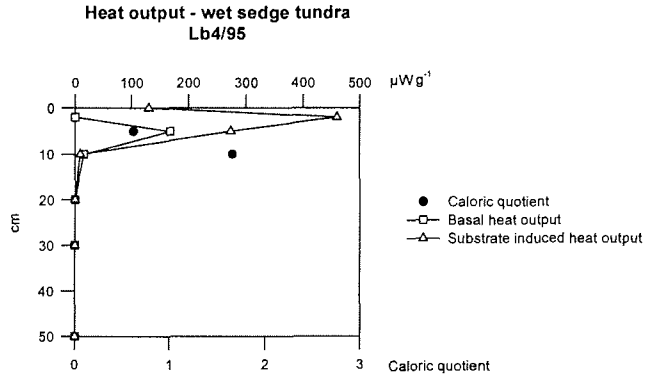


Fig. 5.3.6: Basal and substrate induced heat output and caloric quotient in the wet sedge tundra at Labaz. Missing values were not determined.

5.3.3.2 Substrate induced heat output (SIQ)

Levinson-Lessing

Substrate induced heat output *SIQ* in the soils at Levinson-Lessing was up to 1683.8 μW g^{-1} d.wt. (median 119.5 μW g^{-1} d.wt.). Thus, substrate amendment generally enhanced the overall microbial activity. Between sites, *SIQ* values decreased in the order polygonal tundra, non-sorted steps and non-sorted stripes/nets. Within profiles values generally decreased with depth.

In the polygonal tundra, soils of the wetter micro-sites (LL2/96 and LL4/96) showed greater values. This increase has already been determined for the basal heat output. Yet, with substrate amendment this increase was more pronounced. However, in the mud boil of LL3/96 the substrate induced heat output was lower than without substrate. In the subsoil *SIQ* values decreased remarkably although more pronounced in the soils of the elevated apex/centre.

In the soils of the non-sorted steps, changes in substrate induced heat output along with micro-relief and vegetation were observed. *SIQ* values increased with vegetation cover although this increase was not as pronounced as was observed for the basal heat output. This was partly due to lower heat output in the unvegetated mud pit (LL8.1/96) with substrate amendment than without. *SIQ* values generally decreased with depth although a relative increase in the anaerobic subsoil of LL8/96 could also be established.

Micro-relief and vegetation cover also affected the substrate induced heat output in the non-sorted stripes/nets (LL9/96 and LL10/96). As was established earlier *SIQ* increased with vegetation cover. Substrate amendment enhanced this increase in the case of profile LL9/96 but diminished it for profile LL10/96.

Labaz

Substrate induced heat output *SIQ* in the soils at Labaz was up to 648.4 μW g^{-1} d.wt. (median 38.7 μW g^{-1} d.wt.). Despite a narrower range, substrate amendment generally enhanced the overall microbial activity. Yet, the effect was lower than in the soils at Levinson-Lessing. Between sites, *SIQ* values were greater in the wet sedge tundra than in the hummock and tussock tundra. Compared to the basal heat output, this order was inverse.

In the soil of the wet sedge tundra (Lb4/95) *SIQ* could only be measured in the top 20 centimetres and was enhanced compared to the basal heat output.

A more complex pattern could be established in the soils of the hummock and soils tundra. Substrate induced heat output varied along with the micro-relief as was stated above for the basal heat output. Namely, in the hummock tundra soils *SIQ* values were greater in the drier hummock and decreased in the corresponding frost crack. On the contrary, in the tussock tundra values were greater in the depression. Yet, the heat output could hardly be enhanced by substrate amendment. This increased appeared to be stronger in the subsoil than in the top soil.

5.3.4 Adenosine triphosphate

Levinson-Lessing

The adenosine triphosphate (ATP) contents of the soils at Levinson-Lessing was up to 32.4 µg g^{-1} d.wt.. The median was 0.94 µg ATP g^{-1} d.wt.. The ATP contents decreased in the order non-sorted steps, polygonal tundra soils, and non-sorted stripes/nets. Within profiles ATP usually decreases with depth and varies depending on the micro-relief or sites. Topsoils of vegetated soils always showed greater ATP contents than the adjacent bare soil. On the contrary, ATP contents of the subsoils were often of the same order of magnitude or even greater in the subsoils of the bare micro-site. Water logged sites showed a more even distribution within the profile than the respective drier site.

Tab. 5.3.4-1: ATP contents in the non-sorted steps at Levinson-Lessing.

Profile:		horizon/depth	ATP [µg/g]
8/96	unvegetated mound	AC (0-0.5)	2.99
		AC (0-2)	1.71
		AC (2-4)	1.48
		Cg	5.34
	peat ring	Oi	32.40
		A	14.75
		Bg (5-9)	0.87
		Bg (>9)	0.50
11/96	vegetated mound	A	0.82
		Bg	2.72
	peat ring	Oi	8.74
		Oe	0.90
		Bg	1.70
		x (min)	**0.5**
		x (max)	**32.4**
		mean	**5.8**
		median	**1.7**

This particularly held true in the soils of the non-sorted steps. As can be seen from Table 5.3.4-1, ATP content was 7 to 15 times greater in the vegetation ring than in the adjacent mud pit. In the vegetated soils, this abruptly decreased with the mineral subsoil. In the mud pits, however, ATP increased with depth (profiles LL8.1/96 and 11.1/96).

Table 5.3.4 -2 shows that a uniform pattern of ATP contents along with the micro-relief was lacking in the soils of the polygonal tundra. Whereas the low centred polygon (LL1 and 2/96) showed fourfold greater ATP contents in the wet depression, the corresponding sites in the high centred (LL4/96) and transitionary polygon (LL7/96) showed lower contents. These were a third of the ATP content in the adjacent apex. Furthermore, subsamples of the polygonal tundra revealed "hot spots" of active micro-organisms. Thus, ATP content around the oxidised iron (Fe^{3+}) of the around a water vein was manifold (LL1/96) greater. The same was found in the Fe-oxidation band between the Oe- and Bg-horizon in profile LL4/96 and on the plant

remnants. However, subsamples of the soils in the transitional polygon were in the same order of magnitude as the surrounding horizon.

Tab. 5.3.4-2: ATP contents in the soils of the polygonal tundra at Levinson-Lessing (ND^+ not detectable; ND* not determined).

Profile:		horizon/depth	ATP [µg/g]
Low centred polygon			
1/96	vegetated mound	Oi (0-5)	1.10
		Oi (5-10)	0.24
		Oe	ND^+
2/96	centre	Oi	ND*
		Oe1	2.91
		Oe2	1.60
Special features:			
1/96	Carex roots	Oi	0.98
	Fe-mottling	Bg	7.91
2/96	surface Fe-Ox.		3.58
High centred polygon			
3/96	vegetated mound	Oi	4.67
		Oe	1.31
		Bg	1.02
	frost boil	0-0.5	14.70
		0-4	0.23
4/96	frost crack	Oi	0.64
		Oe	1.18
		Bg	0.81
Special features:			
4/96	transition Oe/Bg	Bg	2.13
Transitionary polygon			
5/96	centre	Oi	11.61
		Oe1	1.27
		Oe2	0.65
		Bg	0.36
		Oef	0.13
6/96	mound	Oa1	3.94
		Oa2	0.43
		Oa3	0.55
		Bg	0.27
		II Oe	0.19
7/96	frost crack	Oe1	0.41
		Oe2	0.32
Special features:			
5/96	Fe-oxidation		0.28
6/96	roots	Oe3	0.50
7/96	roots	Oe1	0.37
		x (min)	**0**
		x (max)	**14.7**
		mean	**2.1**
		median	**0.8**

Lowest ATP contents were found in the soils of the non-sorted steps and stripes (Tab. 5.3.4 -3). As previously has been described for the non-sorted steps, these soils showed variation of ATP contents along with the micro-relief and/or vegetation cover. Thus, values in the unvegetated mound were very low (<0.5 µg g^{-1}). In the soils with vegetation cover, ATP contents were up to ten times greater. Yet, values were greatest in the uppermost centimetres (in the transition between plant debris and humified material, as subsampling of the Oi-horizon revealed (LL10/96).

Tab. 5.3.4-3: ATP contents in the soils of the non-sorted stripes and nets at Levinson-Lessing.

Profile:		horizon/depth	ATP [µg/g]
9/96	unvegetated mound	AC (0-0.5)	0.15
		AC (0-4)	0.11
		C	0.10
	peat ring	Oi	3.07
		Oie (2-3)	0.87
		Oie (3-4)	0.34
10/96	unvegetated mound	A (0-0.5)	0.44
		A (0-11)	0.45
		C	0.19
	peat ring	Oi (0-2)	1.70
		Oi (2-3)	0.60
		A	1.14
		C	1.23
Special features:			
	Oi (0-2)	plant material	0.87
		rhizosphere	13.70
		humified material	2.17
		x (min)	**0.10**
		x (max)	**13.70**
		mean	**1.70**
		median	**0.73**

Labaz

The adenosine triphosphate (ATP) contents of the soils at Labaz were up to 25.2 µg g^{-1} d.wt.. The median was 1.2. µg ATP g^{-1} d.wt.. Thus, ATP contents were greater than in the soils at Levinson-Lessing. The ATP contents decreased in the order hummock and tussock tundra, dry carbonatic brown earth, wet sedge tundra, and podzolised brown earth. Within profiles ATP contents generally decreased with depth. This decrease was usually abrupt changing from A- or O-horizons into the mineral subsoil.

Furthermore, as can be seen from Table 5.3.4 -4, the hummock and tussock tundra soils showed a different distribution of ATP contents along with the micro-relief. In the soil of the hummock tundra, ATP contents were five times greater in the adjacent frost crack (Lb2/95) than in the hummock. On the contrary, in the tussock tundra (Lb3/95), values decreased by a third in the wet depression. In the tussock as well as in the hummock tundra values decreased

with depth but the ratio between the topsoil and the subsoil was narrower in the depression. In both profiles a relative increase of ATP could be observed at a depth of 10 to 20 centimetres (5 to 10 centimetres in the frost crack of the hummock tundra).

Tab. 5.3.4-4: ATP contents in the soils of the hummock and tussock tundra at Labaz (ND not detectable).

Profile			ATP [µg/g]
Hummock tundra			
2/95	hummock	A (0-2) som	3.65
		min.	0.23
		Cg (2-5)	0.34
		Cg (5-10)	0.03
		Cg (10-20)	1.36
		Cg (20-30)	0.83
		Cg (30-40)	1.25
	frost crack	Oe (0-2)	4.51
		Oe (2-5)	0.84
		Oe (5-10)	23.05
		Of (10-20)	1.21
		Of (20-30)	3.00
Tussock tundra			
3/95	tussock	A (0-2)	1.99
		A (2-5)	17.77
		Cg1 (5-10)	0.14
		Cg2 (10-20)	0.19
		Cg2 (20-30)	0.55
		Cg2 (30-40)	ND
		Cg3 (40-50)	ND
	depression	Oe (0-2)	4.16
		Oe (2-5)	4.85
		Oe (5-10)	0.91
		Oe (10-20)	1.74
		ACg (20-30)	ND
		x (min)	**0.0**
		x (max)	**23.0**
		mean	**3.5**
		median	**1.3**

A stratification of the ATP contents was also determined in the dry brown earth (Lb1/95). As can be seen from Table 5.3.4 -5, maximum ATP content of 25 µg g^{-1} d.wt. was found in the A-horizon and decreased remarkably with change into the underlying Bw1-horizon (app. 1 µg ATP g^{-1} d.wt.). ATP contents further decreased with depth. Yet, at a depth of 10 centimetres values increased until a depth of 50 centimetres (4 µg g^{-1} d.wt.).

Tab. 5.3.4-5: ATP contents in the dry brown earth at Labaz.

Profile	Pergelic Cryorthent	Horizon/depth	ATP [µg/g]
1/95		A (0-2)	25.15
		Bw1 (2-5)	1.67
		Bw1 (5-10)	0.71
		Bw1 (10-20)	1.15
		2Cw1 (20-30)	1.62
		Bw2 (30-50)	4.05

Tab. 5.3.4-6: ATP contents in the wet sedge tundra at Labaz.

Profile	Wet sedge tundra	Horizon/depth	ATP [µg/g]
4/95	drainage ditch	Oi (0-2)	1.97
		Oi (2-5)	1.84
		Oi (5-10)	1.13
		ACg (10-20)	ND
		ACg (20-30)	ND
		ACg (30-50)	ND

In the wet sedge tundra (Tab. 5.3.4 -6) and the podzolised brown earth (Lb7/95) ATP could only be determined in the topsoil (Oi- and AE-horizons). In the underlying subsoil ATP was not detectable. ATP contents were lowest in the podzolised brown earth (Tab. 5.3.4 -7.)

Tab. 5.3.4-7: ATP contents in the dry podzolised brown earth at Labaz.

Profile	Pergelic Cryorthent	Depth/horizon	ATP µg/g
7/95		Oi (0-2)	0.24
		Oi (2-5)	0.97
		Oi (5-7)	0.01
		AE (0-10)	0.96
		Bhs (10-25)	ND
		Bwg (25-60)	ND

5.4 Ecological parameters

5.4.1 Fungal to bacterial ratio

Levinson-Lessing

At Levinson-Lessing fungal to bacterial ratio (FB-ratio) was up to 174.1 (median 4.5). Thus, the microbial biomass was clearly dominated by fungi.

In the soils of the polygonal tundra (LL1-7/96), the ratio was narrower due to higher bacterial biomass (median FB-ratio 3.5). Generally, the FB-ratio widened with depth and tended to zero in the supra-permafrost layer, where bacteria dominated. Greater values were found in the apices or the high centre.

In the soils of the non-sorted steps (LL8/96 and LL11/96), median FB-ratio was 5.8. Accordingly, the proportion of the fungi was higher than in the polygonal tundra. This, however, depended on the micro-site. In the vegetated soils ratios were wide and culminated at a depth of approximately 10 centimetres. On the other hand, the FB-ratio was 1 (or smaller) in the unvegetated mound.

In comparison to the non-sorted steps, the FB-ratio narrowed (median 5.5) in the soils of the non-sorted (transitionary) stripes, which was due to higher bacterial biomass. In the unvegetated mounds FB-ratios were nil. In the soils of the vegetated stripes, fungi over took. FB-ratios of profile LL9/96 were narrower than of profile LL11/96.

Labaz

In the soils at Labaz, FB-ratio was up to 170.0 (median 2.7). Thus, microbial biomass was dominated by fungi although the proportion of bacteria increased in comparison to the soils at Levinson-Lessing. At Labaz, FB-ratios were widest in the lower Oe- or upper mineral horizons. This peak was found regardless of sites or micro-sites. Below, FB-ratios verged to nil where bacteria dominated and fungi tended to be absent. Differences could only be established in terms of absolute figures.

Maximum values were found in the wet sedge tundra. In the tussock and hummock tundra, FB-ratios varied along with the micro-relief. In the topsoil of the tussock (Lb3a/95) and the hummock (Lb2a/95), FB-ratios widened with depth. Whereas the A-horizon was dominated by bacteria, fungi over took in the upper Cg-horizon. In absolute figures, FB-ratio was wider in the tussock than in the hummock. On the contrary, the composition of the microbiota differed in the adjacent depression or frost crack. In the frost crack of the hummock tundra (Lb2b/95), the microbiota was dominated by bacteria (with exception of a peak around 10 cm). In the depression of the tussock tundra (Lb3b/95) fungi dominated in the entire organic horizon.

In the uppermost horizons of the dry soils (Lb1 and Lb7/95), fungi and bacteria counterbalanced. FB-ratios widened with depth, although the increase of fungi in profile Lb1/95 was stronger.

5.4.2 Caloric quotient

Levinson-Lessing

The ratio of basal to substrate induced heat output (caloric quotient) was up to 5.1 (median 0.6) in the soils of Levinson-Lessing. Thus, the substrate induced activity prevailed over the basal activity. The caloric quotient narrowed in the following order: non-sorted steps>polygon tundra>non-sorted stripes. Within profiles an apparent pattern was lacking.

In the soils of the non-sorted steps, the caloric quotient was greater 1 when vegetation was lacking. This diminished in the presence of vegetation. The caloric quotient also decreased with depth although relatively greater quotients could also be observed. The latter quotients were ±1. These were determined in the anoxic horizon of profile 8.1. and the aerobic upper centimetres of the subsoil of the vegetation ring (LL11.2/96 and LL8.2/96). In contrast values verged to nil in the anoxic horizon of the soils with vegetation cover.

In the topsoils of the polygonal tundra, the caloric quotient was smaller 1. Again, the quotient increased (i.e., >1) with lacking vegetation as in the mud boil of the high centred polygon (LL3/96). However, the caloric quotient characteristics differed remarkably between the two types of polygons. They differed with respect to micro-site and to depth. In the soils of the low centred polygons the quotient increased with depth. This increase was stronger in the apex than in the wet centre and exceeded 1. In the corresponding profile of the high centred polygon (LL3/96) the quotient decreased with depth although maximum quotient of >1 was determined in the lower organic horizon.

Caloric quotient in the non-sorted stripes were generally very low and verged to nil. Quotients >1 were found in the anoxic mineral subsoil of unvegetated mound (e.g., LL9.1/96) and the organic horizons of the vegetated mound (e.g., 10.2/96).

Summing up it may be stated that the microbial activity was enhanced by substrate amendment. Exceptions were the mineral topsoils of the unvegetated soils, the anoxic subsoil of the unvegetated soils as well as the upper centimetres of the subsoil of the drier elevated micro-sites. Here, substrate induced heat output was below basal heat output, i.e., quotients exceeded 1. The different abiotic properties suggest a different composition of the microbiota at the respective micro-habitats.

Labaz

In the soils at Labaz, the caloric quotient was up to 3.5 (median 0.5). As was observed in the soils of Levinson-Lessing substrate induced microbial activity predominated.

In the wet sedge tundra (Lb4/95) the caloric quotient was only determined in the Oi-horizon since no activity could be measured in the subsoil. Within the Oi-horizon quotients increased

with depth and exceeded 1 in the lower centimetres. In the hummock and tussock tundra, values varied along with the micro-relief although both tundra types differed. The relatively elevated micro-site showed a zigzag pattern of caloric quotients with increasing depth. They both showed a peak (quotient >1) at lower depth of approximately 10 centimetres. Yet, they differ in the topsoil and the underlying subsoil. The hummock (Lb2a/95) showed greater substrate induced activity in the topsoil (caloric quotient <1) and predominating basal activity above the permafrost table. In the tussock (Lb3a/95) on the contrary quotients were nil since no basal activity was measured. In the corresponding depression quotients were always <1 and showed a peak (>1) in the lower Oe-horizon and a relative increase above the permafrost table.

As for the soils at Levinson-Lessing the substrate induced microbiota predominated. Nevertheless micro-habitats with differing caloric quotients were also found in the soils at Labaz. These represented the transitional horizons from the topsoil to the mineral subsoil as well as the supra-permafrost layer.

5.4.3 Microbial inventory

The measurement of trace gas fluxes in the field represent activity studies under natural conditions. Data are usually given as a flux over a given area. For the soils of this study CO_2 (SOMMERKORN, 1998) and CH_4 fluxes (GUNDELWEIN, 1998) were measured. As a consequence an inventory of fungal and bacterial biomass data from Sections 5.3.1 and 5.3.2. was also taken [mg C_{mic} m^{-2}] for further understanding of the mediating microbial population.

Levinson-Lessing

Fungal and bacterial carbon inventories *CI* for the soils at Levinson-Lessing are shown in Table 5.4.3-1. Bulk density changed within profiles and between micro-sites, which results in a different distribution pattern of fungal or bacterial biomass. In contrast to data related to dry weight of soil, decreases of fungi and bacteria within profiles became less pronounced due to increasing bulk density.

As an example given, increasing bulk density between micro-sites in the soils of the non-sorted stripes (LL9/96) and the transitionary polygon (LL5 and 6/96) amplified increases in fungi and bacteria. On the contrary, lower bulk density in wet depressions (LL2/96) or frost cracks (LL4/96) for instance balanced differences out. In the case of the high centred polygon this resulted in an inverse relationship. Fungal *CI* became greater in the frost crack than in the adjacent higher centre. Bacterial *CI*, however, became greater in the centre. An inverse relationship was also observed between the centre and the mud boil of the high centred polygon (LL3/96) and within profile LL1/96. In the latter bacteria increased with depth when given as bacterial *CI*.

Tab. 5.4.3-1: **Bulk density D_b [g cm^{-3}], fine earth bulk density D_{bf} /g cm^{-3}], fungal and bacterial carbon inventory *CI* [mg C m^{-2}] in the upper 4 cm of soils at Levinson-Lessing. Subsoil samples were taken for profile LL1/96 and LL3/96. *values were calculated using an estimated value of bulk density.**

Profile	Horizon/depth	D_b [g cm^{-3}]	D_{bf} [g cm^{-3}]	*CI* [kg m^{-2}]	fungal *CI* [mg C m^{-2}]	bacterial *CI* [mg C m^{-2}]
Polygon tundra						
Low centred						
apex (LL1/96)	Oi (0-4 cm)	0.48		3.9	777.3	68.9
	Oe (6-10 cm)	0.94		8.0	428.6	77.4
Centre (LL2/96)*		*0.34		1.0	*237.1	*8.6
High centred						
Centre	Oi/Oe	0.34		3.0	145.7	135.5
	Bg (2-6 cm)	0.68			3403.0	19.5
	mud boil (0-4 cm)	1.09		2.3	420.4	227.6
Frost crack (LL4/96)		0.09		0.9	101.2	67.8
Transitionary						
Centre (LL5/96)	Oi/Oe1	0.34		2.8	925.4	129.9
Apex (LL6/96)	Oa1/Oa2	0.38		2.9	1733.7	72.6
Non-sorted steps						
LL8.1/96	mud boil	1.29	0.59	0.7	54.1	50.5
veg. ring (LL8.2/96)	A (0-4 cm)	0.75	0.08	0.3	388.8	8.1
Non-sorted stripes						
non-vegetated (LL9.1/96)	AC	1.51	0.52	0.5	0.0	48.2
veg. stripe (LL9.2/96)	Oi/Oie	0.57		3.6	314.8	225.0
veg. stripe (LL10.2/96)	Oi/A	0.57		4.8	712.2	160.9

Labaz

For the soils at Labaz, bulk density values were available for whole profiles. As can be seen from Table 5.4.3 -2 values for fungal and bacterial CI showed also differences in the soils at Labaz other than from simple biomass data. Decreases of fungi and bacteria with depth were less pronounced with increasing bulk density (e.g., Lb2a/95). Conversely, relative increases were enhanced such as the peak at a depth of 10 to 20 cm or in the supra-permafrost layer of profile Lb3a/95. In the corresponding depression an analogous peak became only apparent when fungi and bacteria where given in inventories.

On the contrary, increases in fungi and bacteria between micro-sites (as in profile Lb2/95; Lb3/95) diminished along with lower bulk density. For bacteria this resulted in an inverse relationship. Greater bacterial *CI* was found in the hummock although in the depression the bacterial biomass was greater.

Tab. 5.4.3-2: **Bulk density Db [g cm-3], fungal and bacterial carbon inventory CI [mg C m-2] at different depths in the soils at Labaz. ND not determined (modified from GUNDELWEIN, 1998).**

Profile	Horizon		D_b [g cm^{-3}]	*CI* [kg m^{-2}]	fungal *CI* [mg C m^{-2}]	bacterial *CI* [mg C m^{-2}]
Hummock tundra						
2a/95	A	(0-2 cm)	0.9	1.85	143.5	489.7
	Cg	(2-5 cm)	1.3	0.59	336.7	57.9
		(5-10 cm)	1.3	0.98	599.2	48.1
		(10-20 cm)	1.3	1.69	1968.5	277.7
		(20-30 cm)	1.3	1.69	24.6	95.2
		(30-40 cm)	1.3	2.08	0.0	67.7
2b/95	Oe	(0-2 cm)	0.3-0.6	2.75 - 5.5	104.7-209.4	156.1-312.2
		(2-5 cm)	0.3-0.6	4.12 - 8.24	32.1-64.3	50.1-100.3
		(5-10 cm)	0.3-0.6	6.87 - 13.7	733.7-1467.4	34.4-68.7
	Oef	(10-20 cm)	0.3-0.6	13.74 - 27.48	637.7-1275.5	161.2-322.1
		(20-30 cm)	0.3-0.6	13.74 - 27.48	0.0	53.0-105.9
Tussock tundra						
3a/95	A	(0-2 cm)	0.6	0.58	ND	84.9
		(2-5 cm)	0.6	0.86	00.0	40.2
	Cg1	(5-8 cm)	1.2	0.83	179.8	63.7
	Cg2	(8-10 cm)	1.4	0.59	78.6	27.9
		(10-20 cm)	1.4	2.94	6791.3	135.9
		(20-30 cm)	1.4	2.94	295.9	88.6
		(30-40 cm)	1.4	3.36	0.0	103.9
		(40-44 cm)	1.4	1.34	328.8	127.0
	Cg3	(44-50 cm)	1.2	2.88	185.0	71.4
3b/95	Oe	(0-2 cm)	0.2-0.5	1.34 - 3.36	747.0-1867.0	108.0-269.0
		(2-5 cm)	0.2-0.5	2.02 - 5.04	470.2-1175.5	79.4-198.4
		(5-10 cm)	0.2-0.5	3.36 - 8.4	978.6-2446.4	331.1-827.8
	ACg	(10-17 cm)	0.2-0.5	4.70 - 11.76	3065.0-4279.0	309.0-432.1
		(17-20 cm)	1.3	1.48	2255.3	227.7
		(20-30 cm)	1.3	4.94	0.0	223.0
Wet sedge tundra						
4/95	Oi	(0-2 cm)	0.5	1.68	1039.8	293.8
		(2-5 cm)	0.5	2.52	4600.0	243.1
		(5-10 cm)	0.5	4.2	31191.4	183.5
		(10-12 cm)	0.5	1.68	5725.8	303.0
	ACg	(12-20 cm)	1.4	2.02	5256.5	278.2
		(20-30 cm)	1.4	2.52	186.4	205.9
		(30-40 cm)	1.4	2.52	0	145.0

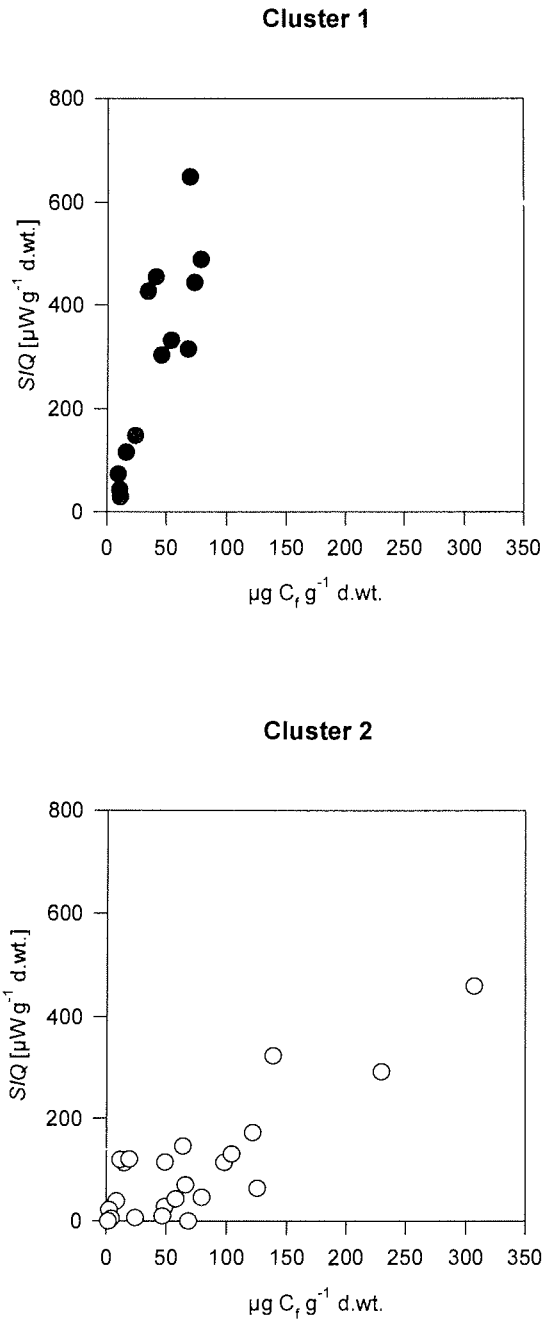


Fig. 5.4.1: Relationship of fungal biomass [µg C_f g^{-1} d.wt.] and substrate induced heat output *SIQ* [µW g^{-1} d.wt.] in the soils with predominant fungal microbial biomass at Levinson-Lessing and Labaz.

5.4.4 Allocation of microbial habitats

Microbial biomass vs. substrate induced heat output

As was mentioned before (4.3.2.2.) substrate induced heat output *SIQ* is a parameter used to determine soil microbial biomass. In this study overall data of fungal and bacterial biomass did not correlate with *SIQ* suggesting a complex microbial community structure. However, individual relationships of *SIQ* to fungal and bacterial biomass became apparent when looking at particular soils or the respective micro-organisms alone. Figure 5.4.1 shows the relationship of the fungal biomass and *SIQ* in the soils with a predominating fungal component of the microbial biomass (FB-ratio >1). The plot shows two discernible clusters. The first cluster is characterised by a steep linear increase of *SIQ* per unit fungal biomass (r^2=0.78). Generally these were mainly organic topsoils of all investigated sites at Levinson-Lessing and Labaz. Most entries were found among the lower Oi- or Oe-horizons. An exception here represented the mineral topsoil of the mud pit of the high centred polygon (LL3/96). At a lower level another cluster showed a linear, more gentle increase of *SIQ* per unit fungal biomass (r^2=0.73). This relationship was generally found for mineral subsoils. Exceptions were organic topsoil horizons of the wet sedge tundra (Lb4/96) and the frost crack in the tussock tundra (Lb2a/95).

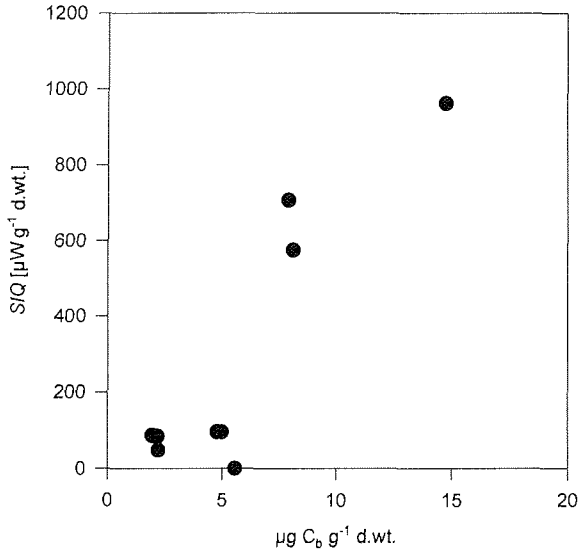


Fig. 5.4.2: Relationship of bacterial biomass [µg C_b g^{-1} d.wt.] and substrate induced heat output in the uppermost 5 cm of soils with predominating bacterial microbiota at Levinson-Lessing.

Soil horizons with a predominating bacterial microbiota (FB-ratio <1) generally showed rather low *SIQ* values. *SIQ* and bacterial biomass only correlated well (r^2=0.83) in the uppermost centimetres of organic topsoils (i.e., Oi-horizons). This relationship was also marked by a

logarithmic increase of *SIQ* values per unit bacterial biomass which was steeper than was observed for fungi. However, as can be seen from Figure 5.4.2 the random sample size was small. Increasing fungi (i.e., greater FB-ratios) did not attribute significantly to increasing *SIQ* values.

Activity of substrate sensitive biomass

Figure 5.4.3 shows the relationship of ATP contents and substrate induced heat output *SIQ* for the soils of both study areas. Three clusters were discernible. Cluster no. 1 is characterised by great *SIQ* values (>250µW g^{-1} d.wt.). Cluster no. 3 showed intermediate values. As for cluster no. 2; *SIQ* values were low but ATP contents were high (>2 µg ATP g^{-1} d.wt.).

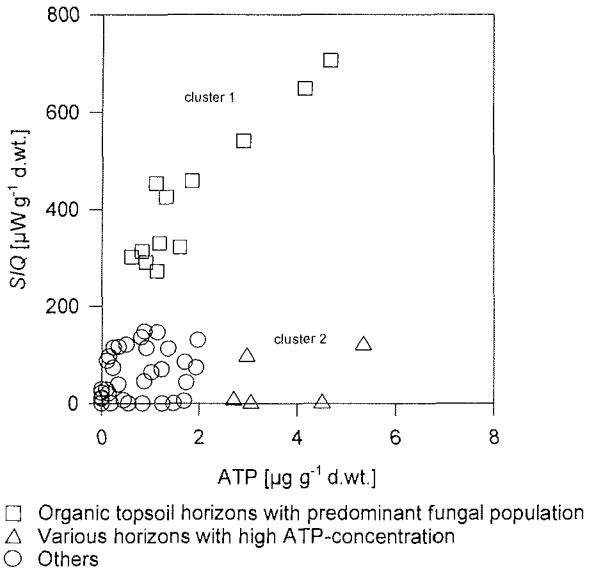


Fig. 5.4.3: Relationship of ATP-contents [µg g^{-1} d.wt.] and substrate induced heat output *SIQ*[µW g^{-1} d.wt.] in the soils at Levinson-Lessing and Labaz.

Cluster no.1 comprises drier (apices of the polygonal tundra, overgrown non-sorted steps, the soils of the vegetation ring) as well as wetter organic horizons (tussock and wet sedge tundra) and subsoil horizons of the wetter micro-sites of the polygonal tundra. As can be seen ATP contents correlated well (r^2= 0.87) with *SIQ* values in these horizons.

Fungal and bacterial biomass was significantly (p=0.10; p<0.01) greater in the horizons of cluster no. 1 than in cluster no. 3. FB-ratios, however, did not diverge. This suggests that the differences were caused by the magnitude of the total active microbial biomass.

In the horizons of cluster no., 2 *SIQ* values were low despite high ATP contents. The overall microbial biomass was low. Yet, this was mainly because of low fungal biomass (median 9.08 $\mu g\ C_f\ g^{-1}$ d.wt.) which was similar to the horizons of cluster no. 3. On the contrary, bacterial biomass in these horizons (median 13.2 $\mu g\ C_b\ g^{-1}$ d.wt.) was significantly higher ($p<0.05$). This was also reflected by the FB-ratio. The latter was also significantly ($p=0.10$) narrower than in the horizons of cluster 1 and thus clearly dominated by bacteria. ATP contents, however, were neither correlated to *SIQ* nor to basal heat output *Q*. Cluster no. 2 comprises the very top centimetres of many Oi-horizons (i.e., generally 0-2 centimetres of the soils of the hummock and tussock tundra as well as the vegetated non-sorted stripe), furthermore the anoxic subsoil of mudpits (non-sorted steps) and the corresponding upper 0.5 centimetres of the unvegetated mudpit.

Active versus restricted microbial biomass

ATP contents neither correlated with fungal nor with bacterial biomass. Nevertheless differences between individual soils were observed when relating ATP to microbial biomass (here: summed up fungal and bacterial biomass, C_{fb}).

In the soils at Levinson-Lessing, median ATP content per unit microbial biomass was 0.03 μg ATP $\mu g^{-1}\ C_{fb}$. At Labaz median value was 0.05 μg ATP $\mu g^{-1}\ C_{fb}$, and significantly ($p<0.10$) different. Maximum values also were up to seven times greater at Labaz than at Levinson-Lessing.

Table 5.4.4 -1 shows that values varied with sites at the respective study area. Similarity between individual sites at Levinson-Lessing and at Labaz could not be established.

Tab. 5.4.4-1: Difference of median ATP:MBM (summed up fungal and bacterial biomass) ratios [µg ATP: µg C_{mb}] and significance level [*p*] between individual sites at Levinson-Lessing and Labaz (PT.: polygonal tundra; Solst.: non-sorted steps with solifluction; Str.: non-sorted stripes; BE: dry brown earth; HT: hummock tundra; TT: tussock tundra; WST: wet sedge tundra; p. BE: podzolised brown earth).

Profiles	ATP:MBM	PT	Solst.	Str.	BE	HT	TT	WST	p. BE
PT (LL1/96-7/96)	0.02		**0.07**	0.67	0.15	0.10	0.38	0.06	0.30
Solst. (LL8/96; LL11/96)	0.19			**0.02**	0.20	0.21	0.46	0.00	0.69
Str. (LL9-10/96)	0.03				0.14	0.08	0.36	0.01	0.25
BE (Lb1/95)	0.56					0.45	**0.79**	**0.12**	0.24
HT (Lb2/95)	0.10						**0.78**	**0.05**	0.39
TT (Lb3/95)	0.03							0.32	0.53
WST (Lb4/95)	0.00								**0.15**
p. BE (Lb7/95)	0.05								

At Levinson-Lessing ATP content per unit microbial biomass was significantly ($p<0.10$) higher in the non-sorted steps of the solifluction slopes. These also showed differences along with the micro-relief. In the unvegetated mud boil (LL8.1/96) values were some 90 % greater than in the adjacent vegetation ring. On the contrary, in the soils of the overgrown step (LL11/96) this relationship was inverse. Values were 30 % greater in the vegetation ring. In the non-sorted stripes, ATP content per unit microbial biomass also increased along with the vegetation cover. Yet, this increase was far less pronounced in profiles LL9/96 (i.e., 10 %) than in profiles LL10/96 (i.e., 60 %). In the polygonal tundra, values were greater in soils of the drier micro-sites than in the corresponding depression or frost crack. Yet, this did not apply to the low centred polygon where no difference could be observed between the micro-sites. Values were higher in the high centred and intermediate polygon. Within profiles, values generally decreased with depth. Exceptions here represented the wet micro-sites of the high and low centred polygon, the drier apex of the intermediate polygon and the subsoils of the non-sorted steps. In the latter this increase with depth was either an absolute (profile LL11/96) or a relative within the subsoil (LL8.2/96).

At Labaz ATP content per unit microbial biomass decreased in the order: dry brown earth > tussock tundra > hummock tundra > podzolised brown earth > wet sedge tundra. Difference between dry brown earth and the tussock tundra as well as between the latter and hummock tundra could not be established. The inconsistency in this relationship was due to a wide range of values in the tussock tundra along with the micro-relief. The wet sedge tundra soil showed a significant lower ATP content per unit microbial biomass than the soils of other sites. Within profiles values generally decreased with depth. Exceptions here could be observed in the soils of the tussock and the hummock tundra. These showed increased ATP contents per unit microbial biomass at a lower depth. In the soil of the hummock tundra this increase was observed at a depth of 5 and 10 centimetres. Values were greater than in the overlying horizons. In the soils of the tussock tundra this increase represented only a relative one and

was observed at a depth of 10 to 20 centimetres. In the dry brown earth increasing values were observed at a depth of 10 centimetres and culminated at a depth of 50 to 60 centimetres.

Active fungi

In soil horizons with predominating fungi, ATP content per unit fungal biomass was up to 3.9 µg ATP $\mu g^{-1} C_f$. Yet, two thirds of the respective samples showed extreme low values of smaller than 0.04 µg ATP $\mu g^{-1} C_f$. Nevertheless fungal biomass was significantly ($p<0.05$) greater. This relationship particularly held true for subsoil horizons and few organic horizons in the non-sorted steps and stripes at Levinson-Lessing. In the low centred polygon, values were lower in the wet centre than in the corresponding apex. This relationship was inverse in the high centred polygon. Values were greater in the drier centre.

In the soils at Labaz, extreme low ATP content per unit fungal biomass were always found in horizons that showed absolute or relative peaks of fungal biomass.

5.4.5 Controls of microbial habitats

Soil pH

Fungi and bacteria were present in soils over the whole range of soil pH. Fungal biomass (FBM) showed a normal distribution pattern (see Fig. A4.1-1) along with pH with maximum FBM at pH ($CaCl_2$) 5.7. On the contrary, no such or only a weak distribution pattern was discernible for bacterial biomass (BBM). Thus microbial community composition as expressed by the FB-ratio was also affected by soil pH as FBM was.

For the tundra soil types (Lb2/95- Lb4/95) at Labaz, maximum FBM values (45-120 µg $C_f g^{-1}$ d.wt.) at soil pH ($CaCl_2$) around 5.1 were found in most subsoil horizons at a depth of approximately 10 centimetres. The soils at Levinson-Lessing showed a different distribution pattern of FBM along with pH. Relatively high FBM values (60-100 µg $C_f g^{-1}$ d.wt.) were found at pH ($CaCl_2$) 6.2. These comprised most organic topsoils of the drier micro-sites of the polygonal tundra as well as of the vegetated non-sorted stripes and steps. Below pH 6.0, FBM was usually smaller than 50 µg $C_f g^{-1}$ d.wt.. Yet, beside the relative peak of a normal distribution pattern, a cluster of higher FBM values (> 60 µg $C_f g^{-1}$ d.wt.) was also found below pH ($CaCl_2$) 6.0, which could be attributed to the vegetation ring of the non-sorted step (LL8/96) and the wet centre of the low centred polygon (LL2/96).

As mentioned above, bacterial biomass (BBM) only showed a weak normal distribution pattern along with soil pH. Yet, two clusters were discernible that fell out of this pattern. In the tundra soil types at Labaz (Lb2-4/95), the uppermost centimetres of organic topsoils showed high BBM values (>20 µg $C_b g^{-1}$ d.wt.) at low pH 5.1 ($CaCl_2$). BBM values between 15 and 22 µg $C_b g^{-1}$ d.wt. were found at higher pH values (6-7.8). This cluster was observed in

the soils at Levinson-Lessing namely in the uppermost centimetres of organic topsoils of the polygonal tundra, the non-sorted stripes and steps. Yet, these horizons were not identical to those for which an increase in FBM has been described before. In the latter O-horizons, on the contrary, BBM values were rather low (usually around 5 µg C_b g^{-1} d.wt). Profile LL11/96 represented an exception.

Within most Oi-horizons at Levinson-Lessing, BBM tended (r^2=0.64) to increase with increasing pH. This relationship did not apply to the centre of the low centred polygon (LL2/96), profile 8.3/96 of the vegetated non-sorted step and profile 9.2/96 of the vegetation stripe. This relationship could also not be established for the soils at Labaz.

Vegetation

Generally the presence of vegetation governed the size as well as the composition of the microbiota. As mentioned in Section 5.4.1 microbial biomass shifted towards higher bacterial biomass in unvegetated soils. Vegetation is also closely related to both quantity and quality of soil organic matter content. Thus, plants affect the nutrient resource for micro-organisms.

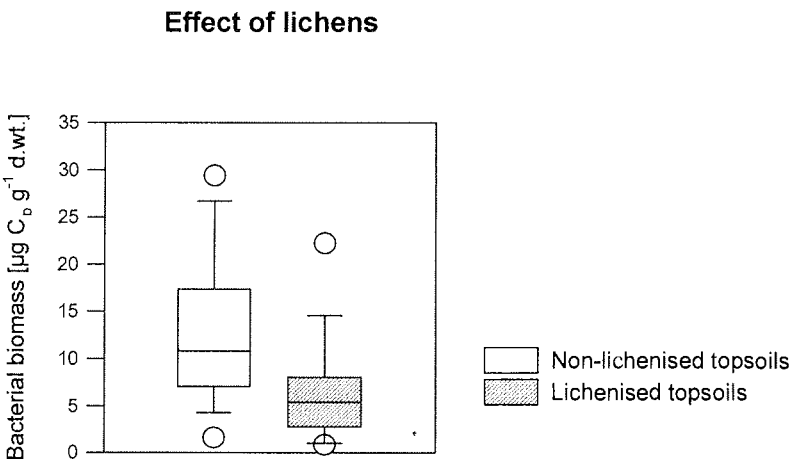


Fig. 5.4.4: Impact of lichens on bacterial biomass BBM [µg C_b g^{-1} d.wt.] in the uppermost centimetres of lichenised and non-lichenised soils.

In both study areas, lichens represented an important component of the vegetation cover at drier sites. As can be seen from Figure 5.4.4-1, bacterial biomass was significantly ($p<0.05$) lower in the uppermost centimetres of soils with lichen stands. At Levinson-Lessing these comprised the drier micro-sites of the polygonal tundra as well as the drier vegetated soils of the non-sorted steps and stripes. At Labaz, lichens were present in the vegetation cover of both brown earth soil types as well as in the elevated hummock of the hummock tundra site.

On the contrary, this relationship could not be established for fungal biomass. Thus, FB-ratios tended to be wider in the lichenised soils. Soil pH was not significantly different.
The impact of plants that form mycorrhizal associations could not be investigated because of the low random sample size of soils with non-mycorrhizal plants (n=4).

Substrate quantity
Substrate quantity was found to affect the microbial biomass and influenced furthermore the microbial community composition and its activity (see Fig. A5-2 and A5-5).
In vegetated dry topsoils as well as in subsoils, bacterial biomass increased with increasing carbon and nitrogen content ($\rho \approx 0.6$-0.8). Fungi only showed greater biomass values with increasing nitrogen content in dry vegetated topsoils ($\rho \approx 0.6$). These also showed a positive correlation of basal *Q* and substrate induced heat output *SIQ* with increasing carbon content ($\rho \approx 0.64$). The latter was also found to increase with carbon and nitrogen content ($\rho \approx 0.85$; $\rho \approx 0.60$). Yet, ATP content did not increase accordingly, which suggests an increasing proportion of glucose sensitive micro-organisms. In subsoil horizons, increasing substrate quantity was found to enhance glucose sensitive activity, which correlated with bacterial biomass ($\rho \approx 0.71$). In dry topsoils, carbon content also increased overall activity (i.e., basal heat output *Q*).

On the contrary in topsoils of wet depressions (see Fig. A5-2), overall microbial biomass was not affected by carbon and nitrogen content. Yet, a negative effect on the composition of the microbiota was observed. The proportion of the autochtonous microbiota (i.e., caloric quotient) decreased with increasing carbon content ($\rho \approx -0.94$) and C/N-ratio ($\rho \approx -0.89$).

Substrate quality
As has just been described for wet topsoils substrate quality as expressed as C/N-ratio showed an impact on composition of the microbiota but less on its size and its activity. In contrast to wet topsoils, substrate quality did not show any affect in dry topsoils. Thus the caloric quotient decreased with wider C/N-ratios ($\rho \approx -0.89$) in wet soils. Substrate quality further affected the glucose sensitive micro-organisms (*SIQ*) in subsoils. *SIQ* was inhibited by wider C/N-ratios ($r \approx -0.9$). Accordingly, the caloric quotient increased with higher C/N-ratios ($\rho \approx 0.63$).

Water logging

In the two study areas, water logging occurred at any depth within soil profiles. The most conspicuous type was water saturation up to the soil surface in wet depressions of micro-sites or in a drainage ditch as at Labaz. These sites had vegetation stands with adaptation to wet conditions (e.g., *Carex spp., Eriophorum spp.*). C/N-ratios in soils at wet (micro-)sites differed significantly ($p<0.05$) from dry topsoils (see Fig. A5-5). Fungal and bacterial biomass values were found to be significantly ($p<0.15$, $p<0.01$) greater in the wetter soils though the activity parameters (i.e., basal heat output, ATP, ATP content per unit microbial biomass) were not.

Impeded drainage within profiles occurred above horizons with lower permeability and above the permafrost table. In supra-permafrost horizons, substrate quantity was significantly different ($p=0.01$). Carbon contents were four times higher horizons although nitrogen content were half of the comparable dry subsoil horizons. The increasing carbon contents mainly affected bacterial biomass ($r\approx0.8$), which was twice the biomass of drier subsoils. Activity parameters did not show any significant difference.

6. Discussion

> This earth is honey to all beings, and all beings are honey to this earth.
>
> Upanishads

6.1 Microbial pool in tundra soils

The data obtained from this study give a detailed picture of the composition of the microbial pool and habitats in arctic tundra soils. Spatial heterogeneity of both fungal and bacterial biomass as well as the energetic state proved to be important parameters for the description and understanding of the decomposer cycle in this environment.

6.1.1 Vertical distribution

In all tundra soils studied, microbial biomass was largely restricted to topsoil horizons, which are the upper 10 to 20 centimetres of the active layer. Fungi and bacteria both decreased with depth. For fungi, this decrease was more pronounced and often marked by a distinct decline or cessation towards the subsoil (e.g., PT, HT, TT, WST). Bacteria also concentrated in the topsoil but occurred throughout the soil profile (SCHMIDT & BÖLTER, unpubl. data; BÖLTER, 1998). This distribution pattern of microbial biomass was reported for the soils of the IBP sites (BUNNELL et al., 1975; CHERNOV et al., 1975; HOLDING, 1981) but also for other biomes (ZVYAGINTSEV, 1994; PAUL & CLARK, 1989). Generally, this distribution pattern was linked to soil organic matter since soil micro-organisms are primarily decomposers. Yet, the results of this study also showed that microbial biomass did not simply follow the distribution of organic matter content. For instance, higher values of microbial biomass were found below organic horizons (e.g., HT and TT), and drier micro-sites show greater microbial biomass despite lower C_{org} contents than adjacent wet sites. Thus, in tundra, soil organic matter did not represent the only factor that influences soil microbiota. The studied soils also differed from those of most other biomes with respect to the shallowness of the total horizons, which micro-organisms predominantly inhabit. Furthermore, microbial biomass was also lower.

Fungi

At Levinson-Lessing the fungal hyphal length was up to 396 m g^{-1} d.wt. with a median of 21 m g^{-1} d.wt.. Although the range of values was wider at the experimental site Labaz (up to 920 m g^{-1} d.wt.), the median was only 4.1 m g^{-1} d.wt.. These values are low compared to those from other biomes (review by KJØLLER & STRUWE, 1982) and even from IBP tundra sites

(HOLDING, 1981). Hyphal fungal length was of the same order of magnitude as respective data of agricultural systems in temperate regions. In the latter, however, fungi represent a minor proportion of the total soil microbial biomass (e.g., BRUSSARD et al., 1990). Fungal hyphal length obtained from this study was within the range from tundra sites in Alaska or Canada (mean values up to 1150 m g^{-1} d.wt., KJØLLER & STRUWE, 1982). Data are given as median values because of asymmetrical distribution. Mean values were higher. Differing sampling techniques may also account for differences in average values of hyphal length. Values for various tundra sites were measured for the uppermost centimetres of the active layer (maximum depth 15 cm; BLISS, 1975). In this study, on the contrary, length of fungal hyphae was measured at all depths of the active layer. As a result samples with low or no fungal biomass were more numerous within the total random sample size. Furthermore, variability of fungi is particularly high (PARINKINA, 1989).

As mentioned above, fungi were confined to the presence of organic matter. Thus, fungal biomass is particularly high in topsoils and decreases with depth. Exceptions were given in unvegetated soils of the solifluction slopes and Leptosols on top of mountains, which may be explained by the absence of carbon sources. In level soils a relative increase or peak of fungal biomass was observed at a depth of approximately 10 centimetres. This coincided with high root densities. In order to enhance nutrient acquisition, many tundra plants form mycorrhizal associations. Although the presence of *Dryas*, *Salix* and *Betula* spp. in the vegetation cover suggests that a great proportion of fungal biomass may be mycorrhizal, this could not be shown by statistical analysis. The random sample size of soils where mycorrhizal associations could clearly be excluded, was too small. Furthermore, vegetation communities with plants that do not form mycorrhizal associations also showed high fungal biomass values. The vegetation of the non-sorted steps and stripes (LL 8/96 to LL11/96) for instance comprised legumes (e.g., *Astragalus* spp.) and other higher plants *Oxitropis* spp., which occasionally have been found to be infected by rhizobia. Yet, the respective soils had acid pH, at which rhizobial nodulation is less likely to occur (KILLHAM, 1994). Acid soil reaction may explain higher fungal biomass values at these sites. Since fungicides were reported to enhance rhizobial infection (TATE, 1995, p. 322), it may be inferred that N_2-fixing bacteria are less competitive in the presence of fungi. In contrast, fungal diversity is higher in these soils (CHERNOV et al., 1975).

Bacteria

According to SCHMIDT & BÖLTER (unpubl. data) total bacterial number (TBN) ranged between 0.2 and $7.4*10^9$ g^{-1} d.wt. at Levinson-Lessing. The experimental site at Labaz showed lower values (BÖLTER, 1998). Provided that total bacterial number was determined by direct observation methods, values of this study were of the same order of magnitude as results from other arctic soils (CHERNOV et al., 1975; BUNNELL et al., 1975) as well as from soils of other biomes. Yet, bacterial biomass was much smaller than in soils of other biomes because of extremely small cell volumes (0.04-0.05 μm^3; SCHMIDT & BÖLTER, unpubl. data; BÖLTER, 1998). Evaluation of TBN data alone may result in a misjudgement of bacteria with respect to microbial biomass. This may partially explain the significance attributed to bacteria by some studies (MATVEYEVA et al., 1975; CHERNOV, et al., 1975). Bacterial biomass data (usually given in g m^{-2}) were generally below fungal biomass (BLISS, 1975; BUNNELL et al., 1975). Bacterial biomass generally decreased remarkably with depth although the following deviations were observed. At Labaz, bacterial biomass was approximately ten times higher in the organic topsoil than in the underlying horizons. Relative increase or peak values may often be observed at a depth of approximately 10 centimetres. This increase was accompanied by higher C_{org} contents (this study, BÖLTER, 1998; GUNDELWEIN, 1998) and probably higher nutrient contents (MATVEYEVA et al., 1975). At Levinson-Lessing, this increase of bacterial biomass was found in a less pronounced manner in the polygonal tundra soils of the Krasnaya valley. Since this feature only occurred in level land with impeded drainage (PT, TT, HT, WST), further explanations may be linked to particular hydrological conditions. The dry podzolised brown earth at Labaz (profile Lb7/95) represented an exception here. Yet, the respective horizon at a depth of 10 to 25 centimetres was characterized by a cemented illuviation zone above a gleyed horizon (for further discussion see Sect. 6.3.2 'frontier'). Bacterial biomass also increased above the permafrost table, which corresponds to findings by LYSAK & DOBROVOL'SKAYA (1982). The layer was characterized by water saturation and a doubling of soil organic matter, which comprises lighter fractions (< 1.6 g cm^{-3}) of fulvic acids as fractionation has shown (GUNDELWEIN, 1998). Since macroscopic organic matter (e.g., fibres, root remains) was lacking, this increase is most likely explained by accumulation and dehydration of dissolved organic carbon (DOC) due to impeded drainage above the permafrost table.

In these subsoils, bacteria were found to prevail over fungi. The statistical data suggested that bacteria throve with increasing substrate quantity (C and N contents) whereas fungi were not affected. In contrast, low temperatures and reducing conditions in these horizons represent stress factors for fungal proliferation (ROBINSON & WOOKEY, 1997; HOLDING, 1981; FLANAGAN & SCARBOROUGH, 1974). Generally the soils of this study were characterized by high fungi to bacteria ratios (FB-ratios). This is explained by overall high C/N-ratios, indicating complex polymer structures of the soil organic matter.
In topsoils, manifold higher fungal biomass resulted in high FB-ratios. These were widest in dry and warm organic topsoils. With the exception of the 'frontier', FB-ratios lowered with depth. In unvegetated soils and wet micro-sites, FB-ratios were also found to be lower than or equal to 1. Thus, microbial composition also varies between sites.

6.1.2 Variation between sites

The experimental sites showed specific forms of micro-relief with regular repetition of elements (see Sect. 2.1.4.2) due to cryogenic processes. These were accompanied with peculiar patterns of soils and vegetation (patterned ground-soil-vegetation complexes). Vegetational succession and freeze-thaw processes both showed independent and interactive effects. This study showed that microbial properties reflect edaphic and vegetational changes between sites.

At level or gently sloping tundra sites, drier apices were surrounded by wet depressions and troughs (TT, HT, PT). Furthermore, these sites were often intersected by drainage ditches (WST) and brooks. As observed for vertical distribution, fungal biomass fluctuated most between wet and drier micro-sites. As mentioned before, fungi predominated in the upper horizons of the drier apices. Fungal biomass values tended to be higher than in the respective wet micro-sites. Thermal conditions, aeration and weakly decomposed organic mats represented a more favourable environment. At wet micro-sites (LL2/96; 4/96; 7/96 as well as Lb2b/95, 3b/85 and 4/95) higher fungal biomass values were found in the horizons between the topsoil and supra-permafrost layer. Bacteria on the contrary prevailed in the uppermost horizons. Since temperature conditions and oxygen levels were more favourable for fungi in the uppermost horizons, this increase of fungal biomass may be explained by vegetational and/or root effects, of for instance *Eriophorum* spp., at these sites (see Sect. 6.3.2 'rhizosphere'). Fungal diversity and biomass is greater in litter and rooting horizons

underneath these vegetation stands (FLANAGAN & SCARBOROUGH, 1974; CHERNOV et al., 1975). In addition, high abundance of fungi exemplifies that fungi tolerate water saturation, a finding supported by FLANAGAN & SCARBOROUGH (1974). The comparison of fungal carbon inventory between these micro-sites shows that higher fungal biomass values often coincided with bulk density values between 0.3-0.4 g cm^{-3}. BUNNELL et al. (1975) have suggested that the respective range might represent optimum bulk density values for fungal growth. However, the respective values also coincide with more decomposed organic topsoils at mesic micro-sites. These alone represent optimum growth conditions for fungi. In contrast to the mentioned study, fungi did not cease at the organic/mineral interface where bulk density values naturally increase (e.g., HT, TT, PT). Consequently, in this study there was no evidence for the impact of bulk density on fungal biomass.

Ammensalism may further explain the absence of fungi in the uppermost horizons. Microscopical investigation revealed that a substantial (but not quantified) proportion of the soil microbiota comprised algae and cyanobacteria. It is known that *Anabaena* and *Nostoc* spp. exude fungicidal compounds (KULIK, 1995).

Generally, bacterial biomass was higher in the wet depressions than in adjacent drier micro-sites which corresponds to findings of other tundra sites. BUNNELL et al. (1975) have reported 55% higher bacterial biomass in polygonal troughs than in the apex. Yet, this study showed that low bulk density values of mossy peat in depressions may also smooth differences out (LL4/96). Mossy peat had a lower bulk density than peat formed from sedges or grasses (as reported by BOTCH et al.; 1995). It has been assumed that higher bacterial biomass in the wet soils is a result of competition rather than adaptation to the wet environment (BUNNELL et al., 1975).

In the soils of the solifluction slopes and the non-sorted stripes (Levinson-Lessing) soil micro-organisms were mainly affected by the presence of vegetation. In bare soils FB-ratios were very low or below 1 which means bacteria prevail over fungi. During the summer months bare soils show steep thermal and moisture gradients (PROŠEK & BRÁZDIL, 1994). Upward movement of soil water may cause moisture deficiency (PARINKINA & PIIN, 1992). These gradients are too strong for fungi to thrive (BUNNNELL et al., 1975). This also explains why fungi showed higher biomass values at deeper horizons where moisture and temperature fluctuations are less pronounced. In addition, root penetration from surrounding vegetation may further affect fungal biomass.

Inhibition of bacteria has been observed in the presence of lichens in the vegetation cover. Ammensalism caused by lichens was also described for other arctic areas (PARINKINA & PIIN, 1992). PARINKINA (1989) states that the carbon content increases in soils with lichen vegetation. In the investigated soils with lichen stands, bacteria were found to correlate with carbon contents. Whereas ammensalism by lichens only affected the upper two centimetres, carbon enrichment may represent a stimulus for bacterial growth in underlying horizons. These findings correspond to the literature (PARINKINA, 1989).

In summary, direct observation methods have proved to be useful in characterisation of the microbial pool. Fungi clearly prevailed in the soils at both experimental sites. Fungi were largely restricted to the pronounced organic horizons and the rooting depth. These findings are in accordance with data from soils of other biomes (e.g., KJØLLER & STRUWE, 1982). Bacteria also dominated in upper organic horizons but inhabit all soil horizons. In unvegetated topsoils, wet micro-sites and the supra-permafrost layer bacteria predominated. Interactions with the composition of the vegetation cover could also be established. This distribution pattern was also described by other authors (e.g., PARINKINA, 1989).

6.2 Spotting the active microbial pool

It is known that only a certain proportion of soil micro-organisms is viable. For fungi the percentage of live mycelium ranges between 10 and 16% (KJØLLER & STRUWE, 1982). The proportion of live bacterial cells on the contrary is higher, namely 60 to 93% (CHERNOV et al., 1975). It is therefore important to investigate the active microbial pool in addition to quantification and differentiation by direct observation methods. ATP content and measurements of heat output are microbial parameters that depend on viable micro-organisms. They furthermore allow differentiation of active micro-organisms from resting or dormant ones and provide further information about the community structure as will be discussed in the following section.

Adenosine triphosphate

All living microbial cells contain ATP which delivers the energy of its phosphate bonds for biosynthetic and catabolic reactions. ATP contents in soil of up to 9.0 µg ATP g^{-1} d.wt. have been reported (JENKINSON & OADES, 1979). For arable soils, ATP contents have been found to be lowest, but varied depending on land use practices (JENKINSON & OADES, 1979; SPARLING & EILAND, 1983). Agricultural and quasi natural grassland systems have shown a wide range from 1.7 to 7.7 µg ATP g^{-1} d.wt. (ROSS et al., 1980). Variation has mainly been explained by differences in nutrient content and nutrient availability of soils (ibid.). In forest systems, ATP contents have been in the upper range (3.1 to 9.0 µg ATP g^{-1} d.wt., JENKINSON & OADES, 1979), which probably also indicates a shift in microbial community structure since fungi contain more ATP per unit biomass than bacteria (AUSMUS, 1973 cf. ROSS et al., 1980). High ATP contents (up to 7.7 µg ATP g^{-1} d.wt.) have also been reported in water-logged paddy soils, but decreased with increasing O_2-depletion (INUBUSHI et al., 1989).

In the soils of this study, median ATP contents were 0.9 µg ATP g^{-1} d.wt. at Levinson-Lessing and 1.2 µg ATP g^{-1} d.wt. at Lake Labaz. Consequently, values are low compared to soils from other biomes and in the same order of magnitude as arable soils from temperate regions. This is in accordance with microbial biomass values. However, extremely high values of up to 32.4 µg ATP g^{-1} d.wt. were found in the uppermost topsoil horizons. Whereas ATP contents of topsoil horizons did not appear to differ significantly from 'frontier' horizons, ATP concentration values (i.e., ATP content per unit microbial biomass) on the contrary did. External ATP sources from vegetation, roots or meso- and macro-fauna may be excluded,

since the chosen ATP extractant (i.e., Tris buffer) is considered to be very specific for microbial cells (VERSTRAETE et al., 1983; VERSTRAETEN et al., 1983). Microbial biomass values in this study comprised fungi and bacteria determined by direct observation methods. Primary producers among micro-organisms such as cyanobacteria and soil algae have not been determined. However, in the Arctic, their presence was reported in the upper horizons of unvegetated soils, in wet depressions and as epiphytic and soil species at drier sites (CAMERON et al., 1978; BUNNELL et al., 1975; HOLDING, 1981; ELSTER et al., 1994). Non-quantified observations during microscopical investigations revealed substantial amounts of cyanobacteria and algae. They may therefore contribute to the extreme ATP contents found in the respective horizons. This is supported by the fact that ATP in these horizons appears to be relatively unaffected by substrate quantity and quality, in which the sites differ. The respective populations were insensitive to glucose amendment for substrate-induced heat output as shown in Table 5.4.4-3 (cluster No. 3). Weak correlation of nitrogen with carbon content in wet topsoils might further indicate another nitrogen source than soil organic matter (such as by N_2-fixation). Yet, on the basis of the present data this conclusion is rather daring. However, the extreme values in ATP content may only partly be explained by algae and cyanobacteria, since algal ATP contents can contribute 0.02-0.28 µg ATP g^{-1} d.wt. in tundra soils (calculated from data by HOLM-HANSEN & BOOTH, 1966; CAMERON et al., 1978)[1]. ATP was most likely be attributed to protozoa (e.g., amoebae, flagellates, ciliates), of which PARINKINA (1989) noted particular high densities in water-saturated sites. In drier topsoils, interference might also come from lichens in the vegetation cover. Furthermore, these higher values of ATP content were concomitant with extreme high values of heat output (see below).

As can be seen from Table 6.2-1, ATP concentrations (i.e., ATP/microbial biomass-ratio) in the literature range from 1:423 (0.0024) to 1:82 (0.012). In this study, ATP to microbial biomass ratios was in this range. Again, extreme ratios were found in the before mentioned topsoil horizons.

[1] mean ATP content of marine algae: 0.074 per cent/dry weight (HOLM-HANSEN & BOOTH, 1966)
maximum algal biomass in tundra soils at a depth of 0-2 cm: 0.6 g d.wt. m^{-2} (CAMERON et al., 978)
bulk density values in this study ranged between 0.08 and 1.1 g cm^{-3}.

Tab. 6.2.-1: ATP concentrations [unit ATP per unit microbial biomass] as given in the literature, molarity converted ATP M_r 602.2 (Boehringer Mannheim).

Soils	ATP concentration	Conversion [µg ATP µg^{-1} C_{mic}]	Ratio	Source
forest humus	3.2 µg ATP mg^{-1} C_{mic}	0.0032	1:312	ARNEBRANDT & BÅÅTH, 1991
arable soils	9.2 µmol ATP g^{-1} C_{mic}	0.0055	1:180	OCIO & BROOKES, 1990
arable soils	-	-	1:167	FRIEDEL, 1993
agricultural and natural grassland	-	-	1:163 1:423	ROSS et al., 1980
arable soils	10.6 µmol ATP g^{-1} C_{mic}	0.0064	1:157	BROOKES & JENKINSON, 1989
various	-	-	1:120	OADES & JENKINSON, 1979
permanent grassland, arable soil	-	-	1:82 - 1:203	SPARLING & EILAND, 1983
paddy soils	9.1 µmol ATP g^{-1} C_{mic} 12.5 µmol ATP g^{-1} C_{mic}	0.0055 0.008	1:181 - 1:167	INUBUSHI et al.,1989

Higher ratios were also found either in horizons just above or below the water table or in the water saturated layer above the permafrost. In addition, this increase in ATP concentration was always very pronounced (i.e., up to 40 times of the overlying horizon). The respective horizons were also characterized by distinct increases of bacteria. In case of the supra-permafrost layer, bacteria even generally prevailed over fungi. The phosphorus status of the soil represents another factor that might have caused high ATP concentrations. NANNIPIERI et al. (1990) have found that the presence of inorganic phosphorus affects the ATP content of soils. It is hence assumed that available phosphorus temporarily accumulates in the respective horizons. In tundra systems, nutrients such as nitrogen and phosphorus are mobilised at snowmelt and during plant senescence although they are highly limited during plant growth (ULRICH & GERSPER, 1978). A considerable amount of nutrients is also lost by leaching (CHAPIN III, 1978), which indicates the impact of water on the nutrient status. Low phosphorus availability has also been determined for the experimental site at Levinson-Lessing (BECKER, 1997). Evidence in support of the conclusion that the phosphorus concentrations are temporarily high at the water table and thus affect ATP concentrations also comes from the presence of water itself. In addition to leaching processes, water saturation will eventually lead to lower redox potentials, which further increases the mobility of phosphorus bound with sesquioxides (SCHEFFER/SCHACHTSCHABEL, 1998, p. 267). Phosphorus that becomes available may then be immobilised by micro-organisms and increase ATP concentrations as suggested by NANNIPIERI et al. (1990). Conditions above the

permafrost table differ slightly in higher phosphorus availability since the microbial P-demand is low at temperatures above freezing point (NADELHOFFER et al., 1992). At Levinson-Lessing higher phosphorus contents were found in horizons influenced by slope water (BECKER, 1997), although this does not necessarily mean that it is available phosphorus. In tundra peat, however, C/P-ratios increase with depth in contrast to C/N-ratios, which reflects the high biological demand for this nutrient (NADELHOFFER et al., 1992). It may thus explain the very low ATP concentrations found in horizons above the water table, the before mentioned 'frontier' horizons. The gradient of ATP concentrations between these depths was very strong. Many tundra plants (e.g., *Dupontia*, *Carex* and *Eriophorum* spp.) only form secondary roots above the water table, where oxygen levels are more favourable for root metabolism (CHAPIN III, 1978). At drier sites many plant species form mycorrhizal associations, without which some plants (e.g., *Salix* spp.) even cannot exist in tundra (MILLER & LAURSEN, 1978). Thus, wet as well as dry sites show specific mechanisms to enhance nutrient acquisition. Yet, these are largely dependent on sufficient aeration. P-deficiency due to nutrient competition with plants may be one explanation for the lower ATP concentrations in the frontier horizons. Further differentiation between frontier horizons of wet and dry micro-sites in this study appeared to be slightly arbitrary, signals of differing ATP concentrations were very weak.

From these discrepancies between microbial biomass and ATP concentrations, it may first be concluded that ATP determination as currently used in soil microbiology does not address primary producers or even protista, which are very common in specific habitats of arctic systems. Probably these also account for high ATP contents as determined in other wet soils reported in the literature (INUBUSHI et al.,1989). Furthermore, in topsoil and frontier horizons of this study, ATP also appeared to be controlled by environmental factors other than the carbon and nitrogen status of the soil. This is surprising because ATP is usually found to correlate with C and N contents (JENKINSON et al., 1979). Yet, this anomaly is supported by a study by ROSS et al. (1980). Therefore, there is intercession for the use of ATP as an estimate for microbial activity rather than microbial biomass (NANNIPIERI et al., in press). ATP contents of microbial populations were also found to be affected by environmental stress to different degrees. In aerobic moist soils, micro-organisms are capable of maintaining high ATP and adenylate energy charge (AEC) levels at those of actively growing cells (BROOKES & JENKINSON, 1989) whereas in anaerobic soils ATP and AEC levels were found to decrease with increasing O_2-depletion (INUBUSHI et al., 1989). It has also been suggested that ATP

contents represent mean values of high ATP concentrations in a small, active population and very low concentrations in the remaining part (BROOKES & JENKINSON, 1989).

Heat output

Heat measurements approved to elucidate the active microbial pool in the soils of this study. As shown in Figure 5.4.4-1, fungal biomass showed different response to glucose amendment. Being heterotrophs most fungi are thought to be sensitive to glucose amendment. A logarithmic increase in respiration per unit biomass is characteristic for active microbial populations (ARNEBRANDT & BÅÅTH, 1991). It is surprising that this relationship held true for wet and dry micro-sites since fungi only thrive under aerobic conditions. One explanation is that the controlled conditions during substrate-induced heat output (*SIQ*) measurements themselves already represented an amelioration of the environment compared to conditions in the field. This conclusion is supported by the relationship of *SIQ* and ATP contents (Tab. 5.4.4.-3). An increase of *SIQ* per unit ATP could only be determined for topsoil horizons at drier micro-sites. VANDENHOVE et al. (1991) have found out that the *SIQ*/ATP-ratio increased significantly with environmental stress. As a consequence, fungi were viable in wet micro-sites, but were restricted in activity. Laboratory conditions were more favourable with respect to aeration and temperature. These may thus represent important controlling factors for fungi since carbon and nitrogen contents appeared to be of minor importance.

On the contrary, fungi appeared less efficient in using glucose as a substrate in mineral horizons (Fig. 5.4.4.2), which comprise 'frontier' and subsoil horizons. In 'frontier' horizons, this was concomitant with low ATP concentrations as previously described. Although ATP concentrations of 1:250 (or 0.004) were low, these are still within the range (Tab. 6.2.-1) Along with lower ATP concentrations, lower *SIQ* values per unit fungal biomass probably indicate that a significant proportion of fungi may not be viable. A study by ZHU et al. (1996) has revealed that only 1.3 to 11% of total fungal length was FDA-active (i.e., a parameter for fungal metabolic activity). Consequently, in 'frontier' horizons, this methodical inaccuracy sums up as fungal biomass increases despite great care with respect to measurement of intact fungal hyphae. On the other hand, caloric quotients were found to be rather high in 'frontier' horizons of drier micro-sites, which may be explained by a lower energetic efficiency due to environmental stress as will be discussed below. Thus, inference of the viable proportion of fungi cannot be made on the present database. Yet, the data rather suggest a low energetic efficiency than a microbial population that is not viable.

A shift in microbial population further explains lower *SIQ* values per unit fungal biomass in 'frontier' horizons, which showed significantly higher FB-ratios than topsoil horizons. Experience with substrate-induced respiration (SIR) demonstrated that inorganic and organic soils formed distinct clusters of C_{mic} to SIR ratios (WARDLE & PARKINSON, 1991; BECK et al., 1997). This was not only explained by different glucose sensitivity (WARDLE & PARKINSON, 1991), but also by a greater proportion of fungi (CHENG & VIRGINIA, 1993) because these produce less CO_2 per unit biomass than bacteria (ANDERSON & JOERGENSEN, 1997). Thus, what looks like a lower glucose sensitivity may only be the effect of decreasing bacterial biomass in 'frontier' horizons. Substrate induced determination of microbial biomass is therefore known to overestimate bacteria (ibid.). When bacteria took over in subsoil horizons, no relationship was found between bacterial biomass and *SIQ* indicating that the respective microbial population is largely insensitive to glucose.

Data on heat output are not readily available since the use of microcalorimetry in studying soils is not wide-spread. Yet, the database is sufficient to allow comparison although caution is required due to poor methodical standardisation (NANNIPIERI et al., in press). Since heat output is most commonly used to estimate microbial biomass, it is usually measured after substrate amendment (i.e., *SIQ* in this study) as described by SPARLING (1983). Furthermore, most studies were done on soils of temperate regions (e.g., RAUBUCH & BEESE, 1995; ZELLES et al., 1987a; ALEF et al., 1988; SPARLING, 1981a) and only one in Antarctica (BÖLTER, 1994). To date, no heat output measurements have been carried out in arctic tundra soils. In generalising data from topsoils of temperate regions, it may be stated that the heat output increased in the order agricultural < grassland < forest soils. Maximum heat output for agricultural soils was reported from 30 to 120 $\mu W\ g^{-1}$ d.wt. (SPARLING, 1983; ALEF et al., 1988), whereas grassland soils reached 80 to 330 $\mu W\ g^{-1}$ d.wt. (ibid.). Values given for forest topsoils range between 500-520 $\mu W\ g^{-1}$ d.wt. (SPARLING, 1983) and 2500-4000 $\mu W\ g^{-1}$ d.wt. (ZELLES et al., 1987a). Thus, heat output of up to 220 $\mu W\ g^{-1}$ d.wt. (BÖLTER, 1994) measured in Antarctic soils falls into the lower range.

In comparison with these data, values of median basal heat output (20.4 $\mu W\ g^{-1}$ d.wt at Labaz; 60.6 $\mu W\ g^{-1}$ d.wt at Levinson-Lessing) as well as median substrate heat output (38.7 $\mu W\ g^{-1}$ d.wt. at Labaz; 119.5 $\mu W\ g^{-1}$ d.wt. at Levinson-Lessing) were within the cited range. Yet, maximum values of up to 1683.8 $\mu W\ g^{-1}$ d.wt. *SIQ* at Levinson-Lessing appear rather high. The upper range of heat output (approximately 300 to 1683.8 $\mu W\ g^{-1}$ d.wt.) was

concomitant with high ATP contents per unit fungal and bacterial biomass (ATP concentrations ATP:MBM > 0.01). Furthermore no clear relationship to microbial biomass was discernible. In addition to the previously discussed algae and cyanobacteria, the vegetation cover at the respective dry sites always comprised lichens. These are therefore assumed to cause interference with heat measurements in the studied soils. This evidence is supported by a study of BÖLTER (1994) who found up to tenfold greater heat output values for lichens.

In this study, heat output generally decreaseed non-linearly with depth (by roughly a third between horizons), which was also established for various investigated soils from the literature (RAUBUCH & BEESE, 1995; ALEF et al., 1988; ZELLES et al., 1987a). Yet, in inorganic soils from Antarctica, this decrease appeared to be stronger (BÖLTER, 1994), which was confirmed by unvegetated soils of this study (e.g., LL10.1/96; LL8.1/96). Exceptions were often found in soils where the microbial population was insensitive to glucose amendment and substrate amendment did not produce any further response in heat output. This has been explained by specific substrate requirements, shifts in microbial population (WARDLE & PARKINSON, 1991) or sufficient *in situ* carbon concentrations (NANNIPIERI et al., in press). Glucose insensitive microbial populations were predominantly found under anaerobic conditions, i.e., soil horizons with chroma of 2 or less and/or underneath the water table, where anaerobic bacteria increase (ROSSWALL et al., 1974). However, this does not apply to soils where the water table was at soil surface (PT, WST, TT, non-sorted stripes LL9.2/96). It is therefore assumed that these differences reflect different substrate requirements, which is supported by a shift to a larger proportion of fungi. Under clearly aerobic conditions, glucose insensitive populations were found in the uppermost centimetres of both unvegetated soils and aerated O-horizons. Since ATP concentrations were also higher and light penetration was possible, it may be assumed that photoautotrophs represent a significant proportion of the microbiota.

The fact that heat output also included organisms other than the taxonomic target groups as well as the fact that some microbial populations were glucose insensitive, form the background, why it is not advisable to estimate microbial biomass from *SIQ* values in tundra soils. CHENG & VIRGINIA (1993), on the contrary, have recommended substrate-induced respiration (SIR) methods for arctic tundra soils. Yet, it has to be stated that in the respective study only the uppermost 5 centimetres of vegetated soils had been sampled, in which

heterotrophic fungi are likely to predominate. In this study, *SIQ* as a tool to estimate microbial biomass, proved to be particularly inappropriate for unvegetated and anaerobic soils. In water-logged soils of a temperate alder forest, comparison of microbial biomass estimates by SIR were clearly greater than by chloroform fumigation extraction methods (DILLY, 1994). Subsoil horizons in particular showed up to fourfold higher values (ibid.).

The ratio of basal heat output *Q* to substrate-induced heat output *SIQ* (caloric quotient) thus provides further information on the microbial population.

Successional stages or environmental stress?

Analogously to the metabolic quotient qCO_2 (basal respiration to microbial biomass carbon) (INSAM, 1990), the ratio between basal and substrate-induced heat output (or respiration) may further be used to analyse the physiological status of microbial communities. In ecosystem theory, the metabolic quotient has been described to decrease with proceeding successional stages reflecting an r-K-selection continuum in favour of K-strategists (ŠANTRUCKOVÁ & STRAŠKRABA, 1991). The r-strategists correspond to Winogradsky's zymogenous micro-organisms that respond rapidly to substrate amendment. These represent successful colonisers during primary stage of succession. K-strategists live at or near the carrying capacity of the ecosystems and correspond to Winogradsky's autochtonous micro-organisms (SCHLEGEL, 1992). Succession selects for K-strategists. These are more efficient in use of substrate and will result in lower metabolic quotients.

At the experimental site Levinson-Lessing, the sampling technique was also designed to detect potential differences between successional forms of patterned ground. In such manner, profile LL11/96 represented an overgrown non-sorted step, which most likely has formed from an unvegetated step like profile LL8/96. The data suggest that the caloric quotient was larger in the unvegetated step which would support the hypothesis of declining caloric/metabolic quotients with progressing succession. The intermediate stage of succession is usually characterized by greater vegetational diversity (e.g., STRASBURGER et al., 1998), which is reflected by the properties of the microbiota (PARINKINA & PIIN, 1992; PARINKINA, 1989). The soils of the solifluction slopes showed highest fungal biomass values when looking at the organic horizons alone. Furthermore, all parameters linked to the active pool (i.e., ATP contents and concentrations, heat output) were within maximum values determined in this study. Temperature regime (i.e., greater thaw depth), aeration, sufficient moisture (i.e., slope water) and nutrient status (BECKER, 1997) were also more favourable. All these factors

indicate that the soils of the solifluction slopes are the most active and dynamic with respect to soil ecology. Finally, the caloric quotient values thus fit into the jig-saw puzzle.

The picture was rather ambiguous in the soils of the polygonal tundra. There was weak evidence that caloric quotients decreased between the low centred polygon (LL1 and 2/96) and the high centred polygon (LL3 and 4/96). Yet, it is subject of dispute whether these represent a successional sequence (e.g., HARRY, 1988). One hypothesis is that high centred forms have evolved from low centred polygons by progressive upthrusting of material adjacent to the growing ice-wedge (ibid.). This option has also been favoured by ecologists (CHERNOV & MATVEYEVA, 1997). On the other hand, it has also been advocated that they develop independently under different hydrological conditions. High centred polygons appear to form under better drained conditions, whereas low centred forms are found in poorly drained areas (TEDROW, 1977, pp. 253). The caloric quotient was also found to increase in response to environmental stress and was therefore used as a respective parameter (RAUBUCH & BEESE, 1995). Increasing caloric or metabolic quotients were found due to environmental stress imposed by low pH (ibid., ANDERSON & DOMSCH, 1993), climatic conditions (ANAN'EVA et al., 1997), or single crop farming (DILLY, 1994). In case of the polygonal tundra, either would result in a decreasing caloric quotient from low centred towards high centred forms, either due to progressive successional stage of the ecosystem or due to amelioration of environmental conditions (i.e., aeration) along this sequence. Thus, from the soil microbiological point of view, this question may not be answered accurately on the database presented.

Yet, the example of the high centred polygon at Levinson-Lessing further illustrates that discussion of succession encounters tundra specific problems as stated by CHERNOV & MATVEYEVA (1997). Due to freeze-thaw dynamics, 'plakor' vegetation at the mesic high centred polygon is intersected by frost-boils either bare of vegetation or with vegetation stands that are characteristic for pre-climax stages. Accordingly, the caloric quotient was found to increase in this study. Yet, again, abiotic factors also deteriorated (e.g., porosity, aeration, desiccation).

As previously discussed, the uppermost centimetres of O-horizons or unvegetated soils showed high caloric quotients concomitant with high ATP concentrations. Fungi tended to be less numerous although there were exceptions from this rule. In topsoils, caloric quotients generally decreased with depth and increasing decomposition, which agrees with the findings of WARDLE (1993). This probably reflects successional stages of the microbial community.

Algae and cyanobacteria showed particularly high abundance at the respective sites. These organisms will be rather insensitive to glucose. Although they represent primary colonisers in soil, equation of substrate-sensitive and -insensitive populations with r-K-strategists appears to be immature at this stage of discussion.

The limited use of caloric and metabolic quotients for the description of successional stages was fostered by the anaerobic soils of this study. In anaerobic horizons above the permafrost table microbial community composition was characterized by a shift towards bacteria, fungi often disappeared and caloric quotients of 1 or higher were generally established. These may partly be explained by stress caused by thawing (ANAN'EVA et al., 1997), low temperatures and oxygen deficiency. Yet, anaerobic bacteria such as methanogens, which had been found to increase with depth (DUNICAN & ROSSWALL, 1974; ROSSWALL et al., 1975) will most likely be adapted to this habitat.

In transition from topsoil to subsoil, the physiology of the microbial community showed the most complex pattern. Caloric quotients increased despite high fungal biomass values and were often concomitant to the lowest ATP-concentrations determined in the soils of this study. The respective horizons indicated reducing conditions (i.e., chroma of 2 or less) in most cases. The latter were linked to the position of the water table, in which wet micro-sites differed from the respective drier ones. At drier micro-sites reducing conditions were found above the water table, which was in the lower part of the soil profile. At wet sites, the water table was at or near surface and reducing conditions were encountered at greater depth (5 - 10 cm). However, the just mentioned microbial properties (fungal biomass, low ATP concentrations, high caloric quotients) occurred at a transitionary depth within profiles at both micro-sites. It may therefore be concluded that anaerobic conditions represent unfavourable conditions for fungi resulting in low activity and high caloric ratios. On the other hand, below this transition, bacteria increased in proportion to fungi and FB-ratios often fell below 1. In the transitionary layer, bacteriological parameters (total number, mean cell volume and bacterial biomass) followed the relative or absolute peak in fungal biomass (SCHMIDT & BÖLTER, unpubl. data; BÖLTER, 1998). This transition in microbial community composition is also supported by MOORE & DALVA (1993), who have found a negative logarithmic response in CH_4 production with decreasing water table. The same study has further shown that methanogenesis is more temperature sensitive than aerobic respiration. Furthermore, in many tundra soils psychrophilic bacteria prevail over mesophilic bacteria at greater depths

(VASSILYEVSKAYA et al., 1975). Consequently, there is strong evidence that the microbial population changes in this transitionary layer between topsoils and subsoils of this study. High caloric ratios may thus either indicate environmental stress, which holds true for fungi in the respective horizons. Yet, since bacteria take over, high caloric ratios may also reflect a transitionary stage of microbial community, where competition for the habitat may be strongest. It was concluded from differences between sites that these properties are linked to the position of the water table. For this reason, this transitionary layer is also highly dynamic over time, all of which has led to formulation of 'frontier' horizons in this study. The 'frontier' as microbial habitat will be discussed in a separate section.

In summary, it may be stated that in this study the caloric quotient not readily distinguished between environment stress and changes in microbial community composition or successional stages. Both signals appear to be superimposed to each other. This is supported by data of WARDLE & GHANI (1995), who therefore object to the broad use of the respective quotients.

6.3 Microbial habitats in tundra soils

In this study patterns of microbial properties are discernible which are closely linked to biotic and abiotic factors. The microbial habitat may thus be described from results of profile description and pedological data (from this study or from references if applicable). In such manner a generalised view of microbial habitats for tundra soils has evolved, which comprise wet and dry topsoils, the 'frontier' and subsoil horizons.

6.3.1 Topsoils

6.3.1.1 Wet topsoils

Wet topsoils represent organic mats of moss or grass-sedge peat. Bulk density was lowest in the mossy peat (i.e., 0.09 g cm^{-3}) and increased with increasing grass and sedge content (i.e., 0.4 g cm^{-3}), which corresponds to literature data (BOTCH et al., 1996). Accordingly, porosity was very high ± 90 vol.% and freely draining macro-pores (i.e., > 1000 µm pore neck diameter) predominated. Since the wet topsoils contain little mineral soil, the high proportion of micro-pores (< 0.2 µm pore neck diameter) is explained by methodical constraints. As described in Section 4.2.4, the calculation of pore size distribution is based on the relationship of volumetric water content at a given suction. It is thus assumed that soil water is only held by capillary forces (MARSHALL et al., 1996; SCHLICHTING et al., 1995). Yet, surface adsorption by organic matter will affect the 'water-retention-curve' and particularly overestimate the proportion of micro-pores. In tundra, organic topsoils are generally water saturated under field conditions, since the water table is at or near soil surface. The respective soils may consequently be pictured as aquatic habitats with a sponge-like structure, which allows organisms to float freely. Compared to their drier counterparts, wet topsoils showed less acid soil reaction as well as higher carbon and nitrogen contents, but with higher C/N-ratios. Yet, the microbial properties seemed to be relatively unaffected by carbon and nitrogen quantity. At first sight, this is surprising because it is rarely questioned that microbiota is positively affected by the respective elements, but C/N-ratios on the contrary showed poor substrate quality indicating nutrient limitation. CHAPIN & BLEDSOE (1992) further report a negative effect of a low nutrient status on N_2-fixers, the abundance of which have been observed during microscopy (see Sect. 6.2). The enzyme system that drives nitrogen fixation (i.e., nitrogenase) requires specific elements for protein synthesis: molybdenum, iron, sulphur and cobalt, but presumably less magnesium (ibid., EADY & POSTGATE, 1974). Analysis of the soils at Levinson-Lessing showed that the nutrient status (BECKER, 1997) appeared to be

favourable for nitrogen fixation to occur. As mentioned before, other microbial properties further supported the significance of primary producers (algae and cyanobacteria). Nitrogen fixation in particular is known for its feedback on methane production, as it furnishes nitrogen (i.e., NH_4^+) as a nutrient for methanogens (CHAPIN & BLEDSOE, 1992). ATP contents and concentrations also suggested the presence of protozoa (Sect. 6.2). This indicates that the microbial loop may be an important component in the energy flux of wet tundra soils.

Generally, fungal and bacterial biomass (given as carbon inventory) were lower in wet topsoils than in the respective drier micro-site. However, at wet depressions of the high centred polygon (LL3-4/96) and the tussock tundra (Lb3/95) this relationship was inverse. These soils differed from all other wet micro-sites in their immediate proximity to mounds of either the vegetated elevated rim or tussocks. Since these mounds were some 20 centimetres higher than the wet depression, greater fungal and bacterial biomass may therefore be a root effect (see section 'rhizosphere' below). Both profiles on the contrary seemed to be quite different with respect to other properties. Different thickness of the active layer for instance indicates more favourable thermal conditions in the tussock tundra than in the wet micro-site of the high centred polygon. As a result, conditions for soil organic matter decomposition also differ (GUNDELWEIN, 1998). According to a study by SOMMERKORN (1998) at the respective sites, Q_{10} values have been higher than in dry topsoils indicating a greater sensitivity to temperature changes.

In summary, wet topsoils represent an aquatic habitat, in which a significant proportion of the energy flux appears to pass through protista and bacteria ('microbial loop'). However, their impact on decomposition may not be answered in the present study and only be inferred from the literature (CLARHOLM, 1994). Although present in lower biomass, decomposers such as fungi did occur in these wet habitats and were viable as microcalorimetric data have shown. Temperature and aeration are likely to control the inhibition of their activity as derived from laboratory conditions and stated in the literature (HOLDING, 1981).

6.3.1.2 Dry topsoils

Dry topsoils generally consisted of organic horizons of varying thickness and the upper mineral horizons. In comparison to their wetter counterpart, dry topsoils showed lower carbon and nitrogen contents as well as narrower C/N-ratios. Soil reaction was more acid. All of which reflected higher degrees of organic matter decomposition. As discussed earlier, microbial biomass occurred in higher abundance in these upper horizons. Although generally decreasing with depth, relative peaks were found in the lower O-horizons and few centimetres

of the underlying mineral soil. In addition to higher degrees of decomposition, the organic horizons showed a more distinct profile differentiation. This was reflected by higher bulk density values, which ranged from 0.4 g cm^{-3} for Oi/A-horizons to 0.9 g cm^{-3} for A-horizons. Porosity was lower than in the wet topsoils but still very high (i.e., 70 to 80 vol.%). Pore size distribution was favourable with respect to aeration and moisture regime. Yet, bulk density increased (i.e., 1.1 to 1.4 g cm^{-3}) and porosity decreased (40 to 60 vol.%) remarkably in unvegetated soils. In addition, larger micro-pores (0.2 to 10 µm pore neck size) represented the biggest proportion, which corresponded to the finer texture of the mud pits. Aeration conditions became more favourable with increasing gravel content. This has been supplemented by texture analyses in a study by MÜLLER-LUPP (1997). The structural properties of unvegetated soils also held true for mineral horizons underneath the organic layers. This structural change in transition further results in moisture and thermal gradients (STONER et al., 1983). Water from precipitation rapidly moves through organic mats. Infiltration then slows down as the higher matric potential of the mineral soil must be overcome. Further downward movement of the wetting front progresses slowly and depends on the soil texture, which may be critical for deep percolation particularly in deeper thawed soils (ibid.). This physical behaviour is important as it indicates stronger accumulation of solutes in the topsoils and therefore affects pedogenesis (GRABETSKAYA & CHIGIR, 1992) as well as the nutrient status (NADELHOFFER et al., 1992; ULRICH & GERSPER, 1978). Thermal properties change in diurnal and seasonal amplitudes (SOMMERKORN, 1998; BOIKE, 1997; PROŠEK & BRÁZDIL, 1994; ROMANOVA & UTKINA, 1973; ROMANOVA, 1970). Within organic mats amplitudes may be very high. Yet, due to low bulk density, organic mats represent a thermal insulation resulting in lower temperatures and variability in the mineral soil. As a consequence, thaw depth generally decreases with increasing thickness of the organic horizons, which was also found in this study. Conversely in winter, when the soil refreezes, the downward movement of the freezing front progresses faster in the organic mats than in the mineral horizons thus forming a 'zero-curtain', which is accompanied by water migration to the freezing front retarding further freezing (RIEGER, 1983). The 'zero-curtain' represents an irregular front and additionally occurs around freezing cells (BOIKE, 1997).

Thus, in transition to the mineral soil, organic mats provide a favourable habitat with respect to temperature variability, moisture conditions and nutrient status. Predominant colonisation underneath the vegetation cover is supported by PARINKINA (1989). In this study, basal heat output and substrate-induced heat output correlated well and was dependent on high levels of

carbon and nitrogen. These properties indicate that the microbiota was mainly zymogenous and sensitive to glucose. This correlation was better for bacteria than for fungi. Since ATP concentrations decreased as the fungal proportion of the microbial biomass increased, the major proportion of fungi seemed to be metabolically inactive or not viable. Yet, insensitivity of fungi to glucose may further be explained by substrate requirements other than simple sugars. The vegetation stands at mesic sites comprised a higher proportion of wood plants (Sect. 5.1.2) than wet sites, which is reflected in the quality of soil organic matter (GUNDELWEIN, 1998). In addition, fungi were more affected by nitrogen levels than by carbon levels. This suggests microbial succession during decomposition as described by GOKSØYR (1975). In drier topsoils, fungi may decompose complex polymers (such as lignin) provided that nitrogen levels are sufficient. Within profiles fungal biomass values were often followed by higher bacterial biomass suggesting that bacteria benefit from fungi. Furthermore, bacteria appeared to require more simple compounds as a substrate due to their stronger affinity to glucose as well as to carbon and nitrogen levels. Fungal decomposition probably provides substrate in the form of leachates, or fungi themselves (e.g., fungal cytoplasm) represent a nutrient source for bacteria. WARDLE (1993) has found a decreasing metabolic quotient during successional stages of decomposition. In this study, there was only weak evidence for a decreasing caloric quotient in this context (e.g., PT, TT, vegetated non-sorted steps). Yet, the respective topsoils encounter decreasing temperatures and increasing oxygen deficiency with depth, which imposes environmental stress. Consequently, an assumed decreasing caloric quotient due to succession would overlay the signal of increasing environmental stress.

The uppermost centimetres of dry topsoils showed quite different microbial properties compared to the transitionary horizons between organic and mineral horizons. ATP contents and concentration as well as caloric parameters indicated a different community structure such as a higher proportion of autotrophs (see Sect. 6.2). In horizons with predominating bacteria, these were found to be sensitive to glucose (Fig. 5.4.4-3). Yet, the trophic relationship remains unclear since it is unlikely that they decompose structurally intact plant material. For the respective horizons, it could be hypothesised that they benefit of primary producers in the same manner as has just been described for lower horizons. It has been suggested in the literature, that bacteria feed on dissolved organic matter leaching from litter surfaces and on exudates of algae and protozoa (CLARHOLM, 1994). Nitrogen fixation by cyanobacteria was also reported to occur in drier topsoils despite decreasing significance in the order wet > mesic > dry topsoils (BLISS, 1997; ALEXANDER, 1974b). In this study, the bacterial population was

found to be inhibited by lichens in the vegetation cover, which was studied in detail for arctic soils by PARINKINA (1989).

In summary, dry topsoil microbial habitat changed stratigraphically from weakly decomposed to humified organic horizons into the mineral topsoil. This was concomitant with an increase in bulk density and a decrease in porosity. As a result, insulation of the organic mats creates a more stable environment with respect to temperature and moisture. Despite high affinity to carbon and nitrogen contents, high microbial biomass was not restricted to organic layers. Relative peaks were determined for the upper mineral horizons, in which nutrient solutes accumulate. Furthermore, there is strong evidence that microbial succession occurred during decomposition spatially (between horizons) and temporally.

6.3.2 'Frontier'

The conception of 'frontier' horizons developed in this study has evolved from strong gradients in microbial properties which suggested a transition in microbial community structure between topsoil and subsoil horizons (see Sects. 6.1.1 and 6.2). Within a depth of 10 to 20 centimetres microbial biomass was found to increase strongly, even reaching maximum values in most soils. Simultaneously, fungi increased manifold stronger than bacteria did as indicated by maximum FB-ratios. Yet, mean bacterial cell volume increased and followed the fungal distribution pattern (SCHMIDT & BÖLTER, unpubl. data; BÖLTER, 1998). As discussed above, ATP concentrations on the contrary were lowest, indicating restricted microbial activity, which was supported by high caloric quotients. These exceeded a value of one, being wider in 'frontier' horizons at drier sites than in wet sites. Higher caloric quotients indicate environmental stress or a changing microbial population (see Sect. 6.2). Either may explain this microbial gradient since the respective horizons showed reducing conditions (chroma 2 or lower) and were found in proximity to the water table. At water-logged, wet sites, reducing conditions only occurred at greater depth, which may be explained by higher oxygen levels in the upper part of the water column. At drier sites, reducing conditions were found above the water table. This implies that conditions may change with fluctuating water table. Furthermore, these conditions are only stable in level or only gently sloping positions, which corresponds to the microbial parameters. Although no relationship could be established between vegetation stands that form mycorrhizal associations and those that do not, there was a clear rhizosphere effect since the respective microbial properties coincided with high root

densities. In general, roots will be metabolically active above the water table (WEBBER, 1978). From these properties it is concluded that 'frontier' horizons represent a stratum of redox potential discontinuity (RPD) interlocking with the rhizosphere.

Redox potential discontinuity

As mentioned above, soils with impeded drainage (PT, TT, HT, WST) showed the respective properties suggesting a link to specific hydrological conditions of plains. The dry podzolised brown earth at Labaz represented an exception here (profile Lb7/95). Yet, the subsoil of the latter (below 25 centimetres) showed gleying features due to water logging. On the contrary, the upper border of 'frontier' horizons was marked by iron oxidation bands (see profile descriptions), which had already been described in other arctic permafrost soils (GRABETSKAYA & CHIGIR, 1992). Below these iron bands, soils showed low chroma values of 2 or less, which thus marks a zone of redox potential discontinuity (RPD) in level tundra soils. The formation of the iron oxidation bands as well as the fact that these occur as relict features in formerly permafrost affected soils (FITZPATRICK, 1972; FITZPATRICK, 1987), indicate that despite short-term fluctuations, the RPD is temporally rather stable.

The occurrence of a RPD has been described in aquatic systems (e.g., OTT, 1988, p. 231) and characterized by decreasing redox potentials with depth and over time. In a marine environment, the redox status of the sediment is further classified as oxic, oxygen depleted postoxic, sulfidic (> 1 µM H_2S concentration) and methanogenic (lower H_2S concentrations) sediment (BERNER, 1981 cf. WALLMANN, 1990). Although this represents a helpful analogy, properties may not readily be transferred to soils, since marine sediments represent an alkaline and highly saline environment with a different decomposer cycle. Only for reed belt sediments of fresh water lakes, decomposition has been reported to be driven by a microbiota comparable to soils. Although no redox potentials were measured during the field campaign of this study, there is strong evidence for a gradient in redox potentials. As already mentioned, there is macroscopic evidence from the profile description (Sect. 5.1.2) such as iron oxidation bands and reduced chroma in the underlying horizons. During soil sampling odour of hydrogen sulphide in anoxic horizons was perceptible. Although the latter is highly subjective, it was still indicative for a particular redox environment. In soils of the experimental site Labaz, soil pH was measured in aqueous and $CaCl_2$ suspension, the quotient of which represents a parameter of exchangeable H^+. 'Frontier' horizons were characterized by a low ratio of pH [H_2O] and pH [$CaCl_2$], which is indicative for reduction reactions since these are

proton-consuming reactions. Furthermore, discontinuity of redox potentials has been supported by other studies. $\delta^{13}C$ studies (GUNDELWEIN, 1998) have shown that methane is formed in the 'frontier' although actual methanogenesis could not be measured. This was supported by activity studies which have shown the presence of methanogens (ibid.). On the contrary, SLOBODKIN et al. (1992) have shown for tundra soils that methane being produced in underlying horizons or adjacent micro-sites is oxidised at the respective depths. Thus, methanogenesis as well as methane consumption occurs in the 'frontier' despite different redox potential requirements. Methanogenesis is strictly anaerobic whereas consumption requires aerobic conditions (SCHIMEL et al., 1993). GUNDELWEIN (1998) states that methanogenesis and methane oxidation occurs at different redox potentials. Yet, a recent study by WAGNER & PFEIFFER (1998) suggests that the respective processes may be synchronous (i.e., in an aerobic environment). This apparent paradox has been explained by synergistic effects of the aerobic and (facultative) anaerobic microbiota at the interface of the RPD in natural environments. Although this question may not be answered from the present study, it is still indicative for a dynamic microbial population at the RPD as has been observed at the respective interface in marine environments (KÖSTER, 1992). In generalising, Table 6.3-1 illustrates microbiologically mediated redox couples, which may be read as a temporal or vertical sequence with increasing oxygen depletion. This gradient also develops around anaerobic pockets (TIEDJE et al., 1984), which occur in tundra soils in the study area of this study (BOIKE, 1997).

Tab. 6.3-1: Sequence of redox couples and associated microbial processes operating in the soil environment, with associated redox potential E_7 [mV] at pH 7 (modified from CRESSER et al., 1993).

Redox couple	Microbial process	E_7 [mV]
$O_2 \rightarrow H_2O + e^-$	Aerobic respiration	+820
$NO_3 \rightarrow N_2 + e^-$; $N_2O + e^-$	Denitrification	+420 [1]
$Mn^{4+} \rightarrow Mn^{2+} + 2\ e^-$	Manganese reduction	+410
organic matter $\rightarrow$ organic acids + e^-	Fermentation	+400
$Fe^{3+} \rightarrow Fe^{2+} + e^-$	Iron reduction	-180
$NO_3^- \rightarrow NH_4^+ + e^-$	Dissimilatory nitrate reduction	-200
$SO_4^{2-} \rightarrow H_2S + e^-$	Sulphate reduction	-220
$CO_2 \rightarrow CH_4 + e^-$	Methanogenesis	-240

[1] Data on significance of denitrification in tundra are contradictory. Whereas some authors state that denitrifiers are rare or absent in tundra soils (MATVEYEVA et al., 1975; BUNNELL et al., 1975), at some sites their numbers have been found to increase those of nitrifiers (PARINKINA, 1986).

The involved micro-organisms have been reported in tundra soils (DUNICAN & ROSSWALL, 1974; MATVEYEVA et al., 1975; BUNNELL et al., 1975; PARINKINA, 1986; VAINSHTEIN & GOGOTOVA, 1992). Because of the relationship of redox potential and pH, reduction processes occur over a wide range of pH. DUNICAN & ROSSWALL (1974) for instance reported sulphate reduction at Eh -200 mV to operate in the range of pH 4.4 to 6.2. Consequently, the position of the water table is crucial for redox reactions to occur (MOORE & DALVA, 1993; SLOBODKIN et al., 1992; WHALEN et al., 1996; SOMMERKORN, 1998; GUNDELWEIN, 1998), the water content and oxygen diffusion (SKOPP et al., 1990) and geochemical conditions (STEINMANN & SHOTYK, 1997). Apart from oxygen production at wet sites (abundance of primary producers), oxygen diffusion may further explain the position of the RPD below the water table. In 'frontier' horizons at drier sites, porosity and low proportion of macro pores was less favourable. This indicates that soil physical properties represent a further control for aerobic versus anaerobic processes as supported by GEBAUER et al. (1996). However, position of the RPD and thickness of the aerobic proportion of the active layer varied remarkably between wet and dry sites. The drier soils of this study showed a greater aerobic proportion than wet sites. Furthermore, thickness of the aerobic layer ranged between 10 and 20 centimetres at drier sites and five to ten centimetres at wet sites. These findings correspond to data by GEBAUER et al. (1996).

In marine environments, it is known that micro-organisms and ciliates interstitially inhabit the RPD (OTT, 1988). In the soils of the present study, manifold higher ATP concentrations below 'frontier' horizons support the hypothesis, that these may inhabit this habitat. In the respective horizons at drier sites, the presence of the water table further represents an ideal habitat for protozoa (COLEMAN & CROSSLEY, 1996). In addition, protozoa represent a characteristic feature of the rhizosphere and are intimately linked to rhizobacteria (CLARHOLM, 1994).

Rhizosphere

The rhizosphere is generally thought to stimulate microbial activity in manifold ways (SØRENSEN, 1997; TATE, 1995; BOLTON et al., 1995; CURL & TRUELOVE, 1986). Yet, despite greater microbial biomass, all parameters that characterize the active pool were found to decrease from topsoil to 'frontier' horizons. This was particularly true for fungi, which correlated with low ATP concentrations. The latter indicated a great proportion of inactive or even decaying fungi. Furthermore, they did not show any correlation with heat output values.

Microscopical investigations revealed that 'frontier' and to a lesser degree subsoils horizons contain a substantial amounts of hyphae depleted of cytoplasm. GUGGENBERGER et al. (in press) found that dead fungi in particular may be regarded as microbial 'litter'. Cell wall residues (e.g., amino sugars) contribute to the intermediate soil organic matter pool that is more recalcitrant to decomposition than carbohydrates. These residues (particularly fungal derived glucosamine) have further been suspected to be of major importance in the formation of organo-mineral complexes as well as in aggregation (TISDALL, 1994; TIESSEN & STEWART, 1988; GOLCHIN et al., 1994). Density fractionation of soil organic matter (som) in the respective horizons showed a distinct increase of the heaviest fraction (>2.4 g cm^{-3}), which contains 2-4% of total som (GUNDELWEIN, 1998). On the other hand, although not metabolising, fungi may still be 'functioning' in transferring nutrients through hyphae from a substrate source to metabolically active parts or plants when in mycorrhizal association. These 'pipelines' are thus important for fungal functioning in soil whether as decomposer or as mycorrhizal symbiont (CLARHOLM, 1994).

In contrast to fungi, carbon and nitrogen contents affected bacteria. Furthermore, basal and substrate-induced heat output also correlated well, which indicates that bacteria feed on simple compounds as described for topsoil horizons. Root exudates are typically simple compounds such as simple sugars, amino acids and organic acids (SØRENSEN, 1997, MARTENS, 1990), which are suitable for a wide range of rhizobacteria. Fungal cytoplasm may provide another nutrient source (GUGGENBERGER et al., in press). In this study, bacteria furthermore appeared to thrive well in the rhizosphere at depth of 20 and 45 cm, which was reflected not only in higher total numbers but also in increased mean cell volume (SCHMIDT & BÖLTER, unpubl. data; BÖLTER, 1998). Yet, no differences in the rhizosphere could be established between different vegetation stands. MATVEYEVA et al. (1975) on the contrary report that roots of different plants stimulate microbiota in different ways. Thus, bacterial biomass was two times greater in the rhizosphere of *Dryas* spp., whereas this increase may be 3 to 30 times greater with *Novosiviersia* (ibid.). Compared to other biomes, many tundra vegetation stands are characterized by high belowground biomass and litter production (WEBBER, 1978), which may be enhanced by short life spans (SHAVER, 1995). According to ZHU et al. (1996) root litter has a stimulating effect on fungal biomass. FEDOROV-DAVYDOV (1998) calculated that more than half the microbial population in tundra soils utilises root litter and exudates as a nutrient source.

In summary, the 'frontier' is characterized by interlocking habitats of redox potential discontinuity (RPD) and rhizosphere. Although microbial biomass in 'frontier' horizons was significantly higher than in the surrounding horizons, this increase did not correspond to the activity parameters. Fungi appeared to be more restricted in activity than bacteria. High caloric ratios indicated environmental stress and a shift in microbial community structure towards the subsoil. Fluctuating reducing and oxidising conditions represent environmental stress. The importance of the water table in this mechanism had already been established in parallel studies at the respective sites (GUNDELWEIN, 1998; SOMMERKORN, 1998) and was confirmed by the present study. This was supplemented by soil physical properties that affect soil water content and oxygen diffusion. The 'frontier' thus appears to be a zone, in which micro-organisms compete for the habitats.

6.3.3 Subsoil

Subsoil horizons generally represent anaerobic mineral horizons above the permafrost table. The only exception represented the transitionary polygon at Levinson-Lessing which showed a buried O-horizon above the permafrost table. As discussed for 'frontier' horizons, thickness of anaerobic subsoil horizons were dependent on the thickness of the active layer and oxygen diffusion. Accordingly, the proportion of subsoil horizons within a profile was greater in wet depressions than in the respective drier sites, which corresponded to findings in the literature (GEBAUER et al., 1996). Subsoils were water saturated above the supra-permafrost layer and marked by a distinct increase in soil organic matter with low C/N-ratios, which correspond to respective data by GUNDELWEIN (1998). This has been explained by precipitation of low molecular organic compounds at low temperatures above the permafrost table (ibid.).
In the respective horizons, bacteria prevailed over fungi, which were even absent in many cases. A peak in bacterial biomass values in the supra-permafrost layer was also determined by LYSAK & DOBROVOL'SKAYA (1982). Substrate induced heat output correlated with carbon and nitrogen levels but was negatively affected by wider C/N-ratios. The fact that caloric quotients increased with wider C/N-ratios indicates that the microbial population was apt for the nutrient resource available in the respective horizons. Heat output was attributed to bacteria and correlated well with the activity dependent parameters.

In summary, the microbial properties in accordance with statistical evaluation allowed a generalised view of microbial habitats in tundra soils, which differed significantly from each

other. Differences between the topsoils of wet and drier micro-sites were greater than between individual 'frontier' or subsoil horizons. As a consequence, variability between sites has only been discussed with respect to the respective horizons. Furthermore, it has to be stated that the individual habitats are likely to interlock depending on active layer thickness and proportion of the aerobic and anaerobic horizons within the profile. Particularly the cumulative wetting effect and 'zero-curtain', which results in accumulation of solutes in the upper part of mineral horizons is likely to interlock with 'frontier' habitats when thaw depth is shallow. Topsoils represent a continuum between wet, aquatic habitats and drier soils characterized by a decomposer cycle. On the other side, these may spatially and temporally interlock with for instance fluctuating water table at soil surface. Rhizosphere effects have been suggested when wet depressions in immediate proximity to vegetated mounds showed very high microbial biomass values. This is justified because of exceptional high belowground biomass production by tundra plants.

6.4 Tundra soils in a changing climate

As confirmed in this study, the decomposer cycle is determined by temperature, moisture and nutrients. Whereas soil temperature and moisture are largely controlled by climatic conditions, nutrient status and availability represent an indirect effect of both abiotic conditions and plant species composition. Yet, all of these factors are intimately linked to each other. In a changing climate, their effects on soil microbial properties are largely unknown. Impact of climate change in this context may thus be discussed in a rather simplistic manner. On the other hand, the presumed increase of CO_2 release and CH_4 oxidation in the Arctic represent plant-microbe-mediated processes, which in return might have a feedback on global climate (CHAPIN III et al., 1992). Since tundra globally covers $7.34*10^6 km^2$ (MATTHEWS, 1983), addressing consequences of climate change at soil microbe level becomes important.

During the last century, temperatures in Alaskan tundra have increased 2 to 4°C (LACHENBRUCH & MARSHALL, 1986 and LACHENBRUCH et al., 1988 cf. OECHEL & BILLINGS, 1992). As a result of atmospheric trace gas emissions such as CO_2, CH_4, and nitrous oxide (N_2O), global temperature might increase ('greenhouse effect'). In the early 1990s, further increase was considered to be highly certain (MAXWELL, 1992; CHAPIN III et al., 1992). More recent data qualify observed higher temperatures in the Arctic within range of historic variability (MAXWELL, 1997). Projections for the Russian Arctic differ from those for other arctic regions. Thus, mean annual air temperature shows no clear trend in climatic scenarios. This is explained by different trends of winter temperatures. Mean summer temperatures, in contrast, are generally expected to increase. In western Siberia (Yamal), an increase in temperature is also expected for winter but decreases towards the east (ibid.). Projections of changes in global water balance differ and are subject of discussion. Thus, climate change may lead to warmer and drier conditions due to increased evapotransipiration (KANE et al., 1997). On the other hand, precipitation is expected to increase (ROWNTREE, 1997) leading to warmer and wetter conditions. In the Russian Arctic, annual precipitation trends range from 0.0 to +2.3% per decade. Yet, summer precipitation is generally expected to increase (MAXWELL, 1997).

At both experimental sites of this study, a temperature increase would result in increased soil respiration, wet (top)soils showing a greater temperature sensitivity than the respective drier ones (SOMMERKORN, 1998). A theoretical temperature increase of 10°C (Q_{10}) would result in 2.2 to 3.0 greater activity at wet sites compared to 1.2 to I.6 greater values at drier sites

(ibid.). Thus, a higher temperature of 1°C would increase mineralisation by 12 to 16% at drier sites and 22 to 30% at wet sites. The potential for greater mineralisation rates at wet sites was supported by data of this study. Substrate induced heat output (*SIQ*) of wet topsoils showed that fungi in the respective horizons were viable. Lower activity under field conditions thus indicated that the microbiota was inhibited most likely due to water logging and low temperatures. In water saturated soils, a temperature increase would increase CH_4 production to a greater extent (VOURLITIS & OECHEL, 1997) because of higher temperature sensitivity (Q_{10} 5.3-16) of methanogenic bacteria (DUNFIELD et al., 1993). In contrast to microbial activity, community composition may not change significantly by temperature changes alone (PANIKOV, 1997)

As can be seen, the position of the water table represents another critical control for decomposition processes in the soils of this study (SOMMERKORN, 1998; GUNDELWEIN, 1998), as has also been established for other arctic soils (FEDOROV-DAVYDOV, 1998; VOURLITIS & OECHEL, 1997; OECHEL & VOURLITIS, 1995; WHALEN et al., 1996; OBERBAUER et al., 1996; MOORE & DALVA, 1993). Yet, the soil moisture regime is a major variable in predicting impact of climate change (see above). Increased annual air temperature along with higher evapotranspiration (i.e., warmer and wetter scenario) is likely to increase thaw depth and to lower the water table (KANE et al., 1992). In the soils of this study, lowering of the water table by 10 cm was found to result in almost complete CH_4 oxidation (GUNDELWEIN, 1998). In contrast, influence of water table on CO_2 efflux is limited, probably reflecting different substrates and microbial populations, lower temperatures and root respiration (SOMMERKORN, 1998; MOORE & DALVA, 1993; GEBAUER et al., 1996). Influence of water table was greatest at a depth of 0-5 cm (SOMMERKORN, 1998; OBERBAUER et al., 1991). For the soils of the experimental sites, this relationship indicates that the bulk CO_2 efflux originates from the respective horizons (SOMMERKORN, 1998), which corresponds to the microbiological data of this study. In addition to these considerations, greater thaw depths and lowering of the water table would result in a shift of 'frontier' horizons. Depending on the physical properties of the soil, this would relieve the stress caused by O_2 deficiency and microbial community structure might shift towards an aerobic population. In wet habitats, a lower water table will reduce ciliates and flagellates that are adapted to feeding in water (CLARHOLM, 1994).

However, climate change may not necessarily induce drier soil moisture regimes. Precipitation is also likely to increase in most areas (i.e., warmer and wetter scenario), as in the Russian Arctic (MAXWELL, 1997). Yet even in the warmer and drier scenario, KANE et al. (1997)

further state that downslope soils may receive additional moisture from hillslope soils. This process would affect many soils of this study. Hence, there is strong evidence that soil moisture regimes may not change to a great extent.

At long-term scales, climate change is expected to affect plant species composition, which bears greater uncertainties since plant species respond differently to changing environmental conditions (CHAPIN III et al., 1997; BILLINGS, 1992). Yet, vegetation affects soil ecology in substrate quantity and quality as well as in competition for nutrients. It has generally been suggested that plant species composition will change towards greater abundance of grasses and deciduous shrubs (KIELLAND & CHAPIN, 1992). Soil drying could increase deciduous shrubs relative to graminoids and mosses (CHAPIN III et al., 1997). Advance of the treeline depends on the onset of the growing season, which might be delayed as a result of later snowmelt (SVEINBJÖRNSSON, 1992). Furthermore, the microbiota of the rhizosphere is very plant specific (PARINKINA, 1974; 1989). Thus, changes in the vegetation cover will be accompanied by changes in the microbial population (KIELLAND & CHAPIN, 1992). It has been suggested that elevated CO_2 concentrations of the atmosphere and increasing temperatures may result in increased plant productivity, which may further be counterbalanced by limited nutrient availability and plant specific water relations (OECHEL & BILLINGS, 1992; OBERBAUER & DAWSON, 1992). Low nutrient availability may increase mycorrhizal infection in order to enhance nutrient acquisition (SVEINBJÖRNSSON, 1992). According to MOORHEAD & LINKINS (1997) greater activity associated with nutrient acquisition, will change the microbial community composition. This is explained by a greater availability of simple carbohydrates, which may lower the decomposition rate of complex polymers. On the other hand, it has been suggested that microbial biomass may increase but not change in composition since plant litter production will increase too (ZAK et al., 1993). Thus, there are many uncertainties in evaluating the long-term effect on plant-microbe relations.

In summing up, it may be stated that even if anticipation of the nature of climatic change was possible, impact on soil ecology of arctic systems might not be. Yet, the soil microbiota of this study showed high potential productivity and sensitivity with respect to temperature and soil water conditions and may therefore be particular vulnerable to climate change.

6.5 Future research needs

The methods used in this study proved to describe the microbial pool and its spatial variability successfully. Yet, in order to elucidate (micro)biologically mediated carbon fluxes in tundra soils future research should address the following aspects:

- This study showed that microbiological investigations should include all depths of the active layer. Changes in microbial properties such as community composition and substrate requirements indicate the potential productivity of tundra soils. This is substantiated by the freeze-thaw dynamics of permafrost affected soils, where frost churning may result in upside-down orientation of subsoil horizons. Furthermore, climate change may cause the soils to thaw to greater depths.
- Tundra soils are characterised by a short growing season, during which edaphic conditions and microbial biomass values change remarkably. It is also known for temperate soils, that microbial parameters such as for example metabolic quotients vary over time (DILLY, 1994). Therefore, a temporal resolution of the sampling technique is desirable. In addition to continuous CO_2 and CH_4 measurements in the field, these would provide further insight in the underlying microbial processes.
- There is evidence from this study that in wet habitats of tundra soils, a substantial proportion of the energy flux might pass through protozoa. The fast turnover of carbon and nutrients through bacteria and protozoa is commonly referred to as 'microbial loop'. For aquatic habitats, the significance of the 'microbial loop' as a link or source of energy flow is subject of dispute. Yet for tundra soils, there is very little information on the respective taxonomic groups and future investigation is recommended.
- Tundra plants show specific rooting strategies and high belowground biomass production. Within the scope of this joint research project, emphasis was put on particulate carbon input from above and belowground. Root litter and exfoliating cells of living roots as well as microbial cell residues will stimulate decomposer micro-organisms. Yet, further input comes from root exudates, upon which different groups will feed. Of equal importance are mycorrhizal associations. In contrast to decomposing fungi, mycorrhizal fungi receive assimilates from above-ground plant parts. Mycorrhiza thus contribute to soil organic matter but are less important in decomposition. The methodology of this study was not designed to capture these processes. Yet, a clear rhizosphere effect was discernible in the studied tundra soils. Further insight in the origin of particulate soil organic matter in the

rhizosphere may be achieved by CP/MAS ^{13}C N.M.R spectroscopy (BALDOCK et al., 1990). Fungal and bacterial cell residues may be investigated by contents of glucosamine and muramic acid (GUGGENBERGER et al., in press). Characterisation of soil pore water and determination of dissolved organic matter with respect to root effects are recommended.

- The hypothesis of a redox potential discontinuity (RPD) needs investigation by redox potentiometers in the field. Yet, both temporal and spatial resolution are required for further characterisation. Confirmation of the presence of a RPD would have implications for geochemical element cycling as well as microbial mediated processes and the microbiota. Marine environments show a dynamic microbiota with respect to carbon cycling at the interface of aerobic and anaerobic layers. Contradictory anaerobic and aerobic processes have also been reported to occur synchronously in water-logged soils of temperate regions. Future investigation should address all these aspects.

7. References

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8. Appendices

A1. Calculation of ATP contents

ATP contents of the soil extract (A-value), the soil extract with standard in the extract (C-value) and the soil extract with standard during measurement (B-value) are read from the standard curve and given in nanograms. The inhibition rate *I* [%] is calculated as follows:

$$I = 100 - \left[\frac{(B - A)}{Std_i} * 100 \right] \tag{1.1}$$

where I inhibition rate [%]

A-value ATP content [ng] of aliquot of the soil extract

B-value ATP content [ng] of aliquot of the soil extract with added ATP standard (Std_i) for measurement

Std_i internal standard during measurement; here: 0.5 or 1 ng ATP

A- and C-values are then corrected for inhibition:

$$Conc_a / Conc_c = \left(\frac{A / C}{100} * I \right) + A / C \tag{1.2}$$

The measured ATP contents A and C (ATP_m) are given in nanograms per gram dry weight of soil using the following equation:

$$ATP_m = \frac{\left[Conc * (V_E + WC) * V_d \right]}{(DW * V_a)} \tag{1.3}$$

where ATP_m ATP content of A or C [ng g^{-1} d.wt.]

Conc ATP content [ng] in the cuvette (obtained from Eqn. 3.4.2)

V_E Extraction volume [ml]; here: 50 ml (or 30 ml)

WC Water content of the soil sample [ml]

V_d Dilution volume [ml]; here: 0.1 ml

DW Dry weight of the soil sample [g]

V_a Aliquot volume of diluted soil extract in cuvette [ml]; here: 0.35 ml

The recovery rate [%] is calculated as follows:

$$\left[\frac{(C - A)}{Std_R} \right] * 100 = RR \tag{1.4}$$

where RR [%] recovery rate [%]

C C-value obtained from Equation 3.4.3

A A-value as obtained from Equation 3.4.3

Std_R Standard added before extraction; here: 1000 ng ATP

The ATP content of the soil sample (A-value as obtained from Eqn. 1.3) is corrected for recovery of added ATP (C-value obtained from Eqn. 1.3) as follows:

$$\frac{(ATP_m * 100)}{RR} = ATP_c \qquad (1.5)$$

where ATP_c ATP content of soil sample [ng g^{-1} d.wt.] corrected for recovery

ATP_m Measured ATP content [ng g^{-1} d.wt.] as calculated by Equation 1.3

RR Recovery rate [%] as obtained from Equation 1.4

A2. Soil maps

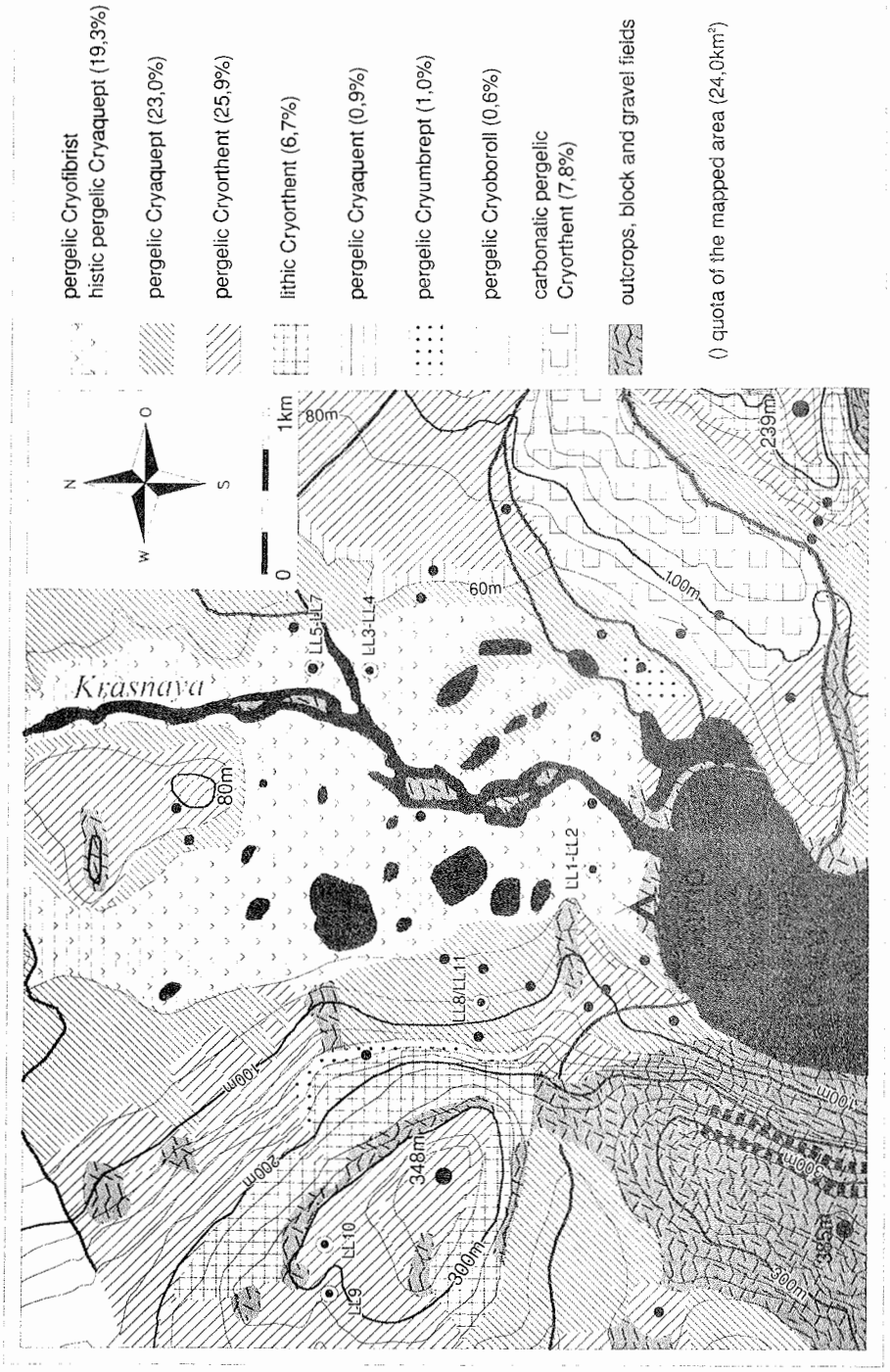

Fig. A2.1-1: Soil map Levinson-Lessing (modified from GUNDELWEIN et al., 1997; GUNDELWEIN, 1998).

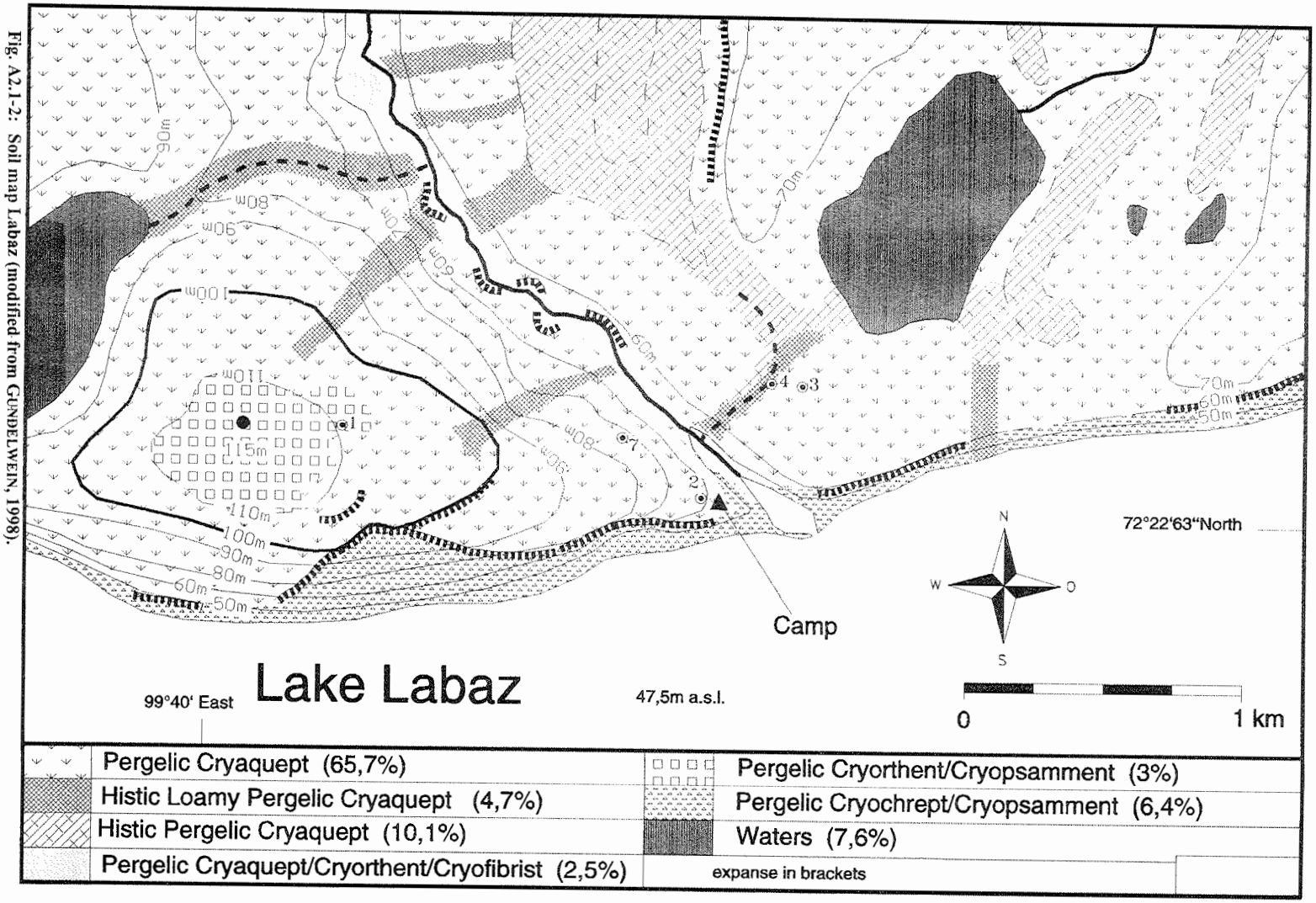

Fig. A2.1-2: Soil map Labaz (modified from GUNDELWEIN, 1998).

High centred polygon

Profile LL3/96: Ruptic-Histic Aquiturbel (Pergelic Cryaquept) (S.T.)
Turbic Cryosol (WRB)
Profile LL4/96: Typic Aquorthel (Pergelic Cryaquept) (S.T.)
Histic Cryosol (WRB)

Relief:	Terrace of river Krasnaya
Altitude:	50 m a.s.l.
Vegetation:	Arctic and arctic-alpine vegetation (100% coverage) Dry centre: mosses (*Tormenthypnum nitens, Hylocomium splendens*), dwarf shrubs (*Dryas punctata*), sedges (*Carex arctosibirica*), lichens (*Thamnolia vermicularis, Dactylina arctica*) Wet frost crack: mosses (*Plagonium elatum*), sedges (*Eriophorum angustifolium, Carex arctosibirca*), dwarf shrubs (*Salix reptans*)
Substrate:	Fluviatile sands
Drainage:	Centre: moderately drained, frost crack: very poorly drained

Profile 3/96 (dry centre):

Depth (cm)	Horizon	Description
- 8 - 5	Oi	Weakly decomposed plant debris, 0 vol.% gravel, no roots, pH [$CaCl_2$] 6.5
- 5 - 0	Oe	Moderately decomposed plant debris, 0 vol.% gravel, very densely rooted, pH [$CaCl_2$] 6.7
0 - 8	Bg	Very dark grayish brown (2.5Y 3/2) sandy loam, weakly stony (1-10 vol.% gravel), dark yellowish brown (10YR 4/6) iron mottling, dipyridyl [+], weakly humic, coherent structure, densely rooted, pH [$CaCl_2$] 6.3, HCl [-], ice veins, oriented stones
>8	pft	Permafrost table

Profile 4/96 (wet frost crack):

Depth (cm)	Horizon	Description
+6 - 4	Oi	Weakly decomposed plant debris, 0 vol.% gravel, no roots, pH [$CaCl_2$] 7.0
4 - 0	Oe	Moderately decomposed plant debris, 0 vol.% gravel, very densely rooted, pH [$CaCl_2$] 7.0
0 - 18	Bg	Very dark gray (5Y 3/1) sandy loam, 0 vol.% gravel, dipyridyl [+], weakly humic, coherent structure, densely rooted, pH [$CaCl_2$] 6.5, HCl [-]
> 18	pft	Permafrost table

Tab. A2.2-1: Profile description high centred polygon (Profile LL3/96 and LL4/96), Levinson-Lessing.

Intermediate polygon

Profile LL5-7/96: Typic Historthel (Pergelic Cryofibrist) (S.T.)
Histic Cryosol / Stagnic Cryosol (WRB)

Relief:	Terrace of river Krasnaya
Altitude:	50 m a.s.l.
Vegetation:	Arctic and arctic-alpine vegetation (100% coverage): Centre: sedges (*Carex stans, Eriophorum angustifolium*), mosses (*Plagomnium elatum*), dwarf shrubs (*Salix reptans*) Apex: dwarf shrubs (*Dryas punctata*), mosses (*Tormenthypnum nitens, Hylocomium splendens*), lichens (*Cetraria cucullata, Thamnolia vermicularis, Stereocaulon spp.)* Frost crack: sedges (*Carex stans*), dwarf shrubs (*Salix reptans, Dryas punctata*)
Substrate:	Fluviatile sands
Drainage:	Centre: poorly drained, apex: imperfectly to moderately drained, frost crack: very poorly drained

Profile LL5/96 (centre):

Depth (cm)	Horizon	Description
-15 - 12	Oi	Weakly decomposed plant debris, 0 vol.% gravel, pH [$CaCl_2$] 6.6
12 - 10	Oe1	Moderately decomposed plant debris, 0 vol.% gravel, pH [$CaCl_2$] 5.4
10 - 0	Oe2	Moderately decomposed plant debris, 0 vol.% gravel, pH [$CaCl_2$] 5.8; Fe^{3+}-band
0 - 5	Bg	Very dark gray (2.5Y 3/1) silty loam, brown iron mottling (7.5YR 4/4), dipyridyl [+], moderately humic, coherent structure, pH [$CaCl_2$] 5.8, densely rooted, stagnating horizon
5- 11	IIOa	Black (10YR 2/1) strongly decomposed organic matter, 0 vol.% gravel, fluviatile sands, pH [$CaCl_2$] 5.6
>11	pft	Permafrost table

Profile LL6/96 (apex):

Depth (cm)	Horizon	Description
-9-6	Oa1	Humified plant debris, 0 vol.% gravel, densely rooted, pH [$CaCl_2$] 5.9
6-2	Oa2	Humified plant debris, 0 vol.% gravel, extremly densely rooted, pH [$CaCl_2$] 6.5
2-0	Oa3	Humified plant debris, 0 vol.% gravel, weakly rooted, pH [$CaCl_2$] 6.4, Fe^{3+}-band
0-6	Bg	Dark olive gray (5Y 3/2) silty loam, 0 vol.% gravel, brown (10YR 3/3) iron mottling, dipyridyl [+], weakly humic, coherent structure, pH [$CaCl_2$] 6.3, no roots
6- 13	II Oa	Black (10YR 2/1) strongly decomposed organic matter, 0 vol.% gravel, fluviatile sands, pH [$CaCl_2$] 6.1
>13	pft	Permafrost table
Note:		Profile showed irregular horizons with respect to thickness and boundaries due to cryoturbation

Profile LL7/96 (frost crack):

Depth (cm)	Horizon	Description
-16- 11	Oi	Weakly decomposed plant debris, 0 vol.% gravel, densely rooted, pH [$CaCl_2$] 6.2
11 - 0	Oe	Decomposed plant debris, 0 vol.% gravel, extremely densely rooted, pH [$CaCl_2$] 6.1
> 0	pft	Silty loam, 0 vol.% gravel, no roots, permafrost

Tab. A2.2-2: Profile description intermediate polygon (Profile LL5/96, LL6/96 and LL7/96), Levinson-Lessing.

Non-sorted steps

Profile LL11/96: Ruptic-Histic Aquiturbel (Pergelic Cryaquept) (S.T.)
Turbic Cryosol / Histic Cryosol (WRB)

Relief:	Upper slope, moderately steeply sloping (15°), east exposition
Altitude:	90 m a.s.l.
Vegetation.	Arctic and arctic-alpine vegetation (100% coverage): dwarf shrubs (*Dryas punctata, Salix polaris, Salix reticula*), *Astragalus spp., Polygonium vivparum*, sedges (*Carex spp.*), mosses, lichens (*Thamnolia vermicularis*)
Substrate:	Kolluvium of fine-grained greywacke
Drainage:	Imperfectly to poorly drained, slope water above permafrost

Profile LL11.1/96 (overgrown mud pit):

Depth (cm)	Horizon	Description
0 - 3	AC	Very dark gray (2.5Y 3/1) sandy loam, 25-50 vol.% gravel, coherent to granular structure, weakly humified, very densely rooted, pH [$CaCl_2$] 6.2
3 - 21	Cg1	Very dark gray (2.5Y 3/1) loamy sand. 2-10 vol.% gravel, coherent structure, no humus, weakly rooted, pH [$CaCl_2$] 5.4, Diyridyl [-]
21 - 51	Cg2	Black (5Y 2.5/1) loamy sand, 0 vol.% gravel, coherent structure, no roots, dipyridyl [-], pH [$CaCl_2$] 5.4, slope water
>51	pft	Permafrost table

Profile LL11.2/96 (vegetation ring):

Depth (cm)	Horizon	Description
-14-11	Oi	Weakly decomposed plant debris, 0 vol.% gravel, extremly densely rooted, pH [$CaCl_2$] 6.2
11-0	Oe	Moderately decomposed plant debris, 0 vol.% gravel, pH [$CaCl_2$] 5.7
0 - 15	Cg	Black (5Y2.5/1) loamy sand, 2-10 vol.% gravel, no humus, no roots, pH [$CaCl_2$] 5.7, dipyridyl [+]
>15	pft	Permafrost table

Tab. A2.2-3: Profile description overgrown non-sorted step at the solifluction slope (Profile LL11.1/96 and LL11.2/96), Levinson-Lessing.

Non-sorted stripes

Profile LL9/96: Typic Aquorthel (Pergelic Cryorthent) (S.T.) Leptic Cryosol (WRB)

Relief:	Foot slope at mountain top plateau, moderately steeply sloping (16°)
Altitude:	260 m a.s.l.
Vegetation.	Arctic and arctic-alpine vegetation (60% coverage): stripes of rock debris (very little vegetation): *Carex reptans* vegetation stripe: *Novosiviersia glacialis*, *Papaver spp. Salix spp.*, *Carex spp.*, *Minuarctic biflora*, mosses spp., lichens (*Cetaria cuculata*, *Thamnolia vermicularis*) *Saxifraga spp.*
Substrate:	Frost shattered rock debris, kolluvium
Drainage:	Poorly drained at vegetated micro-site, imperfectly drained, slope water above permafrost

Profile LL9.1/96 (unvegetated stripe):

Depth (cm)	Horizon	Description
0 - 4	A/C	Very dark gray (10YR 3/1) very sandy loam, 25-50 vol.% gravel, no to very little humus, coherent structure, moderately rooted, pH [$CaCl_2$] 7.2, dipyridyl [-]
4 -60	C	Reddish black (2.5YR 2.5/1) very sandy loam, 50-75 vol.% gravel, no humus to very weakly humic, no roots, pH [$CaCl_2$] 7.4, dipyridyl [-]
>60	pft	Permafrost table

Profile LL9.2/96 (vegetation stripe):

Depth (em)	Horizon	Description
- 4 - 2	Oi	Weakly decomposed plant debris, pH [$CaCl_2$] 7.5
2 - 0	Oie	Moderately decomposed plant debris, pH [$CaCl_2$] 7.6
0- 40	C	Reddish black (2.5YR 2.5/1) moderately sandy loam, 25-50 vol.% gravel, no humus to very weakly humic, moderately rooted, pH [$CaCl_2$] 7.6, dipyridyl [-]
>40	pft	Permafrost table

Tab. A2.2-4: Profile description non-sorted stripes (Profile LL9.1/96 and LL9.2/96), Levinson-Lessing.

A3. Pedological parameters

Tab. A3-1: C- and N-contents, pH value in the polygonal tundra at Levinson-Lessing.

Profile	Horizon/depth	% TC	% N	C/N	pH [$CaCl_2$]
1/96	Oi	20.2	0.9	22.3	6.1
1/96	Oe	21.3	0.8	25.2	6.0
2/96	Oi	33.4	0.6	51.6	5.2
		16.4	0.8	20.0	
2/96	Oe1	19.4	0.9	22.8	-
2/96	Bg	7.6	0.3	25.3	5.5
3/96	Oi	29.1	0.5	58.8	6.5
3/96	Oe	27.0	1.0	27.1	6.7
3/96	Bg	8.2	0.5	16.2	6.3
3/96	frost boil (0-4)	5.2	0.3	15.8	-
4/96	Oi	26.1	0.8	34.7	7.0
4/96	Oe	27.8	0.9	31.4	7.0
4/96	Bg	7.7	0.5	16.0	6.5
5/96	Oi	21.7	0.9	23.0	6.6
5/96	Oe1	18.5	1.0	18.9	5.4
5/96	Oe2	13.4	0.8	16.8	5.8
5/96	Bg	8.3	0.4	20.2	5.8
5/96	II Oe	13.1	0.7	19.1	5.6
6/96	Oa1	20.1	1.1	18.1	5.9
6/96	Oa2	16.8	1.0	16.8	6.5
6/96	Oa3	11.5	0.8	15.1	6.4
6/96	Bg	6.1	0.3	20.4	6.3
6/96	II Oe	10.7	0.5	19.8	6.1
7/96	Oe1	17.0	1.0	17.1	6.2
7/96	Oe2	15.2	0.9	16.7	6.1

Tab. A3-2: C- and N-contents, pH value in the solifluction steps at Levinson-Lessing.

Profile	Horizon/depth	% TC	% N	C/N	pH [$CaCl_2$]
8.1/96	AC (0-2)	2.7	0.2	13.0	5.5
8.1/96	AC (2-4)	3.3	0.3	13.4	-
8.1/96	Cg	3.9	0.3	13.9	5.3
8.2/96	Oi	20.6	0.7	28.6	4.6
8.2/96	A	8.6	0.5	16.2	5.7
8.2/96	Bg (5-9)	3.6	0.3	13.4	5.3
8.2/96	Bg (>9)	3.5	0.3	13.5	-
11.1/96	A	6.2	0.4	14.7	6.2
11.1/96	BG	3.5	0.3	13.6	5.4
11.2/96	Oi	22.3	0.7	33.8	6.2
11.2/96	Oe	22.7	0.8	27.0	5.7
11.2/96	Bg	4.4	0.3	15.1	5.4

Tab. A3-3: C- and N-contents, pH value in the non-sorted stripes/nets at Levinson-Lessing.

Profile	Horizon/depth	% TC	% N	C/N	pH [$CaCl_2$]
9.1/96	surface stones	-	-		
9.1/96	AC (0-0.5)	2.5	0.1	19.0	7.0
9.1/96	AC (0-4)	2.2	0.1	16.0	7.2
9.1/96	C	2.9	0.1	22.0	7.4
9.2/96	Oi	19.3	0.7	29.7	7.5
9.2/96	Oie	11.8	0.5	21.9	7.6
9.2/96	B/C	2.6	0.2	12.9	7.6
10.1/96	A	2.2	0.1	18.0	6.2
10.1/96	C	2.6	0.2	17.2	6.6
10.2/96	Oi (0-2)	26.6	0.6	42.1	6.0
10.2/96	Oi (2-3)	24.6	0.8	32.8	6.4
10.2/96	A	7.2	0.4	17.7	6.2
10.2/96	C1	5.9	0.4	16.0	6.4

Tab. A3-4: C- and N-contents, pH-values in the hummock tundra at Labaz.

Profile	Horizon	Horizon/depth	% TC	% N	C/N	pH [H_2O]	pH [$CaCl_2$]
Lb 2H/95	A (0-1)	0-2	17.5	0.9	19.7	5.1	4.3
	Cg (1- pft)	2-5	1.6	0.1	18.6	6.2	5.3
		5-10	1.8	0.1	16.8	6.2	5.2
		10-20	4.4	0.3	17.3	6.3	5.3
		20-30	1.2	0.1	16.4	6.4	5.8
		30-40	1.7	0.1	19.1	6.6	5.9
Lb 2FC/95	Oe (0-10)	0-2	34.5	1.0	33.1	5.6	4.8
		2-5	26.5	1.2	22.2	5.6	4.7
		5-10	9.6	0.6	17.3	5.8	4.9
	Oef (>10)	10-20	12.9	0.8	16.3	5.8	5.2
		20-30	5.2	0.3	18.1	6.3	5.3

Tab. A3-5: C- and N-contents, pH-values in the tussock tundra at Labaz.

Profile	Horizon	Horizon/depth	% TC	% N	C/N	pH [H_2O]	pH [$CaCl_2$]
Lb 3T/95	Ah (0-5)	0-2	20.2	0.5	38.1	5.3	4.3
		2-5	3.6	0.2	22.4	5.5	4.6
	Cg1 (5-8)	5-10	2.4	0.1	17.7	6.5	5.6
	Cg2 (8-44)	10-20	2.2	0.1	16.6	6.4	5.2
		20-30	2.3	0.1	17.7	6.0	5.2
		30-40	2.2	0.1	17.4	6.1	5.3
	Cg3 (44-50)	40-50	4.7	0.3	18.0	6.5	5.2
Lb 3D/95	Oe (0-17)	0-2	33.2	0.9	36.4	5.8	5.3
		2-5	13.9	0.7	19.3	5.9	5.3
		5-10	17.2	0.9	19.5	5.6	5.2
	ACg (17-27)	10-20	27.2	1.3	21.2	5.65	5.2
		20-30	2.4	0.1	18.4	6.1	5.0

Tab. A3-6: C- and N-contents, pH-values in the wet sedge tundra at Labaz.

Profile	Horizon	Horizon/depth	% TC	% N	C/N	pH [H_2O]	pH [$CaCl_2$]
Lb 4/95	Oi (12-0)	0-2	20.5	0.9	23.0	5.7	5.3
		2-5	42.9	0.9	47.4	-	-
		5-10	14.1	0.9	16.1	5.6	4.7
	ACg (0-33)	10-20	1.9	0.1	18.8	6.1	5.0
		20-30	1.7	0.1	18.4	6.i	5.0
	Cgf (>33)	30-50	2.0	0.1	18.5	6.2	5.3

Tab. A3-7: C- and N-contents, pH-values in the dry uphill soil at Labaz.

Profile	Horizon	Horizon/depth	% TC	% N	C/N	pH [H_2O]	pH [$CaCl_2$]
Lb 1/95	A (0-1)	0-2	8.6	0.5	17.5	6.9	6.6
	Bh (1-23)	2-5	4.3	0.3	15.1	7.5	7.3
		5-10	2.7	0.5	5.5	7.5	7.4
		10-20	1.4	0.1	22.2	7.3	7.0
	Cw (23-34)	20-30	1.0	0.0	24.0	7.7	7.6
	3Bh (34-40)	30-50	0.9	0.0	34.4	8.1	.76
	3 Bw (40-52)						

Tab. A3-8: C- and N-contents, pH-values in the dry podzolised soil at Labaz.

Profile	Horizon	Horizon/depth	% TC	% N	C/N	pH [H_2O]	pH [$CaCl_2$]
Lb 7/95	AE (0-10)	0-2	6.9	0.4	17.7	5.6	4.5
		2-5	5.4	0.3	16.8	5.1	4.3
		5-7	1.8	0.1	15.3	5.3	3.8
	AE (0-10)	0-10	3.2	0.2	16.5	5.3	4.3
	Bsg (10-25)	10-25	0.7	0.0	18.3	5.6	4.2
	Bwg (25-60)	25-60	0.1	0.0	14.0	5.8	4.6

A4. Biovolume and biomass of fungi and bacteria

Tab. A4.1-1: Hyphal length *L* [m g^{-1} d.wt.], fungal biovolume *V* [mm^3 g^{-1} d.wt.], fungal biomass *FBM* [µg C g^{-1} d.wt.], bacterial biomass *BBM* [µg C g^{-1} d.wt.] (SCHMIDT & BÖLTER, unpubl. data) and fungal to bacterial ratio (FB-ratio) at Levinson-Lessing.

Profile		Horizon/depth	L	V	FBM	BBM	FB-ratio
Polygonal tundra							
1/96	vegetated mound	Oi (0-5)	38.84	0.313	40.71	3.61	11.3
		Oi (5-10)	37.04	0.379	49.21	3.31	14.9
		Oe	4.98	0.088	11.46	2.07	5.5
2/96	centre	Oi	6.93	0.089	11.55	14.76	0.8
		Oe1	28.42	1.193	155.08	11.58	13.4
		Oe2	22.31	1.062	138.05	6.23	22.2
Special features:							
1/96	Carex roots	Oi	ND	ND	ND	ND	ND
	Fe-mottling	Bg	30.57	0.468	60.86	ND	ND
2/96	surface Fe-Ox.		0.79	0.011	1.37	ND	ND
3/96	vegetated mound	Oi	3.78	0.022	2.85	7.89	0.4
		Oe	41.19	0.263	34.18	16.05	2.1
		Bg	81.77	0.964	125.33	0.72	174.1
	frost boil	0-0.5	9.34	0.083	10.78	3.76	2.9
		0-4	7.48	0.073	9.52	5.45	1.7
4/96	frost crack	Oi	3.60	0.032	4.14	20.38	0.2
		Oe	34.74	0.413	53.70	18.41	2.9
		Bg	0	0	0	2.25	0.0
Special features:							
3/96	saprophytic fungi	Oe	7.92	0.106	13.84	ND	ND
4/96	transition Oe/Bg	Bg	53.89	0.631	82.02	ND	ND
5/96	centre	Oi	53.62	0.620	80.57	9.78	8.2
		Oe1	26.95	0.263	34.24	9.39	3.6
		Oe2	12.36	0.125	16.24	4.69	3.5
		Bg	5.30	0.249	32.42	10.48	3.1
		II Oe	0	0	0	12.39	0.0
6/96	mound	Oa1	101.39	0.925	120.29	5.18	23.2
		Oa2	85.32	0.742	96.46	3.62	26.6
		Oa3	49.35	0.429	55.79	2.67	20.9
		Bg	3.31	0.012	1.59	3.73	0.4
		II Oe	0	0	0	5.21	0.0
7/96	frost crack	Oe1	41.20	0.379	49.31	10.79	4.6
		Oe2	31.51	0.451	58.65	8.74	6.7
Special features:							
5/96	Fe-oxidation		ND	ND	ND	ND	ND
6/96	roots	Oe3	393.03	3.503	455.34	ND	ND
7/96	roots	Oe1	43.97	0.621	80.72	ND	ND
Non-sorted steps							
8/96	unvegetated mound	AC (0-0.5)	4.42	0.040	5.20	4.99	1.0
		AC (0-2)	2.04	0.017	2.16	2.19	1.0
		AC (2-4)	1.26	0.013	1.67	1.39	1.2
		Cg	4.60	0.089	11.63	2.02	5.8
	peat ring	Oi	82.82	0.561	72.89	7.13	10.2
		A	110.30	0.935	121.50	2.53	48.0
		Bg (5-9)	58.51	0.612	79.56	0.68	117.0
		Bg (>9)	18.49	0.148	19.24	0.87	22.1
11/96	vegetated mound	A	77.55	0.521	67.67	5.42	12.5
		Bg	1.83	0.031	4.08	10.21	0.4
	peat ring	Oi	47.66	0.558	72.59	16.32	4.4
		Oe	224.35	1.763	229.21	4.72	48.6
		Bg	3.49	0.033	4.23	1.87	2.3

-continued -

- continued -

Non-sorted (transitionary) stripes							
9/96	unvegetated mound	AC (0-0.5)	0	0	0	4.81	0.0
		AC (0-4)	0	0	0	1.96	0.0
		C	0	0	0	0.69	0.0
	peat ring	Oi	6.84	0.028	3.67	16.11	0.2
		Oie (2-3)	24.33	0.184	23.93	3.62	6.6
		Oie (3-4)	17.05	0.124	16.11	2.92	5.5
		B/C	ND		ND	ND	ND
10/96	unvegetated mound	A (0-0.5)	0	0	0	1.59	0.0
		A (0-11)	20.97	0.187	24.27	1.39	17.5
		C	45.76	0.526	68.42	1.07	63.9
	peat ring	Oi (0-2)	9.39	0.058	7.60	8.11	0.9
		Oi (2-3)	40.64	0.350	45.56	7.51	6.1
		A	64.24	0.492	63.92	4.44	14.4
		C	51.05	0.508	66.01	0.87	75.9
Special features:							
	peat	Oi (0-2)	12.01	0.093	12.06	ND	ND
		x (min)	**0**	**0**	**0**	**1**	**0**
		x (max)	**393.03**	**3.503**	**455.34**	**20.38**	**174.1**
		mean	**37.13**	**0.379**	**49.31**	**6.13**	**15.7**
		median	**20.97**	**0.187**	**24.27**	**4.71**	**4.5**

Tab. A4.1-2: Hyphal length *L* [m g^{-1} d.wt.], fungal biovolume *V* [mm^3 g^{-1} d.wt.], fungal biomass *FBM* [µg C g^{-1} d.wt.], bacterial biomass *BBM* [µg C g^{-1} d.wt.] (BÖLTER, 1998) and fungal to bacterial ratio (FB-ratio) at Labaz.

Profile		Horizon/depth	L	V	FBM	BBM.	FB-ratio
Lb1/95	Dry brown earth	Ah (0-2)	14.84	0.082	10.65	9.466	1.1
		Bw1 (2-5)	13.86	0.112	14.61	5.983	2.4
		Bw1 (5-10)	17.31	0.080	10.45	0.849	12.3
		Bw1 (10-20)	4.68	0.023	3.01	0.162	18.6
		2Cw1 (20-30)	3.28	0.015	1.96	0.178	11.0
		Bw2 (30-50)	1.79	0.008	1.03	0.117	8.8
2/95	hummock	A (0-2)	3.78	0.050	6.52	22.259	0.3
		Cg (2-5)	8.88	0.066	8.63	1.484	5.8
		Cg (5-10)	11.42	0.071	9.22	0.740	12.5
		Cg (10-20)	12.93	0.116	15.14	2.136	7.1
		Cg (20-30)	0.57	0.001	0.19	0.732	0.3
		Cg (30-40)	0	0	0	0.521	0
	frost crack	Oe (0-2)	16.91	0.134	17.45	26.015	0.7
		Oe (2-5)	1.96	0.027	3.57	5.571	0.6
		Oe (5-10)	43.09	0.376	48.91	2.290	21.4
		Of (10-20)	16.23	0.164	21.26	5.374	4.0
		Of (20-30)	0	0	0	1.765	0
3/95	tussock	A (0-2)	ND	ND	ND	7.078	ND
		A (2-5)	0	0	0	2.234	0
		Cg1 (5-10)	4.35	0.022	2.81	0.995	2.8
		Cg2 (10-20)	48.21	0.373	48.51	0.971	50.0
		Cg2 (20-30)	2.02	0.016	2.11	0.633	3.3
		Cg2 (30-40)	0	0	0	0.742	0
		Cg3 (40-50)	2.32	0.020	2.57	0.992	2.6
	depression	Oe (0-2)	64.87	0.532	69.18	7.018	9.9
		Oe (2-5)	77.74	0.603	78.37	13.229	5.9
		Oe (5-10)	124.92	0.753	97.86	33.111	3.0
		Oe (10-20)	82.44	0.445	57.83	5.839	9.9
		ACg (20-30)	0	0	0	1.715	0
4/95	wet sedge tundra	0-2	79.04	0.800	103.98	29.384	3.5
		2-5	246.86	2.359	306.67	16.209	18.9
		5-10	919.46	9.597	1247.66	7.339	170.0
		10-20	40.28	0.361	46.93	2.484	18.9
		20-30	2.66	0.010	1.33	1.471	0.9
		30-50	0	0	0	0.518	0
7/95	Dry brown earth (podzolised)	Oi (0-2)	0.83	0.012	1.50	1.162	1.3
		Oi (2-5)	1.12	0.004	0.49	0.826	0.6
		Oi (5-7)	1.35	0.006	0.78	0.606	1.3
		AE (0-10)	0.48	0.003	0.39	0.743	0.5
		Bhs (10-25)	2.81	0.017	2.21	1.300	1.7
		Bwg (25-60)	0	0	0	0.157	0
		x (min)	**0**	**0**	**0**	**0.12**	**0**
		x (max)	**919.46**	**9.597**	**1247.66**	**33.11**	**170.0**
		mean	**46.83**	**0.431**	**56.09**	**5.42**	**10.3**
		median	**4.07**	**0.025**	**3.29**	**1.48**	**2.7**

Tab. A4.2-1: Total bacterial number (TBN $n*10^9$ g^{-1} d.wt.), mean bacterial biovolume (MCV μm^3) and bacterial biomass (μg C g^{-1} d.wt.) in the soils of the polygonal tundra at Levinson-Lessing (SCHMIDT & BÖLTER, unpubl. data).

Profile	Sample	TBN [$n*10\ g^{-1}$ d.wt.]	MCV [μm^3]	BBM [μg C g^{-1} d.wt.]
1/96	201	1.48	0.024	3.61
	202	0.97	0.034	3.31
	203	0.44	0.047	2.07
2/96	204	2.80	0.053	14.76
	205	3.07	0.038	11.58
	206	1.32	0.047	6.23
3/96	207	1.52	0.052	7.89
	208	3.12	0.052	16.05
	209	0.16	0.046	0.72
3/96 (mud pit)	252	1.05	0.036	3.76
	253	1.37	0.040	5.45
4/96	210	3.66	0.056	20.38
	211	3.62	0.051	18.41
	212	0.44	0.052	2.25
5/96	213	2.08	0.047	9.78
	214	1.69	0.056	9.39
	215	1.09	0.043	4.69
	216	2.07	0.051	10.48
	217	2.54	0.049	12.39
6/96	218	1.22	0.042	5.18
	219	0.72	0.050	3.62
	220	0.69	0.039	2.67
	221	0.88	0.042	3.73
	222	1.79	0.029	5.21
7/96	223	2.30	0.047	10.79
	224	2.00	0.044	8.74
	x (min)	0.156	0.024	0.719
	x (max)	3.659	0.056	20.383
	mean	1.696	0.045	7.812
	median	1.500	0.047	5.838

Tab. A4.2-2: Total bacterial number (TBN n*10^9 g^{-1} d.wt.), mean bacterial biovolume (MCV µm^3) and bacterial biomass (µg C g^{-1} d.wt.) in the soils of the non-sorted steps at Levinson-Lessing (Schmidt & Bölter, unpubl. data).

Profile	Sample	TBN [n*10^9 g^{-1} d.wt.]	MCV [µm^3]	BBM [µg C g^{-1} d.wt.]
8.1/96	239	1.27	0.039	4.99
	240	0.71	0.031	2.19
	241	0.55	0.026	1.39
	242	0.79	0.026	2.02
8.2/96	243	1.90	0.038	7.13
	244	0.69	0.037	2.53
	245	0.20	0.034	0.68
	246	0.27	0.033	0.87
11.1/96	247	1.37	0.040	5.42
	248	2.37	0.043	10.21
11.2/96	249	7.38	0.022	16.32
	250	1.61	0.029	4.72
	251	0.47	0.040	1.87
	x (min)	0.201	0.022	0.679
	x (max)	7.384	0.043	16.320
	mean	1.507	0.034	4.642
	median	0.791	0.034	2.529

Profile	Sample	TBN [n*10^9 g^{-1}d.wt.]	MCV [µm^3]	BBM [µg C g^{-1} d.wt.]
9.1/96	225	1.05	0.034	4.81
	226	0.62	0.032	1.96
	227	0.27	0.035	0.96
9.2/96	228	3.44	0.047	16.11
	229	1.01	0.036	3.62
	230	0.79	0.037	2.92
10.1/96	232	0.55	0.029	1.59
	233	0.48	0.029	1.37
	234	0.34	0.032	1.07
10.2/96	235	2.17	0.037	8.11
	236	1.90	0.040	7.51
	237	1.05	0.042	4.44
	238	0.28	0.031	0.87
	x (min)	0.273	0.029	0.874
	x (max)	3.440	0.047	16.109
	mean	1.072	0.035	4.256
	median	0.785	0.035	2.915

Tab. A4.2-4: Total bacterial number (TBN $n*10^9$ g^{-1} d.wt.), mean bacterial biovolume (MCV μm^3) and bacterial biomass (μg C g^{-1} d.wt.) in the soils at Labaz (Bölter, 1998).

Profile	Depth	TBN [$n*10^9$ g^{-1} d.wt.]	MCV [μm^3]	BBM [μg C g^{-1} d.wt.]
Lb 1/95	0-2	1.970	0.048	9.466
	2-5	1.156	0.052	5.983
	5-10	0.129	0.066	0.849
	10-20	0.042	0.039	0.162
	20-30	0.035	0.051	0.178
	30-50	0.025	0.047	0.117
Lb 2a/95	0-2	3.352	0.066	22.259
	2-5	0.255	0.058	1.484
	5-10	0.175	0.042	0.740
	10-20	0.434	0.049	2.136
	20-30	0.224	0.033	0.732
	30-40	0.135	0.039	0.521
Lb 2b/951	0-2	3.581	0.073	26.015
	2-5	0.996	0.056	5.571
	5-10	0.373	0.061	2.290
	10-20	1.045	0.051	5.374
	20-30	0.380	0.046	1.765
Lb 3a/95	0-2	1.390	0.051	7.078
	2-5	0.478	0.047	2.234
	5-10	0.220	0.045	0.995
	10-20	0.272	0.036	0.971
	20-30	0.185	0.034	0.633
	30-40	0.212	0.035	0.742
	40-50	0.301	0.033	0.992
Lb3b/95	0-2	1.427	0.049	7.018
	2-5	2.213	0.060	13.229
	5-10	6.807	0.049	33.111
	10-20	1.459	0.040	5.839
	20-30	0.404	0.043	1.715
Lb 4/95	0-2	4.381	0.067	29.384
	2-5	2.706	0.060	16.209
	5-10	1.347	0.055	7.339
	10-20	0.618	0.040	2.484
	20-30	0.376	0.039	1.471
	30-50	0.160	0.032	0.518
Lb 7/95	0-2	0.252	0.046	1.162
	2-5	0.183	0.045	0.826
	5-7	0.208	0.029	0.606
	0-10	0.224	0.033	0.743
	10-25	0.268	0.048	1.300
	25-60	0.071	0.022	0.157
	x (min)	0.025	0.022	0.117
	x (max)	6.807	0.073	33.111
	mean	0.987	0.047	5.424
	median	0.337	0.047	1.478

A5. Ecological parameters

Tab.A5-1: Spearman correlation coefficients ρ for parameters of microbial biomass and activity as well as substrate parameters in wet topsoil horizons. Coefficients in bold letters mark when correlation was accepted. (where FBM: fungal biomass, BBM: bacterial biomass, FB: ratio of fungal to bacterial biomass, Q: basal heat output, SIQ: substrate induced heat output, CALQ: caloric quotient, ATP: ATP content, ATP/MBM: ATP content per unit microbial biomass, C: carbon content, N: nitrogen content, C/N: carbon to nitrogen ratio, n. a.: not applicable).

ρ	FBM	BBM	FB	Q	SIQ	CALQ	ATP	ATP/ MBM	C	N
Frequency	11	11	11	7	10	6	10	10	11	11
FBM										
BBM	0.20									
FB										
Q	0.25	-0.04	0.11							
SIQ	-0.05	-0.06	0.07	0.14						
CALQ	-0.03	-0.49	-0.26							
ATP	0.30	-0.02	0.38	**0.87**	-0.14	**0.80**				
ATP/MBM	-0.49	-0.36	-0.20	0.29	-0.35	**0.67**				
C	-0.20	0.18	-0.10	**-0.81**	-0.05	**-0.94**	-0.03	0.21		
N	-0.16	-0.16	-0.18	-0.51	**-0.67**	-0.25	-0.51	-0.12	0.11	
C/N	-0.04	0.30	0.04	-0.47	0.49	**-0.89**	0.12	0.05	**0.82**	-0.39

Tab.A5-2: Spearman correlation coefficients ρ for parameters of microbial biomass and activity as well as substrate parameters in dry topsoil horizons. Coefficients in bold letters mark when correlation was accepted (where FBM: fungal biomass, BBM: bacterial biomass, FB: ratio of fungal to bacterial biomass, Q: basal heat output, SIQ: substrate induced heat output, CALQ: caloric quotient, ATP: ATP content, ATP/MBM: ATP content per unit microbial biomass, C: carbon content, N: nitrogen content, C/N: carbon to nitrogen ratio, n. a.: not applicable).

ρ	FBM	BBM	FB	Q	SIQ	CALQ	ATP	ATP/ MBM	C	N
Frequency	26	27	26	12	14	12	27	26	27	27
FBM										
BBM	0.39									
FB	n. a.	-0.11								
Q	-0.05	**0.84**	-0.26							
SIQ	0.22	**0.71**	-0.17	**0.68**						
CALQ	-0.21	0.11	-0.11	n. a.	n. a.					
ATP	0.21	**0.67**	-0.19	0.07	0.42	-0.50				
ATP/MBM	-0.45	0.22	**-0.66**	-0.14	0.02	-0.20	n. a.			
C	0.42	**0.79**	0.04	**0.68**	**0.85**	0.01	0.51	0.08		
N	**0.61**	**0.66**	0.29	0.46	**0.60**	-0.05	0.40	-0.09	**0.84**	
C/N	-0.12	0.53	-0.36	0.51	0.51	0.10	0.33	0.25	n. a.	n. a.

Tab.A5-3: Spearman correlation coefficients ρ for parameters of microbial biomass and activity as well as substrate parameters in frontier horizons (at a depth of approximately 10 cm). Coefficients in bold letters mark when correlation was accepted (where FBM: fungal biomass, BBM: bacterial biomass, FB: ratio of fungal to bacterial biomass, Q: basal heat output, SIQ: substrate induced heat output, CALQ: caloric quotient, ATP: ATP content, ATP/MBM: ATP content per unit microbial biomass, C: carbon content, N: nitrogen content, C/N: carbon to nitrogen ratio, n. a.: not applicable).

ρ	FBM	BBM	FB	Q	SIQ	CALQ	ATP	ATP/ MBM	C	N
Frequency	22	22	22	14	15	13	22	22	22	22
FBM										
BBM	0.17									
FB	n. a.	n. a.								
Q	0.41	0.14	0.06							
SIQ	0.56	0.38	0.06	**0.78**						
CALQ	-0.18	-0.30	-0.09	n. a.	n. a.					
ATP	-0.01	0.28	-0.12	-0.13	0.13	-0.51				
ATP/MBM	**-0.57**	-0.09	-0.46	-0.21	-0.01	-0.36	n. a.			
C	0.34	**0.61**	-0.19	0.34	0.57	-0.15	0.21	-0.16		
N	0.35	**0.65**	-0.16	0.19	0.47	-0.34	0.30	-0.11	0.94	
C/N	-0.05	0.29	-0.30	0.41	0.46	0.30	-0.05	-0.09	0.43	0.20

Tab.A5-4: Spearman correlation coefficients ρ for parameters of microbial biomass and activity as well as substrate parameters in subsoil horizons. Coefficients in bold letters mark when correlation was accepted. (where FBM: fungal biomass, BBM: bacterial biomass, FB: ratio of fungal to bacterial biomass, Q: basal heat output, SIQ: substrate induced heat output, CALQ: caloric quotient, ATP: ATP content, ATP/MBM: ATP content per unit microbial biomass, C: carbon content, N: nitrogen content, C/N: carbon to nitrogen ratio, n. a.: not applicable).

ρ	FBM	BBM	FB	Q	SIQ	CALQ	ATP	ATP/ MBM	C	N
Frequency	19	19	19	7	8	4	19	19	19	19
FBM										
BBM	0.06									
FB	n. a.	n. a.								
Q	**-0.69**	0.45	**-0.69**							
SIQ	0.23	**0.63**	0.14	0.27						
CALQ	**-0.89**	**0.74**	**-0.89**	**0.78**	-0.32					
ATP	0.07	-0.14	0.31	**0.69**	0.11	-0.06				
ATP/MBM	-0.06	-0.15	0.19	**0.69**	0.11	-0.06	n. a.			
C	0.06	**0.83**	-0.11	0.19	**0.92**	-0.32	0.04	0.03		
N	0.05	**0.83**	-0.14	0.20	**0.92**	-0.33	0.06	0.06	**0.97**	
C/N	-0.06	0.02	0.05	0.11	**-0.73**	**0.63**	0.18	0.20	-0.03	-0.14

Tab.A5-5: Significance level p (Mann-Whitney U test) of difference of means of data sets for all topsoil (top), wet (wtop) and dry (wtop) topsoil, and all frontier horizons (front: depth of approximately 10 cm) and all subsoils (sub). Bold figures show when difference was rejected (where FBM: fungal biomass, BBM: bacterial biomass, FB: ratio of fungal to bacterial biomass, Q: basal heat output, SIQ: substrate induced heat output, CALQ: caloric quotient, ATP: ATP content, ATP/MBM: ATP content per unit microbial biomass, C: carbon content, N: nitrogen content, C/N: carbon to nitrogen ratio).

p	top vs. front	wtop vs. dtop	wtop vs. front	dtop vs. front	top vs. sub	wtop vs. sub	dtop vs. sub	front vs. sub
FBM	**0.1933**	0.0499	**0.5668**	0.0426	< 0.0001	< 0.0001	0.0001	< 0.0001
BBM	0.1213	0.0002	0.0008	**0.7939**	0.0002	< 0.0001	0.0069	0.0237
FB	0.0212	**0.5387**	0.0727	0.0385	0.0028	0.0252	0.0054	< 0.0001
Q	0.0492	**0.9326**	**0.2047**	0.0570	0.0072	0.0639	0.0068	0.0207
SIQ	0.0179	**0.1599**	0.0198	0.0809	0.0031	0.0164	0.0051	0.0528
CALQ	**0.9362**	**0.6396**	**0.6931**	**0.7237**	0.0333	0.1356	0.0290	0.0315
ATP	**0.2397**	0.1080	0.0281	**0.6729**	0.0014	0.0015	0.0097	0.0281
ATP/MBM	0.0894	**0.7239**	**0.1797**	0.1309	**0.5954**	**0.6464**	**0.6458**	**0.8651**
C	0.1124	0.0010	0.0005	**0.8016**	< 0.0001	< 0.0001	0.0019	0.0037
N	**0.3455**	0.0042	0.0117	**0.9279**	< 0.0001	< 0.0001	0.0026	0.0026
C/N	0.0634	0.0062	0.0010	**0.4880**	0.1526	0.0007	**0.8935**	**0.8857**

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