Soil respiration, microbial respiration and mineralisation in soils of montane rainforests of Southern Ecuador: influence of altitude

Dissertation

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List of Abbreviations

amsl	above mean sea level
BAME	bacterial acid methyl ester
C_{mic}	microbial biomass carbon
CEC	actual cation exchange capacity
DBH	diameter at breast height, i. e. 1.3 m above the floor
DFG	Deutsche Forschungsgemeinschaft
DOC	dissolved organic carbon
DOM	dissolved organic matter
DON	dissolved organic nitrogen
d_Q	distance between first and third quartile
ECSF	Estación Cientifica San Francisco
EGM	environmental gas monitor
FAME	fatty acid methyl ester
HWC	total hot-water extractable organic carbon
HWN	total hot-water extractable nitrogen
LAI	leaf area index
MAP	mean annual precipitation
MAT	mean annual air temperature
MUFA	monounsaturated fatty acid
n/d	not determined
N_{mic}	microbial biomass nitrogen
PC	principal component
PCA	principal component analysis
PE	polyethylene
PLFA	phospholipid fatty acid
$PLFA_{tot}$	total amount of PLFAs

PNP	Podocarpus National Park
PTFE	polytetrafluorethylen
PUFA	polyunsaturated fatty acid
Q1	first quartile
Q3	third quartile
R_H	partitioned soil CO_2 efflux
RBSF	Réserva Biologica San Francisco
RAH	relative air humidity
RC%	root contribution
SATFA	saturated fatty acid
SOC	soil organic carbon
SOM	soil organic matter
T_{min}	temperature of mineral soil
T_{org}	temperature of organic layer
T_{soil}	soil temperature
TIN_{KCl}	total KCl-extractable inorganic nitrogen
TMCF	tropcial montane cloud forest
TN	total nitrogen
TN_{KCl}	total KCl-extractable nitrogen
$TN_{KCl(inorg)}$	total KCl-extractable inorganic nitrogen
$TN_{KCl(org)}$	total KCl-extractable organic nitrogen
TOC	total organic carbon
TOC_{KCl}	total KCl-extractable organic carbon
TSR	total soil respiration
VWC	volumetric water content
VWC_{min}	volumetric water content of mineral soil
VWC_{org}	volumetric water content of organic layer

Chapter 1

Introduction

1.1. Tropical montane cloud forests and climate change

1.1.1. Definition and global distribution

Tropical montane cloud forests (TMCFs) typically occur as a narrow altitudinal zone where cloud cover at vegetation level occurs persistently, frequently or seasonally. There humid mountain slopes with topo-climate conditions favour the occurrence of ground-level clouds during considerable periods of the year (Doumenge et al., 1995). Their lower altitudinal limits grade into montane rain forest; however the distinction is sometimes difficult (Hamilton et al., 1995). At higher altitudes, TMCFs are often bordered by páramo.

On a global scale, TMCFs occur within a wide range of annual and seasonal rainfall regimes, total precipitation may vary between 500 and 10 000 mm per year (Hamilton et al., 1995). These forests develop at different altitudinal positions; in large, inland mountain systems TMCFs are typically found at 2 000 to 3 500 m amsl, in coastal or insular mountains down to 1 000 m amsl and under exceptionally humid, marine and equatorial conditions also considerably lower (Hamilton et al., 1995). Nomenclature for the different types, altitudes and strata is diverse. TMCFs occur in the high tropical Andes of South America, in Central Africa and South East Asia (Doumenge et al., 1995) and Bubb et al. (2004) compiled maps of potential and actual cloud forest distribution (figure 1.1 on the following page).

Tropical montane forests occupy 3.3 million km^2 worldwide, which amounts to 21.2 % of all tropical forest. TMCFs cover an area of 0.38 million km^2, which corresponds to 2.5 % of total tropical forests and 11.7 % of tropical montane forest (Bubb et al., 2004).

1.1.2. Characteristics and ecosystem functions

The vegetation of TMCFs is determined by enveloping or wind-driven clouds that influence atmospheric interaction by reducing solar radiation, water vapour deficit, canopy wetting and general suppression of evapotranspiration. The canopy directly intercepts cloud water and the water use of the vegetation is high, which leads to net precipitation that is higher than rainfall alone (Hamilton et al., 1995). The vegetation is characterised by reduced tree height, increased stem density, gnarled trunks and branches of canopy trees. Crowns usually are dense and compact,

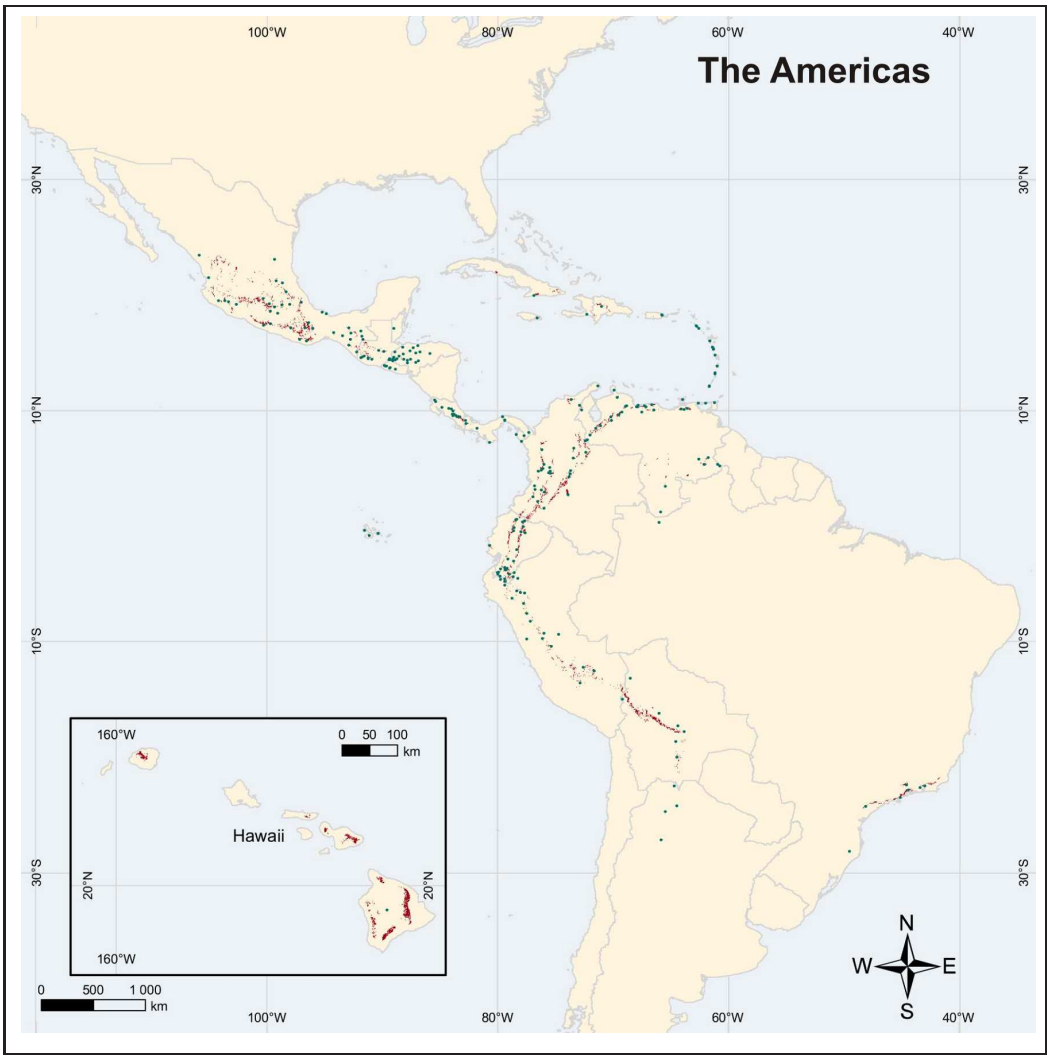


Figure 1.1: Map of the potential and actual distribution of TMCFs.

leaves rather small, thick and sclerophyllic. The proportion of epiphytes is high and the amount of woody climbers is reduced. Biodiversity and endemism are high. Soils are frequently waterlogged and highly organic in the form of mor humus or peat (Hamilton et al., 1995).

Doumenge et al. (1995) summarise the values or functions of TMCFs. First of all, these forests capture and transport water on steep mountain slopes, which contributes to protection of soils against erosion and guarantees the supply of water in downstream areas. As tree crowns intercept wind-driven cloud moisture, they add to net precipitation and therefore to groundwater and streamflow levels. Another value lies in the high faunal and floral biodiversity and endemism, which also adds economic value in terms of wood, medicinal and food plants and touristic issues.

1.1.3. Rates of deforestation and threats

TMCFs and also other tropical montane and submontane forests are subject to rapid deforestation of about 1.1 % per year (Doumenge et al., 1995). Threats are manifold and include

forest conversion to cattle or sheep pastures, extension of subsistence or commercial agricultural cropping by local people. Commercial logging of wood is not an important threat as trees are usually low-statured and forests as a rule inaccessible. However, in some TMCFs wood harvesting for fuelwood or charcoal exerts a major influence. Furthermore, exploitation of non-wood forest products like medicinal plants, orchids, hearts of palm, hunting, clearing for drug production and also tourism and recreation alter the composition of TMCFs and therefore pose a severe threat to these ecosystems (Hamilton et al., 1995).

Discussing the possible impact of global climate change on TMCFs, Hamilton et al. (1995) focus mainly on the impact of extreme events like hurricanes on the fragile and slowly regenerating ecosystem. Bubb et al. (2004) summarised the potential negative impacts of climate change on TMCFs. Climatic conditions will be altered for many mountain habitats and the optimal conditions for TMCFs occur several hundred meters higher in altitude. Consequently, TMCFs could be replaced by other vegetation types and become extinct when they now exist on mountain peaks and cannot spread upslope. Climate change furthermore is thought to change cloud frequency, which would primarily affect distribution of epiphytes and amphibians. Until now, the potential positive feedback of increasing temperatures on carbon dioxide concentrations in the atmosphere has not been addressed yet. Due to the climatic conditions, decomposition of organic material is reduced in montane forests and the soils (including forest floor material) hold considerable stocks of carbon. Thus climatic change in form of higher temperatures and lower soil moisture may accelerate organic matter decomposition and enhance CO_2 emissions of TMCFs. Due to the unique combination of climatic conditions under which TMCFs occur distribution and composition of these forests may be reliable indicators of climate change. However, Foster (2001) points out that the "lack of understanding of the underlying mechanisms of cloud forests morphology make it difficult to predict what the impacts of climate change will be."

1.2. Carbon cycling and climate change

The carbon balance of the world's terrestrial ecosystems is still uncertain. Two different general approaches, top-down calculations based on atmospheric CO_2 concentrations and bottom-up analyses of forest or land-use change inventories, yielded different results as they included different processes and pools of carbon cycling (Houghton, 2003). Globally, a northern mid-latitude C sink of about 2 $Pg\,a^{-1}$ appears robust, even though two different underlying mechanisms are discussed. First, enhanced carbon storage as a result of enhanced atmospheric carbon dioxide concentrations is considered and secondly, it is assumed that enhanced carbon storage is a consequence of ecosystem recovery from past disturbances due to land use. The tropics appear to be a small net source or nearly neutral, either due to large CO_2 emissions as a consequence of land-use change that are balanced by a large sink in undisturbed forests or due to only moderate sources from land-use change and with essentially no change of the sink (Houghton, 2003).

The assessment of consequences of climate change requests a thorough understanding of functional relations controlling turnover of greenhouse gas forming elements like carbon and nitrogen. Soils and organic layers are of special importance as to a depth of 100 cm they sequester twice as much (∼1 580 Pg) carbon as the atmosphere (750 Pg). Jobbágy and Jackson (2000) compiled data of three global databases and calculated the carbon that is stored in 0–300 cm mineral soil

to amount to 2 344 Pg, which is 56 % more than estimated for the top meter. Consequently, even small changes of the soil carbon pool may largely impact atmospheric carbon dioxide concentrations, i. e. feedback mechanisms between soil and atmosphere have to be considered. Recent studies have shown that 20–40 % of the carbon stored in the top meter has turnover times of less than a century (Trumbore, 1997). To address the question how climate change may influence net carbon balance of ecosystems it is essential to know if decomposition of soil organic matter (SOM) or net primary productivity is accelerated. Considering SOM, the magnitude and timing of the response depends on the size of carbon pools that respond quickly to changes in climate and vegetation (Trumbore, 1997). Soils can become sources of carbon dioxide if decomposition of SOM exceeds carbon input into the soil.

A further component of ecosystem carbon cycling is soil CO_2 efflux from the soil to the atmosphere, which globally amounts to approximately 80 Pg C a^{-1}. Tropical and subtropical evergreen broadleaved forests contribute the largest parts of about 22 Pg C a^{-1} (Raich et al., 2003). Through human activity, especially burning of fossil fuels and conversion of forest to other land use forms, about 7 Pg C a^{-1} carbon dioxide enter the atmosphere additionally. It is assumed that increasing carbon dioxide concentrations in the atmosphere are a main cause for higher temperatures in the atmosphere (Rustad, 2001), but as long as it remains unclear how carbon pools and fluxes react to this rise of the temperatures, it also remains unclear how the global carbon cycle will be altered by climate change in the long term.

The area studied in this thesis allows investigation of two different aspects related to carbon cycling and climate change. With respect to soil organic carbon of different decomposability, the definition of functional relations can contribute to a better understanding of carbon turnover in pristine tropical montane forests. Furthermore, along an altitudinal gradient, carbon pools and fluxes can be estimated and evaluated under different vegetation types and climatic conditions. Bruijnzeel and Veneklaas (1998) point out, that quantifying the overall carbon balance of tropical montane forests is essential for further insight into the interrelationships of forest structure and productivity.

1.3. Nitrogen limitation in tropical montane forests

A basic assumption of ecological research in tropical forests is that ecosystem productivity is limited by nutrient availability, but for tropical ecosystems it remains unsure, in how far indices of soil nutrient availability and nutrient use by the plants are interrelated (Silver, 1994). According to Bruijnzeel and Proctor (1995) scientists do not agree on the question if tropical montane forests are P or N limited. However, Tanner et al. (1998) suggested nutrient and especially nitrogen limitation of aboveground net primary production and the reduction of N cycling by low leaf N concentration and reduced leaf litter fall, which results in low plant nitrogen uptake. Plants are considered to take up elements in inorganic forms exclusively (Hodge et al., 2000; Schimel and Bennet, 2004). Consequently, organic matter mineralisation would be the key process determining the availability of nutrients to plants (Schimel and Bennet, 2004). A further basic assumption of nutrient cycling is that plants have disadvantages in competing with micro-organisms for available nutrients, i. e. plants can only take up, what it left over by microbes after mineralisation and immobilisation (Hodge et al., 2000; Schimel and Bennet, 2004). The

same authors suggest that in low-N ecosystems plants may take up organic N, consequently the cited core assumptions of N mineralisation and plant uptake could be invalid.

Vance and Chapin III (2001) summarise the following as a fundamental concept for soils in tropical montane (cloud) forests: decomposition of organic matter containing little N is limited by inadequate N supply to microbial biomass which results in immobilisation of N, reduced net primary production and litter input into the soil. Another concept focuses on the supply of microbial biomass with labile carbon compounds: plants on N-poor soils produce resistant carbon compounds and have low root exudation rates, which reduces litter decomposition by changing size, structure or activity of microbial biomass. Hodge et al. (2000) furthermore point out that soil micro-organisms are limited by the supply with readily decomposable carbon compounds and that most N transformations are conducted by heterotrophic organisms that are dependent on labile organic carbon in the soil.

1.4. Objectives

The central objective of this study was to determine pools and fluxes of carbon and nitrogen cycling in soils of near-natural tropical montane forests, and to detect functional relations of different carbon and nitrogen pools. In detail, analyses included determination of total, mineralisable and readily available carbon and nitrogen contents in organic layers and top mineral soils, as well as total and partitioned soil CO_2 efflux, leaf litter decomposition and nitrogen mineralisation potentials. Size and structure of microbial biomass were studied as well. The studied parameters were evaluated in relation to altitude, i. e. temperature and water budget on soil carbon and nitrogen pools was studied. From the differences of carbon and nitrogen features and dynamics, consequences of possible climate change on carbon sequestration in the studied soil were to be evaluated. Against the background of general assumptions concerning nutrient limitation, from the collected data potential nitrogen and carbon limitation of microbial organic matter decomposition was to be evaluated.

Chapter 2

Research area and study sites

2.1. Location and general aspects

The research area is located in southern Ecuador in the province Zamora-Chinchipe at the border to the province Loja, about 30 km east of the province capital Loja on the northern slope of the Cordillera de Consuelo, a smaller mountain chain on the eastern slopes of the Cordillera Real and one of the main cordilleras of the Andes in this region (Figure 2.1 on the following page).

The study area comprises an altitudinal range from 1 000 to 3 400 m above mean sea level (amsl), study sites are located in the 1 000 ha of the Réserva Biologica San Francisco (RBSF) which is part of the properties of the local foundation Nature and Culture International. This foundation works in the protection of endangered forest ecosystems in southern Ecuador and northern Perú. Two more study sites are located within the borders of Podocarpus National Park (PNP), which is situated south of the RBSF. This national park is one of nine national parks in Ecuador; it covers about 146 280 ha and harbours high biodiversity and endemism (Calderón, 2002). The PNP represents the largest closed forest area in southern Ecuador (Madsen and Øllgaard, 1994). The Estación Cientifica San Francisco (ECSF), the logistic centre of the RBSF, is located at an altitude of 1 860 m amsl at the following co-ordinates: 3°58'18"S latitude and 79°4'45"W longitude (Figure 2.2 on the following page).

The two lower plots at 1 050 ($P_{1\,050\ m}$) and 1 540 m ($P_{1\,540\ m}$) are located close to the lower entrance to the PNP about 4 km south of Zamora, the capital of the province Zamora-Chinchipe. Figure 2.3 on page 9 shows the location of the study sites at 1 890 m ($P_{1\,890\ m}$), close to the ECSF and at 2 380 m ($P_{2\,380\ m}$), also in the RBSF. The highest plot at 3 060 m ($P_{3\,060\ m}$) was upslope of the upper entrance to the PNP, which is called "Cajanuma" (Figure 2.1 on the following page).

The study is part of a joint research project of the Deutsche Forschungsgemeinschaft (DFG),[1] research unit "FOR 402". Further information on current members and projects is available at `www.bergregenwald.de`. Scientific research in the tropical montane forests started in 1997 and was driven by the increasing concern about the preservation and protection of tropical ecosystems, especially in the poorly understood mountain regions. The different projects combine basic research for a better understanding of the ecosystem and processes with applied research to be able to give recommendations for ecologically, economically and socially sustainable management

[1] German Research Foundation

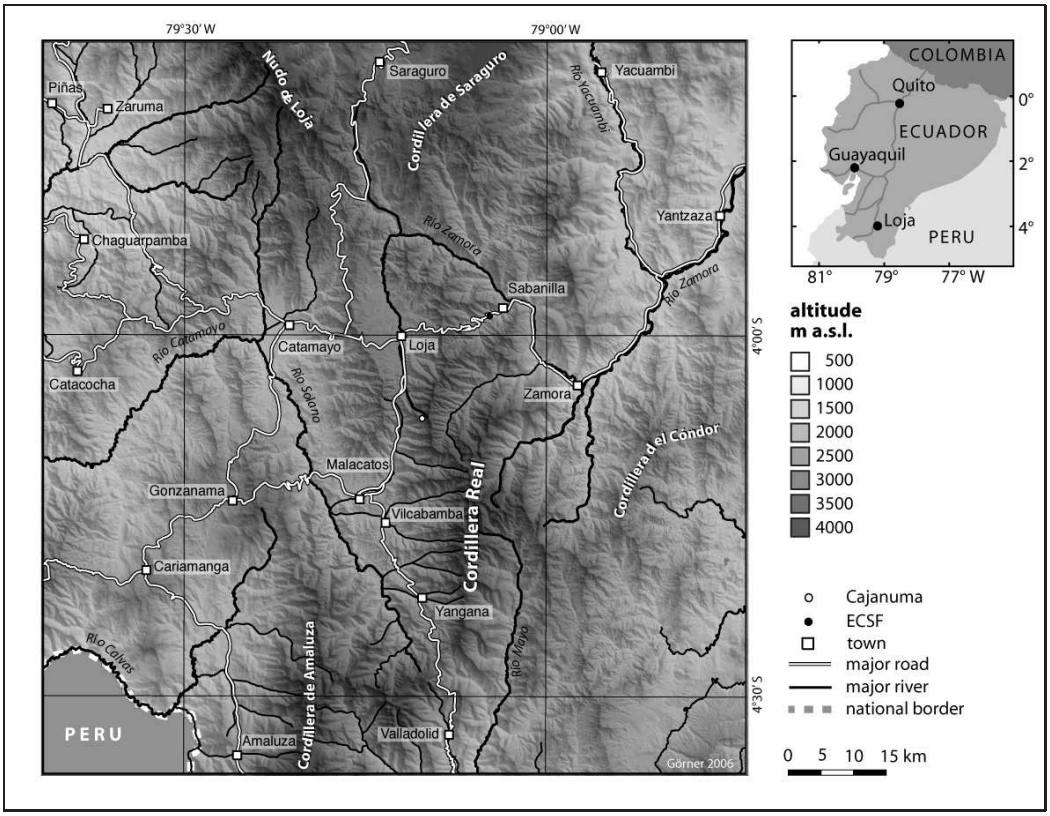


Figure 2.1: Location of the research area. (© 2005 by A. Görner)

Figure 2.2: Overview of ECSF. In the background above the road that connects Loja and Zamora a huge landslide is visible that is characterised by ongoing erosion, especially during the first few days after heavy rain events.

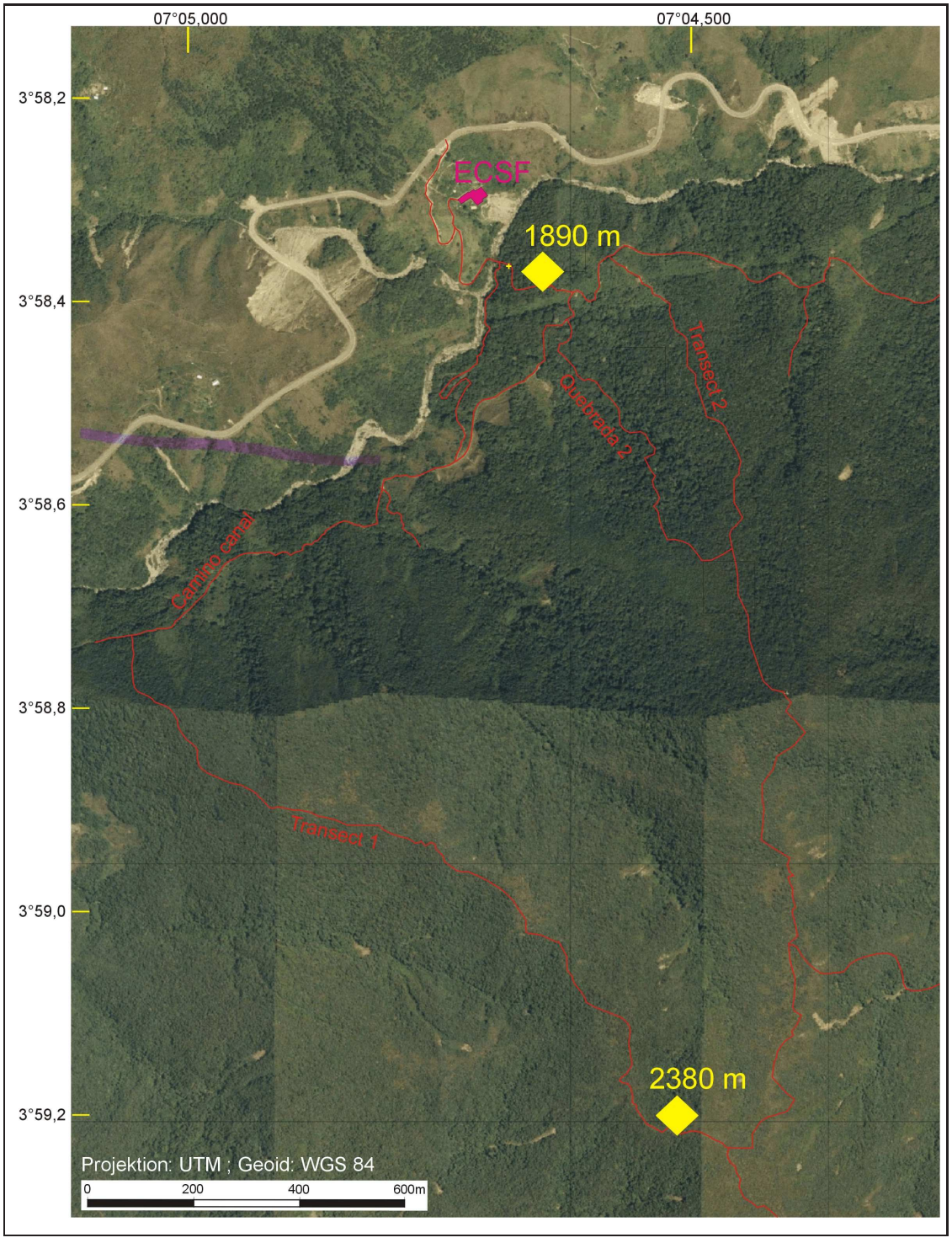


Figure 2.3: Arial photo of the core research area, showing ECSF as well as major transcects and $P_{1\,890\ m}$ and $P_{2\,380\ m}$. (© 2005 by F. Haubrich)

(Beck and Müller-Hohenstein, 2001).

2.2. Climate

The Andean altitudinal depression "Nudo de Loja" is considered a special feature of topography, were the Andes reach a maximum height of only 3 800 m amsl. The depression acts as a natural connection between the humid Amazon lowlands and the arid to semiarid coastal regions (Richter, 2004; Rollenbeck et al., 2005). Three mountain chains stretch from there in southern directions and are strongly dissected by valleys and small basins, which causes very complex and variable climate in this region (Richter, 2004).

The climate of the RBSF has been described thoroughly by scientists of the joint research unit. The climate is perhumid with mean annual precipitation between 2 453 $l\,m^{-2}$ at 1 860 m amsl and 7 786 $l\,m^{-2}$ at 3 182 m amsl (Fabian et al., 2005). Mean annual temperature at 1 970 m is 15.6 ℃, minimal temperatures can drop to about 4 ℃ at 3 400 m, but freezing has not been observed. Air humidity is generally high (Richter, 2004). The area is characterised by humid conditions throughout the year due to dominating trade winds, whose directions vary between E/NE (February) and E/SE (July) and that provide moist and warm air masses that originate in the Amazonian lowlands (Fabian et al., 2005). A primary maximum of precipitation occurs from April to August, a secondary maximum can be observed in some years during December. Above of 2 500 m wetter seasons occur from April to May and in November. The increase of mean annual precipitation along the altitudinal gradient amounts to 230 $l\,m^{-2}$ rain per 100 m, and 240 $l\,m^{-2}$ fog per 100 m (Rollenbeck et al., 2005). Fog and wind-driven rain contribute substantially to precipitation. This contribution increases with altitude as well and ranges between 5 % at 1 800 to 30 % at 3 185 m amsl (Fabian et al., 2005) and is highest in July to August, when wind speed is highest (Rollenbeck et al., 2005). Cloud frequency is high throughout the year and increases with altitude. Clouds that persist close to the ground at the vegetation level have important ecological impact on the ecosystem by supplying it with water through fog and rain and further influence radiation and temperature (Bendix et al., 2004). These features lead to the definition of the primary vegetation of the RBSF as tropical montane cloud forests given by Hamilton et al. (1995).

2.3. Geomorphology, geology and soils

The geomorphology of the research area is characterised by high geomorphologic dynamics; high ridges and steep slopes alternate with deeply dissected valleys which naturally lead to frequent landslides in this area; they cover about 3.7 % of the RBSF (Beck and Müller-Hohenstein, 2001; Wilcke et al., 2003). Geologically, the upper part of the study area is located at the palaeozoic metamorphic belt of the Cordillera Real of the Andes, the Chiguinda unit. According to Litherland et al. (1994) this units consists mainly of quartzite and black phyllites (Figure 2.4(a) on page 12). During Andean orogenesis Palaeozoic sediments were metamorphosed to metasiltstones, metasandstones, slates, phyllites and quarzites, which form a small scale mosaic of different bedrock (Figure 2.4(b) on page 12). Furthermore veins of hydrothermal rock occur. Dominant minerals are quartz, muscovite/illite, chlorite and albite. Ilmenite, zircon and apatite

occur in small amounts (Beck et al., 2007). Soils developed on periglacial cover beds and post-glacial landslides modify the substrate of pedogenesis. This led to a small scale mosaic of different soil types at the RBSF (Schrumpf et al., 2001; Wilcke et al., 2001).

Soils can be generally characterised by low exchange capacity, low pH, thick organic layers and hydromorphic properties (Schrumpf, 1999; Wilcke et al., 2002; Gonsior, 2004), which is considered typical for soils of cool humid tropical montane forests (Bruijnzeel and Proctor, 1995). Dominant soil types are Dystric, Umbric and Gleyic Cambisols; Histosols, Regosols and Leptosols also occur (Schrumpf, 1999; Gonsior, 2004).

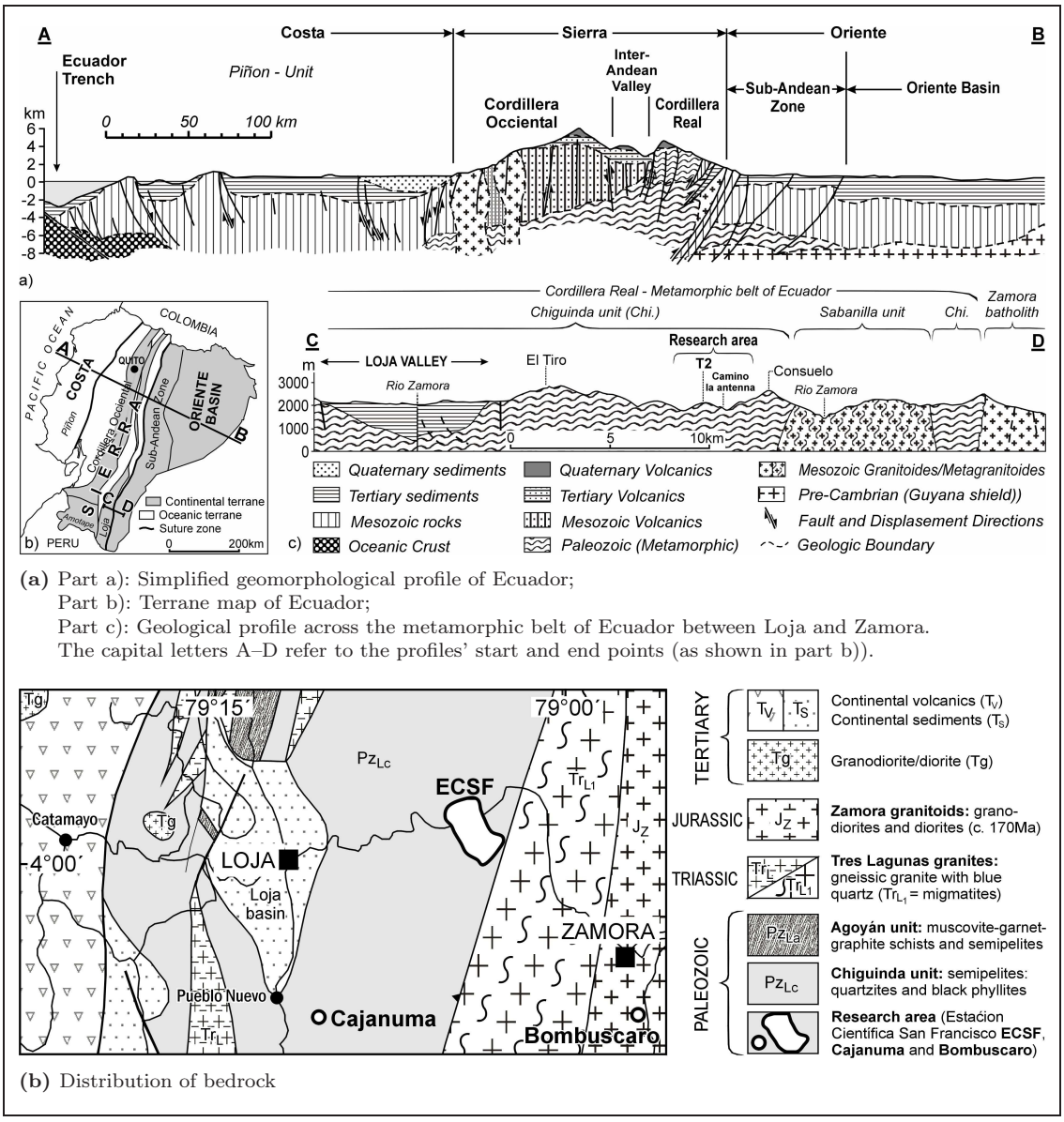
The lower part of the PNP and therefore the two lower plots are located in the Zamora batholith unit which consists of leuco-granidiorites and hornblende granodiorites (Litherland et al., 1994).

2.4. Vegetation

The tropical Andes are characterised by high floral and faunal biodiversity (Myers et al., 2000) as well as high endemism (Mittermeier et al., 1998) and are considered one of the 25 global biodiversity hotspots. Vegetation along the altitudinal range 1 850–2 450 m amsl within the RBSF can be divided into two general types that also change with altitude. There are primary ravine and ridge forests, that differ substantially in their structure (Paulsch, 2002). Ravine forest have higher canopies and diameter at breast height (DBH) than ridge forests that can encounter strong winds and where high radiation input at sunny days can lead to desiccation of the soils. All plots of the presented study were situated closely, but below ridges in the upper part of the slopes.

The genera richest in tree species at RBSF are Euphorbiaceae, Lauraceae, Melastomataceae, and Rubiaceae (Homeier, 2004). Among herbs and shrubs species of Araceae, Asteraceae, Bromeliaceae, Ericaceae, Orchidaceae and Piperaceae account for most of the diversity (Figure 2.5(a) on page 13). Species richness is even higher for mosses and ferns (Homeier, 2004). Figure 2.5(b) on page 13 shows an example of a tree fern. With increasing altitude tree diversity decreases, DBH, tree height and leaf area index (LAI) decrease and the forest canopy becomes more open and trees in general become more stunted, probably due to increased wind speed and depressed nutrient supply (Moser et al., 2007b). At the steep slopes of the investigated area landslides are an inherent factor of vegetation dynamics and increase diversity, as different successional stages exist within short distances (Homeier, 2004). Forest at Cajanuma, the upper part of the PNP, is characterised by stunted stem forms (Paulsch, 2002; Homeier, 2004) and has a maximum height of only 9 m (Moser et al., 2007b). The timberline is situated about 200 to 400 m upslope of the plot, at rather low elevations of 3 200–3 400 m amsl and beyond the timberline patches of alpine páramo can be found (Röderstein et al., 2005). The area there, especially at the mountain ridges is considered pristine, untouched by human influence (Richter, 2004).

The family Melastomataceae was present throughout the whole altitudinal range (Moser et al., 2007b) and also most abundant in the RBSF (Homeier, 2004). Most of the other families showed clear preferences in their altitudinal distribution (Moser et al., 2007b).



(a) Part a): Simplified geomorphological profile of Ecuador;
Part b): Terrane map of Ecuador;
Part c): Geological profile across the metamorphic belt of Ecuador between Loja and Zamora.
The capital letters A–D refer to the profiles' start and end points (as shown in part b)).

(b) Distribution of bedrock

Figure 2.4: Geology of Ecuador and the research area. (© 2005 by F. Haubrich)

2.5. People and human impact

Ecuador counts about 12.4 Mio inhabitants, the main ethnic groups are mestizos (45 %), i. e. people with indigenous and Spanish ancestors, 35 % indigenous, 10 % white and 10 % Afroecuadorians (Auswärtiges Amt, 2005).

In the southern provinces of Ecuador, Loja, El Oro and Zamora-Chinchipe the destruction of natural vegetation and primary forests is considered a general problem. Main actors of this destruction are the so-called campesinos and colonos, population groups that use the areas agriculturally or otherwise to survive but often lack knowledge of ecosystem coherences. Further causes are timber exploitation and uncontrolled fires. Deforestation is proceeding in spite of legal restrictions of timber exploitation (Paulsch, 2002). The most recent land use in the research

(a) Tree ferns and trees covered with bromeliads.

(b) Tree fern in the Rio San Francisco valley.

Figure 2.5: Impression of tropical montane forest.

area began with the construction of the road that connects the province capitals Loja and Zamora in the 1960s (Beck and Müller-Hohenstein, 2001). The construction of these roads directly caused destruction of natural resources, but also indirectly impacts primary forest vegetation as roads facilitate exploitation of valuable timber and tree species in the research area and also at lower altitudes in the Amazonian lowlands (Apolo B., 2002). The land use in the research area along the borders of PNP is characterised by a mosaic of primary forest remnants, forest plantations mostly of *Pinus* spec. and *Eucalyptus* spec., long ago or recently cleared areas, different types of pastures and farmland as well as house gardens (Paulsch et al., 2001; Beck and Müller-Hohenstein, 2001; Pohle, 2004). Landslides and invading ferns (*Pteridium aquilinum* L.) diminish the farmland; some parts are covered by bush vegetation indicating an early stage of succession. Farmland is generally rare; the climatic conditions do not support the cultivation of many crops, especially of the so-called cash crops. The main form of land use in the research area is grazing cattle (Paulsch et al., 2001). Typical land use dynamic is characterised by the burning of primary forest. In some cases single valuable trees are cleared before. Then pasture grasses like *Setaria* spec. and in steeper terrain *Melinis* spec. are planted. Farmers try to inhibit the invasion of ferns by clearing and burning which is counterproductive and favours the even faster invasion of the fern (Figure 2.6 on the following page). Consequently, the land cannot be used as cattle pasture anymore and more primary vegetation will be destroyed. Forest prevails where relief and climate inhibit cattle grazing completely (Paulsch et al., 2001). Primary forest is not considered valuable by the indigenous people (Paulsch et al., 2001; Apolo B., 2002) and if forest is planted, mainly allochthonous and fast-growing tree species are used (Paulsch et al., 2001). Figure 2.7 on the following page illustrates the aforementioned conditions.

Figure 2.6
Pteridium aquilinum L. after pasture burning: the fire destroys the grassroots but not the rhizomes of the fern as they are buried deeper in the soil.

Figure 2.7: View from Cerro de Consuelo: road Loja–Zamora and area north of the road. Smoke plumes indicate fires that are frequent during drier days. Also visible: landslides and small scale vegetation mosaic.

2.6. Detailed description of study sites

The study sites were chosen in accordance with the project "Elevation effects on key processes of carbon cycling in south Ecuadorian mountain forests" led by Prof. Dr. Christoph Leuschner, Department of Ecology and Ecosystem Research, Georg-August-University of Göttingen. This should enable the linking of all collected data in order to thoroughly describe ecosystem functioning along an altitudinal gradient in forests of southern Ecuador. The field work of the co-project was mainly conducted by Gerald Moser who supplied me with data on vegetation and microclimate (see also Moser et al. (2007b)). In the following, I will refer to this data to give a detailed description of the study sites. Furthermore, I will give a description of the soil types that were designated at the study sites. This data was collected in the framework of a Diploma Thesis in the

project "Development of an agroforestry site classification model in the tropical mountain region of southern Ecuador as a basis for sustainable land use planning" by Etienne Bahr at Dresden University of Technology, Institute for Soil Science and Site Ecology.

2.6.1. Plot $P_{1\,050\ m}$

This plot is located close to the eastern border of PNP at S 04°06'54" W 78°58'02" on a lower slope which has an inclination of 26°. The mean annual precipitation (MAP) amounted to approximately 2 230 l m^{-2} during the investigation period (March 2003 to August 2004). The mean annual air temperature (MAT) was 19.4 ℃ and median air humidity 88.7 %. Mean temperature and moisture in the organic layer were 20 ℃ and 9.9 vol%, respectively; in 10 cm mineral soil 19.4 ℃ and 29.7 vol%.

Vegetation at this plot was dominated by trees of the family Myrtaceae, and of the genera *Proteria* (Sapotaceae), *Guatteria* (Annonaceae), *Ficus* (Moraceae) and *Inga* (Mimosaceae). Canopy height was 31.8 m, DBH 17.3 cm and basal area 33.6 $m^2\,ha^{-1}$. Of all study sites, this plot had the highest total biomass that amounted to 317.2 $Mg\,ha^{-1}$. According to a classification of vegetation types of southern Ecuador (Balslev and Øllgaard, 2002), the forest at this site can be considered as "Bosque siempreverde montano bajo", i. e. as evergreen lower mountain forest.

The pH ranged between 4.08 in the upper mineral soil and 4.13 in the lower part of the profile. The actual cation exchange capacity (CEC) was low, decreased from 34.7 μeq (g soil)$^{-1}$ in the Ah-horizon to 22.3 μeq (g soil)$^{-1}$ in the Bv-horizon. Base saturation also was very low and increased from 12.5 % to 19.5 % within the profile. Aluminium saturation was very high and ranged between 78.1 and 84.6 %. Soil texture analysis revealed 49.6 to 53.6 % sand, 13.5 to 15.7 % silt and 30.5 to 35 % clay. According to the World Reference Base for Soil Resources (Food and Agriculture Organization of the United Nations, 1998) this soil was designated as an Alumic Acrisol. We expect that this site was at least slightly influenced by humans as we found small pieces of charcoal and clay shards while excavating the profile. The substrate of pedogenesis might be a mixture of the granodiorite bedrock and colluvial material from upslope. See Figure 2.8(a) on page 17 for a soil profile from $P_{1\,050\ m}$ and Table 2.2 on page 19.

2.6.2. Plot $P_{1\,540\ m}$

The second plot is located upslope of the first at S 04°06'42" W 78° 58'20" and has an inclination of only 10°. MAP reached about 2 300 mm during the period of field work. MAT was 17.5 ℃ and air humidity showed median values of 88.9 %. Mean temperature and moisture in the organic layer were 18.9 ℃ and 12.9 vol%, respectively; in 10 cm mineral soil 18.5 ℃ and 30.3 vol%. At 1 540 m trees of the genera *Axinea* and *Miconia* (Melastomaceae), *Beilschmiedia* (Lauraceae) and *Euterpe* (Arecaceae) dominated species composition. Canopy height was 21.7 m, DBH 11.5 cm and basal area 27.5 $m^2\,ha^{-1}$. Total biomass accounted for 203.8 $Mg\,ha^{-1}$. Vegetation at 1 540 m amsl falls in the same category "Bosque siempreverde montano bajo" as the forest at 1 050 m amsl.

This site is situated on a small plateau and consequently, the soil was less deeply weathered (Figure 2.8(b) on page 17). The soil type at this site can be described by an Ah/E/Cv. Below the eluvial horizon a thin layer of ferrous oxide was visible. CEC, base saturation and aluminium saturation were comparable to the site at 1 050 m: CEC ranged from 19.65 μeq (g soil)$^{-1}$ in the

Cv to 26.4 µeq (g soil)$^{-1}$ in the Ah-horizon. Base saturation was very low in the ferrous oxide band and decreased from the upper part of the profile, 7.5 % in Ah and E-horizon, respectively, to 6.2 % below. Aluminium saturation was more than 90 % in all horizons. Soil pH did not change strongly within the profile and ranged between 4.2 and 4.3. Soil texture was less clayey as at 1 050 m: percentage of sand increased from 60.8 to 71.8 within the profile. The proportion of silt varied little between 20.1 and 25.6 % and the percentage of clay was highest in the top mineral soil (14.7 %). Below, the percentage of clay was almost negligible and ranged between 2.3 and 4.4 % (Table 2.2 on page 19). Due to the low base saturation and high aluminium percentage, this soil type was also classified as Alumic Acrisol.

2.6.3. Plot $P_{1\,890\ m}$

The plot at 1 890 m is located close to the RBSF at S 03°58'345" W 79°04'648" and has an inclination of 31°. MAP amounted to 1 950 mm, MAT was 15.7 °C and air humidity reached 90.7 %. Mean temperature and moisture in the organic layer are 16 °C and 11.6 vol%, respectively in 10 cm mineral soil 16.4 °C and 35.4 vol%. *Graffenrieda* and *Miconia* (Melastomataceae) dominated the stand at 1 890 m; other common genera were *Ocotea* (Lauraceae), *Alchornia* (Euphorbiaceae), *Palicourea* (Rubiacaea) and *Clethra* (Clethraceae). Canopy height was 18.9 m, DBH 12.2 cm and basal area 36.9 m^2 ha^{-1}. Total biomass amounted to 198.8 Mg ha^{-1}. According to the classification of Balslev and Øllgaard (2002) the forest type at 1 890 m is classified as evergreen mountain forest ("Bosque siempreverde montano"). Paulsch (2002) refined existing concepts of vegetation classification in the RBSF. According to him, the stand at 1 890 m can be considered a ravine forest at lower altitudes. The soil type at 1 890 m was classified as Folic Gleysol (Figure 2.9(a) on page 18). In the mineral soil pH increased with soil depth from 4.05 to 4.92. CEC was slightly higher than at lower altitudes and decreased from 60.6 µeq (g soil)$^{-1}$ in the top mineral soil to 15 µeq (g soil)$^{-1}$ in the lower horizons. Base saturation increased from 6.8 to 11.7 % with soil depth. Aluminium saturation was also very high and varied from 85.9 to 89.6 %. Soil texture was dominated by sand and silt (Table 2.2 on page 19).

2.6.4. Plot $P_{2\,380\ m}$

The second plot in the RBSF is located at S 03°59'19" W 79°04'55" at 2 380 m amsl and has an inclination of 28°. During the investigation MAP amounted to 5 000 l m^{-2}, MAT was 13.2 °C and air humidity 93.2 %. Mean temperature and moisture in the organic layer were 14.9 °C and 34 vol%, respectively. The top 10 cm mineral soil were characterised by a temperature of 13.0 °C and soil moisture of 44.7 vol%. Important tree genera at this site were *Purdiaea* (Cyrillaceae), various genera of Melastomataceae, *Podocarpus* (Podocarpaceae), *Ilex* (Aquifoliaceae), *Schefflera* (Araliaceae) and *Clusia* (Clusiaceae). Canopy height was 12 m, DBH 7.4 cm and basal area 27.2 m^2 ha^{-1}. Total biomass was 139.0 Mg ha^{-1}. This stand can be also considered an evergreen mountain forest (Balslev and Øllgaard, 2002). According to Paulsch (2002) the vegetation can be further specified as a microphyll ridge forest.

The soil type at 2 380 m was classified as Haplic Gleysol (Figure 2.9(b) on page 18). In the mineral soil pH varied from 4.07 in the Ahe-horizon to 4.41 and 4.43 in the lower horizons (Sg). CEC was higher than at lower altitudes, changed little between the horizons and ranged between

(a) Soil profile at 1 050 m. **(b)** Shallow soil profile at 1 540 m.

Figure 2.8: Comparison of the soil profiles from plots $P_{1\,050\ m}$ and $P_{1\,540\ m}$.

53.05 and 59.23 µeq (g soil)$^{-1}$. Base saturation was low and varied from 4.3 to 6.8 %. Aluminium saturation was comparable to the other study sites and ranged between 62.0 and 80.7 %. Soil texture was dominated by silt (49.8–55.3 %). Sand and clay accounted for 24.4 to 28.5 % and for 18.8 and 21.6 %, respectively (Table 2.2 on page 19).

2.6.5. Plot $P_{3\,060\ m}$

The highest plot is located at S 04°06'71" W 79°10'581" at an altitude of 3 060 m and has an inclination of 27°. During the investigation period MAP was approximately 4 500 l m^{-2} and MAT 9.4 °C. Air humidity averaged 93.5 %. Mean temperature and moisture in the organic layer accounted for 9.7 °C and 45.3 vol%, respectively. In the top mineral soil mean temperature was 9.8 °C and soil moisture was 49.1 vol%. Abundant tree genera are *Clusia* (Clusiaceae), *Weinmannia* (Cunoniaceae), *Ilex* (Aquifoliaceae), *Faramea* (Rubiaceae), *Hedyosmum* (Chloranthaceae) and various genera of Ericaceae and *Symplocus* (Symplocaceae) (Röderstein et al., 2005; Moser et al., 2007b). DBH was 7.2 cm and basal area 42.2 m^2 ha^{-1}. Total biomass accounted for 174.9 Mg ha^{-1}. Trees were densely covered with mosses and ferns. Paulsch (2002) classified this stand as primary "elfin forest."

The soil type at 3 060 m was classified as a Histic Podzol. Soil pH ranged from 4 to 4.31 in the upper mineral soil horizons. The CEC decreased significantly within the profile from 64.69 to 11.01 µeq (g soil)$^{-1}$. Base saturation was slightly higher than at lower altitudes and varied little from 21.8 to 24.6 %. Aluminium saturation was lower and ranged from 18.1 to 50.2 %. Soil texture was dominated by sand (53.7–72.2 %), silt and clay accounted for 26.5 to 36 % and 0.5 to 10 %, respectively.

All data is summarized in Tables 2.2 to 2.3 on pages 19–20.

(a) Soil profile at 1 890 m. **(b)** Soil profile at 2 380 m. **(c)** Soil profile at 3 060 m.

Figure 2.9: Comparison of the soil profiles from plots $P_{1\,890\ m}$, $P_{2\,380\ m}$ and $P_{3\,060\ m}$.

Table 2.1: Micrometeorological data of the study sites.

plot	location	MAP	MAT	RAH	organic Layer		mineral soil	
		in mm	in °C	in %	T in °C	VWC in vol%	T in°C	VWC in vol%
$P_{1\,050\ m}$	S 04°06'54" W 78°58'02"	2 230	19.4	88.7	20.0	9.9	19.4	29.7
$P_{1\,540\ m}$	S 04°06'42" W 78°58'20"	2 300	17.5	88.9	18.9	12.9	18.5	30.3
$P_{1\,890\ m}$	S 03°58'35" W 79°04'65"	1 950	15.7	90.7	16.0	11.6	16.4	35.4
$P_{2\,380\ m}$	S 03°59'19" W 79°04'55"	5 000	13.2	93.2	14.9	34.0	13.0	44.7
$P_{3\,060\ m}$	S 04°06'71" W 79°10'58"	4 500	9.4	93.5	9.7	45.3	9.8	49.1

Data collected by G. Moser, Georg-August-University of Göttingen.

MAP = mean annual precipitation; MAT = mean annual air temperature;

RAH = relative air humidity

VWC = volumetric water content

Table 2.2: Basic soil characteristics of the study sites.

horizon	**pH**	**CEC**	**base saturation**	**Al saturation**	**texture** in %		
		in µeq (g soil)$^{-1}$	in %	in %	sand	silt	clay
			$P_{1\,050\ m}$				
Oi	5.2	n/d	n/d	n/d	n/d	n/d	n/d
OeOa	4.0	n/d	n/d	n/d	n/d	n/d	n/d
Ah	4.1	34.7	12.5	84.6	53.6	15.7	30.5
Ah–Bv	4.1	26.0	16.9	80.1	49.6	15.3	35.0
Bv	4.1	22.3	19.5	78.1	53.6	13.5	32.9
			$P_{1\,540\ m}$				
Oi	5.1	281.5	0.2	91.1	n/d	n/d	n/d
OeOa	3.9	189.0	18.7	26.6	n/d	n/d	n/d
Ah	4.3	26.4	7.5	91.7	60.8	24.2	14.7
E	4.3	23.3	7.5	90.6	70.7	24.6	4.4
Fe oxide	4.2	22.3	3.8	93.9	76.2	20.1	3.2
Cv	4.2	19.7	6.2	90.9	71.8	25.6	2.3
			$P_{1\,890\ m}$				
Oi	5.6	427.5	91.6	0.6	n/d	n/d	n/d
OeOa	4.2	195.7	59.7	5.2	n/d	n/d	n/d
Ah	4.0	60.6	6.8	85.9	41.7	38.3	19.0
Ah-B1	4.8	32.6	7.7	89.6	44.0	41.5	14.4
B1	4.9	15.0	11.7	86.2	57.9	31.1	9.4
			$P_{2\,380\ m}$				
Oi	5.4	405.6	94.1	2.3	n/d	n/d	n/d
OeOa	4.0	221.4	38.2	41.2	n/d	n/d	n/d
Ahe	4.1	58.2	6.8	62.0	28.5	49.8	21.6
B1 upper	4.4	53.1	4.3	80.7	27.5	52.7	18.8
B1 lower	4.4	59.2	4.9	80.5	24.4	55.3	19.6
			$P_{3\,060\ m}$				
Oi	5.4	361.5	94.0	0.7	n/d	n/d	n/d
OeOa	4.2	282.2	64.2	14.5	n/d	n/d	n/d
Ah	4.0	64.7	22.7	23.8	53.7	36.0	10.0
Ah-E	4.3	13.3	24.6	18.9	71.6	27.4	0.8
E	4.2	11.0	21.8	50.2	72.2	26.5	0.5
Bh	n/d	n/d	n/d	n/d	n/d	n/d	n/d
Bs	n/d	n/d	n/d	n/d	n/d	n/d	n/d

All texture data/all data from plots $P_{1\,890\ m}$–$P_{3\,060\ m}$ collected by E. Bahr,

Dresden University of Technology.

CEC = actual cation exchange capacity

Table 2.3: Vegetation characteristics of the study sites.

plot	H_c in m	basal area in $m^2\,ha^{-1}$	DBH in cm	LAI in $m^2\,m^{-2}$	Σ biomass in $Mg\,ha^{-1}$
$P_{1\,050\ m}$	31.8	33.6	17.3	5.1	317.2
$P_{1\,540\ m}$	21.7	27.5	11.5	4.6	203.8
$P_{1\,890\ m}$	18.9	36.9	12.2	3.9	198.8
$P_{2\,380\ m}$	12.0	27.2	9.8	3.6	139.0
$P_{3\,060\ m}$	9.0	42.2	7.2	2.9	174.9

Data collected by G. Moser, Georg-August-University of Göttingen.

H_c = canopy height; DBH = diameter at breast height; LAI = leaf area index; Σ biomass = Sum of above- and below-ground biomass

Chapter 3

Material and methods

3.1. Soil sampling and sample preparation

Sampling of mineral soil and organic layers was done at different dates throughout the period of field work from July 2003 to Mai 2005. In order to ensure immediate transport and fast processing, soil samples were taken separately for different analysis as described below and summarized in Table 3.1. This approach resulted in major constraints regarding the possibilities of statistical analysis that will be discussed in the section 3.6 on page 33.

For general description of carbon pools and detection of seasonal influences on these the five described plots were sampled representatively once during the wetter (April 2004, precipitation approximately 250 mm) and once during the drier season (November 2004, precipitation approx-

Table 3.1: Sampling dates.

date	**purpose**[a]	**sample size**[b]	**plots**	**analysis runs**[c]
Apr. 2004	TOC, TN, HWC, HWN, all KCl-extractable fractions, C_{mic}, N_{mic}	18 ➠ 6 per plot + horizon	all	2
Nov. 2004	HWC, HWN, all KCl-extractable fractions, C_{mic}, N_{mic}	18 ➠ 6 per plot + horizon	all	2
May 2005	net nitrogen mineralisation	18 ➠ 3 per plot + horizon	all	3
Nov. 2005	gross nitrogen mineralisation	18 ➠ 3 per plot + horizon	$P_{1\,050,\ 1\,980,\ 3\,060\ m}$	2
Nov. 2005	microbial community structure	18 ➠ 1 per plot + horizon	$P_{1\,050,\ 1\,980,\ 3\,060\ m}$	1

[a] See list of abbreviations and respective sections for explanation.

[b] The ➠ indicates a pooling of the 18 individual samples to the specified number of mixed samples.

[c] Some plot samples were analysed more than once. Results were averaged.

imately 100 mm) of the year. At each plot 18 samples were taken; organic layer horizons were sampled using a 20×20 cm wooden frame, which equals an area of 400 cm^2. The two organic layer horizons separated during soil sampling were designated as Oi and OeOa. The former included mainly recently shed litter but also organic material that was initially reduced to small pieces, but whose structure was still completely discernable. The latter horizon consisted mainly of strongly decomposed material whose structure was no longer discernible. This horizon was of a brownish colour and showed highest fine root densities within the soil profile. Within this dense root mat small aggregates of humic matter could be detected, but they seldom formed a discernible horizon. Thus, an Oa horizon was not sampled separately.

Mineral soil was sampled to a depth of 10 cm using a soil auger of 10 cm in diameter, which equals a volume of 785.4 cm^3. For each horizon and plot six composite samples were assembled from three individual samples. These composite samples were subject to further analysis. During soil sampling organic layer thickness was determined at each sampling point. Samples were transported in polyethylene (PE) bags to the laboratory of the ECSF and weighed for determination of stocks. Samples were then homogenized by hand, which involved cutting of the litter layer in approximately 1×1 cm pieces. Stones, coarse woody debris and roots were removed carefully. Then, samples were transported to Germany via airplane within one week and immediately processed in the laboratories of the Institute for Soil Science and Site Ecology of Dresden University of Technology. During transport samples were cooled to approximately 10 °C and it was taken care of that the temperature of the samples did not rise above average temperatures in the investigated soils. Also, samples were not frozen as we expected the impact of such treatment on tropical microbial communities to be more severe than storing them cooled for several days.

3.2. Physical and chemical soil parameters

3.2.1. Dry matter and bulk density

Dry matter was determined gravimetrically for all samples. An aliquot of 10 g was dried at 105 °C to a constant weight. Percentage of dry mass $\%m_{\mathrm{dry}}$ in % was calculated as follows:

$$\%m_{\mathrm{dry}} = m_{\mathrm{d}} \cdot {m_{\mathrm{m}}}^{-1} \cdot 100\% \tag{3.1}$$

with

- m_{d} ▷ mass of dry soil in g
- m_{m} ▷ mass of moist soil in g.

Dry bulk weight $m_{\mathrm{bulk(org)}}$ was calculated for organic layer horizons as follows:

$$m_{\mathrm{bulk(org)}} = m_{\mathrm{s}} \cdot \frac{\%m_{\mathrm{dry}}}{100} \cdot \frac{1}{400\ \mathrm{cm}^2}, \tag{3.2}$$

whereas dry bulk density $\rho_{\text{bulk(min)}}$ was calculated by:

$$\rho_{\text{bulk(min)}} = m_{\text{s}} \cdot \frac{\%m_{\text{dry}}}{100} \cdot \frac{1}{785.4\ \text{cm}^3} \tag{3.3}$$

with

$m_{\text{bulk(org)}}$ ▷ dry bulk density for organic layer horizons in $\text{g}\,\text{cm}^{-2}$
$\rho_{\text{bulk(min)}}$ ▷ dry bulk density for mineral soil in $\text{g}\,\text{cm}^{-3}$
m_{s} ▷ sample weight in g.

3.2.2. Soil acidity $\text{pH}_{\text{H}_2\text{O}}$

Acidity of organic layers and mineral soil was determined electrometrically using a glass electrode (pH-Meter 220, Mettler-Toledo) in deionized water after 4 hours of equilibration of the suspensions. Soil-solution ratio was 1 : 20 for organic layer samples and 1 : 2.5 for mineral soil samples.

3.3. Selected carbon and nitrogen pools

3.3.1. Soil organic carbon and total nitrogen

According to basic rock and reported pH for the investigated area (Wilcke et al., 2002) carbonate content of the studied soils is assumed to be negligibly low. Thus, the designation soil organic carbon (SOC) refers to total organic carbon. For determination of SOC and total nitrogen (TN) an aliquot of each sample was dried (40 ℃ mineral soil; 60 ℃ organic layer) and milled (vibratory disc mill RS 100, Retsch, Germany). Organic layer samples were milled at 700 rpm for 45 seconds and mineral soil samples at 1 400 rpm for 60 seconds. After milling samples were again dried overnight at 40 ℃. SOC and TN were determined after complete dry combustion (CNS-Analyzer vario EL III/elementar, Heraeus) at 1 150 ℃ by a thermal conductivity detector and calculated internally on the basis of the weight of the analyzed aliquot.

Stocks of SOC and TN (in $\text{kg}\,\text{ha}^{-1}$) were calculated based upon average contents for each plot and horizon (content_i in $\mu\text{g}\,(\text{g dry matter})^{-1}$) as follows:

- for organic layer stocks:

$$\text{stock} = \text{content}_i \cdot m_{\text{bulk(org)}} \cdot 0.1, \tag{3.4}$$

- for mineral horizons stocks are related to 10 cm sampling depth each:

$$\text{stock} = \text{content}_i \cdot \rho_{\text{bulk(min)}}. \tag{3.5}$$

3.3.2. Total hot-water extractable organic carbon and nitrogen

For determination of hot water extractable carbon and nitrogen two aliquots of each sample (10 g of mineral soil; 5 g of organic layer) were transferred to 250 ml round-bottomed flasks.

After adding 100 ml deionized water the suspension was boiled for 60 minutes using a reflux condenser. After boiling flasks were immediately closed and cooled to room temperature. Then 2 ml 2 M $MgSO_4$ were added to the suspensions to support sedimentation of the soil particles during centrifugation for 10 minutes at 4 000 rpm at 24 ℃. In the decanted extracts carbon and nitrogen concentrations in $g\,ml^{-1}$ were determined immediately by a CN-analyzer (Multi-NC, Jena Analytik, Germany) by oxidizing organic compounds in the extract at 850 ℃ with oxygen to CO_2 and NO/NO_2. CO_2 is determined at a thermal conductivity detector and NO/NO_2 is determined using a chemoluminescence detector. Contents w in $\mu g\,(g\ dry\ matter)^{-1}$ of total hot-water extractable organic carbon (HWC) and total hot-water extractable nitrogen (HWN) were calculated as follows:

$$w = c \cdot \mathrm{CF} \cdot 100 \cdot \%m_{\mathrm{dry}}{}^{-1} \tag{3.6}$$

with

c ▷ concentration in $mg\,l^{-1}$

CF ▷ concentration factor.

The concentration factor CF is defined as the ratio of the volume of the extraction solution V_{ES} in ml added and the weight of the analyzed aliquot m_{a} in g:

$$\mathrm{CF} = \frac{V_{\mathrm{ES}}}{m_{\mathrm{a}}}.$$

3.3.3. Total KCl-extractable organic carbon and nitrogen fractions

Two aliquots of each sample (10 g of mineral soil; 5 g of organic layer) were transferred in 250 ml PE-bottles. After adding of 100 ml of 0.1 M KCl-solution, bottles were closed tightly and shaken for two hours (180 rpm). Suspensions were then filtered through N-free folded filters (grade 292, 240 mm diameter; Munktell & Filtrak), the first millilitres of the filtrate were rejected. Concentrations of total dissolved nitrogen (total KCl-extractable nitrogen (TN_{KCl})) and carbon were determined at a CN-analyzer (Multi-NC, Jena Analytik, Germany) as described above in section (section 3.3.2 on the previous page). Concentrations of ammonia (NH_4^+-N) and nitrate derived nitrogen (NO_3^--N) were determined photometrically at $\lambda = 540$ nm and $\lambda = 660$ nm, respectively at a continuous flow autoanalyzer (Skalar Analytik GmbH, Germany). The total KCl-extractable inorganic nitrogen ($TN_{KCl(inorg)}$) was calculated as the sum of ammonium derived nitrogen (NH_4^+-N) and nitrate derived nitrogen (NO_3^--N). Nitrite was not considered separately but was included in the nitrate fraction. The total KCl-extractable organic nitrogen ($TN_{KCl(org)}$) was calculated as the difference between TN_{KCl} and $TN_{KCl(inorg)}$. NH_4^+-N and NO_3^--N concentrations (in $mg\,l^{-1}$) were converted into contents ($\mu g\,g^{-1}$) as described in Equation 3.6.

3.4. Nitrogen mineralisation potentials

3.4.1. Net nitrogen mineralisation

Net nitrogen mineralisation was investigated by determining TN, $TN_{KCl(org)}$ and $TN_{KCl(inorg)}$ after 0, 1, 4, 7 and 14 days of incubation. In total 15 aliquots of each field moist sample were incubated in 100 ml PE-bottles at 25 ℃ in the dark. Bottles were sealed with perforated parafilm to keep the samples moist but well aerated. After each incubation period nitrogen fractions in three aliquots of the same sample were determined as described in section 3.3.3 on the facing page. Net mineralisation rates in $\mu g\, g^{-1}\, d^{-1}$ were calculated for each incubation time:

$$\text{Net N mineralisation} = TN_{min(t+1)} - TN_{min(t)}. \tag{3.7}$$

3.4.2. Gross nitrogen mineralisation

Gross nitrogen mineralisation was estimated using the ^{15}N isotopic pool dilution approach. Here, the ammonium (NH_4^+) pool is labelled by adding small amounts of $^{15}NH_4^+$ to the soils studied. As the ammonium pool does not constitute a substrate but a mineralisation product pool, priming effects or stimulation of microbial activity and therefore mineralisation is not expected (Hart et al., 1994). Consequently, the rate at which the isotopic enrichment in the ammonium pool declines can be monitored and is a reliable measure for gross N mineralisation. The determination of gross mineralisation involved two general steps. First, ammonium and nitrate were determined quantitatively as described in section 3.3.3 on the facing page. Secondly, the ^{15}N ratios of these two fractions were determined applying the diffusion method. Gross N mineralisation rate is calculated from

1. the rate of dilution in the ^{15}N enrichment of the NH_4^+ pool as mineralised $^{14}NH_4^+$ enters the pool, and

2. the change in the overall NH_4^+ pool size.

The diffusion method itself is based on the following principle: Ammonium sulphate solution, containing 1.5 atom% $^{15}N{-}NH_4^+$ is thoroughly mixed into 20 g of field-moist sample. 2 µg labelled N per mg N were added as 5 ml ammonium sulphate solution to the respective sample. The small amount was chosen to avoid strong alternation of moisture conditions in the samples. One set of labelled samples is incubated for 1 hour; a second set is incubated for 24 hours at 20 ℃ in airtight glass bottles (500 ml, Schott Duran® Germany). After incubation, NH_4^+ and nitrate (NO_3^-) were determined following the KCl-extraction procedure as described in section 3.3.3 on the facing page; the soil : solution ratio for organic layer horizons was 1 : 10 and for mineral soils 1 : 5. An aliquot of the extracts was transferred to clean airtight glass bottles (500 ml, Schott Duran® Germany). The size of the aliquot depended on the NH_4^+ and NO_3^- concentration of the extract and contained between 25 and 100 µg N in total as the mass spectrometer for $^{15}N : {}^{14}N$ isotope ratio analysis is calibrated for this range. If the concentrations of NH_4^+ and NO_3^- differed strongly, the isotope ratio was analyzed separately for NH_4^+ and NO_3^-. For determination of NH_4^+ the sample solution was adjusted to 2 *M* KCl concentration and 0.2 g MgO were added for alkalinisation. After adding the prepared diffusion filter, bottles were immediately closed and shaken for 72 hours at 90 rpm.

Then, diffusion filters were removed and $^{15}NH_4^+$ content of the filter was determined at the mass spectrometer. Diffusion filters were prepared by cleaning N-free glass fibre prefilters (Sartorius) in diluted hydrochloric acid and subsequently in deionised water. Filters were dried over sulphuric acid in a desiccator. Small filter discs were then acidified with 5 µl 2.5 *M* $KHSO_4$ and wrapped into polytetrafluorethylen (PTFE) tape. This tape allowed diffusion of ammonia (NH_3) to the filter disc but prevented wetting of the filter, as the wet material could not absorb NH_3.

NH_4^+ in the extract reacted with magnesium oxide (MgO) to NH_3, which formed $K(NH_4)SO_4$ with the potassium hydrogen sulphate that was added to the filter disc.

Reaction in the extracted solution: $NH_4^+\text{-}N + MgO \longrightarrow NH_3$
Reaction in the filter: $NH_3 + KHSO_4 \longrightarrow K(NH_4)SO_4$

Each filter absorbs an amount of NH_3 equivalent to 120 µg NH_4^+. As this is the maximum amount one filter can absorb, in the present study per 50 µg N in the solution one filter was added. If the concentration of NH_4^+ is much higher than NO_3^- all NH_4^+ has to be removed from the sample solutions by adding an equivalent number of diffusion filters and treating the samples as described above for determination of NO_3^-. If NH_4^+ and NO_3^- concentrations were similar the same sample can be used for both determinations. For NO_3^- determination 0.4 g of Devarda's alloy (51 % Cu, 44 % Al, 2.9 % Zn) and a prepared diffusion filter were added to the sample solution. Again, samples were shaken for 72 hours at 90 rpm. Diffusion of NO_3^- into the filter occurs according to the following formulae:

Solution: $NO_3^- + MgO + \text{Devarda's alloy} \longrightarrow NH_4^+ \longrightarrow NH_3$
Filter: $NH_3 + KHSO_4 \longrightarrow K(NH_4)SO_4$

The $^{14}N : {}^{15}N$ ratio was determined by mass spectrometry and expressed as ^{15}N atom% (Delta Plus, Finnigan MAT, Germany). Gross mineralisation rate was calculated according to Barraclough (1995) and Smithwick et al. (2005).

Measured ^{15}N atom% were corrected by the ^{15}N contamination of the extraction solution as follows:

$$^{15}\text{N atom\%}_{\text{corr}} = ((^{15}\text{N}_{\text{m}} \cdot (x + \text{cont})) - (0.36978 \cdot \text{cont})) \cdot x^{-1} \tag{3.8}$$

with

^{15}N atom%$_{\text{corr}}$	▷	corrected ^{15}N content in atom% after 1 and 24 h of incubation, resp.
$^{15}N_{\text{m}}$	▷	measured ^{15}N content in atom% after 1 and 24 h of incubation, resp.
x	▷	NH_4^+ concentration in mg l^{-1} in the KCl-extract after addition of labelled ammonium sulphate and 1 and 24 h of incubation, resp.
cont	▷	contamination of extraction solution in mg l^{-1}, results from size of analyzed aliquot in ml $\cdot$ 0.0003 $\cdot$ 1 000 in mg l^{-1}
0.36978	▷	^{15}N content in atom% of extraction solution.

Excess of ^{15}N in the ammonium pool after 1 (APE_1) and 24 h of incubation (APE_{24}) was calculated in atom% as follows:

$$APE_{1;24} = {}^{15}N\ \text{atom}\%_{\text{corr}\,1;24} - 0.3663 \tag{3.9}$$

Gross rates of mineralisation (m in $mg\,kg^{-1}\,d^{-1}$) were calculated as follows:

$$M = (x_1 - x_{24}) \cdot t^{-1} \cdot (\log(APE_1/APE_{24}) \cdot (\log(x_1/x_{24})))^{-1}. \tag{3.10}$$

The NH_4^+-N consumption rate of soil (c in $mg\,kg^{-1}\,d^{-1}$) was calculated as:

$$c = m - (x_{24} - x_1) \cdot t^{-1} \tag{3.11}$$

with

$x_{1;24}$ ▷ total ammonium derived nitrogen in $\mu g\,g^{-1}$ in the soil after addition of labelled ammonium sulphate and 1 and 24 h of incubation, resp.

t ▷ time of incubation in days.

3.5. Size, structure and activity of microbial biomass

3.5.1. Microbial biomass carbon and nitrogen

Microbial biomass was determined by the Chloroform-Fumigation-Extraction method according to Vance et al. (1987). Of each sample a set of two aliquots was weighed into 250 ml PE-bottles (5 g organic layer samples; 25 g mineral soil samples), suspended in 100 ml 0.5 M K_2SO_4 and shaken for 30 minutes at 180 rpm. Suspensions were then filtered (folded filters, 240 mm diameter, grade $589/3\frac{1}{2}$; Schleicher & Schuell) and concentrations of dissolved carbon and nitrogen in the filtrates were determined immediately at a CN-analyzer (Multi-NC, Jena Analytik, Germany; see section 3.3.2 on page 23). A second set of two aliquots was weighed into 50 ml beakers. Samples were placed in a desiccator together with a beaker containing 30 ml of ethanol-free chloroform. The desiccator then was evacuated until the chloroform had boiled for 2 minutes for evenly dispersing the chloroform and samples were fumigated for 24 hours at 20 °C in the dark. After fumigation, the beaker with chloroform was taken out and the desiccator evacuated three times for 5 minutes in order to completely remove the chloroform from the samples. Samples were then transferred into PE-bottles and treated as the non-fumigated samples.

Contents of microbial biomass carbon (C_{mic}) in $\mu g\,g^{-1}$ were calculated as follows:

$$C_{mic} = (c_{C(F)} - c_{C(NF)}) \cdot CF \cdot 100 \cdot \%m_{dry}{}^{-1} \cdot k_{EC}{}^{-1} \tag{3.12}$$

with

$c_{C(F)}$ ▷ concentration of dissolved carbon in extract of fumigated sample in $mg\,l^{-1}$

$c_{C(NF)}$ ▷ concentration of dissolved carbon in extract of non-fumigated sample in $mg\,l^{-1}$

k_{EC} ▷ factor for biomass carbon; here: 0.43 (Martens, 1995).

Contents of microbial biomass nitrogen (N_{mic}) in $\mu g\,g^{-1}$ were calculated accordingly to Equation 3.12 on the previous page:

$$N_{mic} = (c_{N(F)} - c_{N(NF)}) \cdot CF \cdot 100 \cdot \%m_{dry}{}^{-1} \cdot k_{EN}{}^{-1} \tag{3.13}$$

with

$c_{N(F)}$ ▷ concentration of dissolved nitrogen in extract of fumigated sample in $mg\,l^{-1}$

$c_{N(NF)}$ ▷ concentration of dissolved nitrogen in extract of non-fumigated sample in $mg\,l^{-1}$

k_{EN} ▷ factor for biomass nitrogen; here: 0.45 (Jenkinson et al., 2004).

3.5.2. Microbial community structure

3.5.2.1. General aspects

The taxonomic structure of the microbial community was determined by analysing the abundance of phospholipid fatty acids (PLFAs). PLFA analysis uses cell membrane lipids, i. e. structural components of living organisms, as biomarkers for specific groups of organisms and thereby provides a kind of fingerprint of the microbial community (Steenwerth et al., 2002). This analysis does not provide information on the species level, but gives an indication of large taxonomic groups like Gram positive and Gram negative bacteria, actinomycetes and fungi. Phospholipids are rapidly depolymerised upon cell death by enzymes and therefore a reliable measure of viable microbial community composition (Peacock et al., 2001). The function of PLFAs in the cell includes maintenance of nutrient transport and elimination of metabolic products (Ponder Jr and Tadros, 2002).

3.5.2.2. Method

PLFAs were analysed as described by Hamer et al. (2007). In short, all lipids were extracted from 25 g of the respective soil sample, using 237.5 ml of a one-phase mixture of chloroform, methanol and phosphate buffer (1 : 2 : 0.8). The suspension was shaken for two hours at 180 rpm. After 24 hours of resting the $CHCl_3$-phase had separated from the lipid phase and was decanted and evaporated using a rotary evaporator. The lipids in the remaining phase were then separated in neutral, glyco- and phospholipids on a silic acid column (2 g/12 ml, Varian). Subsequently, phospholipids were subjected to mild alkaline methanolysis which separated unsubstituted fatty acid methyl esters (FAMEs) from the hydroxyl substituted ones and the unsaponifiable lipids. FAMEs were further separated according to their degree of saturation. Saturated (SATFAs), mono- (MUFAs) and polyunsaturated (PUFAs) fatty acids were analysed separately in a gas chromatograph with a flame ionisation detector (GC 2010 Shimadzu) after dissolution of the

three fractions in isooctane containing methyl-nonadecanoate (19:0, Sigma-Aldrich). FAMEs were separated in a polar column (BPX 70, 0.25 µm film, 30 m × 0.25 mm, SGE). Peaks were identified by comparison of retention times with different standards (bacterial acid methyl ester (BAME) and FAME mix, 10Me16:0, Sigma-Aldrich).

3.5.2.3. Nomenclature

The fatty acids were designated according to the nomenclature given by RATLEDGE and WILKINSIN (1988) as follows: [total number of carbon atoms] : [number of double bonds], followed by the position (n) of the double bond from the methyl end of the molecule. The type of branching is identified by a (anteiso), i (iso) and cy (cyclopropyl) branching. A methyl branching at the 10^{th} C atom from the carboxyl end is indicated by 10Me. *Cis* and *trans* configurations are indicated by the suffixes c and t, respectively.

3.5.2.4. Calculation

In a first step concentrations of identified PLFAs (c_{PLFA_i}) in µg in the respective sample were calculated as follows:

$$c_{\text{PLFA}_i} = 0.025\ \mu\text{g} \cdot (\text{Area}19:0 \cdot \text{Area}_i)^{-1} \tag{3.14}$$

and corrected by the blank value of the respective peak. The 0.025 µg is the mass of the added standard 19:0. Area_i refers to the integral underneath the peak of PLFA i, whereas $\text{Area}19:0$ is the same below the peak of the standard 19:0.

Secondly, concentrations were converted into contents w_{PLFA_i} (in $\text{nmol}\,\text{g}^{-1}$) as follows:

$$w_{\text{PLFA}_i} = c_{\text{PLFA}_i} \cdot M^{-1} \cdot 1000 \cdot 100 \cdot \text{DS}_i{}^{-1}$$

with

M ▷ molar mass of PLFA i in $\text{g}\,\text{mol}^{-1}$

DS_i ▷ dry weight of analysed sample i in g.

PLFAs were grouped to larger taxonomic units by summing the respective PLFA contents in $\text{nmol}\,\text{g}^{-1}$. Gram positive bacteria included the PLFAs i15:0, a15:0, i16:0 and i17:0. Gram negative included 16:1n7c, cy17:0, 17:1n7c, 18:1n9c, 18:1n7c and cy19:0. Abundance of actinomycetes was indicated by the sum of 10Me16:0 and 10Me18:0. PLFAs 18:2n6,9c and 18:3n6,9,12c are indicators for fungi (PONDER JR and TADROS, 2002; KLAMER and BÅÅTH, 2004).

3.5.3. Total soil respiration

Soil respiration is defined as the total efflux of CO_2 from different sources in the soil to the atmosphere. This process is mainly controlled by the concentration gradient that builds up between air filled pore space (CO_2 partial pressure in the soil 0.2–0.7 kPa) in the soil and the atmosphere (CO_2 partial pressure 0.035 kPa) and diffusion processes. Total soil CO_2 efflux was measured fortnightly at all described plots from July 2003 to September 2004. After this period plots at 1 540 m and 2 380 m were excluded from measurements due to their unfavourable accessibility.

Further constraints of these two plots, especially the one at 1 540 m, will be discussed later. At 1 050 m, 1 890 m and 3 060 m measurements continued until August 2005.

At each plot 16 PE-collars of 5 cm height and 10 cm in diameter were installed randomly and continuously during the respective period of investigation by inserting them approximately 2.5 cm into the organic layer. It was taken care of placing them at least 3 m from big trees, any paths and well frequented spots inside the plots. Furthermore, collars were not placed above coarse roots or cavities in the organic layer. PE-collars were installed one week before the first measurement to guarantee stabilisation of fluxes prior to measurements. Total soil respiration data was collected using a portable closed chamber (SRC-1) connected to an infra red gas analyzer (environmental gas monitor (EGM)-4; both by PP Systems Hitchin, Hertfordshire UK). This system determined CO_2 concentration in the chamber headspace every 4.8 seconds during two minutes or until a concentration change of 100 ppm had occurred. CO_2 emerging from the soil was drawn from the closed chamber by a slowly rotating fan, led into the infra red gas analyzer and back into the chamber. CO_2 strongly absorbs photons in the range of 4.26 µm. The infra red gas analyzer contains a light source emitting at this wave length and a sensor that is sensitive to photons at this wave length. As CO_2 from the closed chamber passes through this sample cell, it reduces the sensor reading. CO_2 concentration is calculated internally from this reduction. The rate of soil CO_2 efflux is calculated internally using a quadratic fitting by plotting the rate of change of the chamber CO_2 concentration. Soil CO_2 efflux was displayed as g CO_2 $m^{-2}\,h^{-1}$.

Due to the high air humidity at all plots, the risk of water vapour condensation inside the analyzer and consequently damage of the system was high. To prevent any damage, an additional tube filled with self-indicating calcium sulphate that absorbed water vapour from the sampled air, was interposed between chamber and analyzer according to the recommendations of the manufacturer of the EGM-4. After switching the system on, it calibrated itself according to ambient air temperature that was entered manually. Furthermore, the system ran a calibration about every 8 minutes. Before each measurement the chamber CO_2 concentration was reduced to ambient air level. A general constraint of closed chamber measurements is the possible underestimation of soil CO_2 efflux which occurs if the concentration in the chamber increases to a point were it substantially alters the concentration gradient between soil and atmosphere, which drives soil CO_2 efflux (Davidson et al., 2002). To overcome this constraint, the system displays an error message if the fitting of the consecutive concentrations of one measurement is not linear, i. e. if the concentration gradient and therefore the soil CO_2 efflux are altered. If the error message was displayed, data was rejected and the measurement repeated. For each measurement, the chamber was placed airtight on the PE-collars and it was taken care not to compact the organic layer around the collar in order not to press CO_2 out of the air filled spaces within the organic layer thus causing a CO_2 flush and overestimation of the flux. For each measurement soil temperature was determined using a sensor directly connected to the EGM-4. Furthermore, soil moisture was determined as volumetric water content (VWC) three times for each soil CO_2 efflux measurement using a handheld sensor (Theta Probe ML2, Delta T Devices Ltd. UK). Soil CO_2 and soil temperature data was logged by the EGM-4 and later downloaded to a PC using software provided by PP Systems. In the following I will refer to total soil CO_2 efflux as total soil respiration (TSR). TSR was determined independently of the prevailing weather conditions as according to observations of Lee et al. (2004) fine-weather observations cannot define the realisable respiration potential

of a soil. Annual carbon efflux in $Mg\,C\,ha^{-1}\,a^{-1}$ from the soil was calculated as follows:

$$\text{Annual carbon efflux} = \text{median TSR} \cdot 8\,760 \cdot 0.2729 \tag{3.15}$$

with

Median TSR	▷	in $g\,CO_2\,m^{-2}\,h^{-1}$
8 760	▷	24 hours · 365 days
0.2729	▷	conversion factor of 1 mg CO_2 in mg CO_2-C.

3.5.4. Diurnal soil CO_2 flux

Due to working routine and long distances to the plots TSR measurements were usually taken at more or less the same time of the day. To evaluate if this gives major bias and to give better estimations of annual CO_2 fluxes, diurnal courses of TSR were observed. For these measurements I chose the plots $P_{1\,050\,m}$, $P_{1\,890\,m}$ and $P_{3\,060\,m}$ due to their favourable accessibility even during night time. In November 2003 preliminary soil respiration data was analyzed, the overall median and the median for each measurement point were calculated. Then three measurement points were selected; one that represented an average value close to the overall median, as well as for maximum and minimum effluxes each to cover the whole range of soil CO_2 efflux at the respective plot. In November 2003 at each of these plots soil CO_2 efflux, soil temperature and VWC at the three selected points were measured hourly for 24 hours.

3.5.5. Heterotrophic soil respiration and root contribution to total soil respiration

The contribution of roots to total soil respiration was determined using the root exclusion method at $P_{1\,890\,m}$ from February 2004 to August 2005 (this plot was installed earlier for a pilot experiment) and at the plots $P_{1\,050\,m}$ and $P_{3\,060\,m}$ from September 2004 until August 2005. At each plot eight 50×50 cm subplots were established by trenching the soil along the sides of the subplots to a depth of 50 cm. Regrowth of roots into the subplots was prevented by inserting double polyethylene sheets along the sides of the subplot and refilling the trenches. At each subplot two collars were installed accordingly to TSR measurements. As control TSR measurements at the same altitudes were used. After exclusion of roots, partitioned soil CO_2 efflux (R_H) corresponds to heterotrophic respiration and was measured at the same dates and within two hours time as TSR at the respective plots. The root contribution (RC%) was calculated for the complete measurement period as the difference between TSR and R_H. It was taken into account that trenching kills roots that provide easily decomposable substrate for decomposers which might enhance R_H and lead to overestimation of heterotrophic respiration. Annual partitioned carbon efflux was calculated accordingly to annual total carbon efflux.

$$\text{RC\%} = (R_H - \text{root carbon}) \cdot \text{TSR}^{-1} \cdot 100 \tag{3.16}$$

with

TSR ▷ annual carbon efflux in g CO_2-C $m^{-2}\,a^{-1}$

R_H ▷ annual partitioned carbon efflux in g CO_2-C $m^{-2}\,a^{-1}$.

For evaluation of the gained data, soil samples were taken from the trenched plots at the end of the experiment. For sampling a soil auger of 35 mm in diameter was used, soil was sampled to a depth of 50 cm. Each sample was weighed and washed on a metal sieve of 250 µm mesh size. All fine root fragments (diameter $\leq$ 2 mm; length $\geq$ 10 mm) were extracted, and living roots were separated from root necromass as described by Röderstein et al. (2005). Then all samples were dried for 48 h at 70 ℃ and weighed.

Root carbon was calculated based on fine root decomposition and fine root carbon data of the investigated plots provided by Gerald Moser, University of Göttingen (see chapter 2 on page 7):

$$\begin{aligned}\text{root carbon} = {} & (\text{amount of roots decomposed during } R_H \text{ measurements in g}\,m^{-2})\times \\ & (\text{carbon content of the roots in } \% \cdot 100^{-1}).\end{aligned} \tag{3.17}$$

3.5.6. Leaf litter decomposition

Leaf litter decomposition was determined using the litterbag methodology. Leaf litter was collected in traps in all of the investigated plots. This litter represented the natural species composition at the respective altitudes and will be referred to as stand litter. For further information of the species composition please see also chapter 2 on page 7. For comparison leaf litter of the early succession species *Myrica pubescens* L. was collected in traps under single trees along the paths in the RBSF from June to December 2003. This litter will be referred to as reference litter. Stand litter was collected between 2001 and 2003 and provided by Marina Röderstein and Gerald Moser (Georg August University of Göttingen). All collected litter was dried at 40 ℃, cut into 1×1 cm pieces and thoroughly homogenized. Litterbags were made of nylon mesh, 12×12 cm in size, the mesh size was 1 mm. Litterbags were filled with 10 g of prepared stand litter from the respective study site. As only small amounts of stand litter from $P_{3\,060\,m}$ and reference litter were available for the decomposition experiment, stand litter bags at $P_{3\,060\,m}$ and all reference litter bags were filled with 5 g only. In January 2004 at each plot 5 sets of ten litterbags of each litter type, in total 500, were placed at the plots on the top of the organic layer, slightly covered with fresh litter and fixed with nylon thread to prevent translocation by animals and consequently loss of the litterbags. After 4 (February 2004), 8 (March 2004), 16 (Mai 2004), 28 (August 2004) and 44 weeks (December 2004) 10 litterbags of each litter type were collected from each plot. Litterbags were dried at 40 ℃ and the dry contents weighed. After 28 weeks of incubation in the field, a substantial growth of fine roots into the litterbags took place. To avoid overestimation of remaining leaf litter mass fine roots were extracted carefully from the remaining contents in the litterbags, as well as visible fungi mycelia. Annual decay rate k was calculated for each litterbag using a negative exponential model (Sundarapandian and Swamy, 1999; de C.G. Mesquita

et al., 1997; Scowcroft et al., 2000; Carnevale and Lewis, 2000):

$$k = -\left[\ln(W_t/W_0) \cdot t^{-1}\right] \tag{3.18}$$

with

W_t ▷ remaining weight at t in g

W_0 ▷ initial weight in g

t ▷ time of exposure in years.

3.6. Statistical analysis

Several authors (Landgraf (2000) and references therein) consider data from living nature a priori as not normally distributed and recommend non parametric tests for correct data analysis. Nielsen and Wendroth (2003) further explain that most natural data cannot be considered normally distributed as most of the natural parameters cannot take on negative values. Thus, for such parameters a physical reality exists, that limits the values close to the range of those observed and distributions of these parameters generally are skewed (Nielsen and Wendroth, 2003). Following these suggestions data gained in the current study was analysed using nonparametric tests. A general constraint of nonparametric tests is their smaller discriminatory power if used for normally distributed data (Voss, 2004) as not all information provided by the data is used. Consequently, I assume that fewer differences will be detected by the applied tests for the normally distributed data sets, than by parametric tests. For unrestricted comparability of statistical analysis the same tests will be applied to all data sets.

3.6.1. Comparison of plots, horizons and sampling dates

Statistical analysis focused on the following aspects:

1. possible correlations between altitude and the investigated parameters, and
2. dependencies between the investigated parameters along the altitudinal gradient.

At this point the fact that data was collected by sampling the plots several times leads to major constraints in statistical analysis. The different parameters were not determined on one single sample; consequently single values cannot be correlated with each other, but median values have to be used for the calculation of dependencies. For this purpose, correlation analysis was carried out. The calculated correlation coefficients take on values between -1 and 1, whereas -1 indicates a completely negative correlation and 1 a completely positive correlation. The closer the coefficient is to zero the weaker is the correlation between the tested parameters. Spearman's rank correlation coefficient r_s tests dependencies between continuous variables using nonparametric methods. This coefficient can be used for ordinally scaled data and does not assume a linear relation (Sachs, 2002).

For each parameter, separately for each investigated horizon, I tested the hypothesis that all data sets originated from the same population (null hypothesis) using the nonparametric version

of the ANOVA, the Kruskal-Wallis test. If the calculated level of significance was smaller than or equal to 0.05 the null hypothesis was rejected, i. e. at least one of the data sets was not part of the population. If this was the case Kruskal-Wallis test was followed by a pair wise comparison of the sample sets applying the Mann-Whitney U test. For this test 0.05 was chosen as level of significance as well. Size of the single data set was n = 6. Due to this small sample size, the option to test the data using higher levels of significance like 0.001 was abandoned. This procedure was applied to compare all plots separately for the sampled horizons (altitudinal gradient) and to compare the different horizons separately for the plots (profile gradient).

For the detection of differences between the two sampling dates it has to be taken into account that samples taken at the same plot at different dates are dependent of each other. Such samples are called tied samples and are tested on differences using special tests. For not normally distributed data, the suitable test is the Wilkoxon test. This test was applied on the data sets, each representing one horizon, plot and sampling date, to detect significant changes of the parameter value between April and November 2004. As six composite samples were analysed, spatial heterogeneity was already reduced and I assume, that detected differences between sampling dates are true differences and not effects of spatial heterogeneity.

3.6.2. Principal component analysis

Microbial community structure as represented by PLFAs was analysed using principal component analysis (PCA), which allows the reduction of the parameters as defined by the identified PLFAs to few decisive factors. Unlike all other statistical analysis applied in this thesis, for reduction of dimensions or factors I used an analytical procedure that is appropriate for normally distributed data only. The main reason to deviate from the principle of using non parametric statistical methods was the dominance of PCA in the relevant literature for analysis of PLFA patterns.

In the case of PLFAs it was not necessary to check the input parameters (i. e. PLFAs) for redundancy as each fatty acid is unambiguously defined by its chemical structure. As a first step the correlation matrix including all extracted PLFAs was calculated. The principal components (PCs) are extracted from this matrix stepwise in such a way that each extraction step explains the maximum of the remaining variation. The more the input parameters are correlated with each other, the fewer principal components are extracted. The number of extracted principal components was determined by combined evaluation of screeplot and the percentage of variation that was explained by the respective principal components. For each principal component factor loadings were calculated that represent the relation between the fatty acid and the principal component. Factor loadings > 0.5 indicate a close relation with the respective principal component. To test if horizons and plots were significantly different from each other the Mann-Whitney-U-Test usually is applied on the factor loadings. This was not possible here, as only one composite sample was analysed for each horizon and plot.

All statistical analysis was performed using Statsoft Statistica® Software, Version 7.1.

3.6.3. Figures

If not indicated otherwise, data will be displayed in box-whisker-plots. Small boxes designate the median, big boxes indicate the 25 to 75 % of data and whiskers show the data range without outliers and extremes.

Chapter 4

Results and evaluation of collected data

This chapter presents results of the current study. In order to provide better understanding and instant evaluation of the collected data, results of comparable studies are presented at the end of each subchapter.

4.1. Soil acidity

The soils of the studied sites are characterised by moderate acidity in the top organic layer and high acidity in the top mineral soil. pH_{H_2O} ranged between 4.9 and 5.9 in the Oi horizon and from 3.9 to 4.9 in the OeOa. For 0–10 cm mineral soil, pH_{H_2O} between 3.8 and 4.4 were observed (Figure 4.1 on the following page). Due to its high variability pH_{H_2O} was not correlated with altitude in the Oi horizon. In the OeOa and 0–10 cm mineral soil pH_{H_2O} declined significantly along the studied altitudinal gradient ($r_s = -0.52$ and $r_s = -0.57$ at $p \leq 0.05$), respectively.

Hamilton et al. (1995) point out that soil properties of tropical montane forests cannot be generalised and that no overriding chemical soil parameter exists. pH of these forests usually ranges between 3 and 7, which corresponds to the range observed in the present study. However, a variety of authors report moderate to strongly acidic soils to prevail in tropical montane forests (Silver, 1994; Rhoades et al., 1998; Schrumpf et al., 2001; Bautista-Cruz and del Castillo, 2005; Schrumpf et al., 2006).

4.2. Selected carbon pools

4.2.1. Soil organic carbon

SOC was determined in April 2004 only, as these parameters were considered very stable during the investigation period. SOC contents generally ranged between 37 and 52 % in the organic layer horizons. This corresponds to carbon stocks between 10 Mg C ha^{-1} at 1 050 m and 33 Mg C ha^{-1} at 2 380 m. Most carbon was stored in the organic layers at 3 060 m; the stock amounted to 68 Mg C ha^{-1}.

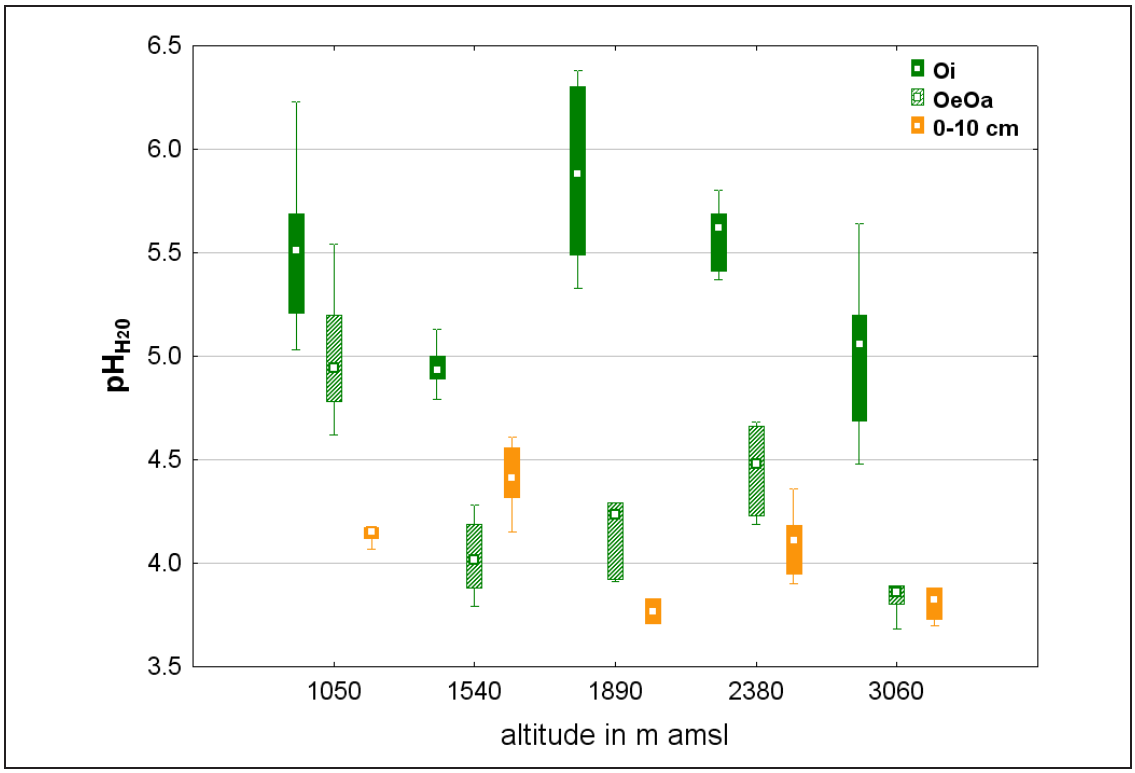


Figure 4.1: Median, quartiles and range of pH_{H_2O} in Oi, OeOa and 0–10 cm mineral soil ($n = 6$), April 2004..

SOC contents increased significantly in the Oi horizon ($r_s = 0.45$; $p \leq 0.05$) from 48.2 % at $P_{1\,050\ m}$ to 51.5 % at $P_{3\,060\ m}$ (Figure 4.2 on the facing page). SOC contents in OeOa varied between 37.6 % at $P_{1\,890\ m}$ and 46.8 % at $P_{2\,380\ m}$ but were not related to altitude (Table 1 on page 138). In the mineral soil (0–10 cm) SOC increased significantly ($r_s = 0.55$; $p \leq 0.05$) from 3.3 % at $P_{1\,050\ m}$ to 11.6 % at $P_{3\,060\ m}$. These contents corresponded to carbon stocks between 30 and 60 Mg C ha^{-1} in the top 10 cm mineral soil (Figure 4.3 on the facing page). At $P_{2\,380\ m}$ comparably little carbon was stored in 0–10 cm mineral soil; the carbon stock was even lower than at $P_{1\,050\ m}$. At all altitudes SOC contents decreased significantly in the soil profile (Table 2 on page 139).

Cumulative stocks of SOC in the organic layer horizons and the top 10 cm of mineral soil increased along the altitudinal gradient from 48.93 Mg ha^{-1} at 1 050 m to 126.19 Mg ha^{-1} at 3 060 m (Figure 4.3 on the facing page), which coincides with increasing SOC contents in the respective horizons. At 2 380 m cumulative carbon stocks are slightly lower than at 1 890 m, which may be attributed to the position of the plot close to a ridge.

SOC was negatively influenced by VWC in the organic layer. Furthermore SOC was negatively related to different nitrogen pools studied: the KCl-extractable total and organic nitrogen and nitrate; N_{mic} and HWN, which suggests a high importance of nitrogen for soil organic matter turnover (tables 6 to 14 on pages 141–149). In both OeOa and 0–10 cm, SOC was positively related to gross nitrogen mineralisation and ammonium consumption rates.

SOC contents of the studied mineral soils are supported by a variety of studies in lowland and also high altitude tropical forests. Rhoades et al. (2000) observed SOC of 6.5 % in the top

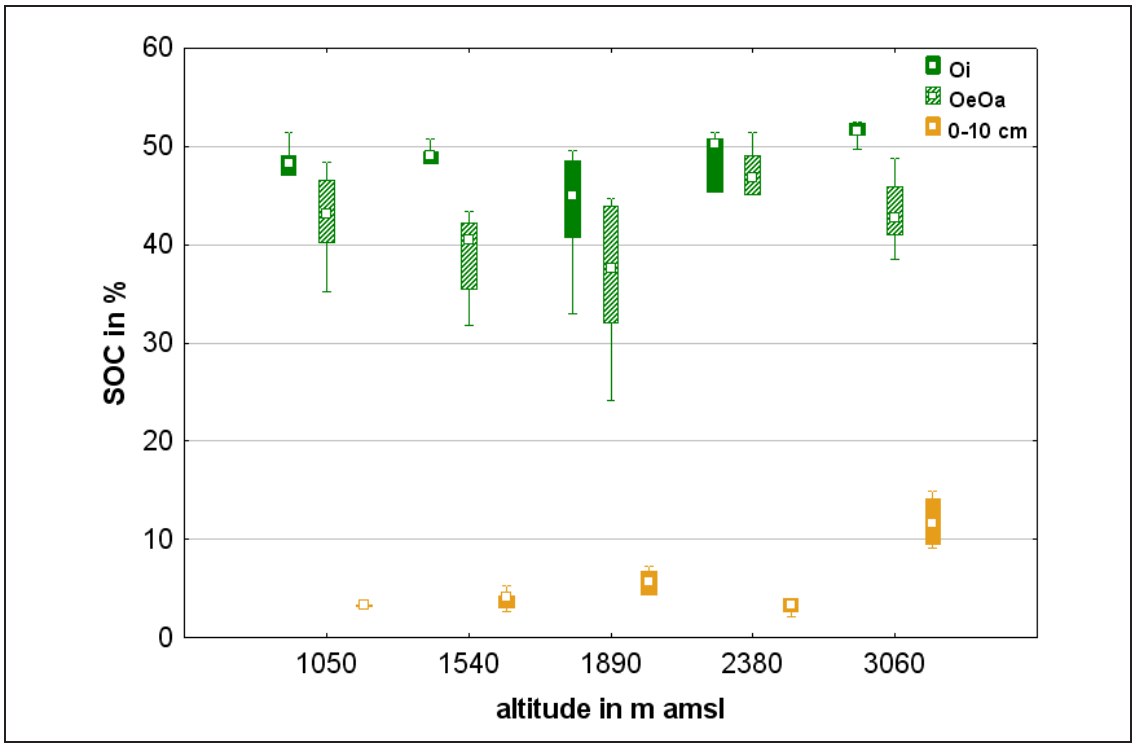


Figure 4.2: Median, quartiles and range of soil organic carbon (SOC) in Oi, OeOa and 0–10 cm mineral soil ($n = 6$), April 2004.

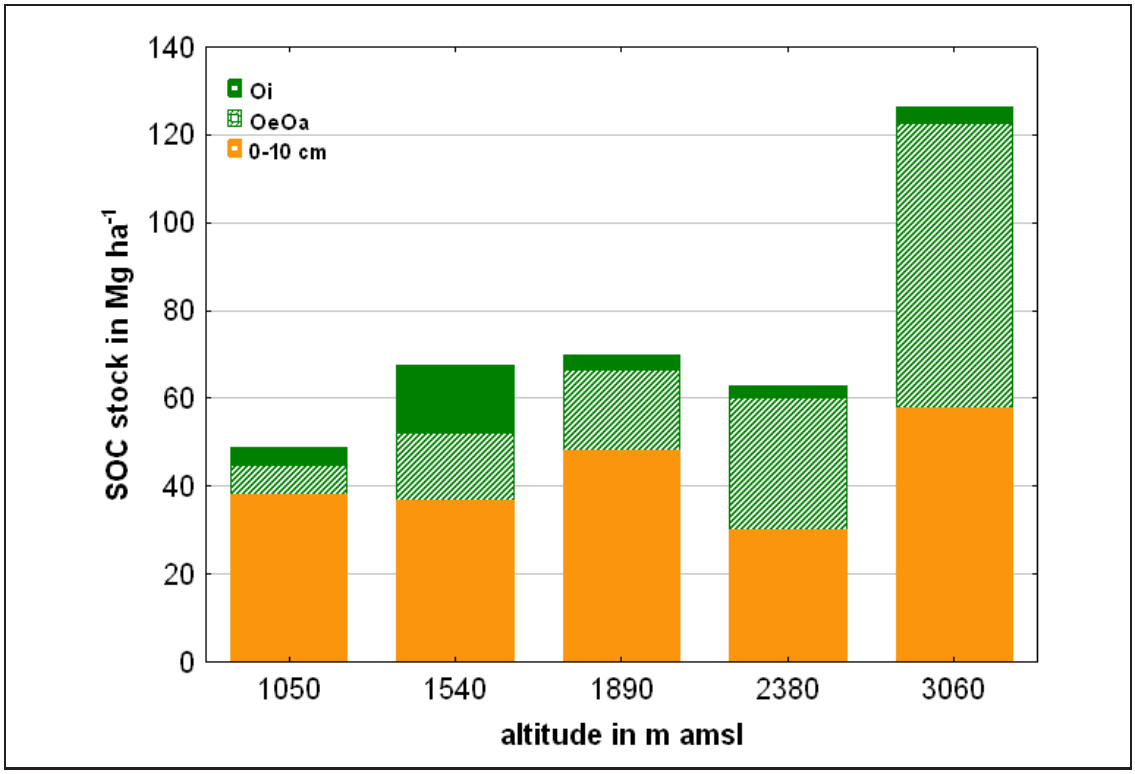


Figure 4.3: Cumulative soil organic nitrogen stocks in Mg ha^{-1} for all studied sites on the basis of median ($n = 6$) SOC.

15 cm of a soil that had developed on andesitic volcanic ash at the western slopes of the Ecuadorian Andes. Different studies in lowland tropical forests of Costa Rica report SOC between 5.1 and 6.8 % in the top 10 cm mineral soil (Krishnaswamy and Richter, 2002) and SOC stocks between 50–140 Mg C ha^{-1} in 0–30 cm mineral soil (Powers and Veldkamp, 2005). For a secondary forest in wet tropical climate of Puerto Rico, Li et al. (2005) report 34.5 Mg SOC ha^{-1} in 0–10 cm mineral soil. Abadín et al. (2002) conducted one of the few studies in soils of tropical ecosystems at high altitudes. In Venezulean páramo (3 350–3 700 m amsl) SOC in 0–15 cm was 7.7 %, thus lower than at the highest study site of the current study. However, data is comparable and the lower SOC in the páramo may be attributed to lower carbon inputs by the vegetation than by the elfin forest at 3 060 m in the PNP. Organic layer horizons or forest floor material is seldom studied for its SOC in tropical ecosystems. Only two recent studies report on SOC content of organic layers in tropical ecosystems: Abadín et al. (2002) observed 45.7 % SOC in the organic layer of tropical páramo and Powers and Veldkamp (2005) report that 1.09 Mg SOC ha^{-1} were stored in the leaf litter of Costa Rican volcanic soils.

4.2.2. Total hot-water extractable organic carbon

In April 2004 HWC in the Oi horizon ranged between 20.2 mg g^{-1} at $P_{1\,050\ m}$ and 25.9 mg g^{-1} at $P_{1\,890\ m}$. HWC was not linearly correlated with altitude, but peaked at 1 890 m. Levels of HWC at $P_{2\,380\ m}$ and $P_{3\,060\ m}$ were comparable to those at $P_{1\,050\ m}$ (Figure 4.4 on the facing page). In the densely rooted OeOa HWC ranged between 16.3 mg g^{-1} at $P_{1\,890\ m}$ and 20.4 mg g^{-1} at $P_{2\,380\ m}$ and was not related to altitude (Table 1 on page 138). Except for the site $P_{1\,050\ m}$ OeOa horizons contained less HWC than Oi horizons. These differences were significant at $P_{1\,540\ m}$, $P_{1\,890\ m}$ and $P_{3\,060\ m}$ (Table 16 on page 150). In the top mineral soil (0–10 cm) HWC significantly increased along the altitudinal gradient ($r_s = 0.74$; $p \leq 0.05$) from 0.9 mg g^{-1} at $P_{1\,050\ m}$ to 3.4 mg g^{-1} at $P_{3\,060\ m}$. Results of the soil analysis in November 2004 supported these findings. HWC ranged at the same levels as in April, only in OeOa at $P_{2\,380\ m}$ and in Oi and 0–10 cm at $P_{3\,060\ m}$ HWC contents were significantly higher than at the first sampling. HWC also showed the same altitudinal trends in the respective horizons, only in 0–10 cm HWC was positively related to altitude ($r_s = 0.66$; $p \leq 0.05$). Without exception, HWC declined significantly in the soil profile at all sites (Table 2 on page 139). Except for sites at 1 050 m and 2 380 m highest HWC were observed in the top organic layer (Oi). Generally, differences between the two organic layers were small and HWC in 0–10 cm was markedly smaller than in the organic layers. With reference to all studied horizons and sites median HWC constituted between 2.7 and 5.4 % of SOC and was not correlated with altitude. In the Oi horizon no significant relations to other soil parameters were detected, except for HWC contents in November 2004 that were significantly related to gross nitrogen consumption. In the OeOa HWC was positively related to C_{mic} and SOC, as well as to gross nitrogen mineralisation and ammonium consumption rates. In the mineral soil HWC was significantly influenced by abiotic conditions; HWC declined at high temperatures and low volumetric water content. Furthermore HWC was inversely correlated with the C_{mic} : SOC ratio, and positively related to total KCl-extractable organic carbon (TOC_{KCl}) and KCl-extractable ammonium, as well as to gross nitrogen mineralisation and ammonium consumption rates (tables 6 to 14 on pages 141–149).

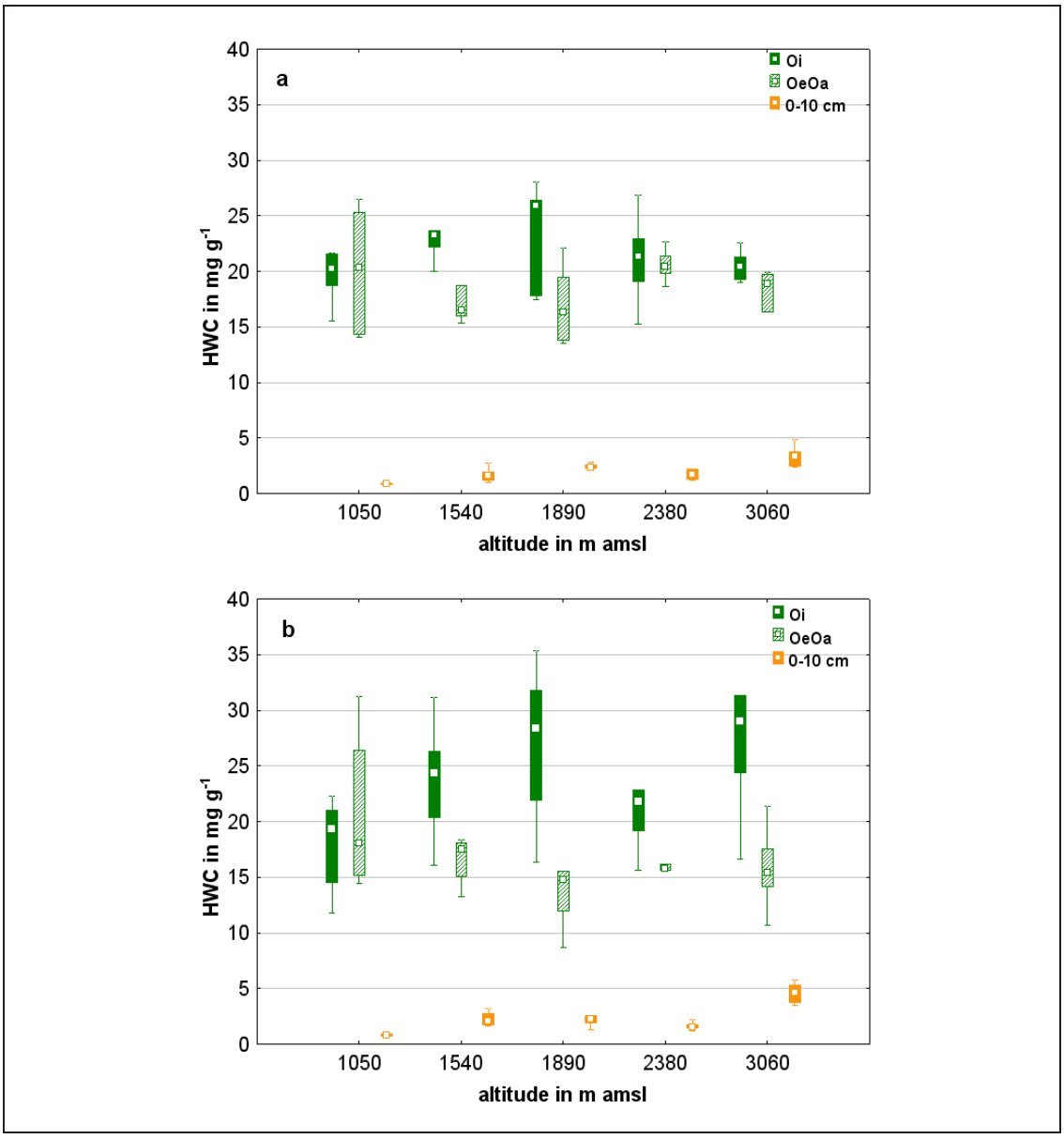


Figure 4.4: Median, quartiles and range of total hot-water extractable organic carbon (HWC) in April 2004 (a) and November 2004 (b) in Oi, OeOa and 0–10 cm mineral soil ($n = 6$).

For different pasture soils in New Zealand Ghani et al. (2003) report hot water extractable carbon contents in different seasons between 1 786 and 5 093 µg g^{-1} soil, thus ranging higher than in the current study. However, in both studies HWC has a high variation that is caused by seasonal changes and management practices in New Zealand and by high spatial differences in the RBSF. Furthermore, the same authors suggest that HWC normally is between 600 and 5 400 µg g^{-1} in mineral soils and that HWC : SOC ratio ranges between 3 and 6 % which supports the current findings. In organic layers under beech in the Ore Mountain region of southeast-Germany HWC varied between 13 and 16 g kg^{-1} (Landgraf et al., 2006) and in peats in New Zealand HWC amounted to an average of 12.2 mg g^{-1} (Sparling et al., 1998). For organic layers and mineral

soils under black locust (*Robinia pseudoacacia* L.) and Scots pine (*Pinus sylvestris* L.) in NE Germany, Landgraf et al. (2005) found hot water-extractable organic carbon contents between 2 and 55 $g\,kg^{-1}$, contents decreased within the soil profile and corresponded to 10–13.8 % of SOC. In fly-ash affected organic layers under *Pinus sylvestris* L. in the NE-German lowlands, Koch et al. (2002) observed HWC contents between 3 and 24 $g\,kg^{-1}$. In mineral soils of the same study HWC ranged from 0.3 to 0.5 $g\,kg^{-1}$. In organic layers of the Saxonian Lowland and the Ore Mountain region, HWC contents amounted to 10–31 $mg\,g^{-1}$ and 14–30 $mg\,g^{-1}$, respectively (Koch, 2006). This corresponded to 4–11 % of SOC . In mineral soils of the same studies, HWC was lower and ranged from 1.1 to 1.8 $mg\,g^{-1}$ and 1–6 $mg\,g^{-1}$, respectively. In both study regions, HWC declined within the soil profile (Koch, 2006). Compared to these findings the HWC in organic layer horizons reported here have to be considered fairly high.

4.2.3. Total KCl-extractable organic carbon

In the top organic layer the average TOC_{KCl} increased from 1 774.7 $\mu g\,g^{-1}$ at 1 050 m along the altitudinal gradient, peaked with 2 685.7 $\mu g\,g^{-1}$ at 1 890 m and was negatively related to altitude at higher elevations (Figure 4.5(a) on the facing page). Thus, TOC_{KCl} was not linearly related to altitude in the Oi horizon (Table 1 on page 138), but was significantly smaller at 3 060 m than at all other plots (Table 32 on page 159). In the OeOa horizon TOC_{KCl} was significantly smaller than in Oi at all plots and declined with increasing altitude ($r_s = -0.51$) from 1 207.8 ($P_{1\,050\ m}$) to 343.6 $\mu g\,g^{-1}$ ($P_{3\,060\ m}$). In this horizon pairwise comparison of plots detected significant differences between $P_{3\,060\ m}$ and all other plots as well (Table 32 on page 159). In the mineral soil (0–10 cm) TOC_{KCl} was even smaller (Table 17 on page 151). TOC_{KCl} ranged from 32.0 ($P_{2\,380\ m}$) to 191.0 $\mu g\,g^{-1}$ ($P_{3\,060\ m}$) and was not related to altitude, but TOC_{KCl} at 3 060 m was significantly higher than at lower altitudes (Table 32 on page 159). From the description can already be concluded that TOC_{KCl} decreased significantly within the soil profile, which is underlined by the results of correlation analysis (Table 2 on page 139).

In November 2004 the described patterns were largely confirmed (Figure 4.5(b) on the facing page). TOC_{KCl} also increased from 1 050 to 1 890 m and then declined but the differences between these two groups were more pronounced. This led to the calculation of $r_s = -0.54$ and therefore indicated a significant decline of TOC_{KCl} along the altitudinal gradient. In OeOa TOC_{KCl} was negatively related to altitude ($r_s = -0.88$) and therefore this relation was even stronger in November than in April 2004. In 0–10 cm mineral soil TOC_{KCl} was also not related to altitude. At all plots, TOC_{KCl} decreased significantly (Table 2 on page 139) within the profile. Significant differences between the two samplings were not systematic and only occurred at $P_{2\,380\ m}$ and $P_{3\,060\ m}$ (Table 47 on page 166). In the Oi horizon at $P_{3\,060\ m}$ and the OeOa at $P_{2\,380\ m}$ TOC_{KCl} was significantly smaller in November, than in April 2004. In 0–10 cm mineral soil at $P_{3\,060\ m}$ TOC_{KCl} was significantly higher in November 2004. This indicates a seasonal variation of TOC_{KCl} at high but not at low altitudes. TOC_{KCl} constituted between 0.08 to 0.59 % of SOC with respect to all studied plots and horizons. The percentage of TOC_{KCl} of SOC was related to altitude in OeOa horizon only ($r_s = -0.56$). Except for $P_{3\,060\ m}$, the TOC_{KCl} : SOC ratio decreased significantly with soil depth (Table 2 on page 139). The plot at 3 060 m differed significantly from all other plots with respect to the TOC_{KCl} : SOC ratio; it was markedly lower than at the other plots in

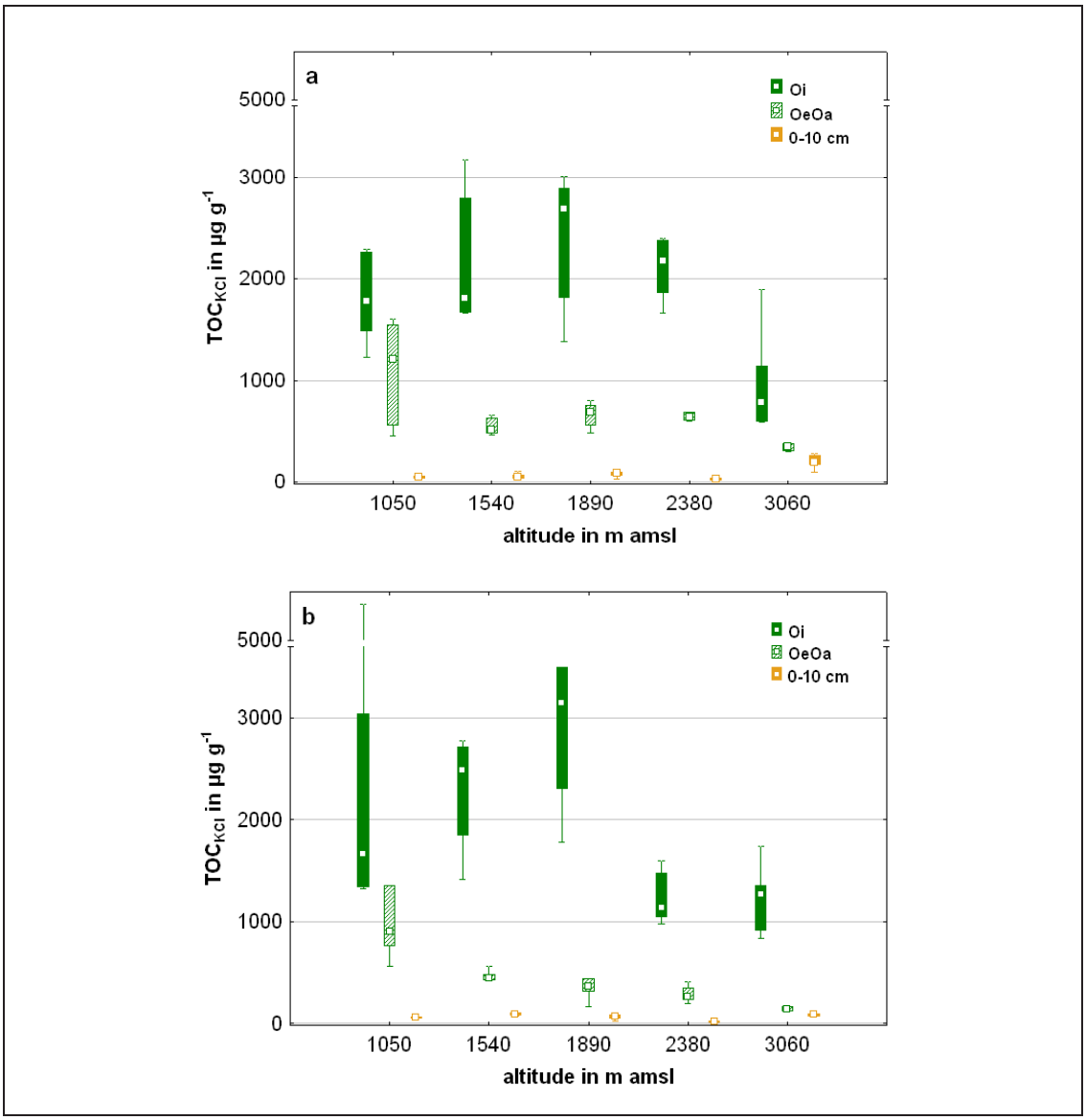


Figure 4.5: Median, quartiles and range of total KCl-extractable organic carbon (TOC_{KCl}) in April 2004 (a) and November 2004 (b) in Oi, OeOa and 0–10 cm mineral soil ($n = 6$).

both organic layer horizons.

TOC_{KCl} in the Oi horizon was influenced by the HWC : SOC ratio, N_{mic} and KCl-extractable organic nitrogen. Furthermore, TOC_{KCl} was correlated with C_{mic} and heterotrophic respiration, which may indicate that TOC_{KCl} is an easily mineralisable substrate. In the OeOa horizon high VWC and SOC : TN ratios led to declined TOC_{KCl}, while HWN, the HWC : SOC ratio, HWN : TN ratio, $C_{mic} : N_{mic}$, C_{mic} : SOC, TN_{KCl} and KCl-extractable nitrate and ammonium were positively related to TOC_{KCl}. In the mineral soil, TOC_{KCl} was inversely related to HWN : TN ratio but positively related to SOC, HWC and KCl-extractable ammonium.

In contrast to the findings of Landgraf et al. (2006) and Böhm (2005) who observed high seasonal variation of TOC_{KCl} in a sandy cambisol in a temperate climate due to prevailing weather

conditions and soil moisture, TOC_{KCl} in organic layers and topsoils under tropical montane forests was rather stable when comparing drier and wetter seasons. However, at high altitudes differences between the two sampling dates occurred. The two authors cited above report average TOC_{KCl} in 0–10 cm up to 30 mg kg^{-1}, which is comparable to TOC_{KCl} at $P_{2\,380\ m}$, but markedly lower than at the remaining plots. Percentage of TOC_{KCl} of SOC varied between 0.11 and 0.36 %, which was comparable to my results. In organic layers under black locust (*Robinia pseudoacacia* L.) and Scots pine (*Pinus sylvestris* L.) in NE Germany, KCl-extractable carbon content was considerably lower than in the present study, and amounted to only 4.12 g kg^{-1} in the Oi (Landgraf et al., 2005).

4.3. Selected nitrogen pools and potential fluxes

4.3.1. Total nitrogen

Considering all horizons and study sites TN varied between 0.2 and 2.2 %. In the top organic layer Oi TN decreased significantly ($r_s = -0.86$; $p \leq 0.05$) from 2.1 % at $P_{1\,050\ m}$ to 0.83 % at $P_{3\,060\ m}$ (Figure 4.6 on the facing page). In the OeOa horizon TN contents ranged higher than in Oi, especially at the three upper plots this difference between the two organic layer horizons was pronounced (Table 2 on page 139). Comparatively to Oi, TN in OeOa declined significantly ($r_s = -0.53$; $p \leq 0.05$) from 2.23 % at $P_{1\,050\ m}$ to 1.40 % at $P_{3\,060\ m}$. TN in the organic layer horizons was significantly higher than in the mineral soil, where TN increased substantially but not significantly from 0.25 % at $P_{1\,050\ m}$ to 0.45 % at $P_{3\,060\ m}$.

TN stocks ranged between 0.06 Mg ha^{-1} at 3 060 m to 0.51 Mg ha^{-1} at 1 540 m in the Oi horizon (Figure 4.7 on page 47). In OeOa TN stocks were considerably higher and positively correlated with altitude: they increased from 0.28 to 2 Mg ha^{-1}. In the mineral soil (0–10 cm) TN stocks further increased as compared to organic layer horizons and ranged from 1.68 Mg N ha^{-1} at $P_{2\,380\ m}$ to 2.94 Mg N ha^{-1} at $P_{1\,050\ m}$. This increase of TN stocks in the profile is attributed to increasing bulk densities. In total, organic layers and top mineral soils at the respective altitudes stored between 3 and 4.5 Mg ha^{-1}. Total TN stocks tended to increase along the altitudinal gradient, but only in the Oi horizon TN stocks were significantly related to altitude ($r_s = -0.9$; $p \leq 0.05$).

In both organic layer horizons, TN was positively related with hot water and KCl-extractable nitrogen species, even though the significance of these correlations was smaller in OeOa than in Oi (tables 6 to 14 on pages 141–149). However, this is an expected result, as HWN and KCl-extractable nitrogen species are subpools of TN. In the Oi horizon abiotic conditions also determined TN, high TN occurred under conditions of increased soil temperatures and low volumetric water content. Furthermore, TN was positively correlated with gross nitrogen mineralisation. In the OeOa horizon the influence of soil temperature subsided, here only VWC influenced TN. Further determinants were HWC : SOC, HWN : TN and the $C_{mic} : N_{mic}$ ratio. In the top mineral soil, KCl-extractable nitrogen was of no relevance for TN, but HWN, N_{mic} and gross nitrogen mineralisation were positively correlated with TN, while high C_{mic} : SOC ratios caused low TN.

In Ecuadorian Andosols of high pH under mature tropical lower montane forests (Rhoades and Coleman, 2004) TN stocks in 0–15 cm mineral soil were 4.98 and 5.51 Mg ha^{-1}. In cultivated

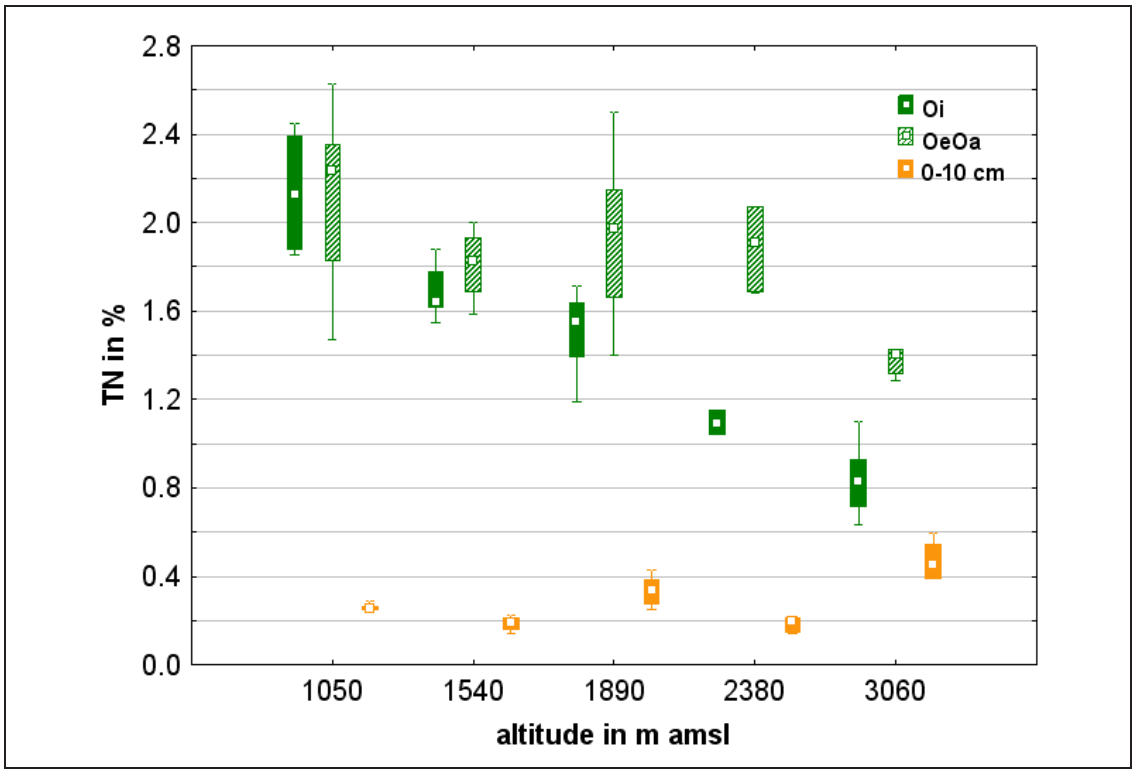


Figure 4.6: Median, quartiles and range of total nitrogen (TN) content in Oi, OeOa and 0–10 cm mineral soil ($n = 6$), April 2004.

soils at altitudes of more than 3 000 m in the Venezuelan paramó (Sarmiento and Bottner, 2002) TN stocks in 0–20 cm mineral soil were 6.6 and 6.9 Mg ha^{-1}, thus higher than at 3 060 m of the current study. The TN content of these soils was between 0.39 and 0.49 % and therefore only slightly smaller than in the mineral soil at 3 060 m. Most of the recent literature provides data for tropical lowland forests rather than for tropical montane forests. In Puerto Rico TN contents at 450 m amsl varied from 0.08 to 0.41 % and were 0.52 % at 950 m (Zou et al., 2005). In a wet lowland tropical forest of Costa Rica TN amounted to 0.6 % (Cleveland et al., 2003) and in mineral soils at the Philippines TN ranged from 0.79 to 1.65 % (Salamanca et al., 2002). TN contents observed in the current study were comparable to the findings in the literature, yet slightly below average. In mineral soils (0–15 cm) of a tropical agroforestry system TN of 0.05 % was even lower than in the soils of this study (Chander et al., 1998). Unfortunately data for organic layer horizons is lacking, as in lowland tropical forests organic layers seldom exist due to rapid litter decomposition. Abadín et al. (2002) provides at least some data. The authors observed average TN contents of 4.1 and 8.2 g kg^{-1} in mineral topsoils and organic layers in Venezuelan parámo soils. However, TN contents in organic layers under tropical montane forest are slightly lower than in organic layers where TN ranged between 2–3 % under beech and fir in Finland (Smolander et al., 2005).

The SOC : TN ratio in the Oi horizon increased significantly with increasing altitude ($r_s = 0.82$; $p \leq 0.05$) from 20.2 at $P_{1\,050\ m}$ to 62.6 at $P_{3\,060\ m}$ (Table 1 on page 138). In the deeper horizons the same trend could be observed; SOC : TN ranged between 17.7 and 30.8 in the OeOa and between

12.9 and 24.2 in 0–10 cm mineral soil (Figure 4.8 on the facing page).

Declining TN contents and wide SOC : TN ratios in the organic layer horizons at higher altitudes indicate low decomposability of the leaf litter. MERILÄ ET AL. (2002) consider C : N ratios below 30 as indicators for N-limitation of leaf litter decomposition. Following this definition, decomposition at $P_{2\,380\ m}$ and $P_{3\,060\ m}$ has to be considered N-limited. At $P_{1\,540\ m}$ and $P_{1\,890\ m}$ SOC : TN ratios in the Oi were 30.47 and 29.11, respectively, consequently decomposition at these altitudes can be regarded as N-limited, too. This assumption is supported by the thickness of the organic layers that averagely range from 10 to 22 cm (Figure 4.9 on page 48). At 3 060 m extreme values reached even 51 cm.

4.3.2. Total hot-water extractable nitrogen

In April 2004 median HWN ranged between 537.9 $\mu g\,g^{-1}$ at $P_{3\,060\ m}$ and 1776.8 $\mu g\,g^{-1}$ at $P_{1\,050\ m}$ in the Oi horizon (Figure 4.10(a) on page 49). In the densely rooted OeOa HWN contents were higher at all sites except for $P_{1\,540\ m}$ and $P_{1\,890\ m}$, and reached maximum contents of 2 386.3 $\mu g\,g^{-1}$ at $P_{1\,050\ m}$. However, differences between the organic layer horizons were significant at $P_{1\,540\ m}$ and $P_{3\,060\ m}$ only (Table 20 on page 152). In both Oi and OeOa HWN was inversely related to altitude ($r_s = -0.85$ and $r_s = -0.62$, respectively at $p \leq 0.005$) (Table 1 on page 138). In the mineral soil (0–10 cm) median HWN contents varied between 71.1 $\mu g\,g^{-1}$ at 1 540 m and 198.4 $\mu g\,g^{-1}$ at 1 890 m, i. e. were significantly lower than in both organic layer horizons (Table 20 on page 152). No significant trend at the altitudinal gradient was detected in this horizon. The sampling in November 2004 largely confirmed these findings (Figure 4.10(b) on page 49). HWN in the organic layer horizons ranged between 637.2 and 1 622.6 $\mu g\,g^{-1}$ and only at 1 890 m a significant difference between Oi and OeOa was detected (Table 20 on page 152). HWN in 0–10 cm differed from the first sampling at $P_{1\,540\ m}$ only. The percentage of HWN of TN averaged between 4 and 10 % (Table 86 on page 182) at all studied sites and decreased significantly in the Oi ($r_s = -0.41$; $p \leq 0.005$) as well as in the OeOa horizon ($r_s = -0.56$; $p \leq 0.005$). In the mineral soil HWN : TN ratio was not correlated with altitude.

HWN was strongly influenced by abiotic conditions in the organic layer horizons, as for TN high temperatures and low volumetric water contents supported high HWN in the Oi, as well as in the OeOa, but in the latter these relations were weaker (tables 6 to 14 on pages 141–149). HWN was high under conditions of high TN and C_{mic}, C_{mic} : SOC ratio and was also positively correlated with gross nitrogen mineralisation. Furthermore, HWN was related to KCl-extractable nitrogen species. High SOC and $C_{mic} : N_{mic}$ ratios indicated low HWN contents in the Oi. In the OeOa HWN was positively related to TN and KCl-extractable nitrogen and high SOC : TN ratios indicated low HWN. In the mineral soil N_{mic} and gross nitrogen mineralisation were significantly correlated to HWN.

In all studied horizons and for both sampling dates, the HWC : HWN ratio was significantly positively correlated with altitude (Table 1 on page 138). Median ratios varied between 10 and 40 in the Oi, between 9 and 30 in the OeOa and between 7 and 25 in the top mineral soil (Figures 4.11(a) to 4.11(b) on page 50). The comparably wide ratios at 1 540 m underline the exceptional position of this plot within the studied altitudinal gradient. Generally the HWC : HWN ratio decreased significantly within the soil profile (Table 2 on page 139).

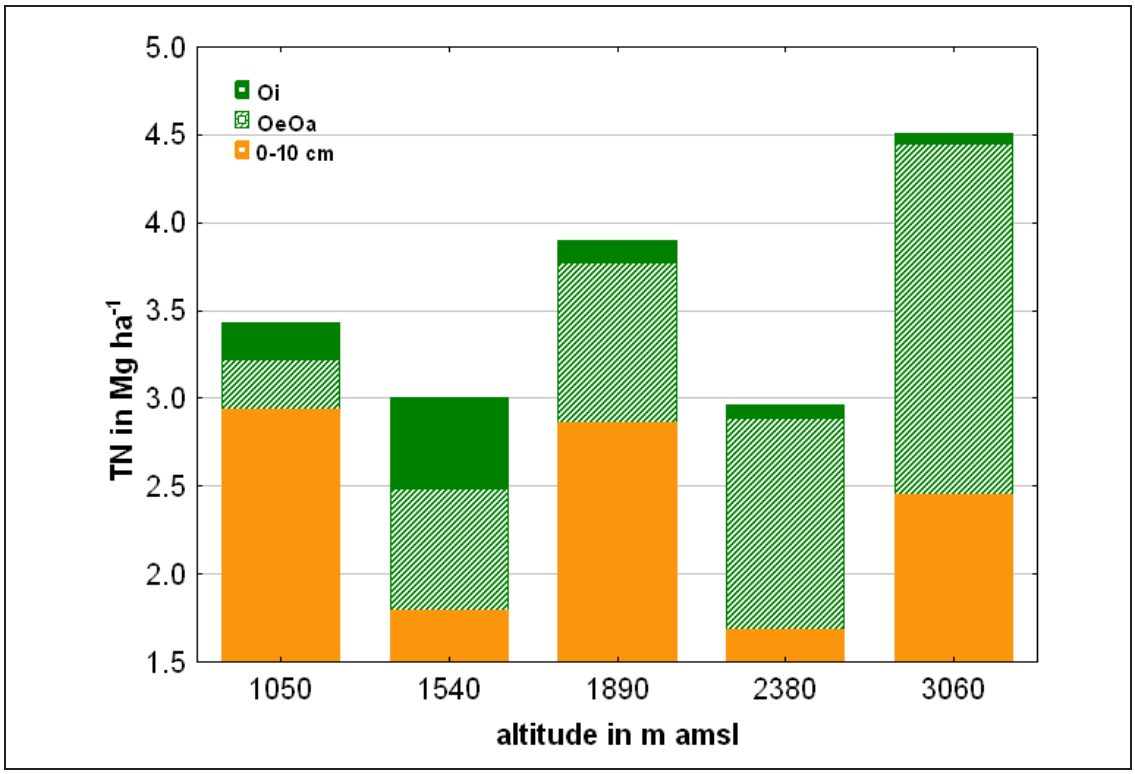


Figure 4.7: Cumulative total nitrogen (TN) stocks in Mg ha^{-1} for all studied sites on the basis of median (n = 6) TN.

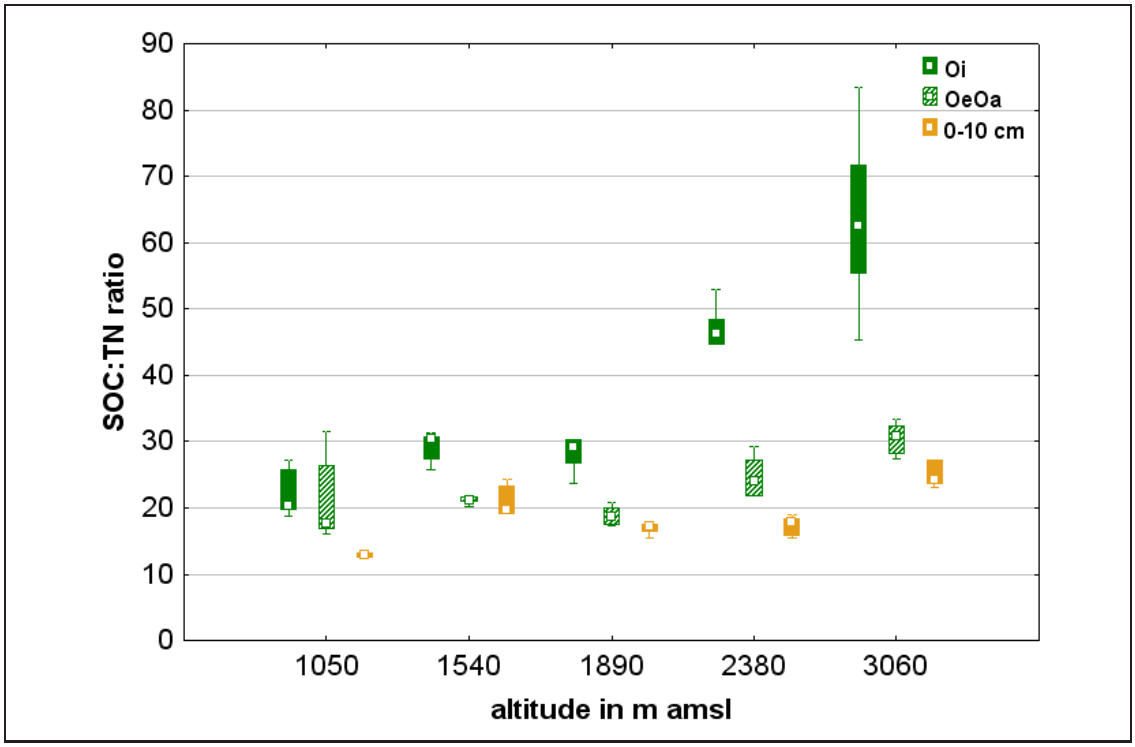


Figure 4.8: Median, quartiles and range of SOC to TN ratio (SOC : TN) in Oi, OeOa and 0–10 cm mineral soil (n = 6), April 2004.

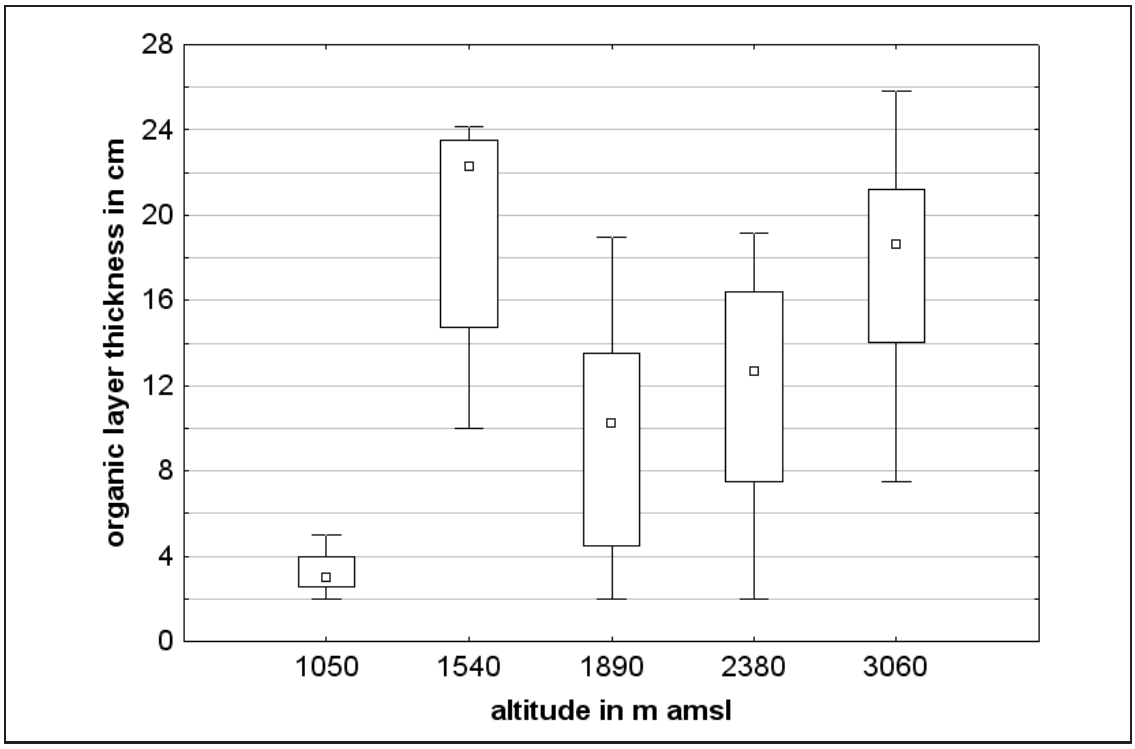


Figure 4.9: Average organic layer thickness at all studied sites ($n = 36$).

Again comparable studies in tropical ecosystems are sparse; very few authors apply the hot water extraction which is also true for agricultural and forested sites in temperate regions. In Dystric and Humic Cambisols in the east German Lowlands HWN was only up to 0.09 g kg^{-1} in 0–10 and 10–30 cm mineral soil (Landgraf et al., 2003). These authors also found comparable HWN : TN ratios between 3 and 9 %. Furthermore HWN was strongly correlated with TN. In organic layers under beech in the Ore Mountain region of southeast-Germany HWN ranged between 0.34 and 0.83 g kg^{-1} (Landgraf et al., 2006), which ranges lower than in organic layers in the RBSF and PNP. Landgraf et al. (2006) did not detect significant differences of HWN in organic layer horizons. Comparably to these findings differences between the studied organic layer horizons of RBSF and PNP were not consistent; at some sites HWN in OeOa was higher than in Oi and vice versa at others.

In organic layers in NE Germany, HWN amounted to 3.3 g kg^{-1} under black locust (*Robinia pseudoacacia* L.) and to 1.1 g kg^{-1} under Scots pine (*Pinus sylvestris* L.) (Landgraf et al., 2005), which was considerably lower than in the present study. The HWN : TN ratio in the Oi amounted to 15 and 6.3 % under locust and pine, respectively, and was about 10 % in the mineral soils.

In sandy soils under fallow in NE Germany, Böhm (2005) observed hot water-extractable N contents between 40 and 70 mg kg^{-1}. Koch et al. (2002) reports HWN between 0.2 and 1.3 g kg^{-1} for organic layers of sandy soils in NE Germany, which corresponded to HWN : TN ratios between 4.6 and 8.1 in organic layer horizons and 2.2 and 2.7 % in 0–10 cm mineral soil. In organic layers under spruce (*Picea abies* L.) and beech (*Fagus sylvestris* L.) HWN ranged from 0.8 to 1.5 mg g^{-1} and generally was below 1 mg g^{-1} in the top mineral soils. In the Ore Mountain

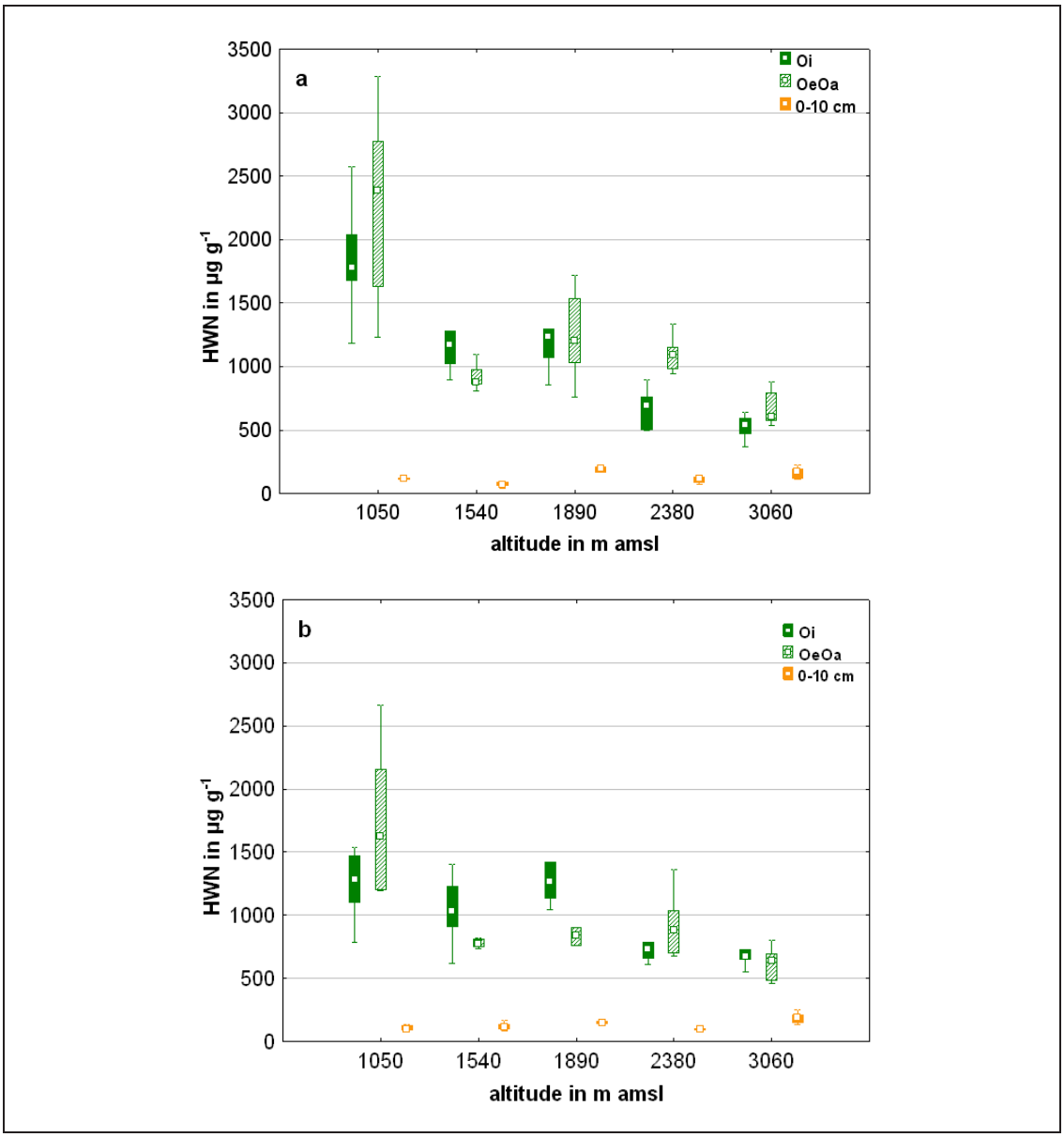


Figure 4.10: Median, quartiles and range of total hot-water extractable nitrogen (HWN) in April 2004 (a) and November 2004 (b) in Oi, OeOa and 0–10 cm mineral soil ($n = 6$).

region the percentage of HWN of TN varied from 5.4 to 11.4 % and the HWC : HWN ratio declined within the profile from 15.1 to 20.8 % (Koch, 2006).

For organic layer horizons under old beech (*Fagus sylvatica* L.) in the Ore Mountain region, Germany, Landgraf et al. (2006) report HWC : HWN ratios of 17 to 46, which are considerably higher than HWC : HWN ratios reported from agriculturally managed sites. In Eutric and Humic Cambisols under succession fallow in NE Germany, HWC : HWN ratios in 0–10 cm mineral soil ranged between 7 and 11 (Landgraf et al., 2003). HWC : HWN ratios in the organic layer horizons at $P_{3\,060\ m}$ were comparable to organic layers under pine (*Pinus sylvestris* L.) in temperate regions (Landgraf et al., 2005).

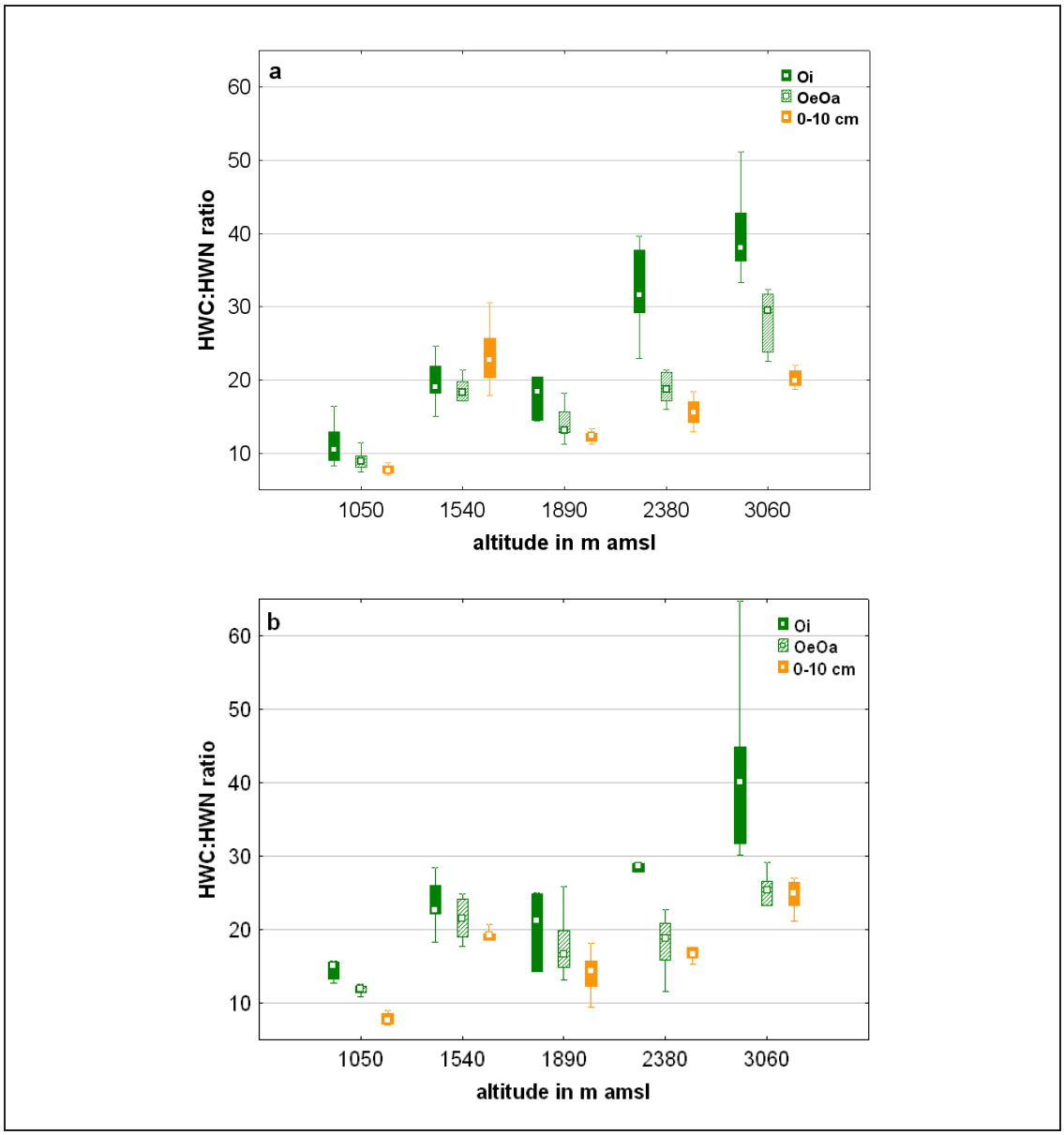


Figure 4.11: Median, quartiles and range of the C : N ratio in the hot water extract for all studied altitudes and horizons.

4.3.3. Total KCl-extractable nitrogen

In April 2004 TN_{KCl} varied strongly in the studied horizons along the altitudinal gradient (Figure 4.12(a) on page 52). In the Oi horizon median TN_{KCl} decreased significantly ($r_s = -0.88$; $p \leq 0.05$) from 1 298.6 $\mu g\,g^{-1}$ at $P_{1\,050\ m}$ to 18.8 $\mu g\,g^{-1}$ at $P_{3\,060\ m}$. This trend is also reflected by the results of the U-Test (Table 36 on page 161), that detected significant differences between all plots, except $P_{1\,540\ m}$ and $P_{1\,890\ m}$, were median TN_{KCl} and also variation of the data were similar. In the OeOa horizon TN_{KCl} contents were significantly correlated with altitude as well ($r_s = -0.827$; $p \leq 0.05$). TN_{KCl} decreased from 1734.7 $\mu g\,g^{-1}$ at $P_{1\,050\ m}$ to 82.3 $\mu g\,g^{-1}$ at $P_{3\,060\ m}$. Differences between the study sites were similarily pronounced as in the Oi horizon (Table 36 on

page 161). In the top mineral soil (0–10 cm) TN_{KCl} was not correlated with altitude and ranged between 23.4 $\mu g\,g^{-1}$ at $P_{1\,540\ m}$ and 71.6 $\mu g\,g^{-1}$ at $P_{1\,890\ m}$ (Table 1 on page 138). U-Tests detected several differences between the sites; TN_{KCl} at $P_{1\,050\ m}$, $P_{1\,890\ m}$ and $P_{3\,060\ m}$ ranged significantly higher than both at $P_{1\,540\ m}$ and $P_{2\,380\ m}$ (Table 36 on page 161).

In November 2004 TN_{KCl} contents covered a smaller range than in April 2004 (Figure 4.12(b) on the following page), which was mainly attributed to changes at 1 050 m. In the Oi horizon median TN_{KCl} of 508.3 $\mu g\,g^{-1}$ was still highest along the gradient, but ranged significantly ($p \leq 0.05$) lower than in April. Consequently, for the second sampling, no significant differences between the three lower sites were detected. TN_{KCl} in November 2004 showed a similar grouping like microbial biomass; TN_{KCl} at $P_{2\,380\ m}$ and $P_{3\,060\ m}$ ranged significantly lower than at the remaining study sites. In the OeOa horizon median TN_{KCl} at $P_{1\,050\ m}$ was also markedly lower, than in April, but due to the high variation differences were not significant. Only at $P_{2\,380\ m}$ differences between the two samplings were significant in the OeOa horizon; TN_{KCl} decreased from 391.4 $\mu g\,g^{-1}$ in April to 140.7 $\mu g\,g^{-1}$ in November 2004. However, in both organic layer horizons, Oi and OeOa, TN_{KCl} decreased significantly along the altitudinal gradient ($r_s = -0.83$, $r_s = -0.86$, respectively at $p \leq 0.05$). In OeOa changes of TN_{KCl} were most pronounced between $P_{1\,050\ m}$ and all other sites; TN_{KCl} at $P_{1\,050\ m}$ was significantly higher. TN_{KCl} at $P_{3\,060\ m}$ was significantly lower than at all other sites (Table 36 on page 161). In 0–10 cm differences between April and November 2004 were detected for three plots (see Table 48 on page 167): at $P_{1\,050\ m}$ TN_{KCl} increased from 49.2 $\mu g\,g^{-1}$ in April to 65.02 $\mu g\,g^{-1}$ in November, at $P_{1\,540\ m}$ from 23.4 to 37.8 $\mu g\,g^{-1}$. At $P_{3\,060\ m}$ TN_{KCl} decreased from 51.8 to 31.1 $\mu g\,g^{-1}$ in November. Contrary to the first sampling, in November 2004 TN_{KCl} was significantly correlated with altitude ($r_s = -0.58$; $p \leq 0.05$). In November 2004 similar differences between the study sites like in April were detected, where TN_{KCl} at $P_{1\,050\ m}$, $P_{1\,890\ m}$ and $P_{3\,060\ m}$ ranged higher than at the remaining sites. Summarising it can also be stated that TN_{KCl} was significantly lower than in the organic layer horizons, but highest TN_{KCl} were always detected in the densely rooted OeOa.

With reference to all sites and horizons median TN_{KCl} constituted between 0.22 and 7.34 % of TN (Table 76 on page 179). At all sites except for $P_{3\,060\ m}$ the percentage of TN_{KCl} was highest in the OeOa horizon. The percentage decreased from 7.34 % at $P_{1\,050\ m}$ to 0.58 % at $P_{3\,060\ m}$. In the Oi TN_{KCl} constituted between 6.04 % (1 050 m) and 0.22 % (3 060 m). Lowest percentages of TN_{KCl} were found in the mineral soil; here they also decreased slightly along the altitudinal gradient. Minimum percentages of 1.13 % were found at 1 540 m. Contrary to the lower sites, at $P_{2\,380\ m}$ percentages of TN_{KCl} were lowest in the Oi horizon. At $P_{3\,060\ m}$ percentages of TN_{KCl} in the mineral soil were higher, than in both organic layer horizons.

4.3.4. Total KCl-extractable organic nitrogen

In April 2004 $TN_{KCl(org)}$ in the Oi horizon decreased significantly ($r_s = -0.55$; $p \leq 0.05$) along the altitudinal gradient, but highest contents were found at 1 540 m (108.5 $\mu g\,g^{-1}$) and 1 890 m (115.4 $\mu g\,g^{-1}$). In OeOa $TN_{KCl(org)}$ also was significantly correlated with altitude ($r_s = -0.73$; $p \leq 0.05$) and ranged between 171.1 $\mu g\,g^{-1}$ at $P_{1\,540\ m}$ and 4.4 $\mu g\,g^{-1}$ at $P_{3\,060\ m}$. Similarly to contents in the Oi horizon, highest $TN_{KCl(org)}$ were found at $P_{1\,540\ m}$. In the mineral soil no significant trend between $TN_{KCl(org)}$ and altitude was detected. Contents ranged between

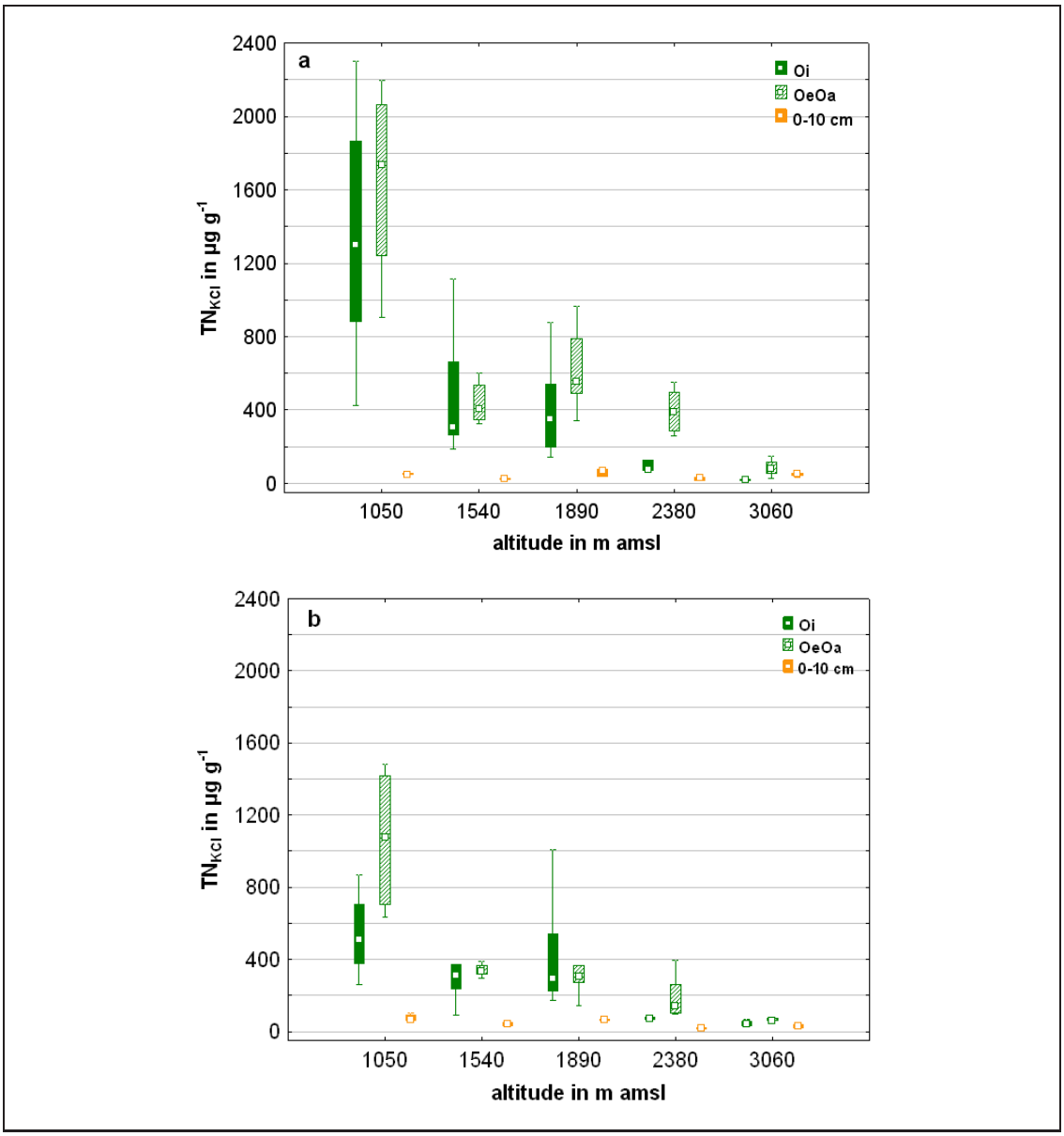


Figure 4.12: Median, quartiles and range of total KCl-extractable nitrogen (TN_{KCl}) in April 2004 (a) and November 2004 (b) in Oi, OeOa and 0–10 cm mineral soil ($n = 6$).

1.1 $\mu g\,g^{-1}$ at $P_{1\,890\ m}$ and 14.2 $\mu g\,g^{-1}$ at $P_{3\,060\ m}$ (Figure 4.13(a) on the facing page).

In November 2004 similar patterns were detected, but highest $TN_{KCl(org)}$ were found at 1 050 m for both organic layer horizons. Comparably to April 2004 $TN_{KCl(org)}$ decreased significantly ($r_s = -0.75$; $p \leq 0.05$) along the altitudinal gradient from 227.5 $\mu g\,g^{-1}$ at $P_{1\,050\ m}$ to 35.2 $\mu g\,g^{-1}$ at $P_{3\,060\ m}$ in the Oi horizon. In the same horizon $TN_{KCl(org)}$ contents were very similar to those of the sampling in April, except for sites at 1 050 and 3 060 m that both ranged significantly higher than in April 2004 (Table 48 on page 167). In OeOa $TN_{KCl(org)}$ ranged in the same span as in April 2004, no differences between the samplings were detected except for the site at 1 540 m. There $TN_{KCl(org)}$ was threefold higher in April than in November. In the mineral soil (0–10 cm)

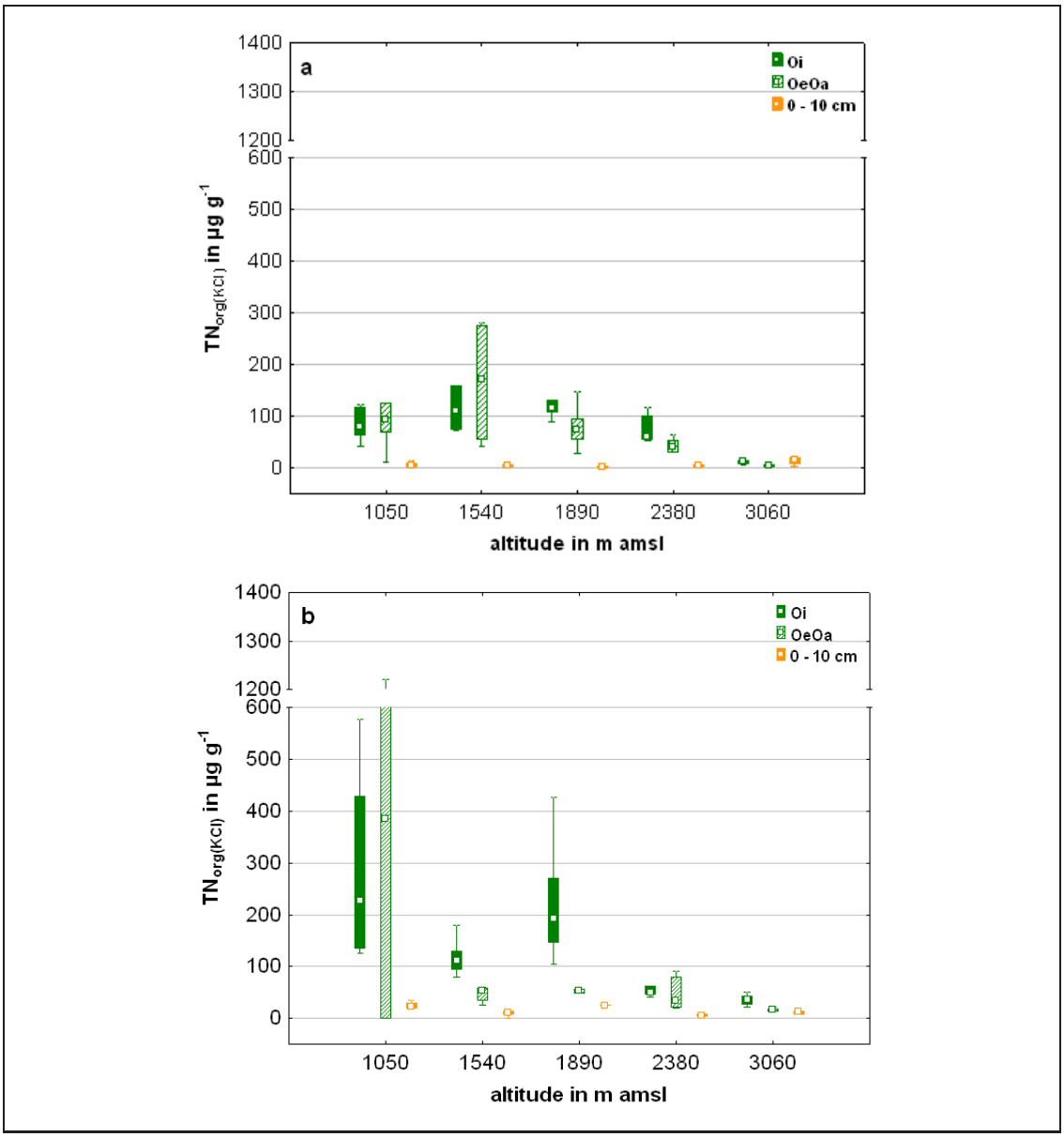


Figure 4.13: Median, quartiles and range of total KCl-extractable organic nitrogen ($TN_{KCl(org)}$) in April 2004 (a) and November 2004 (b) in Oi, OeOa and 0–10 cm mineral soil ($n = 6$).

at $P_{1\,050\ m}$, $P_{1\,890\ m}$ and $P_{2\,380\ m}$ $TN_{KCl(org)}$ as significantly higher than in April. The contents ranged between 5.2 $\mu g\,g^{-1}$ at $P_{2\,380\ m}$ and 25.23 $\mu g\,g^{-1}$ at $P_{1\,890\ m}$ (Figure 4.13(b)). The fact that no systematic differences were revealed and that variation of the data in the organic layer horizons at the two lower sites was generally high, leads to the assumption that the few detected differences between the samplings are rather coincidental.

$TN_{KCl(org)}$ generally constituted less than 1 % of TN (Table 77 on page 179). In both organic layer horizons percentages decreased along the altitudinal gradient but the increase was not monotonic. Highest percentages were calculated for the site at 1 890 m in the Oi and for $P_{1\,540\ m}$ in the OeOa. Furthermore, $TN_{KCl(org)}$ constituted between 9.1 and 77.4 % of TN_{KCl} in the Oi horizon

in April 2004 and between 40.4 and 86 % TN_{KCl} in November 2004. For both samplings the percentage of TN_{KCl} increased along the altitudinal gradient. In April 2004 $TN_{KCl(org)}$ constituted between 3.1 and 33.6 % of TN_{KCl} in the Oi horizon; no altitudinal trend was detected. In the OeOa horizon the $TN_{KCl(org)}$ represented between 18 and 26.2 % of TN_{KCl} and showed no trend between altitudes of 1 540 and 3 060 m in November 2004. At $P_{1\,050\ m}$ the percentage of $TN_{KCl(org)}$ was notably higher (Figure 4.14 on the facing page). In 0–10 cm mineral soil $TN_{KCl(org)}$ varied from 0 to 33.8 % in April 2004. At the second sampling percentages were higher, but also showed only a slight tendency of increasing percentages along the altitudinal gradient (Figure 4.15 on page 56).

For mineral soils under fallow, Böhm (2005) reports KCl-extractable organic nitrogen contents of 1–4 $\mu g\,g^{-1}$, which corresponded to less than 1 % of TN and was lower than in the present study. In organic layers under black locust (*Robinia pseudoacacia* L.) and Scots pine (*Pinus sylvestris* L.) in NE Germany, KCl-extractable organic nitrogen ranged between 0.01 and 1.03 $g\,kg^{-1}$ (Landgraf et al., 2005), which was considerably higher than in the present study. These authors underline that $TN_{KCl(org)}$ was strongly affected by the type of forest stand.

4.3.5. Total KCl-extractable inorganic nitrogen

$TN_{KCl(inorg)}$ included ammonia- (NH_4^+-N) and nitrate-derived nitrogen (NO_3^--N) and generally varied considerably over all plots and horizons (Figure 4.16 on page 57). In April 2004 $TN_{KCl(inorg)}$ decreased significantly in both organic layer horizons Oi and OeOa along the altitudinal gradient ($r_s = -0.88$ and $r_s = -0.73$, respectively at $p \leq 0.05$). Contents in the Oi ranged from 5.9 $\mu g\,g^{-1}$ at $P_{3\,060\ m}$ to 1 179.6 $\mu g\,g^{-1}$ at $P_{1\,050\ m}$ and from 76.3 $\mu g\,g^{-1}$ at $P_{3\,060\ m}$ to 1 443.8 $\mu g\,g^{-1}$ at $P_{1\,050\ m}$ (Figure 4.16(a) on page 57). Thus, highest $TN_{KCl(inorg)}$ were found in the densely rooted OeOa horizon. At 2 380 and 3 060 m differences between the organic layer horizons were significant (Table 23 on page 154). In 0–10 cm mineral soil $TN_{KCl(inorg)}$ ranged significantly lower as it only amounted to values between 18.9 and 72.7 $\mu g\,g^{-1}$. $TN_{KCl(inorg)}$ in the mineral soil was not correlated to altitude in April 2004 (Table 1 on page 138). In November 2004 $TN_{KCl(inorg)}$ showed very similar contents and patterns; very few significant differences between the samplings occurred (Table 48 on page 167), they were most pronounced in both organic layer horizons at $P_{1\,050\ m}$ (Figure 4.16(b) on page 57). In November 2004 $TN_{KCl(inorg)}$ decreased significantly in both organic layer horizons ($r_s = -0.76$ and $r_s = -0.79$ respectively at $p \leq 0.05$) along the altitudinal gradient as well. Contrary to the first sampling, in November 2004 $TN_{KCl(inorg)}$ in 0–10 cm minerals soil was significantly correlated with altitude ($r_s = -0.60$, $p \leq 0.05$).

$TN_{KCl(inorg)}$ constituted up to 6.23 % of TN in the organic layer horizons at $P_{1\,050\ m}$ (Table 78 on page 180). At the remaining sites percentages of $TN_{KCl(inorg)}$ ranged between 0.07 and 2.79 %, in all studies horizons percentages decreased along the altitudinal gradient. In the Oi horizon up to 90.9 % of TN_{KCl} was attributed to $TN_{KCl(inorg)}$ in April 2004 (Figure 4.14 on the facing page). In November 2004 the percentage was smaller; $TN_{KCl(inorg)}$ contributed between 14 and 59.6 % to TN_{KCl} (Figure 4.15 on page 56). For both samplings the percentage decreased with altitude, this trend was more pronounced in April 2004. Compared to Oi the contribution of $TN_{KCl(inorg)}$ in OeOa and 0–10 cm was higher for most of the sites and ranged from 66.4 % at $P_{1\,540\ m}$ to 96.8 % at $P_{1\,890\ m}$ in OeOa and from 66.2 at $P_{3\,060\ m}$ to 100 % at $P_{1\,890\ m}$ in the mineral soil in April

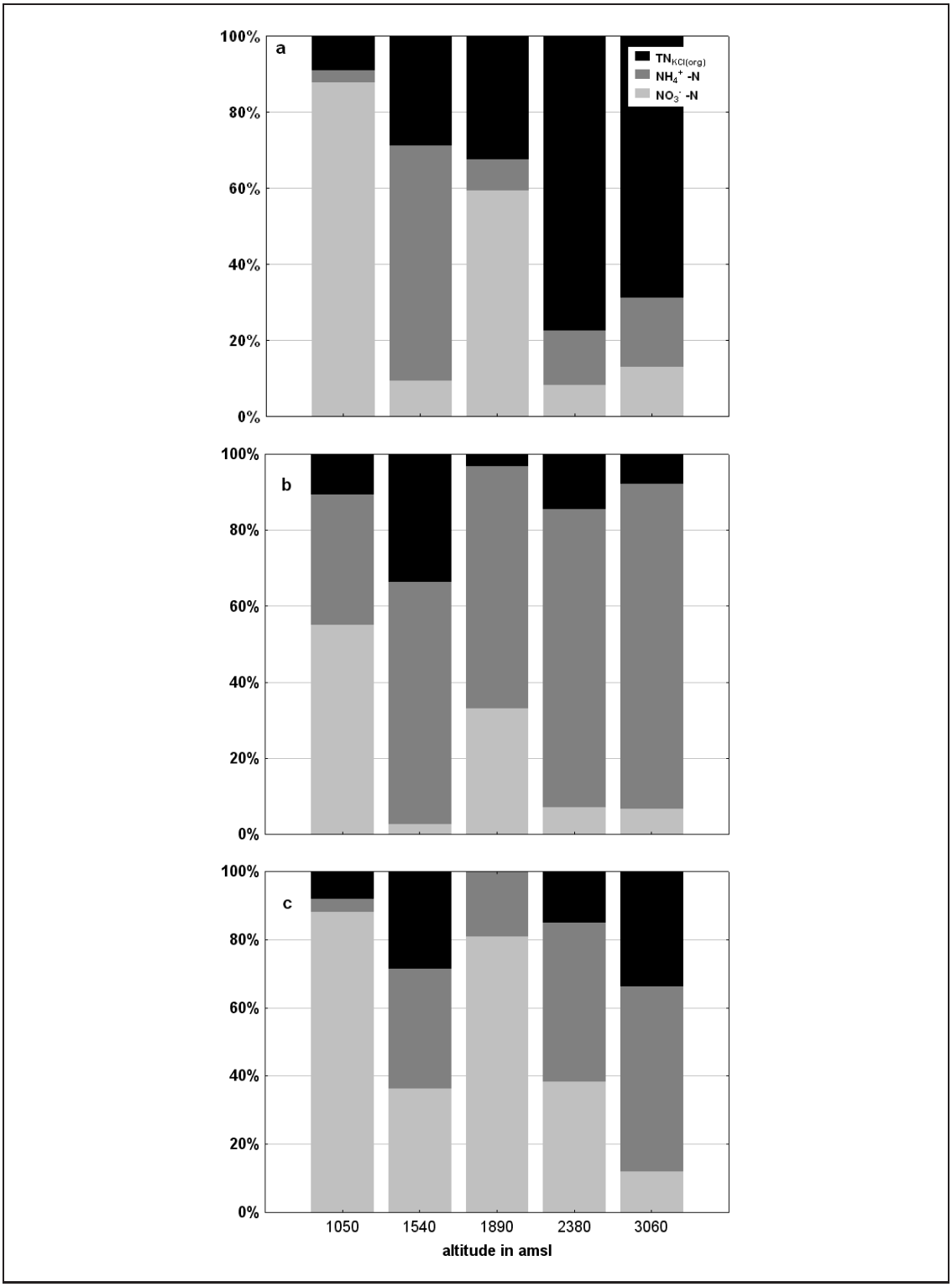


Figure 4.14: Average percentages of $TN_{KCl(org)}$, ammonium and nitrate derived N of TN_{KCl} in Oi (a), OeOa (b) and 0–10 cm mineral soil (c) in April 2004.

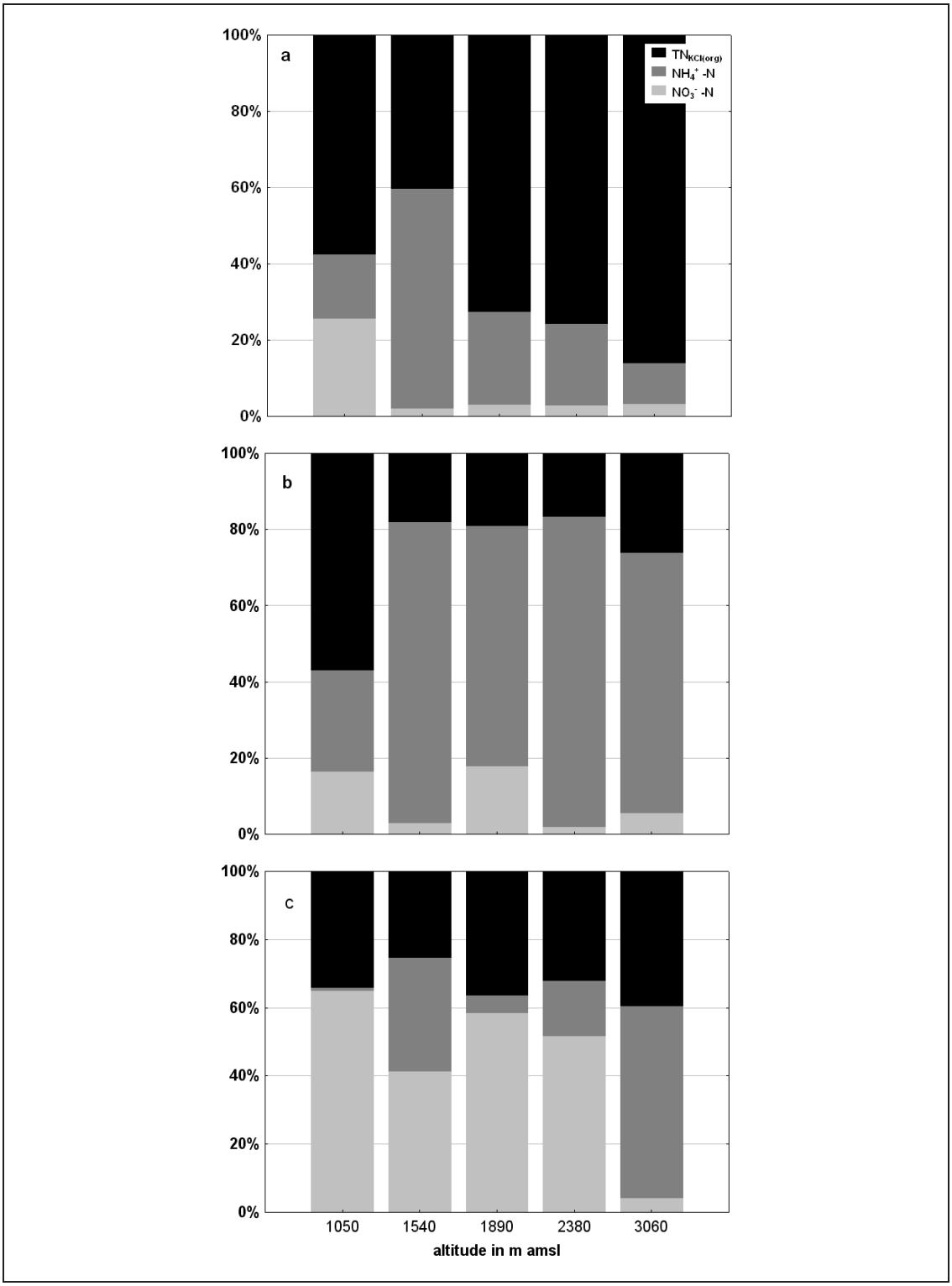


Figure 4.15: Average percentages of $TN_{KCl(org)}$, ammonium and nitrate derived N of TN_{KCl} in Oi (a), OeOa (b) and 0–10 cm mineral soil (c) in November 2004.

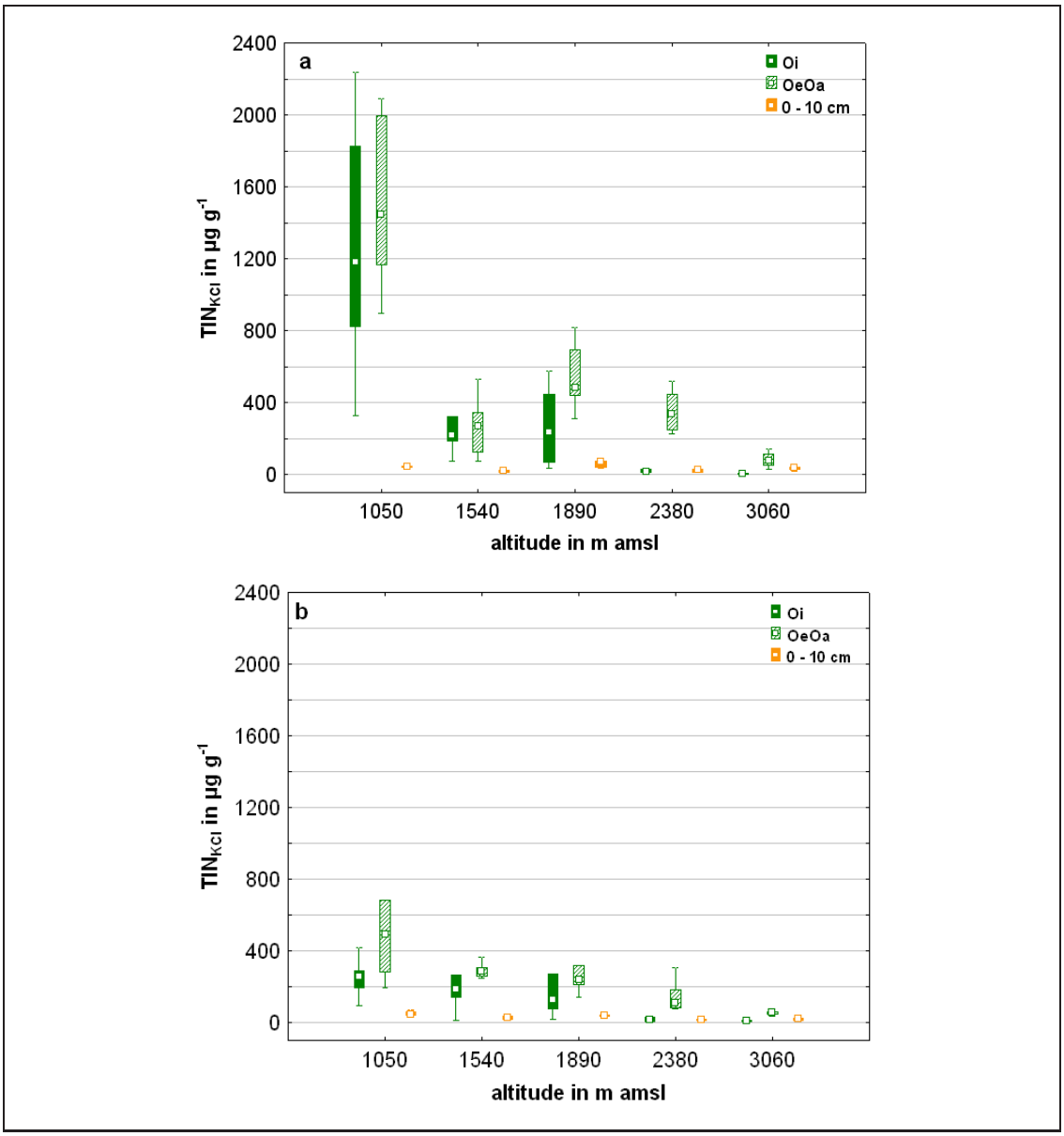


Figure 4.16: Median, quartiles and range of total KCl-extractable inorganic nitrogen (TIN_{KCl}) in April 2004 (a) and November 2004 (b) in Oi, OeOa and 0–10 cm mineral soil ($n = 6$).

2004. In November 2004 percentages of $TN_{KCl(inorg)}$ of TN_{KCl} were similar to the first sampling in OeOa as well as in 0–10 cm. In both horizons $TN_{KCl(inorg)}$ showed no consistent trend along the altitudinal gradient.

Median NH_4^+-N showed patterns similar to $TN_{KCl(inorg)}$ and was significantly ($r_s = -0.72$; $p \leq 0.05$) correlated with altitude. In April 2004 NH_4^+-N of the Oi horizons ranged very low, between 3.4 µg g^{-1} at $P_{3\,060\ m}$ and 40.1 µg g^{-1} at $P_{1\,050\ m}$. Exceptionally high contents occurred at 1 540 m (Figure 4.17(a) on page 59). Median NH_4^+-N in OeOa horizons amounted up to 593.2 µg g^{-1} at 1 050 m and were higher than in Oi of all studied sites except for $P_{1\,540\ m}$ (Table 24 on page 154). This parameter was significantly correlated with altitude as well ($r_s = -0.48$,

$p \leq 0.05$). Contrary to most other data collected in this study, NH_4^+-N in 0–10 cm was positively correlated with altitude ($r_s = 0.80$; $p \leq 0.05$), contents were similar to those in Oi and did not exceed 30 $\mu g\,g^{-1}$.

In November 2004 the observed results differed little from those of the first sampling (Figure 4.17(b) on the facing page). Significant differences between the samplings were found for few sites and horizons (Table 48 on page 167). General trends remained the same: NH_4^+-N contents in Oi and OeOa were inversely correlated with altitude ($r_s = -0.74$ and $r_s = -0.63$, respectively at $p \leq 0.05$). In the mineral soil NH_4^+-N was positively correlated with altitude as well, even though the correlation coefficient was smaller ($r_s = 0.45$; $p \leq 0.05$).

NH_4^+-N constituted less than 1 % of TN in most of the studied horizons (Table 79 on page 180). Exceptions occurred in OeOa of sites $P_{1\,050\ m}$ to $P_{2\,380\ m}$, as well as in Oi of $P_{1\,540\ m}$. Here, NH_4^+-N constituted up to 2.86 %. Thus, the percentage of NH_4^+-N of TN was highest in the root dominated OeOa.

With respect to TN_{KCl}, the percentage of NH_4^+-N differed when comparing the studied horizons, but lacked uniform trends along the altitudinal gradients. Only in 0–10 cm NH_4^+-N tended to be positively related to altitude at both samplings (Figures 4.14 on page 55 and Figure 4.15 on page 56).

Median NO_3^--N declined in all studied horizons and for both samplings significantly ($p \leq 0.05$) at the altitudinal gradient (Table 1 on page 138). In April 2004 median NO_3^--N were comparably low in the Oi horizons; less than 30 $\mu g\,g^{-1}$ at 1 540, 2 380 and 3 060 m. At 1 050 m NO_3^--N was significantly higher than at all other sites and varied strongly (Figure 4.18(a) on page 60). The site at 1 890 m had an intermediate position; NO_3^--N contents were significantly higher than at higher altitudes including a higher variation, but lower than at $P_{1\,050\ m}$. In the OeOa horizon similar contents of less than 30 $\mu g\,g^{-1}$ were determined at all sites except for $P_{1\,050\ m}$. There median NO_3^--N was 955.6 $\mu g\,g^{-1}$ and contents also varied considerably. In the mineral soil median NO_3^--N were 43.4 and 58.53 $\mu g\,g^{-1}$ at $P_{1\,050\ m}$ and $P_{1\,890\ m}$, respectively. At the remaining sites, NO_3^--N ranged below 12 $\mu g\,g^{-1}$. Consequently, median contents declined with increasing soil depth at the three lower study sites. At $P_{2\,380\ m}$ and $P_{3\,060\ m}$ an inverse trend was detected (Table 2 on page 139). The results of the second soil sampling in November 2004 generally supported the findings of April 2004 (Figure 4.17(a) on the facing page). NO_3^--N declined significantly along the altitudinal gradient in all studied horizons (Table 1 on page 138). In the Oi horizons at $P_{1\,050\ m}$, $P_{1\,540\ m}$ and $P_{2\,380\ m}$ NO_3^--N ranged significantly lower than in April 2004, the same was true for OeOa at $P_{1\,050\ m}$ and in 0–10 cm at $P_{3\,060\ m}$. Comparable to the dynamics of NH_4^+-N these results indicate a high variation of KCl-extractable nitrogen species over seasons.

NO_3^--N constituted between 1 and 5.3 % of TN in the horizons of the sites that generally contained more nitrate derived nitrogen, $P_{1\,050\ m}$ and $P_{1\,890\ m}$. At the remaining altitudes less than 1 % of TN was NO_3^--N (Table 80 on page 180). Corresponding to low NO_3^--N contents at sites $P_{1\,540\ m}$, $P_{2\,380\ m}$ and $P_{3\,060\ m}$, percentages of NO_3^--N of TN_{KCl} were consistently lower than at $P_{1\,050\ m}$ and $P_{1\,890\ m}$; they ranged between 2.7 and 13 % in the organic layer horizons (Figure 4.14 on page 55). In comparison, the percentage of NO_3^--N of TN_{KCl} in Oi and OeOa at $P_{1\,050\ m}$ were 87.8 and 55.1 %, at $P_{1\,890\ m}$ 59.4 and 33.1 %. In 0–10 cm these differences were also very pronounced, but percentages of NO_3^--N were higher than in the organic layer horizons, except for $P_{1\,050\ m}$ and $P_{1\,890\ m}$. There NO_3^--N-percentages ranged at similar levels like in Oi

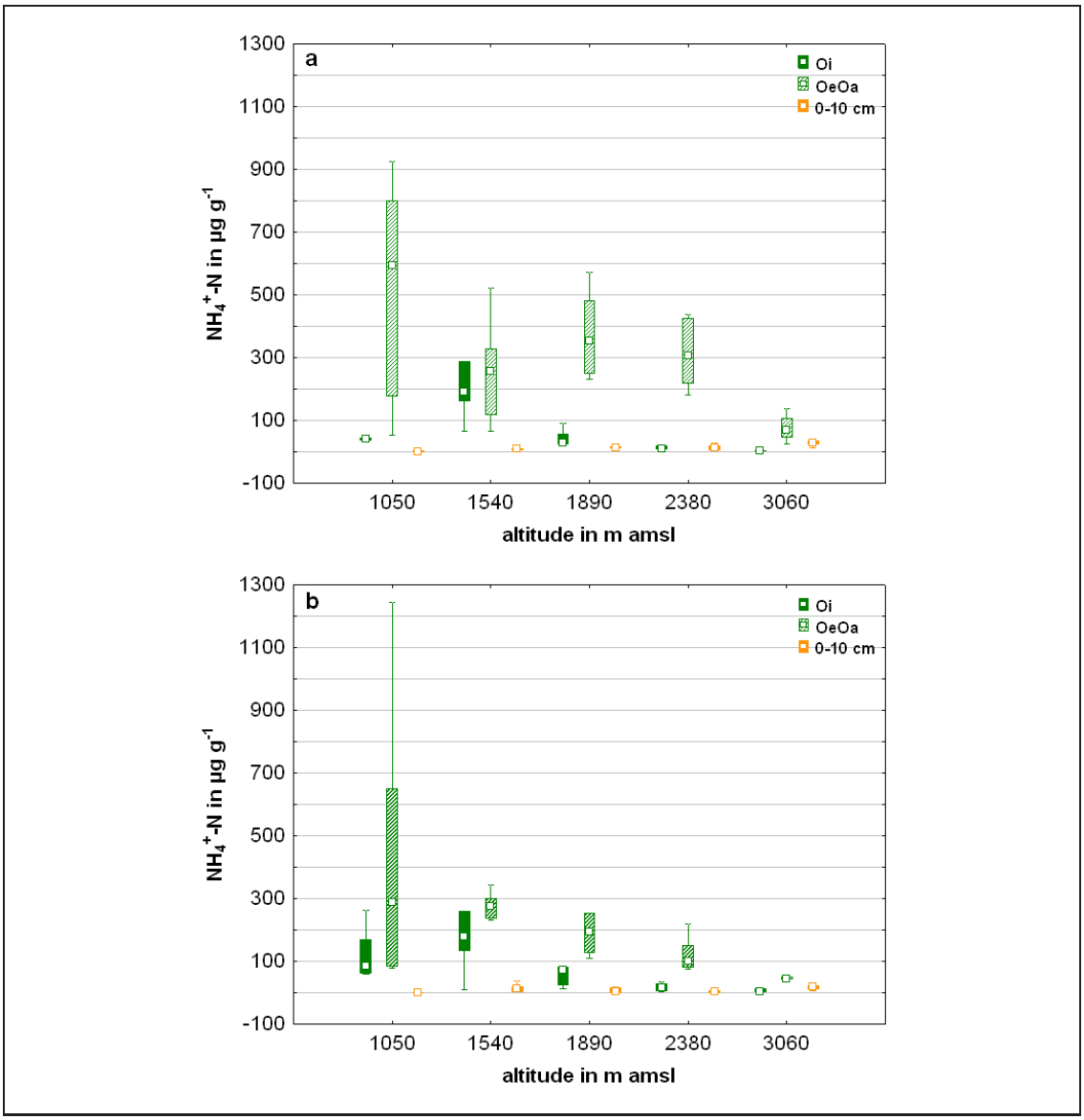


Figure 4.17: Median, quartiles and range of total KCl-extractable ammonium-derived nitrogen (NH_4^+-N) in April 2004 (a) and November 2004 (b) in Oi, OeOa and 0–10 cm mineral soil ($n = 6$).

(Figure 4.14 on page 55). In November 2004 percentages in the Oi horizon were considerably lower at all plots. Highest percentages of NO_3^--N were detected at $P_{1\,050\ m}$, at the remaining sites percentages ranged from 1.9 to 3.2 % (Figure 4.15 on page 56). In OeOa a pattern similar to that of April 2004 was detected, but percentages were lower (Figure 4.15 on page 56). In 0–10 cm most differences between the sampling were detected. At 1 050, 1 890 and 3 060 m percentages were smaller, at 1 540 and 2 380 m higher.

$TN_{KCl(inorg)}$, NH_4^+- and NO_3^--N contents in organic layers and the top mineral horizon were comparable to findings in the recent literature. In the mineral soil under *Pinus radiata* Don. in the temperate humid zone of Spain ammonia contents were 7.37 ± 4.48 mg kg^{-1} (González-Prieto and Villar, 2003). In mineral soils under primary forest along an altitudinal gradient from 700

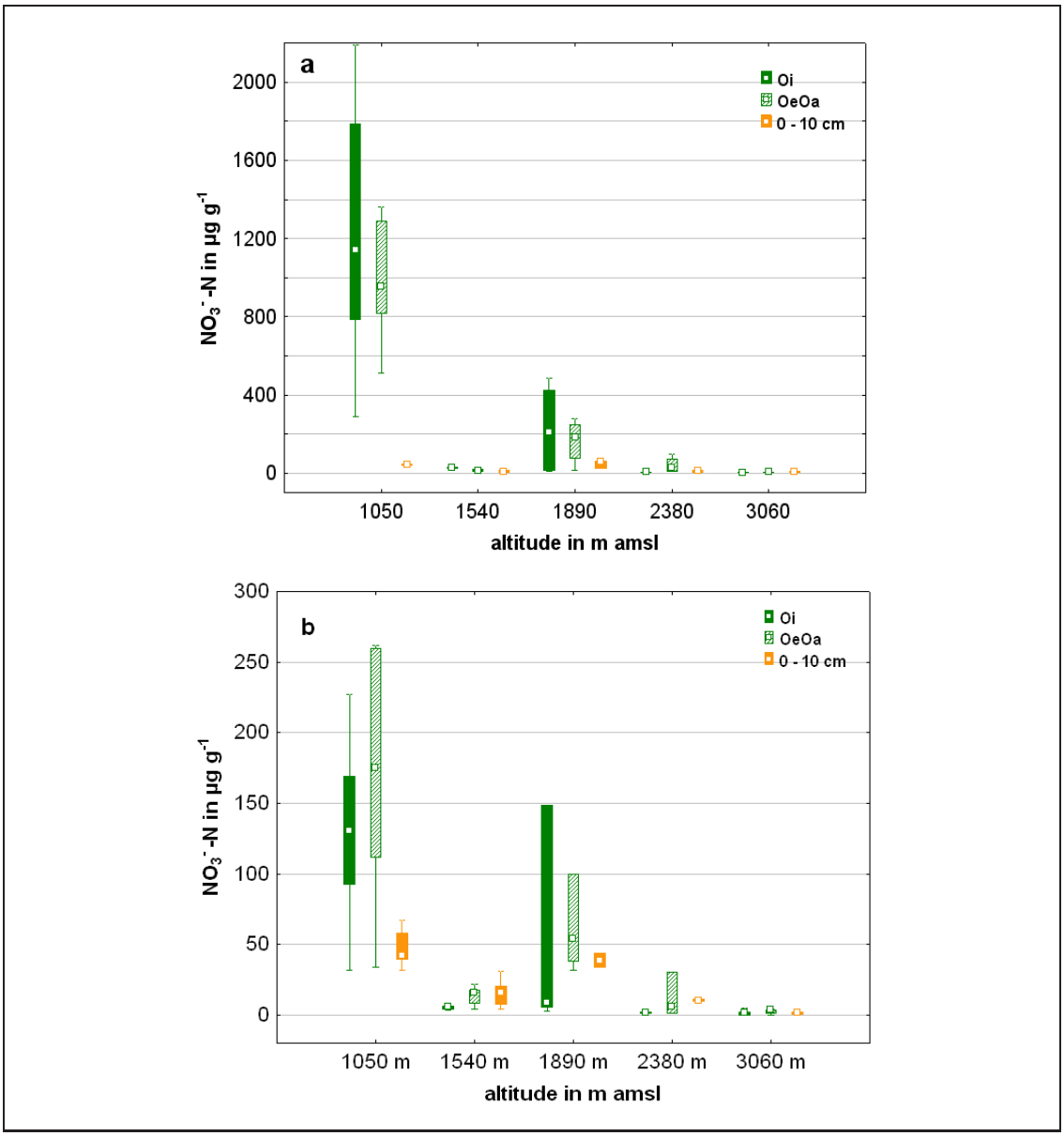


Figure 4.18: Median, quartiles and range of total KCl-extractable nitrate-derived nitrogen (NO_3^--N) in April 2004 (a) and November 2004 (b) in Oi, OeOa and 0–10 cm mineral soil ($n = 6$). Please note the different scaling.

to 3 100 m amsl in Malaysia NH_4^+-N ranged from 15 to 80 µg g^{-1} and NO_3^--N from 0 to 25 µg g^{-1} (Hall et al., 2004). These authors also observed a significant relation between inorganic N and elevation. Nitrate tended to decrease with altitude, while ammonium also decreased in ultrabasic soils and slightly increased in sedimentary soils. In Oxisols and Ultisols under evergreen tropical forest in the Brazilian lowlands (Neill et al., 1997) ammonium contents were influenced by season and varied between 1.27 and 17.59 µg N g^{-1}, the average was 6.47 µg g^{-1}. Nitrate was also related to season and ranged from 1.07 to 11.87 µg g^{-1} and averagely amounted to 5.24 µg g^{-1}.

Another study from the Brazilian lowlands (Neill et al., 1995) reports between 2.62 and 4.86 µg NH_4^+-N g^{-1} and 2.91–4.53 µg NO_3^--N g^{-1} for 0–10 cm mineral soil. These results are

comparable to ammonium contents found at different altitudes in RBSF and PNP, especially at $P_{1\,050\ m}$ and to nitrate contents in the mineral soil at $P_{3\,060\ m}$. Sarmiento and Bottner (2002) studied top mineral soils (0–20 cm) at high altitudes in Venezuelan páramo under special agricultural use, that included long fallow intervals for fertility restoration. These authors observed up to 2.8 mg NH_4^+-N kg^{-1} soil and up to 4.4 mg NO_3^--N kg^{-1} soil and classified these as low. These results are also comparable to contents in mineral soils of RBSF and PNP.

However, similar to other parameters, for inorganic nitrogen no comparative data for organic horizons is provided by the recent literature. Lowland tropical forests seldom have organic layers due to rapid decomposition and therefore I can only relate mineral soil parameters to recent findings.

4.3.6. Net nitrogen mineralisation

Net rates of ammonification, nitrification and mineralisation varied considerably depending on altitude, studied horizon and duration of incubation (Tables 4.1 to 4.3 on pages 61–62).

In the top organic horizon Oi, net ammonification ranged between −29.96 and 1.96 µg NH_4^+-N g^{-1} soil d^{-1} and increased significantly with altitude (Table 1 on page 138), in fact only at 2 380 and 3 060 m positive net ammonification occurred. When considering the detailed ammonification rates for shorter periods of incubation, the plots at 1 050 and 1 540 m have high net ammonification rates during the first 24 h of incubation (Table 4.1), which decrease with ongoing incubation. At 1 890 and 2 380 m net ammonification increases during incubation for 14 days and decreases at 3 060 m.

In the OeOa horizon similar patterns can be observed, net ammonification after 14 days of

Table 4.1: Median net ammonification rates in the respective horizons after 1, 4, 7 and 14 days of incubation.

horizon	day[a]	1 050 m	1 540 m	1 890 m	2 380 m	3 060 m
		net ammonification in µg g^{-1} soil d^{-1}				
Oi	1	38.07	36.84	−35.05	−14.03	4.91
	4	−9.53	1.99	−5.28	−5.47	2.61
	7	−5.11	−11.09	−20.89	−2.40	1.39
	14	−29.96	−10.14	−19.94	0.67	1.96
OeOa	1	37.70	3.11	−12.29	−4.10	28.77
	4	15.69	17.68	2.31	2.65	7.74
	7	11.28	−5.40	10.05	3.85	7.35
	14	4.46	4.65	7.03	7.46	7.45
0–10 cm	1	−0.18	1.39	0.97	2.72	−2.24
	4	−0.11	0.49	0.94	0.51	1.22
	7	0.00	0.52	0.92	0.52	1.14
	14	−0.02	0.55	0.91	0.33	1.00

[a] day of incubation

Table 4.2: Median net nitrification rates in the respective horizons after 1, 4, 7 and 14 days of incubation.

horizon	day[a]	1 050 m	1 540 m	1 890 m	2 380 m	3 060 m
		net nitrification in $\mu g\,g^{-1}$ soil d^{-1}				
Oi	1	15.18	0.28	0.42	0.88	−1.45
	4	10.93	0.06	0.92	0.51	0.54
	7	12.52	0.67	0.48	−0.15	0.00
	14	9.61	−0.10	0.25	0.23	−0.02
OeOa	1	18.44	−3.37	0.35	0.11	−1.85
	4	7.89	−0.20	1.15	1.49	−0.10
	7	10.53	5.93	1.10	1.82	0.17
	14	12.18	0.12	0.53	1.03	0.00
0–10 cm	1	2.84	0.64	−1.75	−0.16	−0.56
	4	1.30	0.26	0.62	0.01	0.08
	7	1.13	0.57	0.79	0.19	0.19
	14	1.50	0.07	0.09	0.13	0.17

[a] day of incubation

Table 4.3: Median net mineralisation rates in the respective horizons after 1, 4, 7 and 14 days of incubation.

horizon	day[a]	1 050 m	1 540 m	1 890 m	2 380 m	3 060 m
		net mineralisation in $\mu g\,g^{-1}$ soil d^{-1}				
Oi	1	53.24	37.12	−34.64	−13.15	3.45
	4	1.40	2.05	−4.36	−4.96	3.14
	7	7.41	−10.43	−20.41	−2.54	1.38
	14	−20.35	−10.24	−19.69	0.90	1.95
OeOa	1	56.14	−0.27	−11.94	−3.99	26.92
	4	23.58	17.47	3.47	4.14	7.64
	7	21.81	0.53	11.15	5.67	7.52
	14	16.63	4.78	7.56	8.48	7.45
0–10 cm	1	2.66	2.03	−0.78	2.56	−2.80
	4	1.19	0.75	1.56	0.53	1.30
	7	1.13	1.09	1.71	0.71	1.33
	14	1.49	0.62	1.00	0.46	1.17

[a] day of incubation

incubation is positively related to altitude as well ($r_s = 0.9$) and increases from 4.46 µg NH_4^+-N g^{-1} soil d^{-1} at $P_{1\,050\ m}$ to 7.45 µg NH_4^+-N g^{-1} soil d^{-1} at $P_{3\,060\ m}$. In 0–10 cm mineral soil net ammonification ranges between −0.02 µg NH_4^+-N g^{-1} soil d^{-1} at $P_{1\,050\ m}$ and 1.0 µg NH_4^+-N g^{-1} soil d^{-1} at $P_{3\,060\ m}$ and is not significantly related to altitude, even though it shows the same trend as in the organic layer horizons.

Net nitrification is inversely related to net ammonification, i. e. tends to decline along the altitudinal gradient. In the Oi, net nitrification after 14 days of incubation is highest at 1 050 m (9.61 µg NO_3^--N g^{-1} soil d^{-1}) and very low at the remaining sites (Table 4.2 on the facing page). In OeOa highest net nitrification also occurs at 1 050 m (12.18 µg NO_3^--N g^{-1} soil d^{-1}) and ranges between 0.00 and 1.03 µg NO_3^--N g^{-1} soil d^{-1} at the remaining plots. In 0–10 cm mineral soil, nitrification rates are even lower. In none of the studied horizons, net nitrification was significantly correlated with altitude (Table 1 on page 138).

Net mineralisation of nitrogen after 14 days of incubation was positively related to altitude ($r_s = 0.9$) in the Oi horizon and increased from −20.35 to 1.95 µg N g^{-1} soil d^{-1}. At $P_{1\,050\ m}$ net mineralisation was high during the first 24 h of incubation but decreased with duration of the experiment to negative values, thus nitrogen was immobilised with ongoing incubation. The same was observed in Oi of $P_{1\,540\ m}$ (Table 4.3 on the facing page). At $P_{1\,890\ m}$ net immobilisation of nitrogen occurred over the whole incubation period. At $P_{2\,380\ m}$ during the first week of incubation nitrogen was immobilised as well, net mineralisation was observed after 14 days. At $P_{3\,060\ m}$ net nitrogen mineralisation occurred during all the incubation, but declined during the 14 days. In the OeOa horizon, immobilisation was observed only during the first 24 h of incubation at 1 540, 1 890 and 2 380 m. At 1 050 and 3 060 m net mineralisation was highest during the first 24 h and declined with ongoing incubation (Table 4.3 on the facing page). Mineralisation rate was not correlated with altitude, but was highest at $P_{1\,050\ m}$, lowest at $P_{1\,540\ m}$ and intermediate at the remaining sites. In the mineral soil (0–10 cm) immobilisation also was observed during the first 24 h only, at sites $P_{1\,890\ m}$ and $P_{3\,060\ m}$. Net mineralisation then ranged between 0.46 and 2.66 µg N g^{-1} soil d^{-1} (Table 4.3 on the facing page), declined during incubation at most of the sites and was not related to altitude (Table 1 on page 138).

Neill et al. (1997) studied Oxi- and Ultisols under moist upland terra firme evergreen tropical forest vegetation and determined net nitrification rates after incubation of mineral topsoils for 7 days. Net nitrification was 0–3.5 µg N g^{-1} soil and net mineralisation ranged from 0.91 to 1.88 µg N g^{-1} soil. Both rates were comparable to nitrification and mineralisation in mineral soils of the current study. These authors also reviewed net mineralisation studied in tropical soils and consider rates between 0.5–2.0 µg N $g^{-1}\,d^{-1}$ in tropical mineral soils as consistent, which is also comparable with my findings. In a study on land use change on Andosols in the lower montane zone of Ecuador (Rhoades and Coleman, 2004) net mineralisation amounted to 0.6 and 1.1 µg N $g^{-1}\,d^{-1}$, which is considered consistent with other studies from Hawaii and Costa Rica. In the same area net mineralisation under single N-fixing (*Inga* spec.) and non-fixing (*Psidium* spec.) pasture trees was very similar to net nitrification, which amounted to 0.8 and 0.4 $\mu g\,g^{-1}\,d^{-1}$, respectively. In a study in southeast Asia (Hall et al., 2004) net nitrogen mineralisation declined along an altitudinal gradient from 650 to 3 050 m amsl and ranged between −1 and 3 µg N $g^{-1}\,d^{-1}$. The studied sites developed on ultrabasic rock and were influenced by anthropogenic N deposition. At sites under primary forest no immobilisation was observed, net

mineralisation was between 1 and 4 $\mu g\,g^{-1}\,d^{-1}$. In mineral soils under tropical moist forest in situ mineralisation was −0.36 to +1.15 $\mu g\,g^{-1}\,d^{-1}$ (Smith et al., 1998).

4.3.7. Gross nitrogen mineralisation

Gross nitrogen mineralisation rates were characterised by a high variation, especially at $P_{1\,050\ m}$, where gross rates in the top organic layer (Oi) ranged from 80 to 213.3 $\mu g\,g^{-1}\,d^{-1}$. In the OeOa horizon gross rates were between 30 and 80 $\mu g\,g^{-1}\,d^{-1}$ and in the mineral soil between 0 and 50 $\mu g\,g^{-1}\,d^{-1}$. In the all other studied horizons of the remaining plots gross mineralisation rates ranged between 0 and 50 $\mu g\,g^{-1}\,d^{-1}$, except for Oi at $P_{1\,890\ m}$. There gross mineralisation was between 107 and 120 $\mu g\,g^{-1}\,d^{-1}$ and therefore comparable to gross rates in the Oi at $P_{1\,050\ m}$ (Figure 4.19). Only in the top organic layer, gross mineralisation was significantly related to altitude ($r_s = -0.79$; $p \leq 0.05$). In the OeOa there was a tendency of decreasing gross mineralisation as well, but in 0–10 cm gross rates tended to increase along the altitudinal gradient.

NH_4^+ consumption rates, i. e. rates of ammonium immobilisation showed very similar patterns (Figure 4.20 on the facing page); highest immobilisation occurred in the Oi horizons at $P_{1\,050\ m}$ and $P_{1\,890\ m}$ and ranged between 80 and 140 $\mu g\,g^{-1}\,d^{-1}$. In OeOa and 0–10 cm at $P_{1\,050\ m}$ NH_4^+ consumption was between 0 and 70 $\mu g\,g^{-1}\,d^{-1}$, thus also was highly variable. In the remaining horizons NH_4^+ consumption rates ranged between 0 and 35 $\mu g\,g^{-1}\,d^{-1}$. Ammonium immobilisation decreased significantly with altitude ($r_s = -0.74$, $p \leq 0.05$), showed no trend at all in the densely rooted OeOa and tended to increase in the upper mineral soil ($r_s = 0.42$; $p \leq 0.05$).

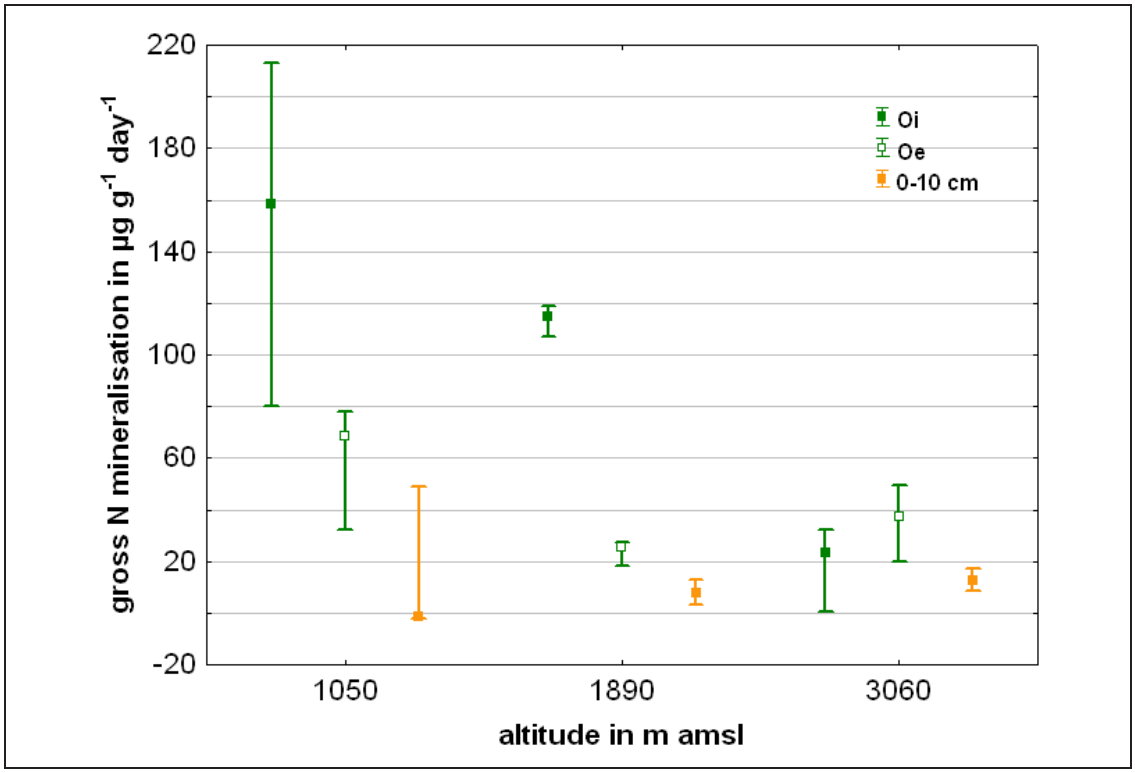


Figure 4.19: Gross nitrogen mineralisation rates at three selected study sites in Oi, OeOa and 0–10 cm. Small boxes represent the median of $n = 3$ replicates, whiskers represent data range.

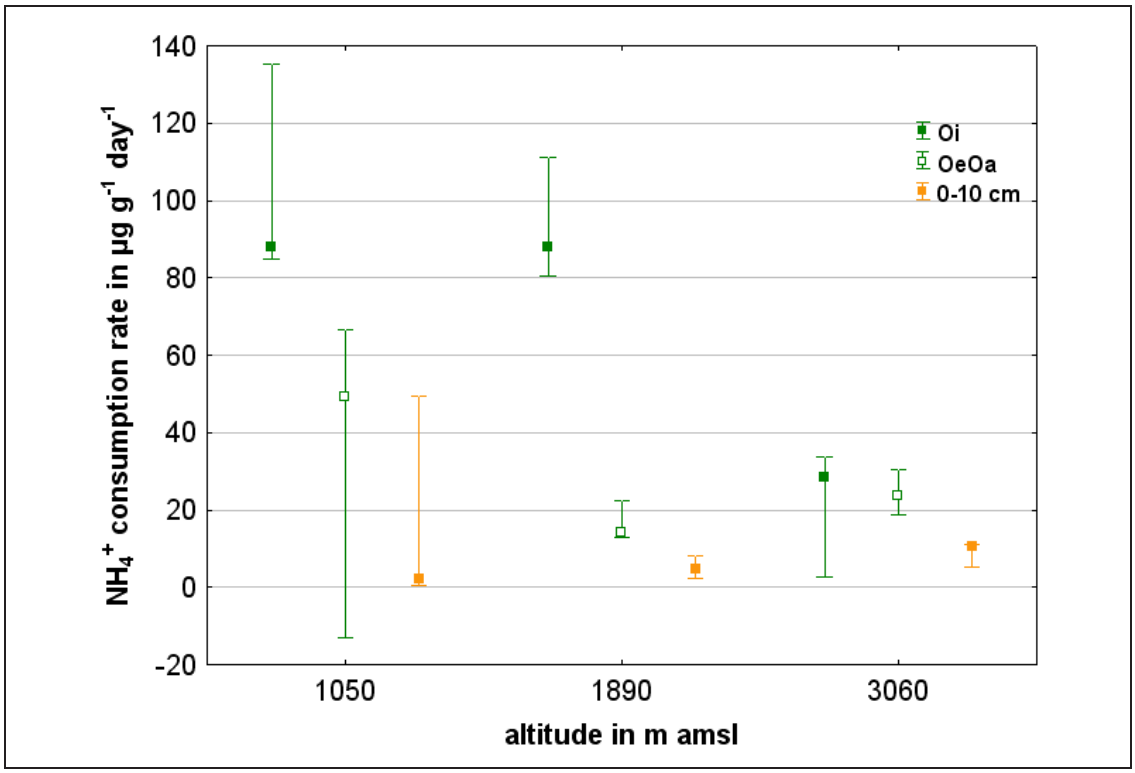


Figure 4.20: NH_4^+ consumption rates at three selected study sites in Oi, OeOa and 0–10 cm. Small boxes represent the median of $n = 3$ replicates, whiskers represent data range.

In the recent literature a multitude of studies on gross transformations of nitrogen transformation was published, but very few for tropical soils and to my knowledge only one study, that investigated gross mineralisation in organic layer horizons in the Boreal Shield region, Canada (Westbrook and Devito, 2004). These authors reported gross ammonification rates of 15 and 8 $\mu g\,g^{-1}\,d^{-1}$ in peatland and upland forest floor samples, respectively. In mineral soils of the same study area gross ammonification was 2 $\mu g\,g^{-1}\,d^{-1}$. Gross mineralisation in Dystric Cambisols under deciduous forests of southern Sweden was between 2.7 and 22.5 $\mu g\,g^{-1}\,d^{-1}$ (Bengtsson et al., 2003). In mature lodgepole pine stand in the Yellowstone National Park under cool and dry conditions gross mineralisation ranged between 0.49 and 3.82 $\mu g\,g^{-1}\,d^{-1}$ and ammonium consumption was between -0.03 and $+4.67$ $\mu g\,g^{-1}\,d^{-1}$ (Smithwick et al., 2005). The authors consider their results as comparable with other studies from other forested ecosystems but at the low end. In agroforestry systems in New Zealand soil gross mineralisation ranged also between 1 and 4 $\mu g\,g^{-1}\,d^{-1}$ (Zaman and Chang, 2004) and in pasture soils between 3 and 6 $\mu g\,g^{-1}\,d^{-1}$ (Mishra et al., 2005). In a sandy clay loam of western Australia gross mineralisation rates were 5.6 and 10.1 $\mu g\,g^{-1}\,d^{-1}$, respectively. Mary et al. (1998) summarized several studies in different ecosystems with gross mineralisation rates between 1 and 200 $\mu g\,g^{-1}\,d^{-1}$. Compared to this data gross mineralisation and NH_4^+ consumption in the studied mineral soils ranged above average. In an unfertilized grassland under humid temperate continental climate and low N deposition of 11 $kg\,ha^{-1}\,a^{-1}$ gross N mineralisation was 4.9–8.2 mg N $kg^{-1}\,d^{-1}$ and gross NH_4^+ immobilisation 3.1–6.7 mg N $kg^{-1}\,d^{-1}$ (Corre et al., 2002). This was comparable to the rates observed in the

mineral soil of the present study. Without comparable studies it proves to be difficult to evaluate gross mineralisation rates determined for the studied organic layer horizons. Compared to in the mineral soil samples, gross rates of the organic layer horizons were consistently higher.

4.4. Size, structure and activity of microbial biomass

4.4.1. Microbial carbon

In April 2004 C_{mic} in the Oi decreased significantly ($r_s = -0.49$; $p \leq 0.05$) from $P_{1\,050\ m}$ (8 405.3 µg C_{mic} g^{-1}) to 4 560.1 and 5 066.18 µg C_{mic} g^{-1} at $P_{2\,380\ m}$ and $P_{3\,060\ m}$, respectively (Figure 4.21(a) on the facing page). This decrease was not linear along the altitudinal gradient but microbial biomass carbon was significantly higher at 1 050, 1 540 and at 1 890 m, than at 2 380 and 3 060 m. Furthermore, spatial variation of microbial biomass carbon was slightly smaller at the two upper plots. C_{mic} in the Oi determined in the second set of samples taken in November 2004 was not correlated with altitude, even though a very similar pattern along the gradient persisted: the three lower plots ranged between 5 953.13 and 8 927.05 µg g^{-1} and increased slightly along the gradient (Figure 4.21(b) on the facing page). The upper plots had substantially lower C_{mic}: 5 061.5 at $P_{2\,380\ m}$ and 5 945.68 µg g^{-1} at $P_{3\,060\ m}$. Thus, C_{mic} in November 2004 at $P_{1\,890\ m}$, $P_{2\,380\ m}$ and $P_{3\,060\ m}$ ranged higher than C_{mic} in April 2004, but the differences between the two samplings were not significant (Table 49 on page 168). In April 2004 C_{mic} in the densely rooted OeOa horizon did not show any significant change along the altitudinal gradient (Table 1 on page 138) even though C_{mic} tended to decline from 5 557.94 µg C_{mic} g^{-1} at $P_{1\,050\ m}$ to 4640.04 µg C_{mic} g^{-1} at $P_{3\,060\ m}$ (Figure 4.21(a) on the facing page). At $P_{2\,380\ m}$ C_{mic} peaked with average contents of 5 990.55 µg g^{-1} and also had the highest variation but was not significantly different from the other plots (Table 33 on page 159). In November 2004 average C_{mic} at $P_{2\,380\ m}$ was 5 061.5 and 8 927.05 µg g^{-1} at $P_{1\,890\ m}$ (Figure 4.21(b) on the facing page). In the OeOa horizon contents were similar to those of the top organic layer (Oi) (Table 18 on page 151). Lowest average C_{mic} content of 3 964.92 µg g^{-1} was detected at $P_{1\,890\ m}$. As in April also in November C_{mic} contents in the OeOa horizons peaked at $P_{2\,380\ m}$with 5 106.42 µg g^{-1}.

In the top mineral soil (0–10 cm) C_{mic} ranged from 518.38 µg g^{-1} at $P_{2\,380\ m}$ to 1 099.56 µg g^{-1} at $P_{1\,540\ m}$ in April 2004 (Figure 4.21(a) on the facing page). Furthermore, C_{mic} was not related to altitude ($r_s = -0.19$; $p > 0.05$). In November 2004 C_{mic} contents in 0–10 cm mineral soil were significantly lower than in the organic layer horizons (Table 18 on page 151) and varied between 443.27 µg g^{-1} at $P_{1\,050\ m}$ and 1 158.85 µg g^{-1} at $P_{1\,540\ m}$ (Figure 4.21(b) on the facing page). For both samplings no significant relation between C_{mic} in 0–10 cm and altitude was observed (Table 1 on page 138).

Summarizing can be stated that microbial biomass carbon showed the same patterns and similar contents along the altitudinal gradient during both seasons with high and low precipitation. This is underlined by a plotwise Wilkoxon test for each horizon that revealed no significant differences between sampling dates (Table 49 on page 168), except for 0–10 cm at $P_{1\,050\ m}$, were C_{mic} was significantly higher in April 2004. The very few differences may be explained by the high spatial variation of microbial biomass carbon, which may mask possible differences between sampling dates. However, the data does not support the theory that microbial biomass varies

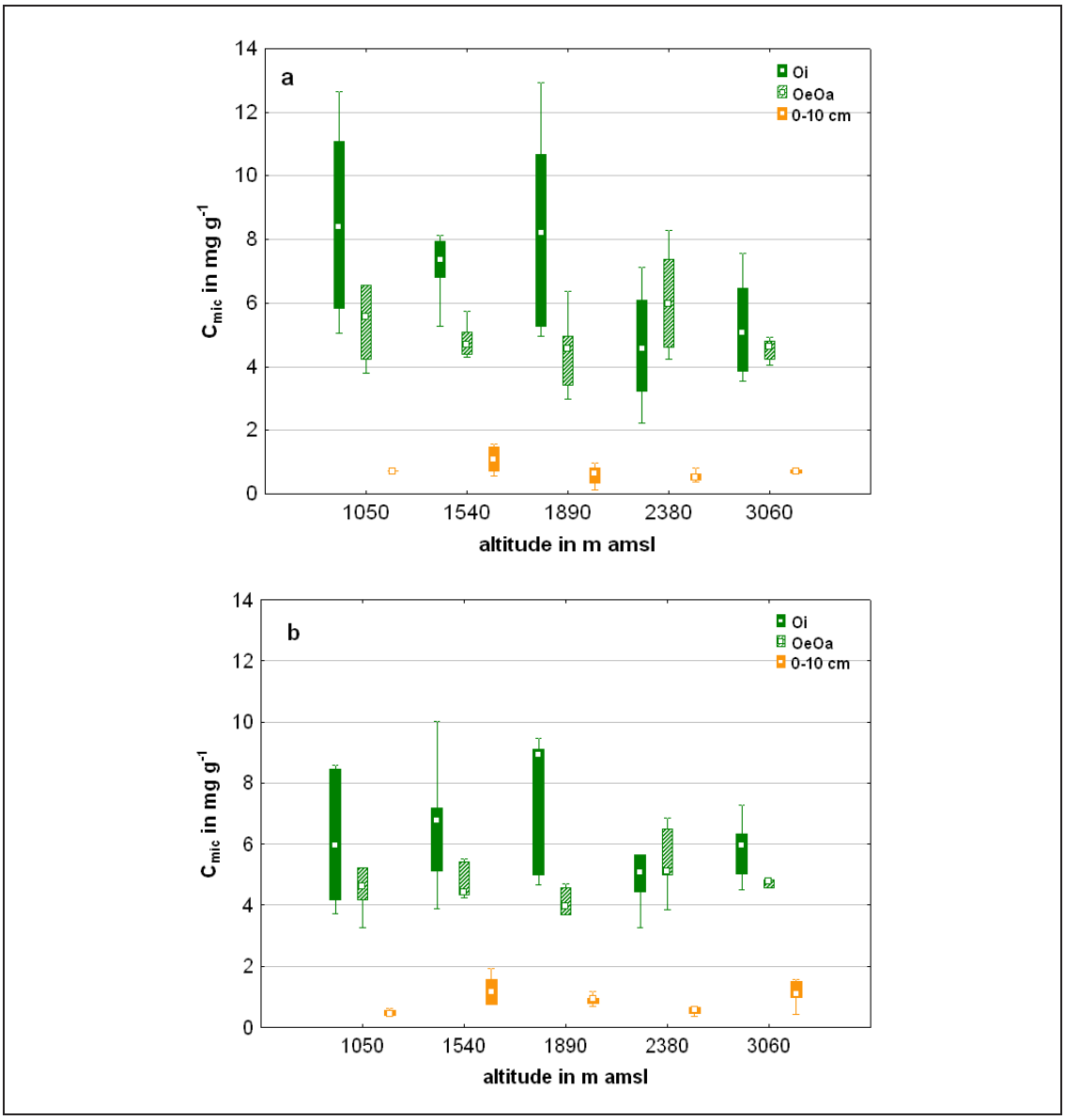


Figure 4.21: Median, quartiles and range of microbial biomass carbon (C_{mic}) in April 2004 (a) and November 2004 (b) in Oi, OeOa and 0–10 cm mineral soil ($n = 6$).

strongly with season in the investigation area.

In the Oi horizon, C_{mic} was significantly correlated with volumetric water content in the organic layer, the SOC : TN ratio, HWN, N_{mic}, TN_{KCl}, KCl-extractable nitrate and organic nitrogen (tables 6 to 14 on pages 141–149). High heterotrophic respiration and gross mineralisation and ammonium consumption rates were also related to C_{mic}. In the OeOa horizon C_{mic} was positively related to SOC, HWC, N_{mic} and negatively correlated with the $C_{mic} : N_{mic}$ ratio. Furthermore, microbial carbon was higher at plots with higher heterotrophic respiration and gross mineralisation and ammonium consumption rates. In the mineral soil (0–10 cm) C_{mic} was related to KCl-extractable ammonium content of November 2004 only.

4.4.2. Microbial nitrogen, C_{mic} : N_{mic} and C_{mic} : SOC ratio

In April 2004 N_{mic} in the Oi horizon decreased significantly with increasing altitude ($r_s = -0.59$; $p \leq 0.05$). Similar to C_{mic}, N_{mic} data was clustered (Figure 4.22(a) on the facing page): at 1 050, 1 540 and 1 890 m N_{mic} ranged between 1 184.75 and 1 356.6 $\mu g\, g^{-1}$ and all plots were significantly different from 3 060 m (Table 41 on page 163). At $P_{2\,380\ m}$ and $P_{3\,060\ m}$ N_{mic} was 760.6 $\mu g\, g^{-1}$ and 618.7 $\mu g\, g^{-1}$, respectively. N_{mic} contents of both organic layer horizons at $P_{3\,060\ m}$ showed consistently smaller variation than at all other plots. In the OeOa horizon N_{mic} also decreased along the altitudinal gradient from 1 179.9 $\mu g\, g^{-1}$ at $P_{1\,050\ m}$ to 682.0 $\mu g\, g^{-1}$ at $P_{3\,060\ m}$, but peaked at $P_{2\,380\ m}$ with contents similar to those in the Oi of the three lower plots. Thus, no significant relation between N_{mic} and altitude was detected in the OeOa. In the top mineral soil (0–10 cm) N_{mic} was significantly smaller than in the organic layer horizons (Table 26 on page 155). N_{mic} ranged from 96.5 to 140.4 $\mu g\, g^{-1}$ and was not significantly correlated with altitude, as well.

In November 2004 microbial biomass nitrogen contents were similar to those in April 2004 (Figure 4.22(b) on the facing page). Wilkoxon tests detected only few differences between the two sampling dates: at $P_{1\,050\ m}$ N_{mic} in 0–10 cm was significantly higher for the first sampling than in November 2004. At $P_{1\,890\ m}$ N_{mic} in the same horizon was significantly higher in November than in April 2004 (Table 49 on page 168). At $P_{3\,060\ m}$ N_{mic} contents in the Oi and OeOa horizons were significantly higher: 848.1 and 962.2 $\mu g\, g^{-1}$, respectively. As for the first sampling, in none of the investigated horizons a significant correlation between N_{mic} and altitude was detected. Besides the dependencies between N_{mic} and C_{mic} already described, N_{mic} in the Oi horizon was influenced by SOC ($r_s = -0.9$), the HWC : SOC ratio and TOC_{KCl} and C_{mic} : SOC ratio. In the OeOa horizon only N_{mic} and C_{mic} were significantly related to each other. In the mineral soil, N_{mic} increased at high TN.

The ratio of microbial carbon to microbial nitrogen did not show significant trends in April 2004. In the Oi median C_{mic} : N_{mic} slightly increased from 6.00 ($P_{1\,540\ m}$) to 10.44 ($P_{3\,060\ m}$) (Figure 4.23(a) on page 70). In the OeOa the ratio ranged between 4.83 ($P_{2\,380\ m}$) and 6.65 ($P_{1\,890\ m}$). In the mineral soil, all plots had similar median ratios, at 1 540 m the ratio was exceptionally high (10.33). In November 2004 significant trends were detected in Oi and 0–10 cm (Table 1 on page 138). In the top organic layer, median ratios increased from 5.90 at $P_{1\,050\ m}$ to 7.86 at $P_{2\,380\ m}$ and 6.83 at $P_{3\,060\ m}$. In the OeOa C_{mic} : N_{mic} ratio declined significantly along the altitudinal gradient, and varied between 5.98 at 1 050 m and 4.94 at 3 060 m. In the mineral soil, no significant trend was detected, ratios ranged between 3.77 (1 050 m) and 6.41 (3 060 m) (Figure 4.23(b) on page 70). Again, in the mineral soil at 1 540 m exceptionally wide ratios were observed. C_{mic} : N_{mic} declined in the soil profile at all altitudes, except for 1 540 m, where the ratio was higher in the top mineral soil than in organic layer horizons. Wilkoxon tests detected significant differences between the two sampling dates in none of the horizons at $P_{2\,380\ m}$ and $P_{3\,060\ m}$ (Table 49 on page 168). At $P_{1\,050\ m}$ in each horizon differences were observed: in Oi and 0–10 cm C_{mic} : N_{mic} were higher in April 2004, in OeOa the ratio was significantly smaller than in November 2004. At $P_{1\,540\ m}$ differences were restricted to OeOa and 0–10 cm: in both C_{mic} : N_{mic} was significantly wider in April 2004. At $P_{1\,890\ m}$ C_{mic} : N_{mic} were also significantly wider in April 2004 in Oi and 0–10 cm.

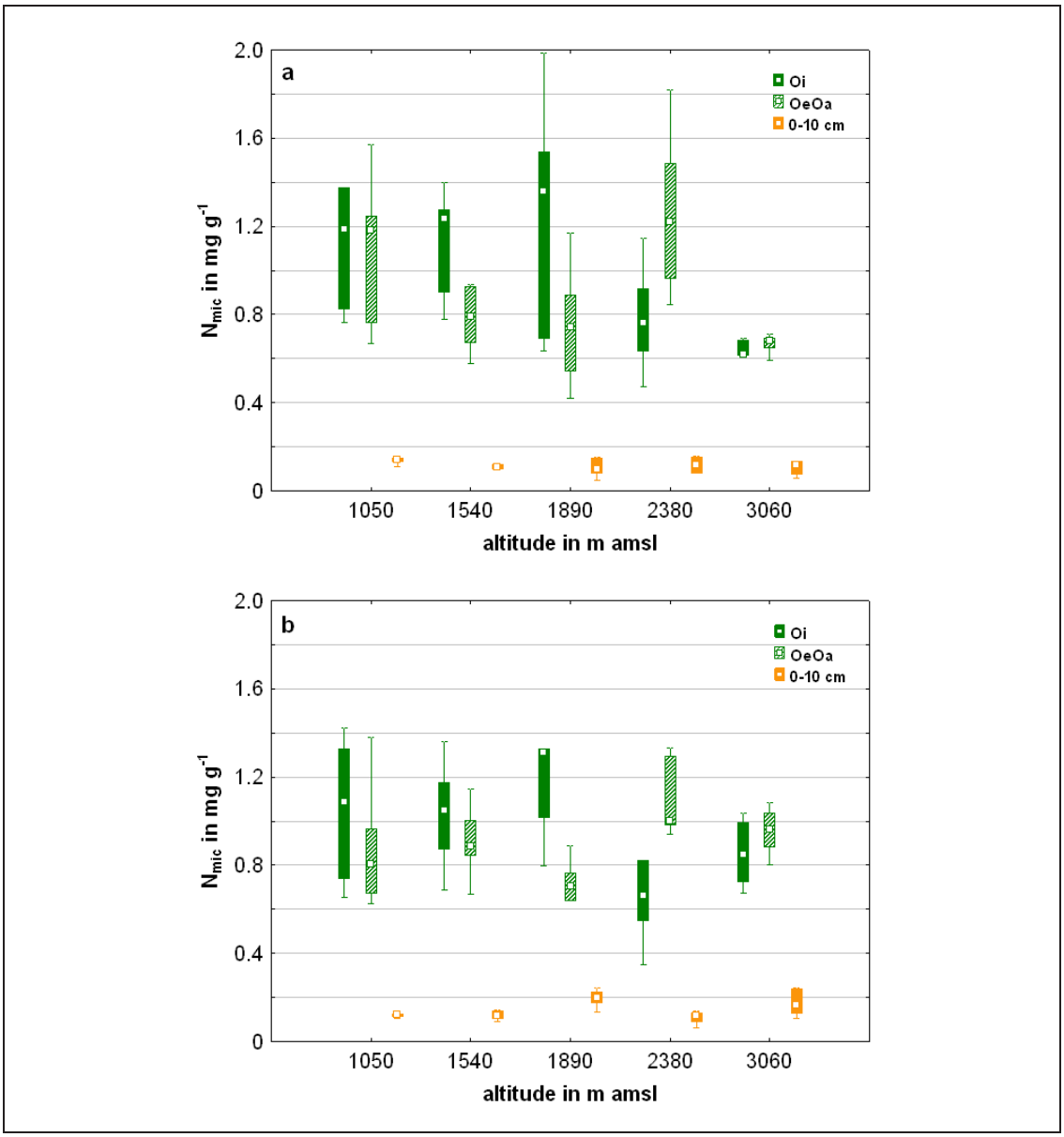


Figure 4.22: Median, quartiles and range of microbial biomass nitrogen (N_{mic}) in April 2004 (a) and November 2004 (b) in Oi, OeOa and 0–10 cm mineral soil ($n = 6$).

The proportion of microbially bound carbon of soil organic carbon (C_{mic} : SOC ratio) decreased along the altitudinal gradient in all studied horizons. In the Oi and 0–10 cm mineral soil this decrease was significant (Table 1 on page 138). In the Oi C_{mic} : SOC ratios ranged from 0.90 ($P_{2\,380\ m}$) to 1.74 ($P_{1\,050\ m}$). At the three lower plots C_{mic} : SOC ratios were smallest in the densely rooted OeOa, and ranged between 1.05 ($P_{3\,060\ m}$) and 1.36 ($P_{1\,050\ m}$) in this horizon (Figure 4.24 on page 71). Except for $P_{3\,060\ m}$, C_{mic} : SOC was highest in the mineral soil, it ranged between 0.66 (3 060 m) and 3.07 (1 540 m).

For mineral soils comparable results have been reported in the recent literature. Chander et al. (1998) observed microbial carbon contents between 229 and 261 $\mu g\,g^{-1}$ in 0–10 cm mineral

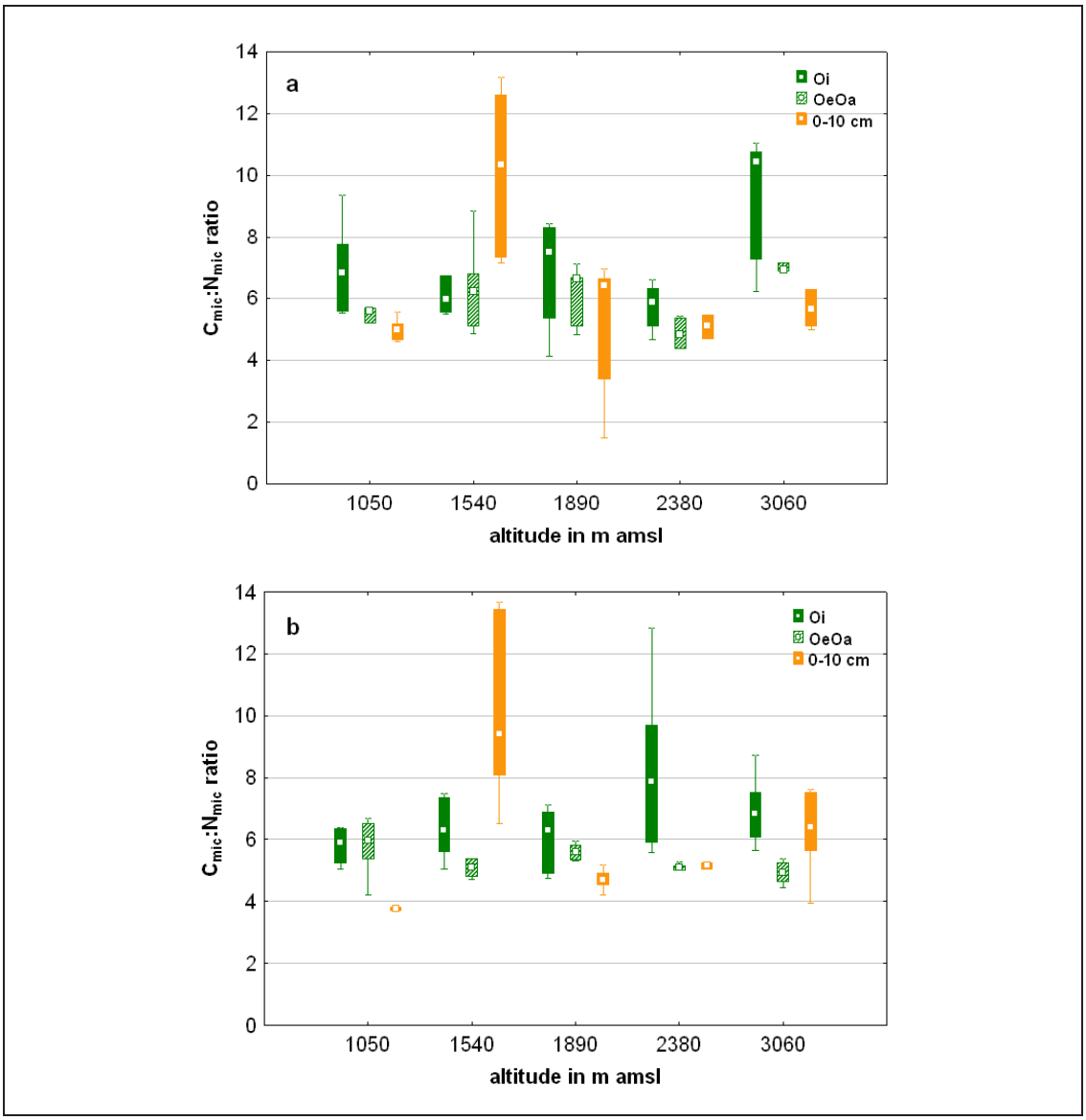


Figure 4.23: Median, quartiles and range of microbial C : N ratio ($C_{mic} : N_{mic}$) in April 2004 (a) and November 2004 (b) in Oi, OeOa and 0–10 cm mineral soil ($n = 6$).

soil of tropical agroforestry systems in India. This corresponded to C_{mic} : SOC ratios between 3.68 and 4, which is higher than in soils of RBSF and PNP. In a lowland tropical forest of Puerto Rico, Ruan et al. (2004) found between 1.05 and 1.71 mg microbial carbon per g soil. In topsoils (0–10 cm) under the same vegetation type in Costa Rica microbial carbon ranged from 0.95 to 0.99 mg g^{-1} and microbial nitrogen varied from 0.23 to 0.25 mg g^{-1} (Cleveland et al., 2003). With respect to microbial carbon, both studies are comparable to the C_{mic} contents in the soils of this study, but microbial nitrogen was markedly lower in tropical montane forest soil than in lowland forests. Li et al. (2005) found microbial carbon to be variable when comparing rainy and dry season in a lowland tropical forest of Puerto Rico. C_{mic} was 0.8 and 0.46 mg g^{-1}, respectively. The microbial carbon content in alkaline soils derived from basic rock and alluvial sediments under

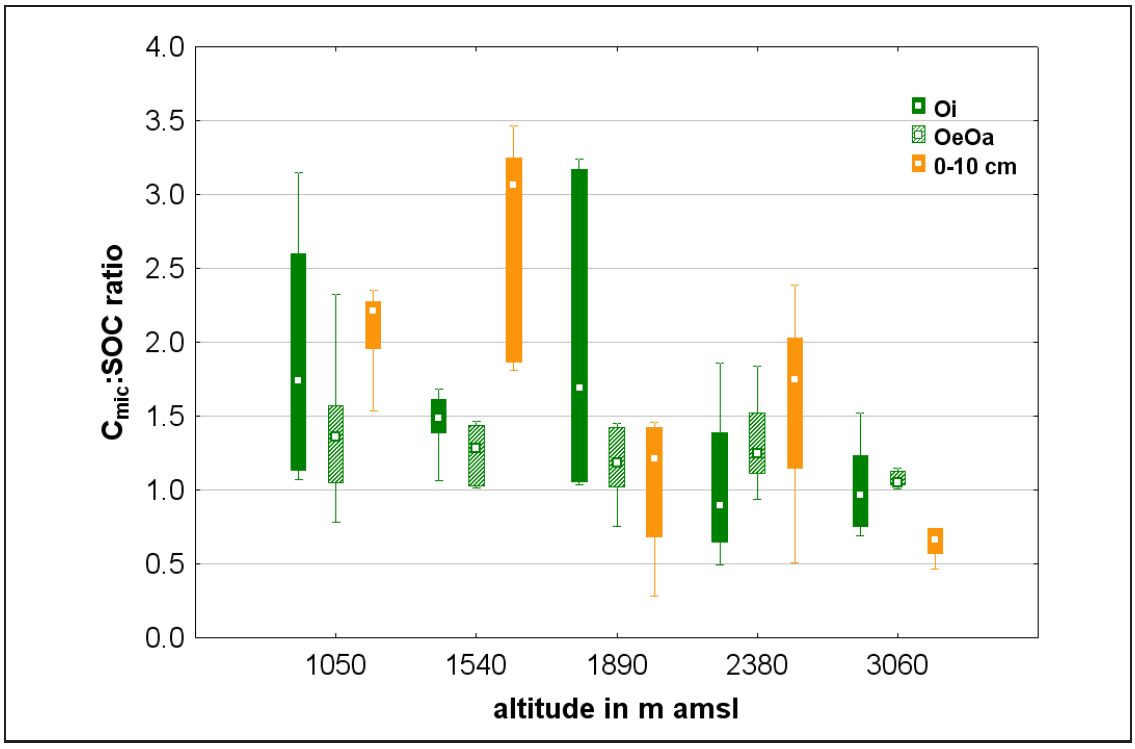


Figure 4.24: Median, quartiles and range of the proportion of microbial carbon of soil organic carbon (C_{mic} : SOC) in April 2004 in Oi, OeOa and 0–10 cm ($n = 6$).

different secondary forest types on the Philippines (Salamanca et al., 2002) was consistently smaller than in the current study and ranged only from 0.21 to 0.49 mg g^{-1} soil, microbial nitrogen only ranged from 0.01 to 0.04 mg g^{-1}, which resulted in average C_{mic} : N_{mic} ratios of 14.1. The C_{mic} : SOC ratio was 2.8. Soils under wet tropical climate in south Andaman (Dinesh et al., 2003) contained on average 0.6 mg microbial carbon g^{-1} and 0.05 mg microbial nitrogen g^{-1} soil. The C_{mic} : SOC ratio was 2.44. Sarmiento and Bottner (2002) studied top mineral soils (0–20 cm) at high altitudes (about 3 000 m amsl) in the northern Andes, Venezuela, under fallow and agricultural management. They observed microbial carbon contents of 0.6 and 0.3 mg g^{-1} under fallow and management, respectively, which corresponded to 0.64 and 0.34 % of SOC. Compared to results observed at 3 060 m PNP páramo soils under extensive agricultural management contained markedly less microbial biomass.

I found only one study published in recent literature that not only deals with mineral soils but also with organic layers or forest floor material in tropical ecosystems. Priess and Fölster (2001) studied soils and forest floor material in the Highlands of Guyana, southern Venezuela, at altitudes between 800 and 1 500 m amsl. Microbial carbon in the mineral soil amounted to 0.9–1.5 mg g^{-1} and in the organic layer to 2.4–3.5 mg g^{-1}. The authors of this study consider their values high in comparison to other tropical soils. This evaluation is supported by the results of the current study. Mineral soils contained microbial carbon and nitrogen comparable to published results, whereas organic layer horizons in RBSF and PNP had significantly higher microbial biomass. This leads to the assumption, that in tropical montane forests microbial biomass is concentrated in the organic layers and that the organic horizons play the significant role in microbial dynamics. According to

Priess and Fölster (2001) the C_{mic} : SOC usually ranges between 1 and 5 % in the tropics. In the current study, C_{mic} : SOC in Oi at $P_{2\,380\ m}$ and $P_{3\,060\ m}$ were slightly lower than 1, as well as C_{mic} : SOC in 0–10 cm at $P_{3\,060\ m}$. This indicates that soil organic carbon at high altitudes is very stable and is subject to slow turnover.

4.4.3. Microbial community structure

The total amount of PLFAs ($PLFA_{tot}$) in the Oi horizon was highest at $P_{1\,890\ m}$ (2 005.6 nmol g^{-1}), and lowest at $P_{3\,060\ m}$ (536.4 nmol g^{-1}). At $P_{1\,050\ m}$ intermediate $PLFA_{tot}$ of 1 028.2 nmol g^{-1} was observed (Figure 4.25 on page 74). In the OeOa horizon $PLFA_{tot}$ decreased from 2 084.6 nmol g^{-1} at $P_{1\,050\ m}$ to 944.7 nmol g^{-1} at $P_{3\,060\ m}$, thus ranged in the same span as in the Oi. In the mineral soil $PLFA_{tot}$ increased from 1 050 to 3 060 m from 42.19 to 276.19 nmol g^{-1}. $PLFA_{tot}$ was significantly correlated with C_{mic} ($r_s = 0.73$, $p \leq 0.05$) and N_{mic} ($r_s = 0.87$, $p \leq 0.05$).

The amount of PLFA that was extracted from the samples was in the range given in the literature for soils in Mediterranean climate (Steenwerth et al., 2002; Fierer et al., 2003), and higher than reported for temperate soils (Peacock et al., 2001; Ponder Jr and Tadros, 2002). I found only few studies that investigated PLFAs in tropical soils: Burke et al. (2003) report between 30 and 50 mg $PLFA_{tot}$ per kilogram dry soil for mineral soils of lower montane rain forest in northern Ecuador. Bünemann et al. (2004) report $PLFA_{tot}$ between 47.6 and 77.1 nmol g^{-1} in the top 15 cm of mineral soils under agricultural management and P fertilization in Kenya. Significant correlations of $PLFA_{tot}$ and microbial biomass carbon were also reported by Zelles (1999); Yao et al. (2000); Bailey et al. (2002); Bååth and Anderson (2003) and Bünemann et al. (2004).

In total, 30 fatty acids were extracted from the samples and 17 of these could be identified as specific biomarkers. Table 4.4 on the facing page gives an overview of the relative abundances displayed as Mol% of each fatty acid in all investigated samples. The fatty acid 16:0 was abundant in all samples, its proportion ranged between 10.49 and 28.57 Mol%. This fatty acid occurs widely in plants and micro-organisms and therefore is no specific biomarker. Furthermore, a relatively high abundance in all samples was detected for 18:1n9c and 18:1n7c, both indicators of Gram negative bacteria. The fungal marker 18:2n6,9c was also one of the dominating fatty acids. Relatively high proportions contributed the PLFA cy19:0, which indicated high abundances of Gram negative bacteria and anaerobic eukaryotes (Steenwerth et al., 2002) in the investigated organic layers and mineral soils.

Gram positive bacteria had summed abundances between 3.37 and 22.21 Mol% (Table 4.5 on page 75). Gram negative bacteria showed the highest proportions in the OeOa layers and in 0–10 cm mineral soil at all altitudes, their contribution to the microbial community ranged between 22.55 and 62.42 Mol% with a minimum of 6.54 Mol% in the Oi at $P_{3\,060\ m}$. Actinomycetes was the smallest group, their proportion ranged between 1.36 and 6.28 Mol%. At 1 050 and 3 060 m the relative abundances of all these groups increased notably, yet not significantly with soil depth. At $P_{1\,890\ m}$ Gram negative bacteria increased, while the other groups decreased slightly with maximum relative abundances in the densely rooted OeOa layer. The proportion of fungi ranged from 7.13 to 37.79 Mol% in all plots and horizons and showed an overall, but also not significant decrease with soil depth at 1 050 and 3 060 m. At $P_{1\,890\ m}$ the abundance of fungi also decreased in the

Table 4.4: Relative abundances in Mol% of phospholipid fatty acids (PLFAs) at the different sites and horizons.

PLFA	1 050 m			1 890 m			3 060 m		
	Oi	OeOa	0–10 cm	Oi	OeOa	0–10 cm	Oi	OeOa	0–10 cm
14:0	0.64	0.67	0.06	0.75	0.89	0.00	1.58	1.11	0.88
14:1	0.97	0.66	0	0.57	0.20	0.53	0.00	0.00	0.24
15:0	0.66	0.58	0	0.72	0.91	0.00	0.42	0.58	0.88
i15:0	2.76	5.40	14.81	3.45	8.14	4.90	2.05	4.11	6.12
a15:0	1.35	1.74	2.80	1.50	2.50	1.20	0.98	1.49	2.42
15:1n5c	2.80	0.45	0	0.12	0.13	0.69	0.34	0.28	0.39
16:0	19.06	18.50	21.73	20.57	20.21	12.08	27.23	16.54	13.52
i16:0	0.85	1.74	0	1.05	2.60	0.00	0.00	0.30	0.40
16:0 10Me	1.08	2.51	1.11	1.38	4.20	3.57	1.14	2.60	3.42
16:1n7c	1.44	3.59	0	4.17	3.22	3.09	0.00	4.71	4.98
17:0	0.90	0.79	0	0.82	0.85	0.00	0.56	0.20	0.15
17:0 cy9.10	1.12	1.66	3.02	1.26	2.04	1.24	1.38	1.18	1.99
i17:0	0.62	1.27	4.60	0.62	1.46	0.00	0.35	0.76	1.46
17:1n7c	0.93	0.75	0.00	0.87	0.46	0.76	0.00	0.62	0.99
18:0	6.33	5.15	5.54	2.97	3.61	3.46	3.91	2.59	2.82
18:0 10Me	0.32	0.78	5.17	0.32	1.31	1.78	0.23	0.77	1.35
18:1n9c	10.36	12.55	0	12.98	9.16	15.34	1.54	13.48	15.69
18:1n7c	6.67	8.60	0	7.06	5.87	18.33	0.95	9.50	13.72
18:2n6,9c	28.27	20.58	7.13	27.91	14.70	7.22	36.80	25.00	11.51
18:3n6,9,12c	8.84	3.58	0.00	5.93	1.91	0.31	0.96	5.89	1.42
18:3n3,6,9c	0.41	0.32	0	0.35	0.22	0.18	14.34	0.55	0.35
19:0 cy9.10	2.03	5.82	32.22	2.43	13.13	23.66	2.66	6.40	14.18
20:0	0.40	0.41	0	0.35	0.48	0.00	0.06	0.00	0.00
20:1n9c	0.20	0.28	0	0.39	0.26	0.65	0.00	0.24	0.33
20:2n6,9c	0.17	0.17	0	0.19	0.16	0.00	0.00	0.00	0.02
20:3n3,6,9c	0.00	0.18	0	0.13	0.06	0.00	0.00	0.00	0.00
20:4n6	0.53	0.97	0	0.83	0.89	0.48	1.20	0.00	0.16
22:0	0.14	0.30	0	0.15	0.31	0.00	0.26	0.21	0.00
22:1	0.00	0.00	0	0.00	0.00	0.53	0.00	0.00	0.24
24:0	0.17	0.00	1.81	0.16	0.12	0.00	1.03	0.89	0.00

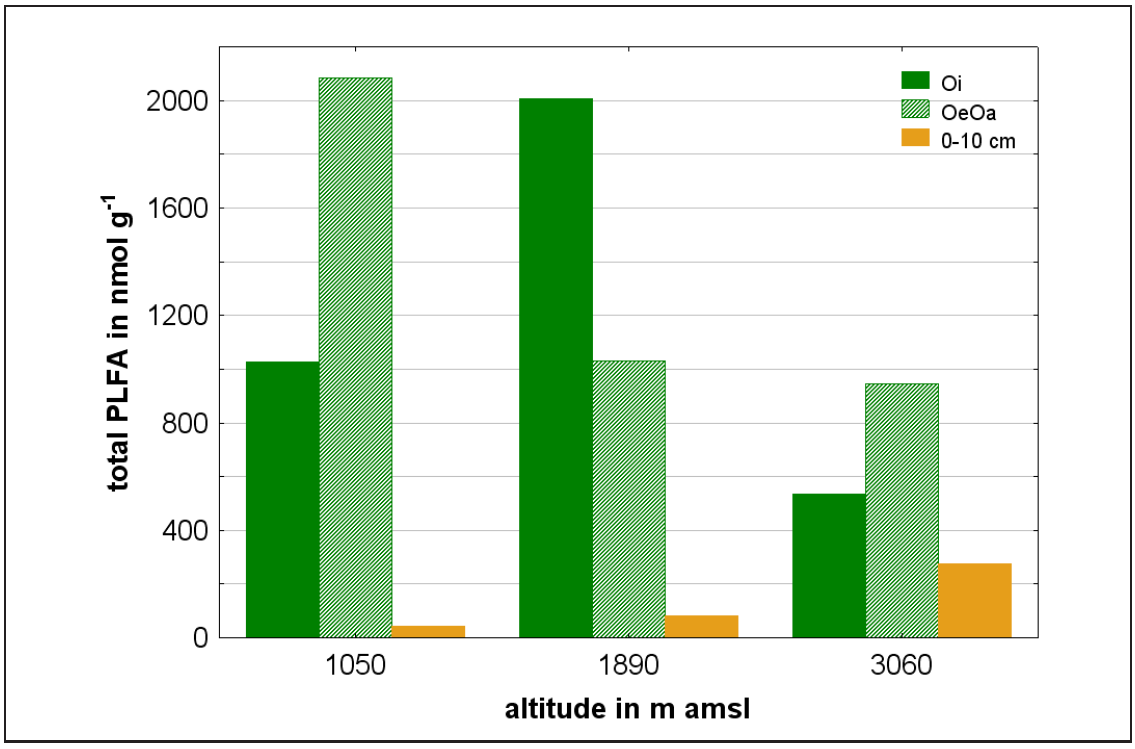


Figure 4.25: Total amount of PLFAs ($PLFA_{tot}$) in composite samples of Oi, OeOa and 0–10 cm of $P_{1\,050\ m}$, $P_{1\,890\ m}$ and $P_{3\,060\ m}$, respectively.

profile, with minimum values in the OeOa. In none of the investigated horizons the described taxonomic groups were related to altitude. Summed relative abundances for the microbial guilds Gram negative and fungi were higher than reported in the recent literature and the proportion of Gram positive and actinomycetes were lower than generally reported for different types of land-use in different climates (Fritze et al., 2000; Yao et al., 2000; Merilä et al., 2002; Fierer et al., 2003; Bünemann et al., 2004). Thus, microbial community composition in the tropical montane forests soils generally is characterised by a dominance of fungi and Gram negative bacteria; the former are more abundant in the Oi, the latter in the densely rooted OeOa and in the top mineral soil. This conclusion is also based upon reported fungal : bacterial ratios that typically range from 0.07 to 0.33 (Fritze et al., 2000; Malmivaara-Lämsä and Fritze, 2003; Leckie et al., 2004). The ratios determined for tropical montane forest soils ranged from 0.11 to 0.35 in the mineral soils (Table 4.5 on the facing page), which is well within the range given above. In the organic layer horizons fungal : bacterial ratio ranged between 0.38 and 3.35 which indicates an overall dominance of fungi in the organic layer, but especially at $P_{3\,060\ m}$.

From the 30 fatty acids found in the studied samples PCA extracted 8 PCs that explained the complete variation in the PLFA patterns (Table 91 on page 185). PC 1 explained 34.36 %, PC 2 26.50 % and PC 3 15.65 % of the total variation. These three PCs together explain 76.52% and are therefore assumed as sufficient for further analysis. The PLFAs i15:0 (Gram positive), 10Me18:0 (actinomycetes) and cy19:0 (Gram negative and anaerobic eukaryotes) produced the highest loadings for PC 1 (Table 92 on page 185). For the second principal component 22:1 and 20:1n9c (both unidentified), 18:1n7c (Gram negative) and 16:0 (not specific) had highest loadings.

Table 4.5: Summed abundances of larger taxonomic groups of microbial community and fungi : bact ratios in all studied plots and horizons.

plot	horizon	Gram+ in Mol%	Gram− in Mol%	actinomycetes in Mol%	$bact_{tot}$ in Mol%	fungi in Mol%	fungi : bact
1 050 m	Oi	4.89	22.55	1.40	28.83	37.11	1.29
1 890 m	Oi	6.62	28.77	1.70	37.09	33.83	0.91
3 060 m	Oi	3.37	6.54	1.36	11.27	37.79	3.35
1 050 m	OeOa	10.15	31.31	3.28	44.74	24.17	0.54
1 890 m	OeOa	14.70	33.88	5.51	54.08	20.56	0.38
3 060 m	OeOa	6.67	35.90	3.37	45.93	30.88	0.67
1 050 m	0–10 cm	22.21	35.24	6.28	63.74	7.13	0.11
1 890 m	0–10 cm	6.10	62.42	5.35	73.87	25.55	0.35
3 060 m	0–10 cm	10.40	51.55	4.77	66.72	13.28	0.20

Two biomarkers of Gram positive bacteria (a15:0 and i16:0) contributed highest loadings to PC 3. Differences in the abundances of these PLFAs cause the biggest part of variation of microbial community structure as defined by the PLFA patterns in the investigated soils and organic layer horizons.

Figure 4.26 on the following page visualizes the differences and similarities in PLFA patterns of the respective plots and horizons. Along the axis of PC 1, thus dependent on the combined effects of i15:0, 10Me18:0 and cy19:0, the investigated samples can be distinguished into three groups according to their PLFA patterns: Oi and OeOa at $P_{1\,050\ m}$ and Oi at $P_{1\,890\ m}$ have a very similar microbial community structure, which is also true for PC 2. Secondly, all horizons at $P_{3\,060\ m}$ and the remaining horizons at $P_{1\,890\ m}$ are very similar with respect to PC 1, but they differ more along the axis of PC 2. The mineral soil at $P_{1\,050\ m}$ differs strongly from all other samples with respect to PC 1. Thus, the PLFA pattern in the mineral soil of $P_{1\,050\ m}$ was dominated by Gram positive bacteria and Gram negative bacteria. Related to PC 1 most of the organic layer samples from the different altitudes were very similar, thus had similar abundances of a15:0, i17:0, 10Me18:0 and cy19:0. In relation to PC 1 OeOa and 0–10 cm at $P_{3\,060\ m}$ and mineral soil at $P_{1\,890\ m}$ formed two intermediate groups. PC 2 was loaded by three indicators of Gram negative bacteria (17:1, 18:1n9c, 18:1n7c). Related to PC 2 differences between Oi layers were small along the altitudinal gradient and also small along the depth gradient. However, calculation of Spearman's correlation coefficient revealed no significant correlations between relative abundances of the functional guilds and altitude and soil depth respectively.

These results contradict the assumption that increasing $C_{mic} : N_{mic}$ ratios indicate a shift in the microbial community structure. This finding is supported by the work of Salamanca et al. (2002) and Dinesh et al. (2003), who were not able to link high $C_{mic} : N_{mic}$ ratios to high fungal biomass. Different ratios of fatty acids like trans : cis, cyclopropane fatty acids to their monoenoic precursors (cy17:0 + cy19:0 : 16:1n7c + 18:1n7c) and the sum of all saturated PLFAs in relation to the sum of all monounsaturated PLFAs (Navarrete et al., 2000; Ponder Jr and Tadros, 2002; Fierer et al., 2003) serve for the evaluation of the physiological status of

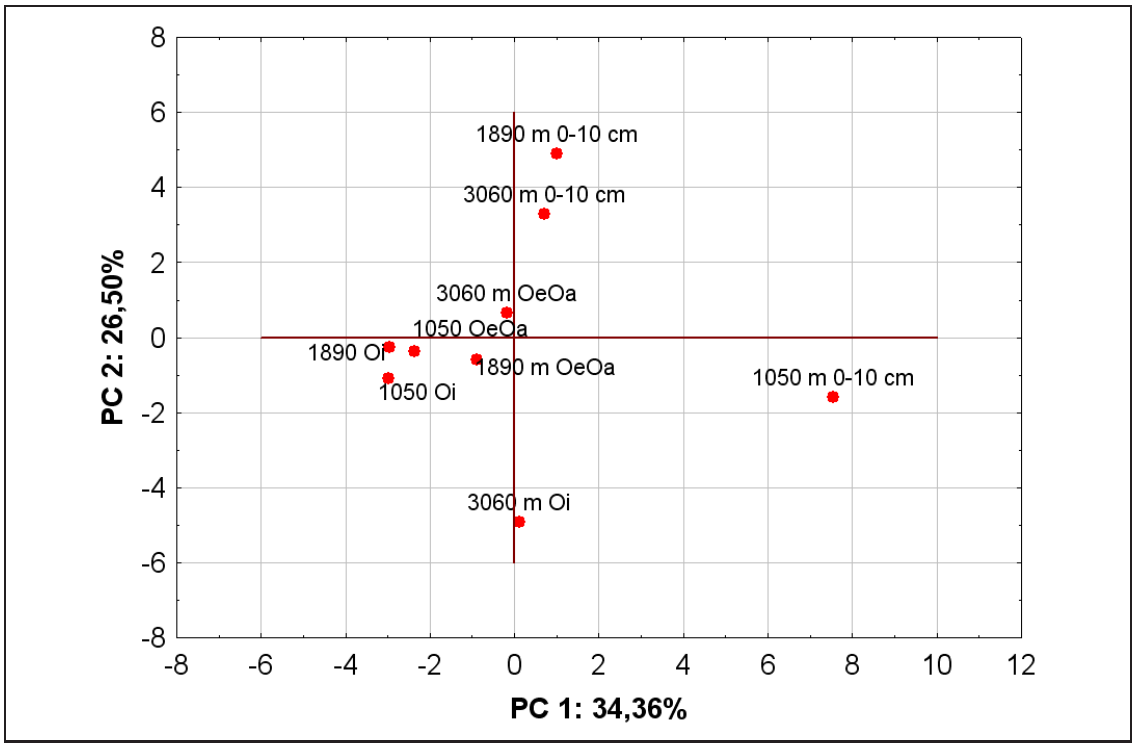


Figure 4.26: Scatter diagram of scores for principal components (PCs) 1 and 2 from the principal component analysis (PCA) of the phospholipid fatty acids (PLFAs) in Oi, OeOa and 0–10 cm mineral soil of $P_{1\,050\ m}$, $P_{1\,890\ m}$ and $P_{3\,060\ m}$.

microbial communities. At $P_{1\,050\ m}$ in the organic layer cy : precursor ratio was small, as well as in the Oi at $P_{1\,890\ m}$ and in OeOa and top mineral soil at $P_{3\,060\ m}$ (Table 4.6 on the facing page). The highest ratio of 2.6 occurred in the Oi at $P_{3\,060\ m}$ and in OeOa and 0–10 cm at $P_{1\,890\ m}$. In the current study no trans-PLFAs were found at all and the ratio of all saturated to all monounsaturated (SATFA : MUFA) ranged between 1.3 and 3.3 and was exceptionally high in the Oi of $P_{3\,060\ m}$ (Table 4.6 on the facing page).

Summarizing it can be stated that no significant change of microbial community structure occurred in any of the investigated horizons along the altitudinal gradient. Oi at $P_{3\,060\ m}$ was characterised by an exceptionally high fungi : bacteria ratio and on the basis of several stress indicators distinguished as nutrient-limited. In comparison to recent literature all plots were characterised by a low relative abundance of actinomycetes.

4.4.4. Total soil respiration

Along the investigated altitudinal gradient average TSR declined significantly ($r_s = -0.83$; $p \leq 0.05$) with increasing altitude (Figure 4.27 on page 78). Highest average TSR was measured at $P_{1\,050\ m}$ and $P_{1\,540\ m}$ and averaged 0.56 and 0.72 g CO_2 $m^{-2}\,h^{-1}$ over the whole measurement period, respectively. Lowest average values of 0.15 g $CO_2\,m^{-2}\,h^{-1}$ occurred at both $P_{2\,380\ m}$ and $P_{3\,060\ m}$. Except for these two plots differences between the study sites were significant (Table 45 on page 165). However, there was a clear separation between $P_{1\,050\ m}$, $P_{1\,540\ m}$ and $P_{1\,890\ m}$ on the one hand, and $P_{2\,380\ m}$ and $P_{3\,060\ m}$ on the other. Overall variability of TSR is indicated by

Table 4.6: Ratios and stress indicators derived from phospholipid fatty acid (PLFA) abundances for all studied sites and horizons.

plot	horizon	cy : cy precursor	SATFA : MUFA	trans : cis	i : a	fung : bact	bact : fung
1 050 m	Oi	0.4	1.6	no	3.1	1.3	0.8
	OeOa	0.6	1.8	trans	4.8	0.5	1.9
	0–10 cm	no precursor	no MUFAs	detected	6.9	0.1	8.9
1 890 m	Oi	0.3	1.4	no	3.4	0.9	1.1
	OeOa	1.7	3.3	trans	4.9	0.4	2.6
	0–10 cm	1.2	1.3	detected	4.1	0.3	2.9
3 060 m	Oi	2.6	15.5	no	2.5	3.4	0.3
	OeOa	0.5	1.4	trans	3.5	0.7	1.5
	0–10 cm	0.9	1.4	detected	3.3	0.2	5.0

boxes and whiskers in Figure 4.27 on the following page and decreased with increasing altitude (Table 50 on page 169).

Figures 4.28(a) to 4.28(e) on page 79 give more detailed information on spatial and temporal variation of TSR at the respective sites. Data for each sampling day is represented by error bar plots and the length of the error bars holds information on the spatial variability at each sampling date. The course of the error bar plots gives information on temporal variation of TSR. Even though these figures are based on biweekly measurements that were distinct from each other, the error bar plots are connected to highlight the course of TSR over the complete measurement period (see also Tables 51 to 55 on pages 169–171). Median TSR fluctuated strongly during the period of measurement but consistent seasonal patterns that coincide with periods of higher and lower precipitation could not be observed. At the plots $P_{2\,380\ m}$ and $P_{3\,060\ m}$ median TSR was less variable during the period of measurement, probably due to the unfavorable climatic conditions like high precipitation and soil moisture increase and low soil temperature at higher altitudes, that become more and more limiting for TSR. Spatial variability at each day of measurement at the respective plot was also considerably high and also decreased with increasing altitude (Figures 4.28(a) to 4.28(e) on page 79). Summing up, TSR has to be considered a parameter highly variable in space and time for the complete research area.

The exemplary determination of diurnal CO_2 efflux underlined the high variability of TSR during the day and showed higher variation at measuring points with higher average TSR as well (Figure 4.29 on page 80). At $P_{1\,050\ m}$ and $P_{3\,060\ m}$ peaks of TSR at "high TSR" occurred around midday, in the early evening and shortly after midnight. For the other measurements no peaks were detected. It can be assumed that TSR of the investigated tropical montane forests is not subject to a pronounced diurnal course. Doff Sotta et al. (2004) determined diurnal TSR in a primary forest of the Amazon lowlands. In contrast to my results, they found TSR to be significantly lower during the night. At daytime TSR was higher and also showed higher variation.

The lacking of a systematic diurnal course of soil respiration allowed the calculation of daily fluxes independently of the time of the day during which measurements were conducted. Con-

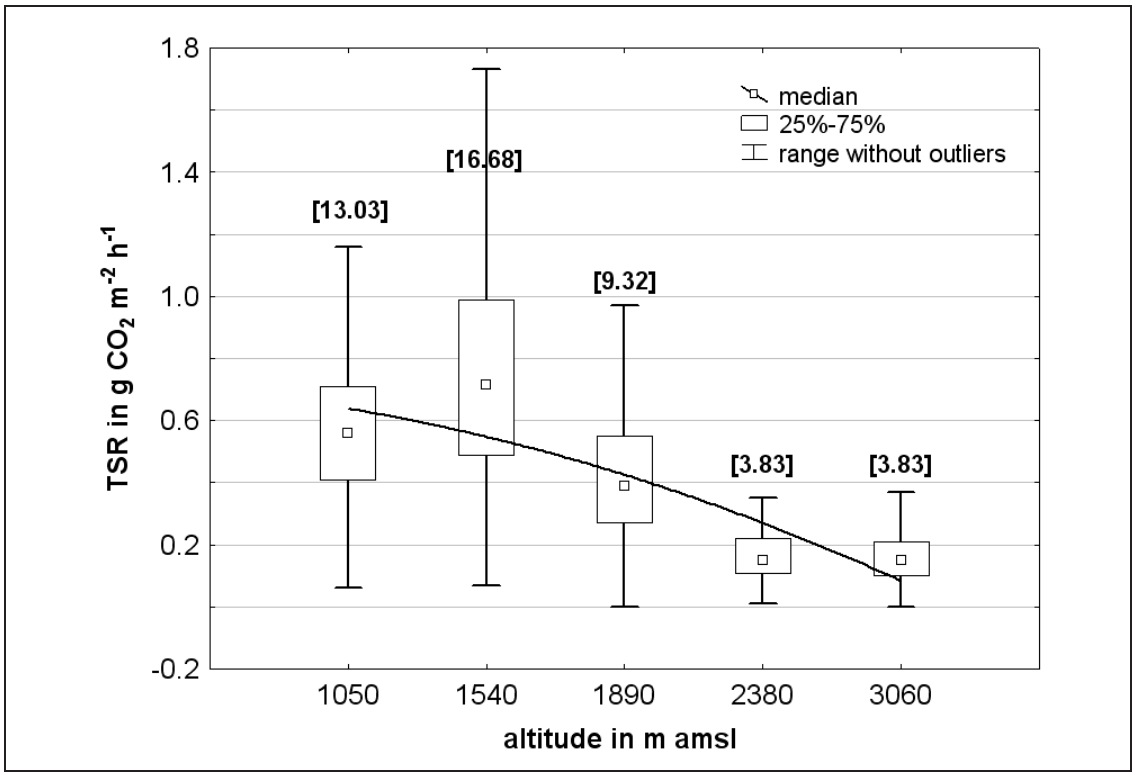


Figure 4.27: Median, quartiles and range of total soil respiration (TSR) at all studied sites and including all data collected from June 2003 to August 2005. Figures in brackets indicate annual C fluxes in $Mg\,ha^{-1}$.

sequently, average annual fluxes based on the biweekly measurements between July 2003 and September 2004 at 1 540 and 2 380 m as well as between July 2003 and August 2005 at the remaining sites were calculated without any further correction. Soil respiration fluxes amounted to 16.68 $Mg\,ha^{-1}$ at 1 540 m and 3.83 $Mg\,ha^{-1}$ above 2 380 m elevation (Figure 4.27).

Total soil respiration in soils of lower montane tropical forests ranges amongst the highest worldwide, while fluxes at higher altitudes are similar to those reported for boreal and cold temperate biomes (Raich et al., 2003). These values are comparable to results summarized by Bond-Lamberty et al. (2004). The results of the current study are well supported by the data from other studies in Brazil, Hawaii and Costa Rica (Raich and Tufekcioglu, 2000). Doff Sotta et al. (2004) and Schwendenmann et al. (2002) investigated the spatio-temporal dynamics of CO_2 efflux in primary forests in Central-Amazonia and in Costa Rica, respectively. Their soil respiration rates were in the same order of magnitude like the presented data at lower elevations. Schwendenmann et al. (2002) showed that respiration rates were almost constant without any clear seasonal variations. They also showed that respiration rates in highly weathered Oxisols were significantly higher than on younger fluvial sites.

4.4.5. Factors controlling TSR along the altitudinal gradient and at stand level

TSR was not directly related to precipitation over the whole altitudinal gradient but appeared

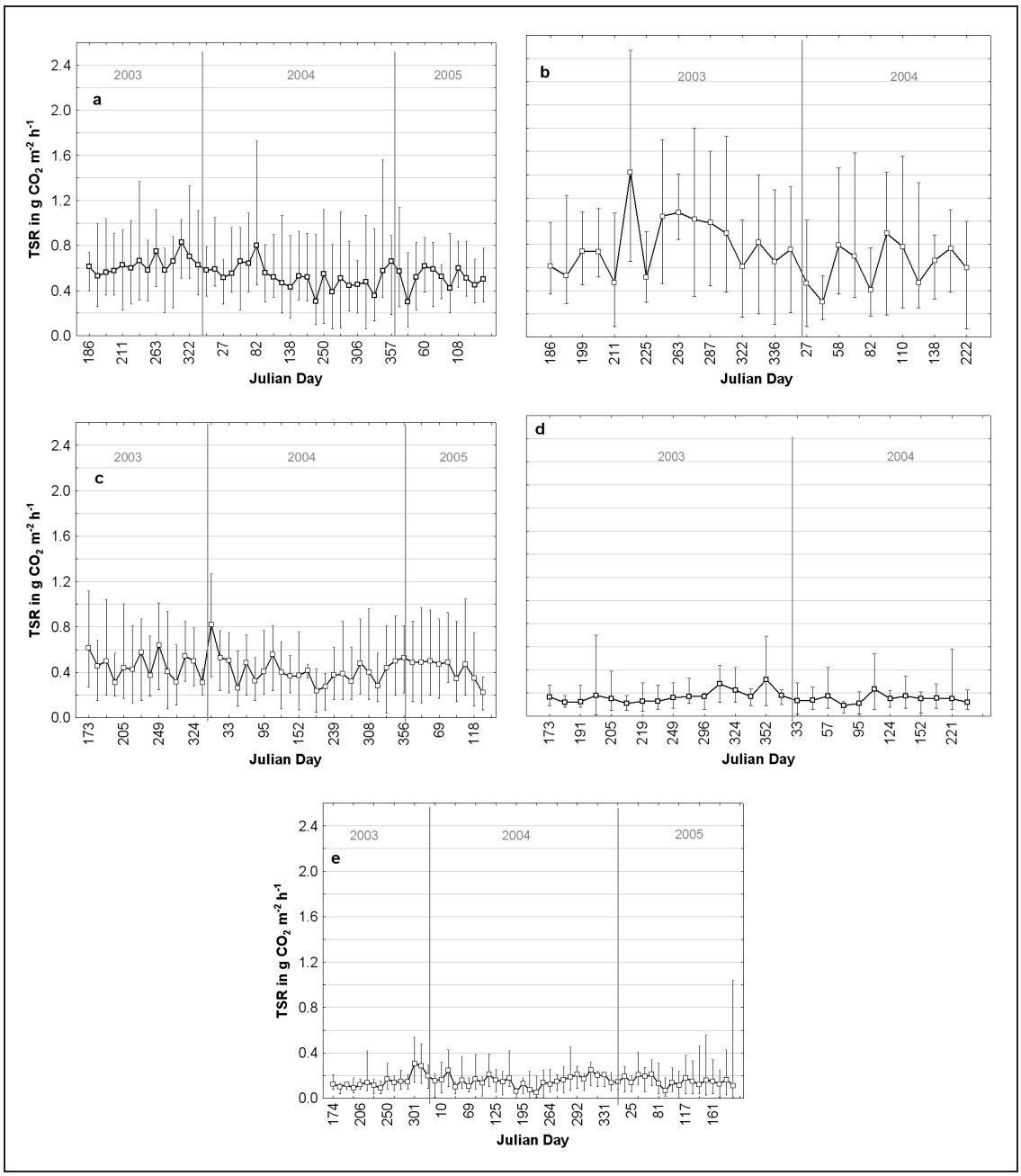


Figure 4.28: Median, quartiles and range of total soil respiration (TSR) $P_{1\,050\ m}$ (a), $P_{1\,540\ m}$ (b), $P_{1\,890\ m}$ (c), $P_{2\,380\ m}$ (d) and $P_{3\,060\ m}$ (e). Each box-whisker-plot represents data for one measurement day ($n = 16$).

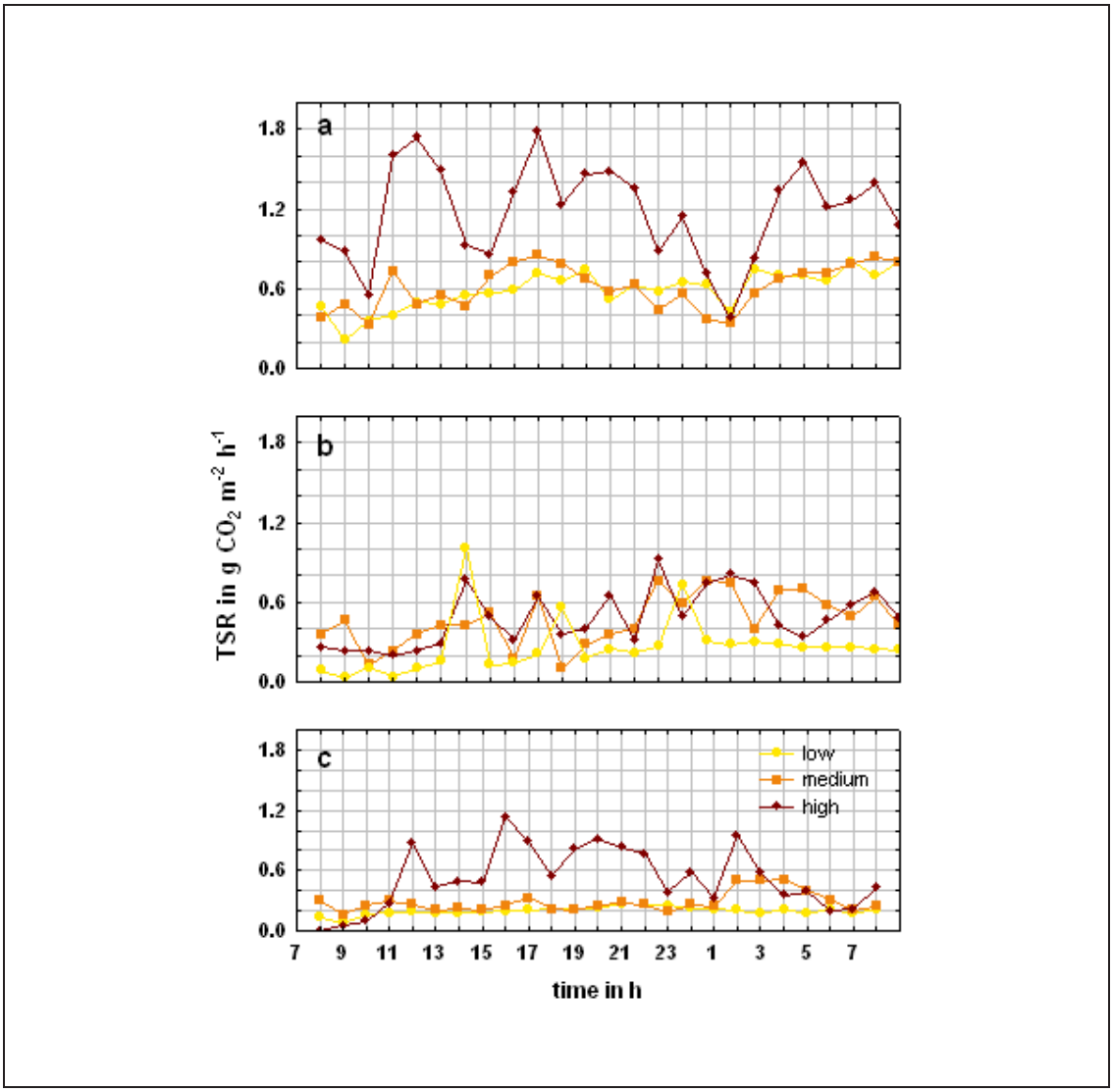


Figure 4.29: Diurnal total soil respiration (TSR) at $P_{1\,050\ m}$ (a), $P_{1\,890\ m}$ (b) and $P_{3\,060\ m}$ (c) in December 2003, measured at three selected measurement points.

to be influenced by VWC and soil temperature (T_{soil}) as measured automatically at the micro climate stations of each study site (Data provided by Christoph Leuschner and Gerald Moser; see also section 2.6 on page 14). TSR was correlated with VWC in the organic layer ($r_s = -0.72$; $p \leq 0.05$) and in the mineral soil ($r_s = -0.76$; $p \leq 0.05$) and positively linked to temperature in the organic layer ($r_s = 0.76$; $p \leq 0.05$) and the mineral soil ($r_s = 0.78$; $p \leq 0.05$). The two factors were also related to altitude: T in the organic layer and mineral soil decreased significantly ($r_s = -0.95$ and $r_s = -0.96$, respectively; $p = 0.05$) with altitude, while VWC increased ($r_s = 0.86$ and $r_s = -0.88$, respectively; $p = 0.05$).

At the stand level, the influence of VWC and T_{soil} was analyzed on the basis of data taken by handheld sensors. For each measurement collar TSR was correlated to VWC and T_{soil} data collected during the study period. Significant relations between TSR and VWC and TSR and T_{soil} could be found for only very few collars (Table 5 on page 140). Consequently, VWC and T_{soil}

were no suitable predictors of variation of TSR at the stand level, but exerted a strong control on total soil CO_2 efflux over the whole altitudinal gradient.

TSR was significantly correlated to only a few of the studied soil parameters: total soil CO_2 efflux was positively related to KCl-extractable ammonium contents and gross nitrogen mineralisation in the Oi horizon for both sampling dates and to KCl-extractable organic nitrogen. (tables 6 to 14 on pages 141–149). Furthermore, TSR was linked to biotic components of the ecosystem that were investigated by Gerald Moser at the same study sites during the same investigation period. TSR was positively correlated with leaf litter fall ($r_s = 0.975$; $p \leq 0.05$), which suggests that heterotrophic soil respiration is mainly driven by the availability of easily decomposable organic compounds and also nitrogen supplied by senescent leaves (Raich and Tufekcioglu, 2000). Furthermore, TSR increased consistently with increasing leaf area index ($r_s = 0.872$), which also indicates that recently assimilated photosynthates regulated TSR via root respiration (Lavigne et al., 2003).

4.4.6. Heterotrophic soil respiration and root contribution to total soil respiration

Root contribution to TSR was inversely related to altitude. It decreased from 41.15 % at 1 050 m to 15.49 % at 1 890 m and to 7.78 % at 3 060 m. Figure 4.30(a) on page 82 shows, that R_H at 1 050 m was much less variable in time than TSR throughout the investigation period. From fine root litter decomposition data determined at the very same plots (Gerald Moser; pers. comm.) it was concluded that during the investigation period more than 50 % of the cut fine roots were decomposed. As R_H shows a general decline and little fluctuation root decomposition is considered to be more or less even. At 1 890 m periods of enhanced and strongly fluctuating R_H occurred right after the trenching and lasted for more than one year (Figure 4.30(b) on page 82). At this altitude about 60 % of the cut fine roots were decomposed during the course of the experiment but this decomposition apparently fluctuated stronger, than at 1 050 m, causing peaks in the soil CO_2 efflux. At 3 060 m only 5 % of the cut roots were decomposed within one year. Enhanced R_H at the end of the measurements (Figure 4.30(c) on page 82) may indicate that decomposition is accelerating after approximately one year. At both $P_{1\,890\ m}$ and $P_{3\,060\ m}$ overall variation of TSR and R_H were very similar. At 1 050 and 1 890 m no living roots and less than 0.001 g dry dead necromass per cm^3 soil remained after the trenching experiment, both plots did not differ significantly. At 3 060 m no living roots were remaining, but the root necromass was significantly higher than at lower altitudes. These findings match the enhanced R_H at the end of the experiment and can be explained by either suppressed dead root decomposition or higher root biomasses at higher altitudes.

In a review Bond-Lamberty et al. (2004) compiled data of studies that determined root contribution but did not include root exclusion studies in the tropics. They reported root contributions of 41.2 (subtraction method; Brazil), 62.9 (isotope method; Brazil) and 70 % (extraction method; Benin) from different lowland tropical forests. Compared to these results R_H at 1 050 m is considered consistent. Root contribution at 1 890 m ranges within the span of 10–90 % given by Hanson et al. (2000). Compared to this span the values gained at 3 060 m are quite low, but the review did not include data from tropcial montane cloud forests (TMCFs) at high altitudes. In a

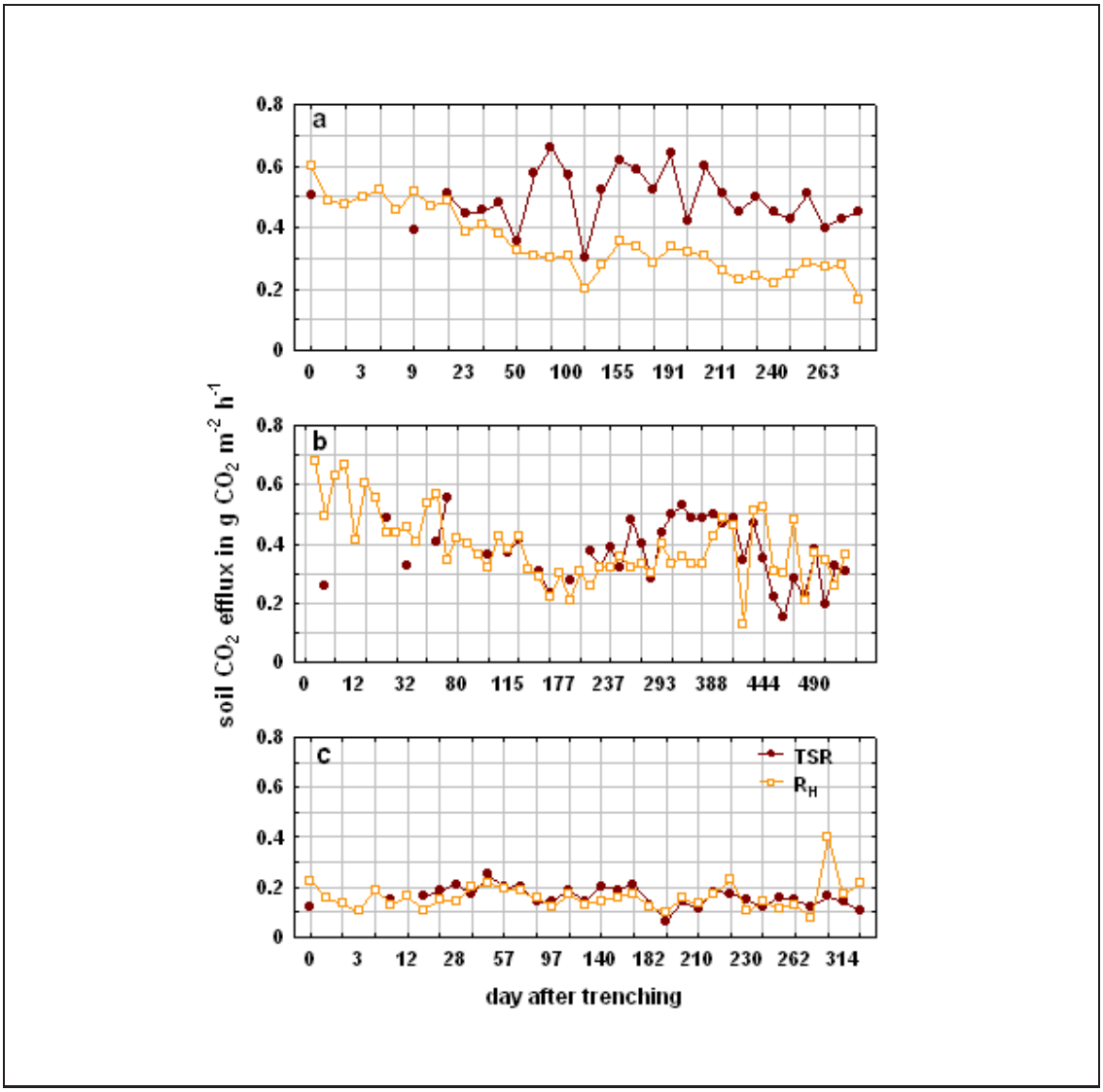


Figure 4.30: Median total soil respiration (TSR) and partitioned soil CO_2 efflux (R_H) at $P_{1\,050\ m}$ (a), $P_{1\,890\ m}$ (b) and $P_{3\,060\ m}$ (c) at each measurement day after trenching.

cool temperate ecosystem, Lavigne et al. (2003) found root contribution to total soil CO_2 efflux to be positively correlated with soil temperature along a gradient of average soil temperatures between 1 and 7 ℃ and RC% ranged between 30 and 55 %. Even though soil temperatures at the studied sites ranged from 9.6 to 19.4 ℃ I assume this relation to be of significant influence along the investigated gradient and therefore the results consistent.

4.4.7. Leaf litter decomposition

Remaining leaf litter after incubation in the field decreased significantly over the incubation period at all study sites (Figure 4.31 on page 84), between 36.3 (at 3 060 m) and 50.25 % (at 1 050 m) of the initial stand leaf litter were decomposed within the 44 weeks of exposure (Table 90 on page 184). At $P_{1\,050\ m}$ the relative remaining litter mass did not differ significantly after four

and eight weeks. With ongoing incubation, the reference litter was decomposed faster than the stand litter (Table 46 at page 165). After 44 weeks 45.8 to 56.3 % of the stand litter was left and between 29.4 and 47.8 % of the reference litter remained (Figure 4.31(a) on page 84). At $P_{1\,540\ m}$ no differences in the decomposition of the two litter types were detected, but Figure 4.31(b) on the following page shows that the reference litter was decomposed slower during the first 8 weeks of exposure in the field. After 44 weeks 55.9 and 55.4 % of stand and reference litter remained, respectively. At $P_{1\,890\ m}$ there was a tendency of faster decomposing reference litter for most of the incubation period, after 28 weeks significantly less reference than stand litter remained (Figure 4.31(c) on the following page). But after 44 weeks these differences had levelled off: the stand litter was reduced to 54.2 % and reference litter to 55 % of the respective initial mass. At $P_{2\,380\ m}$ reference litter was significantly faster decomposed during weeks 4 to 28 of the incubation period. But after 44 weeks 63.7 % of the stand litter remained, which was less than 71.1 % of the reference litter. This indicates that decomposition of the reference litter was faster at the beginning but stagnated after 28 weeks (Figure 4.31(d) on the following page). At $P_{3\,060\ m}$ reference litter was decomposed more slowly than stand litter (Figure 4.31(e) on the following page). After 44 weeks 74.6 and 71.3 % remained, respectively. Weight of remaining leaf litter of both litter types was positively correlated with altitude at the respective sampling dates, i. e. leaf litter decomposition was slower at high altitudes for stand and reference litter, respectively (Table 1 on page 138).

For all study sites and both litter types correlations between duration of exposure and litter mass loss were highly significant (Table 3 on page 140). However, using a linear model for describing leaf litter decomposition is not suitable, because such a model would include negative values if duration of exposure is long enough. Therefore, for description of decomposition a negative exponential model was used (de C.G. Mesquita et al., 1997; Carnevale and Lewis, 2000; Gholz et al., 2000; Scowcroft et al., 2000). Annual decay rates, also referred to as k values, are displayed in Table 93 on page 186.

From the figures and k values for the different incubation times it can be deduced that decomposition was fast during the first four weeks at $P_{3\,060\ m}$ and during the first eight weeks at all remaining sites. Then mass loss slowed down, remaining weight at the third sampling even increased at some plots. At 1 050 and 1 540 m decomposition was accelerated at the fourth sampling (28 weeks), at the remaining plots k values had increased for the fifth sampling (44 weeks). Annual decay rates ranged between 0.20 and 1.47 for the stand litter and between 0.13 and 1.38 for the reference litter (Table 93 on page 186). The initial C : N of the stand litter ratio increased with increasing altitude (Figure 4.32 on page 85), but leaf litter decomposition was influenced by the initial C : N ratio only during the first 4 weeks of incubation in the field (Table 4 on page 140). The k values calculated on the basis of the remaining litter weight after 8 and more weeks were not related to the initial C : N ratio.

In a study in southern Ethiopia with subhumid climate decomposition of two well represented tree species was investigated. After 16 weeks 59 % of *Albizia gumifera* Gmel. and 43 % of *Cordia africana* Lam. were decomposed (Teklay and Malmer, 2004). Gholz et al. (2000) report a wide range of k values from different tropical sites. In Panama leaf litter of *Drypetes glauca* Vahl., a tropical hardwood tree species, was decomposed faster (k value 3.7), than at four different sites in Costa Rica and Puerto Rico, of which one was a tropical montane cloud forest. k values ranged from 0.362 to 1.209 at the tropical lowland forest sites. At the TMCF site (1 250–1 800 m amsl)

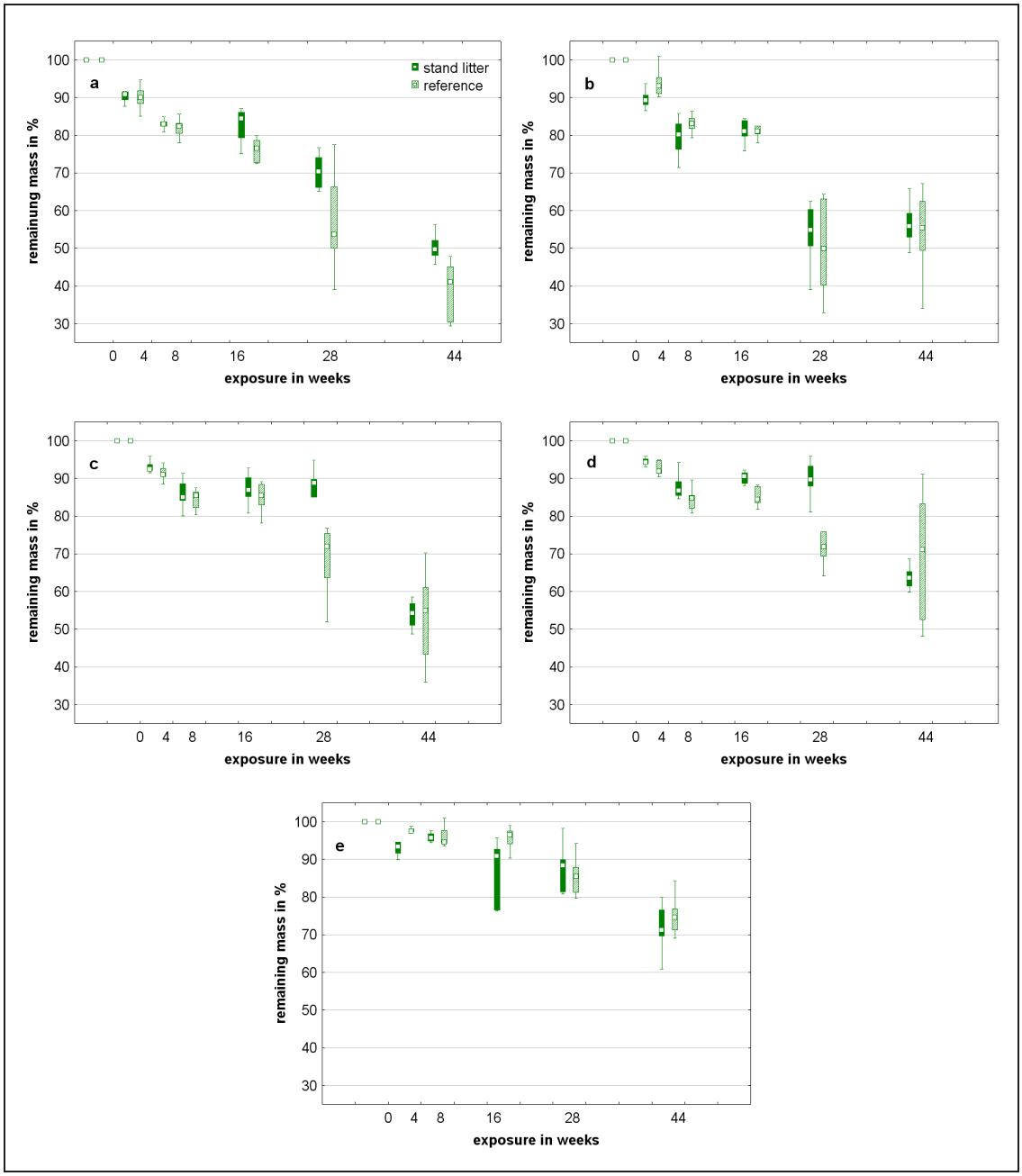


Figure 4.31: Median, quartiles and range of remaining stand and reference litter after incubation in the field at $P_{1\,050\ m}$ (a), $P_{1\,540\ m}$ (b), $P_{1\,890\ m}$ (c), $P_{2\,380\ m}$ (d) and $P_{3\,060\ m}$ (e).

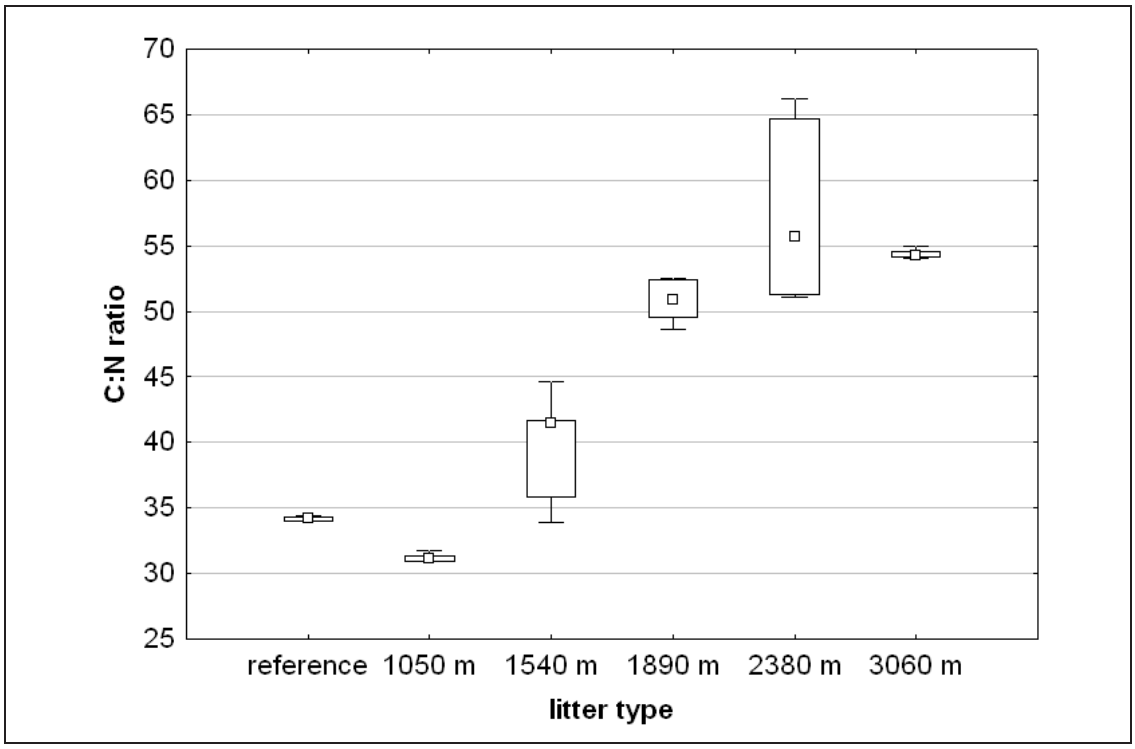


Figure 4.32: Median, quartiles and range of the initial C : N ratio of reference litter and stand litter collected at $P_{1\,050\ m}$, $P_{1\,540\ m}$, $P_{1\,890\ m}$, $P_{2\,380\ m}$and $P_{3\,060\ m}$, respectively.

annual decay rate was 0.403 which ranges within the span of annual decay rates calculated on the basis of 44 weeks of exposure along the altitudinal gradient of the present study. The decrease of leaf litter decomposition along the investigated gradient was also consistent with a study in Hawaii (Scowcroft et al., 2000). There k values for leaf litter decomposition in a humid climate decreased along two altitudinal gradients from 700 to 1 660 m amsl and 915 to 1 555 m amsl on relatively young soils from 0.26 to 0.14 and from 0.9 to 0.51, respectively.

Annual decay rates in a secondary *Cecropia*-dominated humid forest that were calculated after 560 days of exposure were between 0.41 and 0.61, which also corresponds to data of the current study if it is taken into consideration that following the negative exponential approach k values should be smaller, than calculated after 44 weeks (de C.G. Mesquita et al., 1997). In a tropical forest in India between 38.96 and 72.66 % remained after 90 days litter exposure in the field (Sundarapandian and Swamy, 1999). In a study in the savannah of Gran Chaco, Argentina, annual k values for typical and abundant tree and shrub species ranged from 0.04 to 0.15 for the first year of decomposition (Howard and Howard, 1979). Mass loss after 44 weeks at $P_{3\,060\ m}$ in the current study was comparable to temperate conditions in Central Europe. Heim and Frey (2004) found *Fagus sylvatica* L. leaves to loose between 19 and 33 % of their initial mass within one year of decomposition. Ritter (2005) reported mass loss for *Fagus sylvatica* L. between 31 and 39 % within one year.

Chapter 5

Discussion

5.1. Carbon pools: factors and distribution

Soil organic matter (SOM) is the sum of all organic C-containing substances, and consists of a mixture of plant, animal and microbial residues in various stages of decomposition, and of substances synthesized microbially or chemically from the breakdown products, and of the remains as well as living bodies of soil micro-organisms (McColl and Gressel, 1995). Simple organic compounds like amino acids and sugars constitute the substrate for microbial metabolism. This pool is supplied via the decomposition of more complex macromolecules like polysaccharides, proteins, lipids and lignin. The latter group also provides the main constituents of humic substances. It has to be emphasised that SOM is the non-living component of organic matter; microbial biomass is not included in this definition (Trumbore, 1997; Ågren and Bosatta, 2002; Krishnaswamy and Richter, 2002). It is well known that the relevance of SOM results from its function as indicator for soil fertility and filter, buffer, transformation and element cycling processes in the soil. However, many authors doubt the informational value of SOM alone for the evaluation of soil fertility. Schulz (2004) points out that SOM has long turnover times and consists of different pools that are differently protected against mineralisation. For evaluation of soil fertility or soil quality, these pools should be determined and evaluated (Schulz, 2004). A basic assumption is that SOM can be divided at least into two pools. The inert pool is closely related to clay content and does not have to be considered primarily in studies of C and N dynamics (Schulz, 2004). The decomposable pool is further divided into fractions, each decomposing at their specific rate, which is also the basis of virtually all simulation models of decomposition in the soil (Magid et al., 2002). Recent research on SOM dynamics has concentrated on identifying and measuring biologically meaningful pools and fluxes (Magid et al., 2002). Soil quality should be evaluated by studying carbon pools that have short turnover times (Abadín et al., 2002; Bending et al., 2004). For temperate regions a variety of different SOM pools and SOM models has been discussed in the recent literature, but reliable models for tropical regions are lacking (Diels et al., 2004). The carbon derived from SOM is termed soil organic carbon (SOC). The conversion factor that allows the conversion of SOC into SOM ranges between 1.4 and 3.3, and is usually around 1.724 (Schulz, 2004). For the correct use of the term SOC it should be noted, that SOC as determined by complete combustion of soil samples, also includes the microbial carbon and

therefore is not equivalent to SOM.

In the present study total soil organic carbon stock increased along the altitudinal gradient which was recognisable in organic layer thickness and also SOC content in the top mineral soil and also indicated by reduced leaf litter decomposition at high altitudes. This increase is mainly attributed to increasing soil moisture and declining temperatures, i. e. the reduction of microbial activity due to unfavourable climatic conditions. Soil conditions at 3 060 m were characterised by continuous water saturation of the organic layer and temperatures below 10 °C, which is comparable to humid temperate regions. Additionally, the relation of SOC stocks to SOC : TN (total nitrogen) ratios and different available nitrogen pools indicates the high importance of nitrogen in limiting decomposition of SOM at high altitudes. A variety of studies support the conclusions of the present study that main factors of impeded SOM decomposition are soil temperature and soil moisture (Conent et al., 1998; Jobbágy and Jackson, 2000; Veldkamp et al., 2003). The monitoring of SOC storage and cycling in the studied soils is of high importance for evaluation of their carbon sequestration potential and possible effects of climate and land use change. The presented data show that tropical mountain forest store large amounts of carbon in and on the mineral soil. Even though these forest types cover only small areas, they are important for C sequestration. The carbon stored in the soils of the study area can be released by land use change, burning and conversion into pastures and as a consequence of climate change through acceleration of SOM decomposition.

The hot water extractable carbon contains simple organic compounds and easily depolymerisable hydrocarbons, i. e. includes the microbially bound carbon (Körschens et al., 1990; Jandl and Sollins, 1997; Körschens et al., 1998). The size of this carbon pool characterises the organic matter supply, especially the carbon that can be mineralised in short to medium terms (Körschens et al., 1990, 1998; Hagedorn et al., 2002). Schulz (2004) considered the hot water extraction as a simple, reliable method for determining the mineralisable carbon (total hot-water extractable organic carbon (HWC)) in the soil. The HWC is assumed an indicator sensitive for small changes (Ghani et al., 2003; Schulz, 2004). Landgraf et al. (2006) explained the positive correlation between HWC and microbial biomass carbon (C_{mic}) with the fact that hot water extracted microbial metabolites and degradation products. Generally, HWC contents in soils are influenced by vegetation and land use (Landgraf et al., 2003; Böhm, 2005). Mineral soils under forests have higher HWC than under agricultural management, as a consequence of higher biomass input and root litter accumulation (Landgraf et al. (2005); Böhm (2005) and references therein). According to Leinweber et al. (1995) major constituents of the hot water extract are carbohydrates and nitrogen-containing compounds like amino acids and amides. It is concluded that root exudation and microbial cell lysis predominantly supply HWC (Leinweber et al., 1995; Schulten and Leinweber, 1999).

In the present study, HWC was not consistently correlated with C_{mic} in the studied horizons, which leads to the conclusion that in the Réserva Biologica San Francisco (RBSF) microbial carbon is no dominant proportion of HWC. This is supported by the findings of Jandl and Sollins (1997), who do not consider HWC a reliable estimate for microbial carbon either.

According to a classification of Körschens et al. (1998) soils with HWC contents larger than 400 mg kg^{-1} are considered well supplied with organic matter. As this classification is only valid for A-horizons of arable soils under conditions of 6 to 10 °C and 400 to 800 mm annual precipitation it

cannot be directly transferred to the studied soils in the RBSF. However, it supports the conclusion that HWC contents and therefore carbon mineralisation potential are fairly high at all sites of the studied transect. HWC contents and HWC : SOC ratios were not correlated with altitude and total soil respiration (TSR), consequently the potentially decomposable carbon pool is not considered to be limiting microbial activity. In the mineral soil HWC increased significantly at high altitudes and was related to declining C_{mic} : SOC ratios, temperatures and increasing soil moistures, which supports the conclusion that carbon mineralisation is reduced at high altitudes due to small relative quantities of microbial biomass and abiotic conditions that restrict microbial activity. As a source of microbially decomposable carbon and substrate for heterotrophic respiration (Jandl and Sollins, 1997), high HWC suggest that not carbon supply is limiting mineralisation in the mineral soil, but other factors like abiotic conditions and nitrogen supply.

Hot water extraction is an estimate of carbon that is potentially mineralised in short to medium terms. However, for many authors it still remains unclear how to define labile organic carbon as a substrate for heterotrophic respiration and appropriate analytical methods (Zou et al., 2005). In that context, dissolved organic matter (DOM) including dissolved organic carbon (DOC) and dissolved organic nitrogen (DON) is considered an important substrate for micro-organisms (Hishi et al., 2004), especially as microbial uptake mechanisms require water (Marschner and Kalbitz, 2003). The same authors define "DOM" as all organic substances smaller than 0.45 µm that are suspended in aqueous solutions. Furthermore, they point out that in a strict sense DOM is sampled with lysimeters only, but it is acknowledged that in many studies DOM is extracted with water or low-concentrated salt solution like 0.1 M KCl as well. Following this definition, total KCl-extractable organic carbon (TOC_{KCl}) in the present study can be considered an indicator of potentially dissolved organic carbon. The importance of this carbon pool for heterotrophic microbial activity remains inconsistent. Wagai and Sollins (2002) do not consider leachable C (DOC) as substrate for heterotrophic respiration and consider the relevance of water extractable C to be unclear. Suominen et al. (2003) conclude from their study that concentration and properties of DOC and DON, extracted by water, are controlled by microbial activity, but also by sorption and desorption. In a cool temperate forest ecosystem, water extractable carbon was an important index of microbial carbon (Hishi et al., 2004) but this was mainly assumed from the high percentage of carbohydrates in the water extracts. Bending et al. (2004) conclude that microbial parameters like C_{mic}, microbial biomass nitrogen (N_{mic}), basal respiration and enzyme activities are more effective and consistent indicators of management induced changes to soil quality (as defined by soil organic matter pools) than biochemical parameters like the size and composition of different C and N pools. Böhm (2005) used the same method for determining TOC_{KCl} as in the present study and came to the conclusion that TOC_{KCl} is no reliable indicator for the supply of soils with organic matter and that the carbon compounds of this pool are neither microbially bound nor a main substrate for micro-organisms. Landgraf et al. (2006) compared size and composition of cold and hot water extractable carbon in temperate forest floors and point out that these are of different composition and stability. They suggest that hot water extractable carbon is a better predictor of easily decomposable organic matter than cold water extractable, as is contained more easily available substances such as carbohydrates, phenols and lignin monomers that are released by boiling during the extraction procedure from structured organic litter residue.

However, in their review Marschner and Kalbitz (2003) highlight the importance of a

standardised methodology for the determination of DOM, DOC and DON and point out that in naturally structured soils certain amounts of DOM may not be accessible for microbial degradation, while also extraction methods have severe constraints.

In the present study, TOC_{KCl} in the organic layer horizons was not correlated to TSR, and C_{mic} and also showed no significant trends along the altitudinal gradient. In the mineral soil TOC_{KCl} tended to increase along the altitudinal gradient, which may be attributed to dislocation of dissolved carbon from the increasingly thick organic layers to mineral soil, adsorption and low mineralisation under high moisture conditions at high altitudes (Turunen and Moore, 2003). This allows the conclusion that TOC_{KCl} is no indicator for readily available substrate for microbial degradation.

5.2. Nitrogen pools and mineralisation potentials

Among plant nutrients nitrogen holds an exceptional position as N is absent in most primary substrates and is obtained from the atmosphere by either biological N fixation or atmospheric deposition (Vitousek and Farrington, 1997). Nitrogen in the soil is subject to many transformations, in most cases nitrogen limits crop yield, can contribute to eutrophication of surface water bodies and reduce the quality of drinking water (Vitousek and Farrington, 1997). The same authors furthermore point out that gaseous N compounds may contribute to the anthropogenic green house effect. It is well documented that more than 90 % of the N in most surface soils occurs in organic forms and can be categorized into (i) organic residues and (ii) soil organic matter or humus (Appel, 1999). Nitrogen influences plant nutrition directly and indirectly via microbial activity and a considerable part resists microbial attack and is therefore unavailable for plant uptake (Kelley and Stevenson, 1995). Therefore, organic matter dynamics are closely related to N dynamics.

In the present study, the significant decrease of soil TN along the studied transect is paralleled by a significant decline of total leaf N content along the same gradient which also leads to an increase of the C : N ratio in fresh leaves (Unger, 2005). This change of leaf N concentration was attributed to declining temperatures and increasing wind speed at high altitudes (Unger, 2005). Soethe et al. (2007) observed a decline of N concentrations in young tree leaves, shrubs and herbs of the three upper study sites and considers only the vegetation at 2 380 and 3 060 m to be deficient in N. Concurrently, leaf carbon concentrations at all forest stands studied were high in comparison to other studies from the tropics (Unger, 2005). This results in increasing leaf C : N ratios along the altitudinal gradient and gives a first indication of plant production being N-limited at high altitudes. Biological N fixation and atmospheric deposition are the main N input mechanisms into ecosystems (Galloway et al., 2004) and it has to be evaluated if differences may attribute to the observed altitudinal trend of TN. Fabian et al. (2005) state for the RBSF that between 1 860 and 3 185 m above mean sea level pH, ion concentrations and electrical conductivity of precipitation did not show any dependency on altitude, i. e. the atmospheric matter input can be assumed equal for the three upper study sites. The inputs of ammonium, nitrate and sulphate are seasonally highly variable and annual wet N deposition was calculated to range between 1.5 and 4.4 kg NH_4^+-N ha^{-1} and 0.5 to 0.8 kg NO_3^--N ha^{-1}. This implies a light but constant fertilization of the study area; biomass burning in the Amazonian lowland has been identified as dominant sources of this nitrogen

input (Fabian et al., 2005). From this data can be concluded that atmospheric deposition does not alter the altitudinal distribution of nitrogen. Estimates of biological N fixation in the tropics are sparse, but the relative richness of potential N_2-fixing plants in tropical forests suggests that this process is of major importance (Galloway et al., 2004). However, even though detailed data on forest stand composition exists (Homeier, 2004; Röderstein et al., 2005; Moser et al., 2007b) it remains a task to quantify biological N fixation in tropical mountain forests. If biological N fixation is, like overall microbial activity, strongly determined by soil moisture and temperature then it would decline along the altitudinal gradient as well and would contribute to the described reduced N supply to vegetation and soil micro-organisms at high altitudes of the gradient investigated. However, this remains a hypothetical suggestion but investigations of biological N fixation in the study region might enhance the understanding of N cycling in tropical montane forests. Due to increasing organic layer thickness stocks of TN increased along the gradient, which also implies that reduced organic matter turnover is crucial for N availability to plants and microbes.

The term "N-limitation" has been mentioned several times in this thesis and it will be further evaluated in how far the nitrogen supply may influence ecosystem processes like plant uptake and growth and soil organic matter decomposition in the study area.

Tanner et al. (1998) point out that limitation of any nutrient in an ecosystem is only shown if the rate of a particular process is increased by addition of that nutrient, which can in a strict sense only be determined experimentally. In addition, two more aspects have to be considered: firstly, the nutrient limitation of overall ecosystem processes does not necessarily imply nutrient limitation of every single species or individual. Secondly, in most cases more than one element (N, P) or resource (active radiation, water) limit ecosystem processes.

Tanner et al. (1998) conclude from a limited set of studies that nutrient limitation to above-ground net primary production may be widespread in montane tropical forests. In comparison to lowland tropical forests less N and also P is cycled in montane forests as a result of reduced litterfall and low N and P concentrations in the leaves. N leaf concentrations decreased with an increase in altitude in different transects and from the amount of a nutrient that is discharged in the leaf litter fall the amount of plant uptake can be deduced, i. e. low leaf litter nitrogen concentrations suggests low nitrogen uptake rates (Tanner et al., 1998). However, this does not solve the question if the uptake depends upon leaf litter fall or vice versa. Low leaf nitrogen concentrations could also be a result of high immobilisation as a consequence of soil organic matter build-up due to incomplete decomposition. Tanner et al. (1998) do not discuss this point any further, even though humus dynamics and possible nutrient limitations to the decomposers may give helpful hints.

In order to evaluate mineralisation-immobilisation turnover in the studied gradient against the background of increasing organic layer thickness and reduced leaf litter decomposition with increase in altitude, soil nitrogen pools of different availability and gross/net nitrogen mineralisation in organic layers and top mineral soils were determined. In that context, the hot water extraction gives a measure of mineralisable N in soils (Körschens et al., 1990). Böhm (2005) suggests HWN to be a feasible indicator of humus content changes and for detection management changes and of short time changes of the mineral N content in soils.

In the present study, total hot-water extractable nitrogen (HWN) amounted to stocks be-

tween 50 and 100 kg N ha^{-1} in organic layers and between 130 and 220 kg N ha^{-1} the mineral soil (0–10 cm). The potentially mineralisable nitrogen pool in the organic layers increased along the gradient, which is attributed to increasing organic layer thickness. These findings allow the assumption that nitrogen is held back in the slowly decomposing material at high altitudes which further supports the hypothesis, that high altitude forest stands are increasingly N-limited. Furthermore, HWN content decrease was paralleled by an increase of the HWN : TN ratio and HWC : HWN ratio. During mineralisation of organic matter, per unit carbon a definite amount of nitrogen is requested, consequently wide C : N ratios hinder mineralisation and lead to accumulation of the potentially mineralisable substrate, which results in the stabilisation of the organic matter and immobilisation of nitrogen. Thus, in the ecosystem context, N pools are fairly large at high elevations but also very stable and passive.

As a result of the presented data, HWN is considered a feasible indicator of mineralisable nitrogen in the studied forests and is recommended for the evaluation of nitrogen limitation in montane tropical forests. Thus, the presented results support the conclusion of Curtin et al. (2006) who consider HWN an indicator for soil N supplying power and predictor of plant N uptake.

The readily available nitrogen pool as determined by KCl-extraktion (TN_{KCl}) (Appel, 1998; Dou et al., 2000) in the organic layer decreased considerably along the gradient from almost 40 kg ha^{-1} at 1 050 m to about 12 kg ha^{-1} at 3 060 m. Thus, high mineralisable nitrogen stocks occurred together with low readily available stocks. In terms of contents, both HWN and TN_{KCl} decreased significantly in the organic layer horizons, which further support the hypothesis of N-limitation at higher altitudes (Tanner et al., 1998). Within the readily available N pool, organic KCl-extractable nitrogen is the fraction that is the immediate precursor of inorganic N and that is in a dynamic equilibrium with inorganic N (Dou et al., 2000). Along the transect studied, the percentage of this organic N tended to increase in the Oi horizon and mineral soil, in the densely rooted OeOa no changes were observed. To sum up, nitrogen contents of different compartments like vegetation (Soethe et al., 2007), total, mineralisable and available N in organic layers and top mineral soil, as well as microbial biomass N decreased with increasing altitudes, which strongly supports the hypothesis of N-limitation of high altitude tropical forests per se. Second, the potentially mineralisable N pool increased, which does not imply high but restricted mineralisation. This process in turn leads to the storage of high N stocks in organic forms, resistant to microbial attack. Consequently, this nitrogen is not rendered available for plant uptake and nitrogen cycling is impeded. Ammonium and nitrate concentrations showed high seasonal variation, which cannot be related to seasonality of litter fall or amount of precipitation.

Fabian et al. (2005) found the composition of precipitation to vary strongly between seasons which was especially true for pH, electric conductivity, sulphate, nitrate and ammonium concentration in rain and fog water in the study area. This may give an explanation for the variation found in the studied samples and indicates that element concentrations of the studied forest stands are influenced by external factors as well.

Net nitrogen mineralisation rates are considered a key factor for plant uptake and an indicator for plant availability and are the result of two basic processes. Firstly, net mineralisation involves the decomposition of organic N compounds to inorganic N, mainly ammonium and nitrate and secondly the immobilisation of these inorganic forms by soil micro-organisms. One basic assumption in discussing nutrient limitation of net primary production is that plants can take up only

inorganic forms of nitrogen, i. e. nitrate and ammonium (Mittermeier et al., 1998; Schimel and Bennet, 2004). Furthermore, it is assumed that microbes generally are better competitors for inorganic nitrogen than plants; consequently the N supply for plants is determined by microbial uptake and mineralisation and for higher plants only the nitrogen that is mineralised beyond microbial supply is available (Runge, 1970; Schimel and Bennet, 2004). This will be discussed in relation to TSR in the following section. Recently, it has been suggested that mechanistic approaches may improve the understanding of the relation between soil organic matter and N mineralisation. These approaches define two processes as fundamental for net nitrogen mineralisation, the N supply or gross mineralisation rate and the concurrent N immobilisation, i. e. the removal of N from the mineral pool (Herrmann, 2003). As net and gross mineralisation deviate considerably from each other, the former can only be an "index" for N availability and only gross mineralisation can give an estimate of N cycling (Schimel and Bennet, 2004). Zaman and Chang (2004) point out that gross mineralisation rates give information about total microbial activity and assuming that plants can compete effectively with soil micro-organisms for inorganic N forms gross rates could be a better indicator of potential nutrient availability.

The most striking pattern of the net N mineralisation was the positive relation with altitude. If net mineralisation rates are an indicator for nitrogen availability, the observed altitudinal trend conflicts with previous assumptions of increasing N limitation with increase in altitude. Consequently, the conceptual model presented by Knops et al. (2002) may rather explain the presented results. They summarise different studies showing that different net N mineralisation rates were not caused by differences in gross mineralisation but by differences in microbial N immobilisation. In the present study, determination of gross rates showed high NH_4^+ consumption at 1 050 m, which is an indicator for high microbial activity at this site. It has been pointed out that high supplies of readily available carbon may support the immobilisation of nitrogen by microbial uptake (Knops et al., 2002; Dilly et al., 2003). Even though labile carbon contents were neither correlated to net N mineralisation rates nor to altitude, there is an indication that labile carbon may have influenced microbial nitrogen uptake. For grassland ecosystems, several studies have shown that larger plant productivity leads to increased microbial N immobilisation and smaller net nitrogen mineralisation, as higher plant productivity was accompanied with higher supply of microbes with labile carbon for example from root exudation. For the studied altitudinal gradient Moser et al. (2007b) report higher total biomass and leaf area index (LAI) at the lower sites which allows the conclusion that productivity is also higher. Consequently, low net N mineralisation at low altitudes is attributed to larger productivity, supply of carbon to microbes and higher N immobilisation. The reliability of net N mineralisation rates as an indicator for N availability thus must be questioned. Furthermore, in low and intermediate fertilisation studies it has been assumed that increased nitrogen availability does lead to increased productivity and nitrogen storage in plants and SOM, but not to a proportional increase in nitrogen mineralisation (Knops et al., 2002). Consequently, for a thorough understanding of nitrogen mineralisation, the determination of gross mineralisation and consumption rates is considered more useful than the determination of net mineralisation rates.

However, high N immobilisation in Oi horizons along the studied transect remains contradictory. According to Herrmann (2003) net immobilisation of nitrogen occurs if the material to be microbially decomposed cannot meet nutrient requirements of soil micro-organisms. Highest

immobilisation occurred for stands where the C : N ratio of freshly fallen litter was between 20 and 30. In general it is assumed that net immobilisation of nitrogen only occurs in substrates with C : N > 30 (Hodge et al., 2000). Gonzáles-Priéto and Villar (2003) could explain high ammonification and nitrification rates by coarse soil texture, low C : N ratio, high exchangeable P and K and base saturation. However, in the present study, highest immobilisation was observed for lowest litter C : N ratios.

In the OeOa at 1 050 m net mineralisation was highest and the other study sites had very similar rates, irrespective of altitude. Compared with the other horizons net mineralisation was highest in OeOa horizons at all altitudes, i. e. high N availability for plant uptake occurred at high root densities. The correlation of net mineralisation rate to HWN and TOC_{KCl} in this horizon suggests that hot water extractable nitrogen may constitute an important substrate for mineralisation and that labile carbon in the root zone also supports mineralisation. This would correspond to the concept that sufficient supply of microbes with labile carbon is decisive for any mineralisation, i. e. activity and growth process and also the use of N (Heath and Huebert, 1999). The lacking of an altitudinal gradient and the comparably high net rates in the OeOa also contradicts N limitation at high altitudes. In the mineral soil net mineralisation occurred at all sites without any correlation with altitude or other parameters determined in the study. Noteworthy net nitrification only occurred at 1 050 m, which is in accordance with the general assumption that net nitrification in acidic soils increases at higher pH and lower C : N (Jussy et al., 2004). Thus, the probability of N leaching and loss of N is also higher at low altitudes. Hall et al. (2004) propose that the absence of nitrification may be attributed to the assumption that nitrifying micro-organisms are weak competitors for N compared to heterotrophic microbes and plants, which suggests that populations are small where N is limiting net primary production. This might also be a strategy to avoid further N loss by leaching in N limited ecosystems. At the three upper sites of the same transect in RBSF Soethe (2006) consider root length densities to be sufficient for effective nitrate retention as they tended to increase at high altitudes.

Both gross mineralisation and gross NH_4^+ consumption in the Oi significantly declined with increasing altitude, which indicates a decline in microbial activity. Due to the methodological approach to determine these parameters for three sites only, I refrained from calculating correlations with all other parameters and have to evaluate relationships on the basis of altitudinal changes. Declining gross mineralisation rates coincide with the decline of several others parameters, mainly size of nitrogen pools of different availability, increase of SOC : TN ratios, organic layer thickness and the mineralisable nitrogen pool. On the contrary to net mineralisation, gross mineralisation results are in full accordance with the hypothesis of N-limitation at high altitudes. Bengtsson et al. (2003) suggest that respiration rate and adenosine triphosphate content are better indicators of gross mineralisation and immobilisation than C : N ratio of the decomposed substrate and found their results comparable to other studies, where highest NH_4^+-Immobilisation coincided with low C : N ratios. However, gross NH_4^+ consumption could be overestimated by the addition of the ^{15}N-marker as the additional substrate may stimulate microbial immobilisation (Davidson et al., 1991). Thus, Accoe et al. (2004) suggest considering gross NH_4^+ consumption as an indicator of potential rather than actual immobilisation. The same authors again emphasize that quality and quantity of SOC should be considered as key factor of N turnover as it determines the availability of carbon for microbial activity. In case of carbon limitation microbial activity and

growth are suppressed which results in reduced nitrogen uptake by microbes. However, SMITHWICK ET AL. (2005) do not assume that theories of N-limitation can be corroborated by gross mineralisation studies. First of all, they consider mineralisation and consumption as indicators for biochemical cellular processes rather than for SOM transformation processes. Secondly, they state that N-limitation may be a question of the ability of plants and associated micro-organisms to take up organic N. As recent studies found relations between microbial community structure and gross mineralisation rates, they suggest using stress indicators of PLFA analysis for evaluation of N cycles. This could also answer the question in how far the microbial community influences N cycling.

5.3. Size, structure and activity of microbial biomass

The soil microbial biomass includes organisms smaller than 500 μm^3 (JÖRGENSEN and BROOKES, 1991) and therefore comprises bacteria, fungi, algae and actinomycetes as well as micro fauna, e. g. amoebas, flagellates and ciliates. Already in 1977, JENKINSON postulated microbial biomass as "the eye of the needle through which all organic material that enters the soil must pass." Organic matter is converted by micro-organisms, in this process they generate energy and produce metabolites that support their maintenance and growth (MARTENS, 1995). In that sense soil microbes function as sinks of carbon and nutrients. Upon cell death carbon and nutrients are released and soil microbes become nutrient sources. The source/sink function of soil microbes is of enhanced importance in tropical ecosystems that are characterised by a high seasonality of temperature and precipitation (RUAN ET AL., 2004). By this immobilisation and mineralisation of nutrients, soil microbial biomass has a key position in plant nutrition (O'DONNELL ET AL., 2001) and for this reason, soil microbial parameters are proposed as indicators of soil fertility (DINESH ET AL., 2003). In decomposing and transforming of soil organic matter, soil micro-organisms also mediate the emission of gases that contribute to the anthropogenic greenhouse effect. In general, the content of microbial carbon and nitrogen are considered reliable indicators for the size of the soil microbial biomass and a variety of determining factors is being discussed extensively in the recent literature. Furthermore, microbial carbon is considered the most labile soil organic matter pool and is subject to fast turnover (LANDGRAF, 2001). For this reason, microbial carbon is an indicator for changing environmental conditions for example due to changing land use or during succession of ecosystems (SARMIENTO and BOTTNER, 2002). Among the factors that influence the size of the microbial biomass are changes of soil temperature and moisture, nutrient and substrate availability, soil acidity, clay content and cation exchange capacity (MACHULLA ET AL., 2001; RUSTAD, 2001) but also by vegetation parameters like litter input (CHANDER ET AL., 1998; RUAN ET AL., 2004) and age and growth phase of vegetation (LANDGRAF, 2001).

In the present study, determining factors of C_{mic} varied in the respective horizons. In the top organic layer volumetric water content exerted major influence which is in accordance with other studies (LANDGRAF, 2001; MACHULLA ET AL., 2001; PRIESS and FÖLSTER, 2001; LI ET AL., 2005). Furthermore, C_{mic} declined due to large SOC : TN ratios, declining HWN, TN_{KCl}, nitrate and organic nitrogen. These correlations very clearly indicate an N-limitation of the microbial biomass at high altitudes of tropical montane forests. This conclusion is underlined by significantly decreasing N_{mic} contents. Thus, the size of the microbial biomass is predominantly determined by

nitrogen availability. However, in the densely rooted OeOa horizon neither microbial carbon nor nitrogen were significantly related to altitude, but C_{mic} clearly depended on SOC and HWC. As HWC includes rhizodeposits (Leinweber et al., 1995; Schulten and Leinweber, 1999), this correlation underlines the importance of plant-derived carbon compounds for microbial growth. In the mineral soil, C_{mic} was not consistently determined by any of these factors, and N_{mic} was positively correlated with TN.

The studied soils sequester high carbon stocks, but not the size of SOC but its availability is decisive for microbial activity (Wagai and Sollins, 2002). Thus, due to high recalcitrance of organic matter or formation of organo-mineral complexes in the mineral soil SOC availability can be limited (Wagai and Sollins, 2002). For soils in humid, warm temperate climate of the Argentinean Pampa, Alvarez et al. (2000) agree with the general assumption that microbial biomass, mineralized C and light fraction C (debris of rapid turnover) are indicators of changes in soil management. They consider light fraction C as a substrate for microbial respiration and suggest that the proportion of active microbial biomass increases at high availability of labile carbon. However, in the present study, C_{mic} was not only related to total carbon, but also to HWC, which is, as earlier stated, an indicator of C mineralisation potential. Chander et al. (1998) found leaf litter fall to positively influence C_{mic}, due to enhanced organic matter input into the soil. On the contrary, in a lower montane wet forest, Ruan et al. (2004) suspected C_{mic} to be influenced by leaf litter fall, but found C_{mic} to peak approximately one month before litterfall. The authors ascribed this to reduced plant nutrient uptake and retranslocation of carbon and nutrients in the plant shortly before litterfall, which would then result in enhanced nutrient availability and belowground carbon input. Röderstein et al. (2005) studied leaf and root litter dynamics during 2001 and 2002 at the three upper plots of the present study and found leaf litter to peak during the driest and wettest month of the study period at 1 890 m. The authors consider irregularly occurring strong valley winds as possible causes for leaf litterfall peaks. Root necromass showed peaks in the same months at 3 060 m, but for the study area no consistent trend was detected. In order to fully enlighten possible correlations between above and belowground litter dynamics and microbial biomass, these parameters should be determined at the same time intervals. From the available data a correlation cannot be deduced here. But this may also be attributed to the high spatial variation of C_{mic}. However, despite the peaks identified, in the study area litter fall occurs during the whole year (Röderstein et al., 2005) and thus constitutes a stable source of available substrate for microbial turnover. Similar microbial biomass for both sampling dates in spite of variation in precipitation can be explained by relatively stable moisture in the organic layers, i. e. water storage in the organic layers buffers precipitation peaks. In that context microbial biomass is not assumed to undergo strong fluctuations. The lacking of an altitudinal gradient of C_{mic} and N_{mic} in the OeOa may be a result of rhizodeposition and a stable and high supply of micro-organisms with available carbon.

The ratio of C_{mic} and SOC is generally considered an indicator for microbial activity (Wardle and Ghani, 1995) and carbon turnover in soils (Landgraf, 2001; Landgraf et al., 2005). The significant decrease of this ratio along the altitudinal gradient in Oi and 0–10 cm mineral soil therefore indicates a decrease of carbon that is available for microbial activity and a slowed turnover of biomass at high altitudes. It is hypothesised that the lacking of such a gradient in the OeOa layer may be explained by high mycorrhizal activity in this densely rooted part of the

organic layer. In the Oi at 2 380 and 3 060 m as well as in OeOa and 0–10 cm mineral soil at 3 060 m $C_{mic}:SOC$ are below or close to 1 % which further underlines the assumption of reduced carbon turnover at high altitudes (Jörgensen et al., 1994). Higher $C_{mic}:SOC$ at the lower plots generally indicates that the microbes assimilate carbon more efficiently at these altitudes, which also explains the lower organic layer thickness at these sites. In a long-fallow agricultural system in the páramo of the Venezuelan Andes the $C_{mic}:SOC$ ratio ranged from 0.3 to 0.6 (Sarmiento and Bottner, 2002). In comparison to other agriculturally managed soils that had $C_{mic}:SOC$ ratios between 0.5 and 4.5, these ratios were considered very low and indicated high stability and long turnover of soil organic matter (Sarmiento and Bottner, 2002). Wardle and Ghani (1995) point out that both microbial carbon and $C_{mic}:SOC$ ratio are appropriate indicators of a change of microbial activity and sensitive to disturbances. In the present study, the altitudinal decrease of $C_{mic}:SOC$ was inversely correlated with soil moisture and positively related to soil temperature, which clearly shows that the microbial biomass is quantitatively limited under wet and cold conditions.

5.4. $C_{mic}:N_{mic}$ ratio and microbial community structure

In the recent literature it is debated whether the $C_{mic}:N_{mic}$ ratio is a reliable indicator for the soil microbial community composition. Generally, it is assumed that fungi and bacteria have different C:N ratios; variations from 3 to 6 are given for bacteria and 7 to 12 for fungi (Jenkinson, 1988; Bååth and Anderson, 2003). Thus, changes of $C_{mic}:N_{mic}$ ratios may indicate a shift in microbial community structure. Traditionally, soil microbes have been considered ubiquitous "black boxes", i. e. passive catalysts of organic matter decomposition that are controlled by abiotic parameters like nutrient availability, temperature and pH. This assumption excludes the possibility that the composition of microbial biomass can have an impact on organic matter degradation. Furthermore, correlations between mineralisation abiotic factors were not always significant. Thus, it is now taken into consideration that organic matter decomposition may be a function of microbial community composition and partly independent of abiotic factors. One possible explanation would be that only certain microbial populations can successfully perform initial steps of decomposition (Waldrop et al., 2000). Recently, the determination of microbial community structure by extracting and identifying phospholipid fatty acids (PLFAs) has become increasingly important. PLFAs are structural components of living cells that are rapidly depolymerised upon cell death and therefore cannot react with soil colloids (Nannipieri et al., 2003). Changes of PLFA-patterns are related to changes of abundance of different microbial guilds and can be interpreted in comparison with pure cultures of micro-organisms or known biosynthetic metabolic pathways (Nannipieri et al., 2003). Until now no interrelationships between microbial diversity and soil functions has been proven, which can be explained by the redundancy of soil functions (Nannipieri et al., 2003). Generally, the total amount of PLFAs is closely correlated with microbial carbon (Yao et al., 2000; Bailey et al., 2002; Bååth and Anderson, 2003; Bünemann et al., 2004; Leckie et al., 2004) and PLFAs do not provide information on the species level as different species contain the same PLFA (Zelles, 1999). Thus only information on larger taxonomic guilds is available (Zelles, 1999; Steenwerth et al., 2002). From their studies, Waldrop and Firestone (2004) concluded that plant and microbial communities are closely related, as the plant-derived substrates

are an important determinant for microbial community composition.

High $C_{mic} : N_{mic}$ ratios in the Oi at $P_{3\,060\ m}$ corresponded to higher fungal abundances. However, relations between abundances of functional guilds and $C_{mic} : N_{mic}$ ratios are inconsistent along the studied transect and it is concluded that the $C_{mic} : N_{mic}$ ratio is no reliable indicator of a shift in microbial community composition so far. Different authors (Salamanca et al., 2002; Dinesh et al., 2003) were also not able to link high $C_{mic} : N_{mic}$ ratios to high fungal biomass in secondary wet tropical forests. Dilly et al. (2003) observed $C_{mic} : N_{mic}$ ratio between 3 and 9 in temperate mineral soil and attributed this variation to differences in the nutrient supply and biological N-fixation by Frankia and not to high bacterial abundances. High fungal abundances in the Oi at $P_{3\,060\ m}$ are supported by the findings of Ruan et al. (2004) who observed a positive correlation between fungi abundance and soil moisture.

Different ratios of fatty acids like trans : cis, cyclopropane fatty acids to their monoenoic precursors (cy 17:0 + cy 19:0 / 16:1n7c + 18:1n7c) and the sum of all saturated PLFAs in relation to the sum of all monounsaturated PLFAs serve for evaluation of the physiological status of microbial communities (Navarrete et al., 2000; Ponder Jr and Tadros, 2002; Fierer et al., 2003). Cyclopropyl PLFAs are synthesized from their precursors if growth is hindered as caused by substrate limitation (Bossio et al., 1998; Butler et al., 2003), thus high ratios indicate starvation, slow-down of bacterial growth and increasing carbon limitation (Navarrete et al., 2000; Fierer et al., 2003). In the present study high ratios at $P_{3\,060\ m}$ and $P_{1\,890\ m}$ indicated that conditions in the horizons must be comparatively unfavourable for microbial growth. The trans : cis ratio also is well accepted as a indicator of starvation and/or toxic conditions, and in healthy, unstressed microbial communities the ratio usually does not exceed 0.05 (Navarrete et al., 2000). In the current study no trans-PLFAs were found at all, consequently, the microbial populations sampled are considered healthy and active at least based on the data from other ecosystems. According to the conclusions of Bossio et al. (1998) exceptionally high SATFA : MUFA ratios in the Oi at $P_{3\,060\ m}$ indicate limitation of microbially available carbon. Fierer et al. (2003) also concluded, that increasing saturated fatty acid (SATFA) contribution allows the assumption that low contents of organic carbon and/or nutrients reduce microbial growth. In conclusion, microbial populations at high altitudes in the RBSF are not considered to be limited by the C mineralisation potential but by low soil temperature, high soil moistures and low nitrogen supply and therefore by reduced actual carbon mineralisation.

5.5. Total soil respiration and determining factors

Quantifying soil CO_2 efflux is one of the key components of the ecosystem carbon balance (Le Dantec et al., 1999; Savage and Davidson, 2003) and amounts to 80 Pg C on a global scale and tropical and subtropical evergreen broadleaved forests contribute about 22 Pg C annually (Raich et al., 2002). Fluxes in and out of terrestrial ecosystems can have a significant impact on atmospheric carbon dioxide concentrations and have to be fully understood before the consequences of climate change can be evaluated (Norman et al., 1997). It is assumed that increasing carbon dioxide concentrations in the atmosphere are a main cause for higher temperatures in the atmosphere (Rustad, 2001), but as long as it remains unclear how carbon pools and fluxes react on this rise of the temperatures, it also remains unclear how the global carbon cycle will be altered

by climate change in the long term.

Placing chambers over the soil is considered the most direct way of quantifying total soil CO_2 efflux. Such chamber based measurements have been used for several decades now and potential sources of error of this methodology are supposed to be fully understood (Davidson et al., 2002). In the present study an environmental gas monitor (EGM) was used that consisted of a dynamic closed chamber fitted to an infra red gas analyzer, which determined CO_2 concentration change in the sampled air. This methodology has some general constraints. Soil CO_2 efflux is driven by concentration gradients between the air-filled pore space of the soil and the atmosphere. Placing the chamber over the soil allows the accumulation of CO_2 in the chamber and may cause alteration of the concentration gradient which would lead to an underestimation of soil CO_2 efflux up to 15 % (Davidson et al., 2002). In the present study, this was prevented by short measurements of only 2 minutes or until a concentration change of 100 ppm had occurred. Furthermore, the EGM internally checked the slope of the concentration rise in the chamber and gave a "non-linear fit" warning if the concentration rise in the chamber was not linear, i. e. slowed down due to alteration of the concentration gradient. In such cases, measurements were rejected and repeated. Davidson et al. (2002) also argue that the act of placing the chamber on the soil might cause disturbance and overestimation of fluxes through compaction of the organic layer. In the present study it was taken care of fitting the chamber carefully to the collars, without stepping closely to the collar and pressing the chamber onto the collars. The "non-linear fit" warning also served to recognize potential sources of error in this case, too. If one presses the chamber onto the soil and causes flushes of CO_2 the concentration rise is very high during the first seconds of measurement and later declines. In such a case the "non-linear fit" warning would be displayed and the measurement be repeated. Furthermore, the EGM delays the commencement of the measurement for several seconds to buffer possible flushes after fitting the chamber. The EGM is fitted with a ventilation fan to mix chamber air that runs at a speed of 0.9 $m\,s^{-1}$. This fan is considered to disrupt the boundary layer of CO_2-rich air close to the soil surface and therefore lead to an overestimation of soil CO_2 efflux, especially in comparison to LiCor systems (Le Dantec et al., 1999; Davidson et al., 2002). In the present study this must be considered the only constraint but the interpretation of the altitudinal gradient should not be affected by such an inherent error. However, Kabwe et al. (2002) compared different systems for determining soil CO_2 effluxes and concluded that dynamic closed chamber systems connected to an infra red gas analyzer can yield reliable information for a wide range of efflux rates. Furthermore, Litton et al. (2003) found no differences between the EGM and LiCor systems.

Even though there is a general consensus on the importance of soil moisture and temperature on soil CO_2 efflux, strength and direction of these relations have to be carefully evaluated depending on the studied ecosystem. In the present study, spatial and temporal variation of TSR was high at all sites, which was in accordance with other studies. Doff Sotta et al. (2004) consider the distribution of roots and microbes in the organic layer as main causes for small scale variation of TSR. Martin and Bolstad (2005) explained short time variation of soil CO_2 efflux mainly by the varying activity of roots and in the rhizosphere, while variation within one year was attributed to variation of soil temperature and soil moisture. In the investigated tropical mountain forests in-site variation of TSR was not controlled by volumetric water content (VWC) or soil temperature (T_{soil}), which is attributed to the relatively stable conditions in the soil due to the climate: air

temperatures vary little during the day and the year (Richter, 2004) which leads to stable soil temperatures within the plots and to a highly significant altitudinal gradient. The volumetric water content of the investigated sites varied little during the measurement period as during several days without rain only the upper centimetre of the organic layer dry out and enough moisture is stored in the organic layer to support microbial respiration. The only occasion, when soil moisture was limiting microbial activity, was in January 2004 at $P_{1\,890\ m}$ when a prolonged dry period of approximately three weeks occurred and soil efflux was reduced to zero.

In old-growth forest stands soil moisture and temperature appear to exert the major influence on soil CO_2 efflux (Doff Sotta et al., 2004; Martin and Bolstad, 2005). In a tropical savanna (Michelsen et al., 2004) volumetric water content was not assumed a good indicator for TSR. In the Amazon lowlands the soil water status was revealed as the key factor for soil respiration, and in contrast to my findings even short dry periods caused a significant decrease of the respiration activities (Doff Sotta et al., 2004).

Concerning the whole altitudinal range from 1 050 to 3 060 m VWC and T_{soil} significantly control total microbial and root activity, as expressed by soil CO_2 efflux (Vanhala, 2002). McGroddy and Silver (2000) also found decreasing soil temperatures and increasing soil moisture along an altitudinal gradient from 180 to 1 000 m in the humid tropics. There TSR was highest at 780 m and the authors of this study conclude that soil temperature and soil moisture in the observed range are not limiting for TSR and that other factors must cause the observed variation in TSR. Further studies from other ecosystems support the conclusion that soil temperature and soil moisture are principal determinants of TSR (Conent et al., 1998) and that mainly extreme moisture conditions limit soil respiration under otherwise favourable soil temperatures (Scott-Denton et al. (2003); Lee et al. (2004) and references therein). Low soil moistures directly influence the activity of microbial biomass and have indirect impact on the availability of photosynthesis products as a substrate for root and rhizosphere respiration (Scott-Denton et al., 2003). Summarizing can be stated that in the present study, abiotic conditions become increasingly limiting for TSR as precipitation and soil moisture increase and soil temperature declines at high altitudes.

Besides the described abiotic paramters a wide variety of biotic and soil parameters are discussed in the recent literature as determinants for soil CO_2 efflux. In a review paper on the interaction of vegetation and soil respiration, availability of C substrates for micro-organisms, plant root densities and activities, soil organism population levels, soil physical and chemical properties, soil drainage and also vegetation composition were summarized as important factors of total soil CO_2 efflux (Raich and Tufekcioglu (2000) and references therein). McGroddy and Silver (2000) identified root biomass and SOC as determinants of TSR. For the investigated forest sites the authors report a negative correlation of TSR with the carbon pool including root biomass, organic layer and soil organic carbon. Along a sequence of young lodgepole pine stands of different age and density in the Yellowstone National Park, USA, plant activity was determined as major control of TSR (Litton et al., 2003). Martin and Bolstad (2005) determined soil temperature, soil water content, nutrient availabilities, total respiring tissue, primary production and litter production as main predictors for TSR in a broadleaved temperate forest.

For interpretation of the collected soil respiration data, it should be kept in mind that total soil respiration is the result of two main processes: respiration of free soil microbes that mineralize

organic matter and respiration of roots and associated micro-organisms. Consequently, determinants of TSR have to be carefully evaluated, whether they exert influence on root or microbial activity. In addition to soil temperature and soil moisture, in the present study, TSR was positively correlated to available ammonium content of the Oi horizon and KCl-extractable organic N content of the Oe horizon. Furthermore, TSR data was related to leaf area index and leaf litter fall (section 2.6 on page 14).

Based on the observation that fine root densities were negligible in the Oi horizon, I assume that the CO_2 efflux evolving from the Oi horizon is mainly a result of microbial activity. High TSR rates in the Oi were not only correlated with ammonium content but also concurrent with high gross N mineralisation and ammonium consumption rates. This points at high microbial activity in the Oi at low altitudes. The availability of ammonium apparently determined organic matter mineralisation, but at the same time both C and N mineralisation may be controlled by a third parameter or process, as they both are closely related to soil temperature and volumetric water content. This suggests a strong control of microbial activity by abiotic soil properties. Furthermore, the significant relation between leaf litter fall and TSR along the altitudinal gradient supports the hypothesis that microbial activity may also be nitrogen limited. Reduced soil N input via leaf litter fall is assumed to be a main factor of reduced gross N mineralisation and ammonium consumption rates that result in reduced ammonium contents and TSR. Vance and Chapin III (2001) studied substrate limitations to microbial activity in taiga forest soils by investigating the response of microbial activity as expressed by CO_2 efflux on nitrogen and carbon addition in situ and in laboratory incubations. For organic layers under spruce they were able to link low soil respiration to low microbial nitrogen uptake, thus identifying N availability as important factor of microbial activity. In their laboratory experiments, addition of N did not lead to increased microbial activity, which led to the assumption that a further reason for low activity was organic matter quality. Several other authors (Raich and Tufekcioglu, 2000; Lavigne et al., 2003; del Grosso et al., 2005; Van Hees et al., 2005) emphasised that the size of different labile or active carbon pools, typically including recent leaf, needle and root litter and microbial biomass, are an important source for heterotrophic respiration. In the present study, leaf litter fall, i. e. the supply of detritus and thereby rapidly decomposable carbon and nitrogen pools, was a main control of microbial activity and mineralisation. Not only the total amount of litter declined, but also the SOC : TN ratio of the Oi horizon increased, which reduces N input into the soil even more.

In the tropical montane forests studied, the OeOa horizons were densely rooted at all altitudes, thus it is assumed that root and rhizosphere activity will considerably influence CO_2 efflux from this horizon. In the OeOa the main determinant of TSR was KCl-extractable organic N, which is considered readily available (Appel, 1999) and in dynamic equilibrium with the mineral N compounds (Landgraf, 2000; Böhm, 2005; Landgraf et al., 2005) thus a substrate readily supporting microbial activity. However, under the assumption that root activity is positively related to N supply, the correlation between organic N content and TSR raises the question of the relevance of organic nitrogen uptake for root activity and plant nutrition. Until recently, one of the core assumptions in nitrogen mineralisation research was that plants only take up or use inorganic N forms via the mineralisation of soil organic matter (Hodge et al., 2000; Schimel and Bennet, 2004). Since the early 1990s, several studies focused on the question whether plants can also take up low molecular organic nitrogen forms (Schimel and Bennet (2004) and references therein).

In different studies scientists came to the conclusion that organic nitrogen may play an important role in plant nutrition. Schimel and Bennet (2004) summarized studies from arctic, boreal, alpine, wetland and even desert ecosystems, where plants are able to use amino acids for their nutrient supply. From this review, Schimel and Bennet (2004) conclude that organic N use by plants may be a common phenomenon, at least in ecosystems, where N supply is limited. However, it is not yet clear, to what extent organic N sources can meet nutrition requirements of plants (Hodge et al., 2000). In their review, Hodge et al. (2000) also summarized several major constraints of the studies that showed organic N uptake by plants. Many of these studies were conducted under unrealistic temperatures and nutrient additions and the absence of competing micro-organisms. Hodge et al. (2000) further point out that glycine, often used as substrate in organic N uptake studies, is a poor substrate for micro-organisms and does not serve to study direct competition for organic N sources between plants and micro-organisms. Hodge et al. (2000) consider the true ecological significance of the described phenomenon to remain equivocal.

Ectomycorrhizal fungi have been shown to directly utilize organic N sources (Smith and Read, 1997) and Hawkins et al. (2000) demonstrated that also arbuscular mycorrhizas utilized glycine and transferred it to the plant root, even though the underlying mechanism could not be identified. Contrarily, Hodge et al. (2000) again point out that it remains unclear if arbuscular mycorrhiza directly contributes to organic N uptake, if the N source concomitantly constitutes a substrate for microbial uptake. For ericoid and ectomycorrhiza organic N uptake has been proven in several studies (Hodge et al., 2000) (and references therein). For the RBSF Kottke and Haug (2004) highlight the importance of arbuscular mycorrhiza, but also ectendomycorrhiza and ectomycorrhiza occur and have been described recently (Haug et al., 2005; Setaro et al., 2006). Against the background of the cited studies and the importance of organic N content in the densely rooted OeOa horizon for TSR, the question arises to what extent organic N uptake may play a role in plant nutrition of tropical mountain forests and in how far mycorrhiza may be involved. However, the results of the present study also show that besides organic nitrogen, available inorganic nitrogen species were closely but non-significantly related to TSR. This indicates that inorganic nitrogen supply in the OeOa horizon also plays an important role for TSR.

The influence of the studied parameters in the mineral soil on TSR was small. Here, abiotic soil conditions exerted the strongest, even though non-significant, influence, i. e. reduced TSR was attributed to low soil temperature and high volumetric water content of the mineral soil. As a result of low TSR rates, SOC stocks in the mineral soil and the size of the mineralisable carbon pool (HWC) increased.

Leaf area index was identified as a further determinant of TSR. First of all this index is a measure for the density of canopies, but may also give an indication of assimilate production of plants or plant communities, i. e. the higher the LAI, the better the assimilate supply of the plant, which would lead to enhanced root activity and respiration. Between one and two thirds of the proportion of daily assimilated carbohydrates that is translocated to the roots, is respired within the same time (Lambers et al., 2002). In pot experiments, Hütsch et al. (2002) found up to 18 % of the photosynthetically fixed carbon to be exudated into the soil. Between 64 and 84 % of these root exudates were microbially respired within few days. Other studies also underline that current photosynthesis is the main source for autotrophic respiration and point out that between 10 and 40 % of total net C assimilation is transferred from living plant roots to the

soil (Warembourg and Lafont (2003) and references therein). Therefore, I hypothesize that increased LAI influence TSR via fine root activity and exudation of assimilated carbon, but it remains unclear to what extent, as the partitioning of assimilates in the plant and the release of root exudates has not been studied in the field yet (Hütsch et al. (2002) and references therein). Following this hypothesis a high LAI indicates good supply of roots and their associated micro-organisms, which may involve enhanced root exudation, and lead to higher activity and soil CO_2 efflux. In a pot experiment with ^{14}C-labelled non-woody plants of different families, Warembourg and Lafont (2003) found respiration of functional autotrophs to be significantly determined by the quantity of soluble root exudates and concluded that respiration of microbes in the rhizosphere must rely on root exudation. Furthermore, root N content had a significant influence on rhizosphere respiration. Litton et al. (2003) came to a similar conclusion as their studies resulted in a strong dependency of soil surface CO_2 flux on plant activity, as estimated by above- and belowground biomass. Their results agree with different studies (Larionova (1998); Litton et al. (2003) and references therein) that showed that net primary production and the flux of carbon assimilates to roots are important factors of total soil respiration. Other studies also hypothesized that aboveground biomass significantly determined TSR. Doff Sotta et al. (2004) used the basal area of lowland Amazonian forest stands to estimate TSR but did not detect a significant relation. They concluded that basal area was not related to litter fall and fine root production and therefore could not estimate TSR. In a modelling approach that included data from different vegetation covers under temperate climate, del Grosso et al. (2005) determined phenology and autotrophic respiration as main factors of TSR. According to the findings of Raich and Tufekcioglu (2000) vegetation had only secondary influence on TSR, they attributed TSR to feedbacks between temperature, availability of water and substrate parameters.

5.6. Partitioning soil CO_2 efflux and heterotrophic soil respiration

Soil CO_2 efflux originates from three major sources: (i) root respiration including (ii) microbial respiration derived from rhizodeposition, and (iii) microbial respiration from mineralisation of above- and belowground litter (Sulzman et al., 2005). Kuzyakov (2006) even differentiated soil CO_2 efflux into five groups: (1) microbial decomposition of SOM in root free soils without undecomposed plant remains, (2) microbial decomposition of SOM in soil affected by roots and/or plant residues, (3) microbial decomposition of dead plant remains, (4) microbial decomposition of rhizodeposits of living roots and (5) root respiration. As at this time no reliable method is available for measuring these partitioned fluxes, Högberg et al. (2004) postulated a concept that separated functional autotrophs from functional heterotrophs by the origin of the carbon source they use. The former receive photosynthates directly or indirectly from the plant canopy, and therefore include (4) and (5) as defined above. The carbon source for the latter group is soil organic matter, derived from above- and belowground sources and includes (1) to (3) (Högberg et al., 2006).

In a review Hanson et al. (2000) discussed methods for separating root and soil microbial contributions to soil CO_2 flux. They defined root respiration as the sum of all rhizosphere pro-

cesses, which includes respiration of living root tissue, the respiration of symbiotic mycorrhizal fungi and associated micro-organisms, and the respiration of organisms dependent on root exudates and recent dead root tissue in the rhizosphere (Wiant, 1967; Hanson et al., 2000). This definition is in accordance with the definition of "functional autotrophs" given by Högberg et al. (2004) and also Kutsch et al. (2001) gave an analogous definition but used the term "rhizomicrobial respiration." The methods for partitioning the contributions of the different functional groups can be grouped into three broad categories: component integration, root exclusion and isotopic approaches (Hanson et al., 2000). In the present study on soil CO_2 efflux in tropical montane forests, subplots were trenched and total and partitioned soil CO_2 efflux was determined. This approach falls in the category of root exclusion methods and has some general constraints that have to be carefully evaluated. Firstly, cutting of the roots possibly eliminates water uptake by roots from the soil, which may alter soil water content in the trenched plots and thus activity of aerobic microbes (Hanson et al., 2000). In the present study soil moisture was not measured directly in the trenched plots, but as soil temperature did not differ between control and trenched plots at all altitudes and as it is usually positively correlated with soil moisture within the same ecosystem, the soil water content of the trenched plots is not assumed to have changed due to the treatment. Secondly, cutting of the roots enhances the availability of decomposable substrate for the functional heterotrophs, which enhances their respiration; i. e. root exclusion by trenching is supposed to overestimate heterotrophic respiration and underestimate root contribution (Hanson et al., 2000; Lee et al., 2003). This constraint has been addressed only recently by relating trenching studies to root litter decomposition in the respective ecosystems and according to the climatic conditions (Epron et al., 1999; Lavigne et al., 2003; Lee et al., 2003; Rey et al., 2002). In the present study, the decomposition of roots was included in the calculation of root contribution to soil CO_2 efflux. Thus, root contributions to total soil respiration at the investigated plots are considered reliable estimates. A further constraint of the trenching method in deeply weathered soils or in those with very thick organic layers may be the restricted depth of trenching that can be achieved in steep and difficult terrain. Trenching depth in the present study was 50 cm and was chosen according to results of Soethe (2006) that showed negligibly low fine root length densities below this depth. I therefore conclude that root contribution was correctly estimated by the applied method, which is supported in a review by Bond-Lamberty et al. (2004), who found trenching studies to give adequate results as compared to other methods.

In the present study root contribution to total soil CO_2 efflux as well as the total carbon respired by roots declined with increasing altitudes. At the same plots Moser et al. (2007b) observed an increase of total fine root biomass at high elevations and a shift in carbon allocation from aboveground biomass to belowground biomass at the high-elevation plots. They consider this shift a compensation of reduced nutrient availability through increased root biomass at high altitudes. Following this argumentation and the frequently cited correlation that high allocation to roots causes high fine root activity and therefore high root respiration (Kutsch et al., 2001) and that low nutrient supply leads to enhanced respiration of assimilated carbohydrates by the roots (Lambers et al., 1998), declining autotrophic respiration along the studied altitudinal gradient do not fit in. However, in a study along a humid tropical elevation gradient from 180 to 1 000 m, root contribution was not determined, but the situation was very similar to the present study: soil moisture and fine root biomass increased, soil temperature and TSR declined with increasing

altitude (McGroddy and Silver, 2000). Furthermore, fine root biomass was positively related to SOC. The authors attributed their findings to reduced root turnover in moist soils and to reduced efficiency of decomposers under anaerobic conditions. Concerning the results of the present study, I hypothesize that low soil temperatures and high soil moisture are not only responsible for reduced nutrient availability and high belowground biomass (Moser et al., 2007b), but also reduce root activity and therefore root contribution to soil CO_2 efflux, which would lead to the observed trend of declining root contribution along the altitudinal gradient. Reduced root contribution to soil CO_2 efflux at high altitudes indicates that the overall root activity of these forest stands is smaller than at lower plots, but the relative root activity may be higher for the single tree. Lavigne et al. (2003) found the LAI to be a factor of autotrophic respiration and concluded that recently assimilated carbohydrates must control root respiration. Bond-Lamberty et al. (2004) also consider the availability of photosynthetic carbon as the limiting factor of autotrophic respiration. For the studied altitudinal gradient, Moser et al. (2007a) consider decreasing LAI and leaf photosynthetic capacity as main factors of reduced total photosynthetic carbon gain. In summary, these findings support the hypothesis that reduced respiration of functional autotrophs is a function of reduced LAI and total carbon gain at high altitudes. However, the carbon balance of slow growing plants under limited nutrient availability, high water saturation and low soil temperatures needs further detailed investigation (Lambers et al., 1998), as from the given facts it cannot be explained how carbon allocation to different parts of the plants may change as a result of decreasing total carbon gain.

Different authors could not correlate the size of microbial biomass as indicated by C_{mic} to activity parameters like respiration and enzyme activities (e. g. Lou et al. (2004)). Wang et al. (2003) found only weak correlation between C_{mic} and TSR and suggested that a close relation between the two parameters requires sufficient supply with mineralisable carbon and a relatively constant microbial activity. Nannipieri et al. (2003) also emphasises that C_{mic} is not necessarily an indicator for microbial activity. In the present study high C_{mic} was related to high heterotrophic respiration, gross mineralisation and gross ammonium consumption and TSR declined concurrently. This indicates that the size of the microbial biomass did influence microbial activity to a certain point. Litton et al. (2003) explained the positive relation between TSR and stand age with increasing C_{mic} and belowground biomass. In a lowland tropical forest of Puerto Rico, soil CO_2 efflux was positively correlated to total and active fungal and bacterial biomass, respectively. There was no direct significant dependency of TSR on microbial carbon or nitrogen as indicators for microbial biomass. Microbial carbon was highly variable, especially in the organic layer horizons, which was also true for TSR at the respective plots. This leads to the assumption that a heterogeneous distribution of micro-organisms causes spatially variable soil respiration. The lacking of a close correlation between TSR and microbial biomass indicates that the quantity of microbial carbon and nitrogen alone is not necessarily relevant for the activity of micro-organisms. Furthermore, TSR is a measure of the combined activity of microbes and roots and therefore may not be correlated with microbial biomass. As shown by the C_{mic} : SOC ratio, microbial biomass can be an indicator of TSR in relation to the soil organic carbon pool, which leads to the conclusion that the availability of the substrate determines microbial activity. Wang et al. (2003) also found only weak correlation between microbial carbon and total soil respiration, which was in correspondence with other studies. They concluded that a close relation

can only exist, if microbial biomass was sufficiently supplied with available substrate and if the microbial biomass itself was of continuous activity.

5.7. Leaf litter decomposition

Production and decomposition of plant litter are important ecosystem functions, as they provide input of organic matter and energy into the soil and are decisive for nutrient cycling and humus formation (Kainulainen and Holopainen, 2002; Fioretto et al., 2003). The rate of organic matter turnover, i. e. litter decomposition is of particular importance in nutrient poor ecosystems (Coûteaux et al., 2002). Nutrient mineralisation from fresh plant litter occurs via the enzymatic activities of the microbial communities that become established on the litter surfaces (Kourtev et al., 2002). Litter decomposition and nutrient mineralisation are controlled by micro- and macro climate and a variety of biotic factors like the presence of invertebrate fauna, activity of decomposing organisms, litter type and therefore litter quality (Coûteaux et al., 2002; Kainulainen and Holopainen, 2002; Vasconcelos and Laurance, 2005). In the present study, remaining litter was dependent on time of exposure and altitude. Declining leaf litter decomposition along the investigated altitudinal gradient reflected the increase of organic layer thickness. Leaf litter decomposition was monitored over 44 weeks and the faster decomposition as indicated by higher decay rates during the first weeks of exposure is attributed to the leaching of water-soluble components from the leaves (O'Neill and Norby, 1996; Heim and Frey, 2004; Magid et al., 2004). The cutting of the litter before filling the bags might also have enhanced the leaching of soluble plant compounds. During the following weeks decay rates declined which may be partly an effect of the colonisation of the litter by microbes which increases the remaining dry weight in the litter bag. Furthermore, after leaching of soluble compounds the increasing residual plant mass is characterised by less decomposability (Sundarapandian and Swamy, 1999) and the remaining organic matter is gradually stabilised by the formation of humus. The fact that during the first 16 weeks average remaining litter increased at some time at investigated plots maybe explained by collection and preparation of the litter. As all litter was collected in traps, the bags had no soil contact prior to drying, homogenization and distribution at the plots. Consequently, freshly fallen litter was not yet inoculated with soil micro-organisms. Thus, colonization of the litter started at the moment when the litterbags were placed at the plots, which increased the remaining litter weight and led to slower decomposition during the first 16 weeks. The observed pattern of leaf litter decomposition underlines the importance of the colonisation of the freshly fallen plant material by soil micro-organisms for decomposition.

In the study I used a mesh size of 1 mm, which excludes macrofauna from the fragmentation of the litter (Cortet et al., 2002). Up to now, no studies haven been conducted in the RBSF concerning soil macrofauna, but as far as personal observations from all soil scientists that have worked in the area go, only very little macrofaunal activity was observed (Maraun et al., 2007). I therefore assume that the current decomposition study does not underestimate the decomposition rates due to exclusion of soil macrofauna.

The ingrowth of fine roots into the litterbags during the final period of the experiment coincided with increased k values, which leads to the assumption that fine root activity and exudation supports leaf litter decomposition. This argument is supported by a study in Congolese Euca-

lyptus plantations (Laclau et al., 2004). This study investigated how alien species are able to develop appropriate strategies that allow them to grow on poor tropical soils. This was realized by a thick, dense root mat that directly takes up nutrients from throughfall, stem flow and leachates. Furthermore nutrients are taken up directly from decomposing plant material. Cuevas and Medina (1988) came to a similar conclusion as they observed an accelerated leaf litter decomposition if the litter was in contact with fine roots. Their conclusion was that a nutrient release mechanism exists, that is mediated by these fine roots and/or their associated micro-organisms.

To test the influence of litter quality on decomposition, two different types of litter were used in the study. The reference litter can be considered to be of homogeneous composition and the variation of its decomposition at the respective sites at the respective exposition times and along the altitudinal gradient should give estimation of the importance of site conditions and abiotic factors for decomposition. The stand litter was of different composition at the five study sites and, compared to reference litter decomposition, its decomposition gives an idea of the influence of litter quality and site conditions on leaf litter decomposition. However, the comparison of stand and reference litter decomposition did not reveal general differences or universal patterns. There were only few significant differences which lead to the assumption that leaf litter decomposition was controlled rather by abiotic factors than by litter quality. This assumption is supported by the fact that the initial C : N ratio of the reference litter was significantly different from the initial C : N ratio of stand litter of the other plots. It was wider than at $P_{1\,050\ m}$ and significantly smaller than at all other plots. Only k values after four weeks of decomposition were significantly related to the initial C : N ratio. Consequently C : N ratio had a consistent influence on initial leaf litter decay. However, if C : N ratio is considered an important determinant of litter decomposition, then reference litter should have been decomposed significantly slower at $P_{1\,050\ m}$ than stand litter at the same site as reference C : N ratio was significantly lower, but this was not the case. For the other study sites, that all had significantly higher C : N ratios, reference litter was not consistently faster decomposed. Consequently, C : N ratio alone cannot predict leaf litter decomposition in different stands of tropical mountain forest of Southern Ecuador, which is in accordance with a study in lowland Brazil (Luizão et al., 2004). There are several possible explanations; firstly, site conditions overrule the higher substrate quality as expressed by the C : N ratio of the reference litter. Another reason may be that decomposer communities cannot adapt to the quality of the reference litter as this species usually does not occur in closed stands. Maraun et al. (2007) found single species leaf litter to be more slowly decomposed than mixed litter and attributed this to either higher humidity in mixed litter or to the fact that mixing of litter may stimulate the decomposition of low quality litter. Last but not least, the C : N ratio alone may not be an appropriate indicator of litter quality. Hobbie et al. (2004) point out, that leaf litter quality is not only defined by the N content and in the recent literature several parameters of leaf litter quality have been considered important for decomposition: total nitrogen and lignin content and lignin : N and C : N ratios (O'Neill and Norby, 1996; Heim and Frey, 2004). Furthermore manganese concentrations appear to be a good indicator of decomposability, as the activity of the fungi-derived enzymes, that catalysate lignin depolymerisation is dependent on the manganese concentration (Heim and Frey, 2004). Hartemink and O'Sullivan (2001) found the lignin+polyphenol : N ratio to exert a strong influence on leaf litter decomposition. Concentration of condensed tannins should be carefully evaluated as an indicator for inhibited leaf litter decomposition (Teklay and Malmer,

2004). On a global scale summer drought and temperature sum exert a strong influence in litter decomposition (Liski et al., 2003) but under locally equal climatic conditions substrate quality has the dominant influence (Heim and Frey, 2004). For the study area, Wilcke et al. (2007) found no indications that reduced organic matter turnover at high altitudes are caused by high lignin or polyphenol contents and considered frequent waterlogging and decreasing temperatures as controlling factors. Their suggestion that also increasingly unfavourable nutrient supply might contribute to reduced turnover is supported by the findings of Maraun et al. (2007). They determined the availability of C, N and P as limiting for basal trophic taxa in particular fungi and decomposer soil mesofauna.

Chapter 6

Summary

6.1. Summary and theses

Impacts of land use and climate change in tropical forests on the global carbon budget are of principal interest in the recent research, as these forests amount to about 48 % of the world's forested area. Interest has been focused on lowland tropical forests mainly, but tropical montane forests occupy about 20 % of all tropical forests. Soils of tropical montane forests are frequently waterlogged and characterised by high soil organic carbon stocks. Furthermore, along altitudinal gradients, changes in stand structure and net primary production can be observed that have not been fully explained yet. As causes reduced microbial activity and nitrogen turnover in soils of tropical montane forests have been suggested. Against the background of climate change, carbon turnover mechanisms in soils of these forests are of special interest.

The present study therefore aimed at determining and quantifying relevant carbon and nitrogen pools as well as nitrogen mineralisation potentials. Furthermore, size, activity, and structure of microbial biomass were characterised. The collected data was supposed to provide basic knowledge on carbon and nitrogen cycling in tropical montane forest soils. Thus, evaluation of the susceptibility of their carbon stocks for climate change as well as nitrogen and carbon limitation of microbial organic matter decomposition was possible.

Field work of this study was conducted during 2003–2005 at an altitudinal transect that included five study sites between 1 050 and 3 060 m amsl. Total soil respiration was recorded biweekly over two years, the contribution of roots to total soil CO_2 efflux over one year. Soils of the study sites were sampled twice and biochemical and microbial parameters were determined.

The principal results of the study can be summarised as follows:

Total soil organic carbon stock increased along the altitudinal gradient which was recognisable in organic layer thickness and also SOC content in the top mineral soil and also indicated by reduced leaf litter decomposition at high altitudes. This increase is mainly attributed to increasing soil moisture and declining temperatures, i. e. the reduction of microbial activity due to unfavourable climatic conditions. In that context, tropical montane forest soils are susceptible to climate change as rising temperatures may accelerate organic matter decomposition and cause an increase in soil CO_2 efflux.

Hot water extractable carbon served as an indicator for the carbon mineralisation potential

in the studied organic layer and mineral horizons. In general the carbon mineralisation potential was high at all sites studied and was positively correlated with altitude. This indicates reduced decomposition and increased organic matter stabilisation in mineral soils at high altitudes and underlines the importance of high altitude tropical forest soils for carbon sequestration.

The size of the microbial biomass in the organic layer horizons was spatially variable and determined by different factors. In the top organic layer the availability of nitrogen exerted a major role on microbial biomass size and declining nitrogen contents led to reduced microbial biomass at high altitude forest stands. In the fermented and partly humified organic horizon that was characterised by high fine root densities, microbial biomass was controlled by the size of total (SOC) and mineralisable (HWC) pool, which leads to the conclusion that rhizodeposits are an important substrate for microbial growth and that microbial activity and growth is dependent on labile carbon compounds.

For the studied soils, the $C_{mic} : N_{mic}$ ratio is not considered an adequate indicator of changes in microbial community structure, as changes of this ratio did not consistently correspond to changes in PLFA patterns.

Over the studied altitudinal gradient, PLFA patterns did not indicate a significant change in microbial community composition even though exceptionally high fungal abundances occurred in the top organic layer at 3 060 m and the community composition in the mineral soil at 1 050 m was clearly different from the remaining samples. All studied horizons were characterised by comparably low abundances of actinomycetes and high abundances of fungi and Gram negative bacteria as compared to other vegetation and land use types. The physiological status of microbial communities is characterised by limitation of microbially available carbon.

The negative correlation of total, mineralisable and mineral nitrogen contents with altitude in organic layer horizons reflected increasing N-limitation of organic matter decomposition at high altitudes.

High hot water extractable nitrogen stocks in concurrence with low readily available nitrogen stocks support the conclusion of reduced organic matter turnover at high altitudes, as they indicate high mineralisation potential but reduced actual mineralisation and availability for plant uptake and microbial growth. As HWC : HWN and SOC : TN increased concurrently with an increase in organic layer thickness and SOC stocks, these ratios are considered reliable indicators for limited organic matter turnover and increasing carbon sequestration.

Net nitrogen mineralisation rates contradict the conclusion that explains increased organic matter decomposition reduction at high altitudes. Net mineralisation rates were not consistently correlated with altitude in the studied horizons.

Declining gross nitrogen mineralisation and ammonium consumption at high altitudes corresponded to declining nitrogen contents and the increase of SOC : TN ratios, organic layer thickness and the mineralisable nitrogen pool. These results suggest the reduction of microbial activity as a result of low nitrogen availability.

From the collected data, general N-limitation of organic matter turnover can be deduced. However, fertilizer experiments, that include other possibly limiting elements like phosphorus, are strongly recommended for the detailed investigation of further controls on decomposition and mineralisation.

Total soil respiration is spatially and temporally highly variable. On the stand level, abiotic

parameters like volumetric water content and soil temperature were no reliable determinants of total soil respiration. Over the whole investigated altitudinal gradient, volumetric water content, soil temperature, leaf litter fall and leaf area index served to reliably estimate total soil respiration.

A main control of TSR was ammonium content in the top organic horizon (Oi). Thus, the availability of mineral nitrogen determined carbon mineralisation. In that context, low TSR at high altitudes point at nitrogen limitation of microbial activity at the upper study sites. This conclusion is supported by lower gross mineralisation and ammonium consumption rates and reduced soil N input via leaf litter fall at high altitudes.

The close correlation between organic KCl-extractable nitrogen and TSR further supports the conclusion, that microbial activity is N-limited in high altitude tropical forests of Southern Ecuador. It furthermore raises the question of the importance of organic plant uptake for plant nutrition in the studied forest stands.

The influence of the studied soil parameters in the mineral soil on TSR was small. Here, abiotic soil conditions exerted the strongest, even though non-significant, influence, i. e. reduced TSR was attributed to low soil temperature and high volumetric water content of the mineral soil. As a result of low TSR rates, SOC stocks in the mineral soil and the size of the mineralisable carbon pool (HWC) increased.

The size of microbial biomass was no overruling factor of TSR. This is attributed to the contribution of root and rhizosphere activity to total CO_2 efflux. It is concluded that also the activity of the microbial biomass controls total soil CO_2 efflux.

The contribution of root and rhizosphere respiration to total soil CO_2 efflux declined along the studied altitudinal gradient and was mainly attributed to low soil temperatures and high volumetric water contents. Under these conditions root and rhizosphere activity are reduced.

The application of the trenching method for determination of root and rhizosphere contribution to total soil CO_2 efflux is considered adequate only, if the following aspects are considered: the amount of carbon that is respired additionally due to enhanced substrate supply after cutting of the roots should be determined and the soil carbon flux from trenched plots should be reduced by this amount. Secondly, rooting depth of fine roots should be regarded for determination of trenching depth.

In tropical montane forests the litterbag methodology has some general constraints that have to be addressed carefully. Fine roots develop thick fine root mats in the fermented and partly humified organic horizon and grow into the litterbags, which leads to an overestimation of the remaining leaf litter. Furthermore, high fungal abundances and the formation of mycelia in the litterbags have the same effect.

Declining leaf litter decomposition along the investigated altitudinal gradient reflected the increase of organic layer thickness and was mainly attributed to declining soil temperatures and increasing volumetric water content.

In all studied forest stands, litter type of lower C : N ratio was not faster decomposed than litter representative for the respective forest stands over the complete duration of the incubation. Low C : N ratios only supported initial leaf litter decomposition. It is concluded that the C : N ratio of the litter is no reliable indicator for leaf litter decomposition.

From the comparison of the data collected in this study with the recent literature it became obvious that only few studies include organic layers in their studies. It is highly recommended

to consider organic matter pools and fluxes, especially in studies on nutrient limitation, carbon sequestration potential and ecosystem element budgeting.

Due to the high spatial variability of the studied parameters, statistical analysis of the collected data was restricted. For future studies this aspect should be considered.

6.2. Zusammenfassung und Thesen

Die Auswirkungen von Landnutzungsänderungen und dem Klimawandel in tropischen Wäldern auf den globalen Kohlenstoffkreislauf gelten heute als eine der Hauptinteressen der Forschung, da tropische Wälder mit 48 % einen wesentlichen Teil der weltweit bewaldeten Fläche einnehmen. Forschungsvorhaben waren und sind vor allem auf die tropischen Tieflandregenwälder ausgerichtet, jedoch nehmen tropische Bergregenwälder insgesamt ca. 20 % der tropischen Waldfläche ein. Die Böden dieser Bergregenwälder sind sehr oft durch Wassersättigung und hohe Vorräte organischen Kohlenstoffes gekennzeichnet. Ein weiteres Kennzeichen tropischer Bergregenwälder ist die systematische Veränderung der Bestandesstrukturen und Nettoprimärproduktion entlang von Höhengradienten, deren Ursachen bisher nicht völlig erklärt werden können. Als Gründe werden unter anderem eine Verminderung der mikrobiellen Aktivität und des Stickstoffumsatzes im Boden angenommen. Vor dem Hintergrund eines Klimawandels sind genaue Kenntnisse der Prozesse des Kohlenstoffumsatzes dieser Böden von besonderem Interesse.

Die vorliegende Arbeit hatte daher zum Ziel, aussagekräftige Kohlenstoff- und Stickstofffraktionen sowie Mineralisationspotentiale zu bestimmen und zu quantifizieren. Des Weiteren wurden Größe, Aktivität und Struktur der mikrobiellen Gemeinschaft bestimmt. Die erhobenen Daten lieferten grundlegende Informationen zum Umsatz von Kohlenstoff und Stickstoff in Böden tropischer Bergregenwälder. Daraus sollte im Folgenden die Anfälligkeit der Kohlenstoffvorräte für Änderungen des Klimas, sowie potentielle Einschränkungen des Abbaus der organischen Substanz durch Kohlenstoff- oder Stickstoffverfügbarkeiten abgeschätzt werden.

Die Feldaufnahmen erfolgten von 2003 bis 2005 entlang eines Höhengradienten, der fünf Untersuchungsflächen auf Höhen zwischen 1 050 und 3 060 m ü. NN einschloss. Die Gesamtbodenatmung wurde im genannten Zeitraum zweiwöchentlich bestimmt, die Bestimmung des Anteils der Feinwurzeln am gesamten CO_2-Fluss des Bodens wurde von 2004 bis 2005 vorgenommen. Die Böden der Untersuchungsflächen wurden zwei Mal repräsentativ beprobt, an den Proben wurden Kohlenstoff- und Stockstoffgehalte unterschiedlicher Verfügbarkeiten sowie mikrobielle Parameter bestimmt.

Die grundlegenden Ergebnisse der Untersuchungen lassen sich wie folgt zusammenfassen:

Die Vorräte des gesamten organischen Kohlenstoffes in Auflagen und Oberboden nahmen entlang des Höhengradienten zu, was durch zunehmende Mächtigkeiten der organischen Auflagen, steigende Kohlenstoffgehalte im obersten Mineralboden und abnehmende Blattstreuabbauraten charakterisiert war. Diese Veränderungen werden wesentlich durch zunehmende Bodenwassergehalte und abnehmende Bodentemperaturen mit zunehmender Höhe ü. NN begründet, welche zu einer Reduktion der mikrobiellen Aktivität führten. Somit stellen organische Auflagen und Mineralböden unter tropischen Bergregenwäldern wichtige Kohlenstoffsenken dar. Es kann davon ausgegangen werden, dass veränderte klimatische Bedingungen im Sinne von erhöhten Temperaturen und abnehmenden Bodenwassergehalten den Abbau des organischen Materials beschleunigen

können und somit Kohlenstoff in Form von CO_2 aus dem Boden in die Atmosphäre abgegeben wird.

Der heißwasserlösliche Kohlenstoff ist ein wichtiger Indikator des potentiell mineralisierbaren Kohlenstoffes in organischen Auflagen und Mineralböden des Untersuchungsgebietes. Das Mineralisierungspotential von Kohlenstoff war generell als hoch einzustufen und positiv mit der Höhe ü. NN korreliert. Auch dieses Ergebnis unterstreicht den eingeschränkten Abbau und die damit einhergehende Stabilisierung der organischen Substanz mit zunehmender Höhe sowie die Bedeutung der untersuchten Böden als Kohlenstoffsenke. Gleichzeitig weisen aber die hohen Mineralisierungspotentiale darauf hin, dass veränderte klimatische Bedingungen, welche den Abbau organischer Substanz begünstigen, zu erhöhter Mineralisation des organischen Materials und damit zu erhöhten CO_2-Flüssen in die Atmosphäre führen können.

Die Größe der mikrobiellen Biomasse zeigte eine große räumliche Variabilität und war in den untersuchten Horizonten von unterschiedlichen Faktoren bestimmt. Im obersten Auflagenhorizont hatten der Ammoniumgehalt und damit die Verfügbarkeit von Stickstoff einen signifikanten Einfluss. Im OfOh-Horizont, der durch sehr hohe Feinwurzeldichten gekennzeichnet war, waren die Gesamt- und mineralisierbaren Kohlenstoffgehalte (HWC) die bestimmenden Faktoren für die Größe der mikrobiellen Biomasse. Aufgrund der Zusammensetzung und Beschaffenheit des HWC wird geschlussfolgert, dass Wurzelexudate ein wichtiges Substrat für mikrobielles Wachstum darstellen und dass die mikrobielle Biomasse demzufolge durch die Verfügbarkeit von labilen C-Verbindungen bestimmt wird.

Für die untersuchten Böden korrespondierten Änderungen des $C_{mic} : N_{mic}$-Verhältnisses nicht mit Änderungen der Struktur der mikrobiellen Gemeinschaft, wie sie durch Analyse der PLFA festgestellt wurde. Demzufolge wird das $C_{mic} : N_{mic}$-Verhältnis nicht als zuverlässiger Indikator einer Änderung der Fettsäuremuster angesehen.

Im untersuchten Höhengradient wiesen die Fettsäuremuster nicht auf eine einheitliche Änderung der Zusammensetzung der mikrobiellen Gemeinschaft hin. Der Oi-Horizont in 3 060 m Höhe ü. NN unterschied sich durch besonders hohe Pilzabundanzen deutlich von den anderen Höhenstufen, des Weiteren zeigte der Mineralboden auf 1 050 m deutliche Abweichungen. Im Vergleich zu anderen Vegetations- und Landnutzungstypen zeigten alle untersuchten Waldböden relativ niedrige Vorkommen von Aktinomyceten, sowie große Häufigkeiten von Pilzen und Gram negativen Bakterien. Der physiologische Status der mikrobiellen Gemeinschaft war durch geringe Mengen mikrobiell verfügbaren Kohlenstoffes gekennzeichnet.

Der negative Zusammenhang zwischen Gesamt-, mineralisierbaren und mineralischen Stickstoffgehalten mit der Meereshöhe in den organischen Auflagen vor dem Hintergrund zunehmender Mächtigkeiten der organischen Auflagen erlaubt die Schlussfolgerung, dass die Verfügbarkeit von Stickstoff mit zunehmender Meereshöhe den Abbau der organischen Substanz limitiert.

Hohe heißwasserlösliche und gleichzeitig niedrige KCl-extrahierbare Stickstoffgehalte zeigen, dass die untersuchten Auflagen und Böden ein hohes N-Mineralisierungspotential aufweisen und dieses aber nicht genutzt wird und damit die Verfügbarkeit von N für den mikrobiellen Umsatz sowie die Pflanzenaufnahme eingeschränkt ist. In diesem Zusammenhang erwiesen sich die HWC : HWN-, HWN : TN- und SOC : TN-Verhältnisse als Indikatoren für die Beurteilung der Stickstofflimitierung des Abbaus organischer Substanz.

Die bestimmten Nettomineralisationsraten zeigten in den jeweiligen Horizonten keine einheit-

lichen Trends entlang des Höhengradienten und waren z. T. positiv mit der Meereshöhe korreliert. Dieses Ergebnis widerspricht der Schlussfolgerung einer N-Limitierung des Abbaus des organischen Materials.

Abnehmende Bruttomineralisation des Stickstoffes und abnehmende Ammoniumimmobilisierung entlang des Höhengradienten wiesen im Zusammenhang mit abnehmenden N-Gehalten, dem Anstieg des SOC : TN-Verhältnisses und der Auflagenmächtigkeit und dem N-Mineralisierungspotential auf eine Einschränkung der mikrobiellen Aktivität in Folge geringer Verfügbarkeit von N hin.

Trotz der aufgeführten Indikatoren für eine N-Limitierung von Umsetzungsprozessen des organischen Materials in den untersuchten Waldböden werden ausführliche Düngeexperimente als notwendig erachtet, um die Frage der Stickstofflimitierung vollständig zu klären.

Die Gesamtbodenatmung ist räumlich und zeitlich hoch variabel. Auf dem Niveau des einzelnen untersuchten Waldbestandes waren volumetrischer Bodenwassergehalt sowie Bodentemperatur keine zuverlässigen Schätzer der Gesamtbodenatmung. Im gesamten Höhengradienten wurde die Gesamtbodenatmung jedoch signifikant durch den volumetrischen Bodenwassergehalt, die Bodentemperatur, Blattstreufall und Blattflächenindex beeinflusst.

Die Gesamtbodenatmung wies einen positiv signifikanten Zusammenhang mit dem Ammoniumgehalt des kaum durchwurzelten LOf1-Horizontes auf. Daraus wird geschlussfolgert, dass die Verfügbarkeit von Ammonium einen wesentlichen Einfluss auf die C-Mineralisierung hat. Dieser Zusammenhang stützt die Annahme, dass die mikrobielle Aktivität in der obersten Streulage durch die Verfügbarkeit von mineralischem Stickstoff beeinflusst bzw. limitiert wird. Diese Annahme wird weiter durch niedrige Bruttomineralisationsraten und Ammoniumimmobilisierung, sowie einen reduzierten Blattstreu- und damit Stickstoffeintrag auf den oberen Untersuchungsflächen untermauert.

Die enge Korrelation zwischen Gesamtbodenatmung und KCl-extrahierbaren organischen Stickstoff im OfOh-Horizont weist ebenfalls auf die Bedeutung des Stickstoffes für den Abbau des organischen Materials hin. Weiterhin wird durch diesen Zusammenhang die Frage aufgeworfen, ob die Aufnahme von organischem Stickstoff durch die Pflanzen in den untersuchten Waldbeständen von Bedeutung ist.

Der Einfluss der untersuchten Bodenparameter im Mineralboden auf die Gesamtbodenatmung war gering. Hier wurden niedrige Bodentemperaturen und hohe Bodenwassergehalte als wesentliche Einflussfaktoren ausgeschieden. Hohe Kohlenstoffvorräte, sowie hohe Gehalte an mineralisierbaren C im obersten Mineralboden resultieren aus den niedrigen Gesamtbodenatmungsraten.

Die Größe der mikrobiellen Biomasse hatte keinen direkten Einfluss auf die Gesamtbodenatmung. Dies wird unter anderem damit begründet, dass die Gesamtbodenatmung auch die Aktivität der Wurzeln und der in der Rhizosphäre lebenden Organismen einschließt. Es wird geschlussfolgert, dass die Aktivität der mikrobiellen Biomasse die Gesamtbodenatmung beeinflusst.

Der Anteil der Wurzel- und Rhizosphärenatmung an der Gesamtbodenatmung nahm entlang des Höhengradienten deutlich ab, was ebenfalls hauptsächlich niedrigen Bodentemperaturen und hohen Bodenwassergehalten zugesprochen wird, da unter solchen Bedingungen die Aktivität von Wurzeln und assoziierten Organismen eingeschränkt ist.

Die Anwendung der Wurzelausschlussmethode mittels Trenching zur Bestimmung der Wurzel- und Rhizosphärenatmung wird nur dann als zulässige Methode angesehen, wenn die folgenden

Aspekte berücksichtigt werden: Durch das Durchtrennen der Wurzeln steht den Bodenmikroorganismen vermehrt abbaubares Substrat zu Verfügung. Die Menge des zusätzlich mineralisierbaren Substrates muss bestimmt und mit dem CO_2-Fluss der manipulierten Flächen verrechnet werden, um eine Überschätzung der mikrobiellen Atmung zu vermeiden. Weiterhin muss die Wurzeltiefenverteilung bei der Anlage der Trenchingplots berücksichtigt werden.

In den untersuchten Waldbeständen hatte die angewendete Methode zur Untersuchung des Streuabbaus grundsätzliche Einschränkungen, die berücksichtigt werden müssen. Die Feinwurzeln bilden in der Auflage dichten Wurzelfilz und wachsen in die Litterbags ein, was zu einer Unterschätzung der Abbauraten führen kann. Weiterhin verursacht die Bildung von Pilzmycelien ähnliche Effekte.

Abnehmende Abbauraten der Blattstreu entlang des untersuchten Höhengradienten spiegeln die Zunahme der Auflagenmächtigkeiten wider und werden maßgeblich durch zunehmende Bodenwassergehalte und abnehmende Bodentemperaturen verursacht.

In allen untersuchten Waldbeständen wurde der Streutyp mit engerem C : N-Verhältnis unter Berücksichtigung des gesamten Versuchszeitraumes nicht schneller abgebaut, als Streutypen mit weitem C : N-Verhältnis. Niedrige C : N-Verhältnisse förderten den raschen Streuabbau nur während der ersten vier Wochen. Damit kann das C : N-Verhältnis der verwendeten Streu nicht als zuverlässiger Indikator für den langfristigen Abbau der Blattstreu angesehen werden.

Im Vergleich der vorliegenden Daten mit der aktuellen Literatur wurde ersichtlich, dass nur wenige Studien die organischen Auflagen in ihre Untersuchungen einbeziehen. Die vorliegende Studie zeigt jedoch die Bedeutung der Auflagen für Kohlenstoff- und Stockstoffumsätze und für die Bewertung von Vorräten. Daher wird empfohlen, organische Auflagen in Untersuchungen, besonders im Hinblick auf C-Sequestrierung, Nährstofflimitation und bei der Erstellung von Nährstoffbudgets für bestimmte Ökosysteme, einzubeziehen.

Infolge der sehr hohen räumlichen Variabilität der untersuchten Bodenparameter waren die Möglichkeiten zur statistischen Auswertung eingeschränkt. In folgenden Studien im Untersuchungsgebiet sollte dieser Umstand stärker berücksichtigt werden.

6.3. Resumen de tesis

Los efectos de los cambios del uso del terreno y del cambio climatico en los bosques tropicales en el ciclo del carbono total son de interés principal de la presente investigación, porque los bosques tropicales cubren un 48 % del aréa forestal del mundo. Estudios fueron y estan concentrandose en los bosques tropicales bajos, pero bosques tropicales montañosos cubren un 20 % del aréa forestal tropical. Frecuentamente la saturación de agua y los contenidos elevados de carbono son caracteristicos para los suelos de estos bosques. Adémas, en los bosques tropicales se encuentra un cambio de la estructura y una declinación de la producción primaria neta con el aumento de la altitud, estas causas no se han identificado completamente. La declinación de la actividad microbiana y la transformación de nitrogeno en el suelo se discuten como factores principales. Para la evaluación de los posibles efectos del cambio climatico, conocimientos exactos sobre el ciclo de carbono y nitrogeno del suelo son de interes especial.

Por eso, el objectivo de la tesis presentada fue la determinación y la cuantificación de fracciones differentes de carbono y nitrogeno y potenciales de mineralización. Adémas la cantidad, actividad

y estructura de la masa microbiana fueron determinados. Los datos colectados dan información basica sobre la transformación de C y N en capas organicas y suelos minerales de los bosques tropicales montañosos. En conclusión de esta información la sensibilidad del carbono secuestrado en el suelo por el cambio climatico y restricciones potenciales de la descomposición de la materia organica fueron evaluados.

El trabajo del campo fue realizado durante los años 2003 hasta 2005 en una gradiente altitudinal, que incluyó cinco sitios de investigación entre 1 050 y 3 060 m sobre nivel del mar. La respiración total de suelo fue determinado bimensualmente. Además, la parte de los raíces finos en la respiración total fue determinado durante un año entre enero de 2004 y agosto de 2005. La toma de muestras de las capas organicas y suelos minerales representativa de todos los sitios de investigación fue realizado en noviembre del 2003 y abril del 2004 para la determinación de los parámetros microbianos y de los ciclos de carbono y nitrogeno.

Los resultados fundamentales se puede resumir como sigue:

Los contenidos del carbono organico total en las capas organicas y suelos minerales se incrementarón con el aumento de la altitud que se refleja en capas organicas mas amplias, contenidos mas altos del carbono secuestrado en los suelos minerales y descomposición mas lenta de las hojas en altitudes elevadas. Estos cambios estan establecidos pincipalmente por contenidos volumetricos altos de agua y temperaturas bajas del suelo, que resultan en la declinación de la actividad microbiana.

Por eso, las capas organicas y los suelos minerales de los bosques tropicales montañosos constituyen filtros de carbón muy importantes. Por la reducción de la transformación de carbono en altitudes elevadas debido a condiciones abioticos, se deduce que cambios del clima pueden acelerar la descomposición de la materia organica y por lo tanto aumentar el flujo de CO_2 del suelo a la atmosféra.

La fracción de carbono soluble en agua hirviendo (HWC) fue un indicator acreditado del potencial de mineralización. Generalmente, las capas organicas y suelos minerales examinados se caracterizaron por potenciales altos de mineralización, que incrementarón con la elevación de la altitud. Este resultado también subraya la descomposición reducida de la materia organica y la importancia como filtro de carbón. Potenciales de mineralización altos también muestran la sensibilidad alta del carbono secuestrado por cambios climaticos.

La cantidad de la masa microbiana demostró una variación espacial grande y fue determinado en los distintos horizontes por factores diferentes. En el Oi, la masa microbiana fue correlacionado significativamente con el contenido de ámonio disponible. En el OeOa, que fue caracterizado por densidades muy altos de raíces finas, SOC y HWC fueron determinantes de la masa microbiana. A base de la composición y la calidad de HWC se concluye que las excreciónes de raíces son un substrato importante para el crecimiento microbiano y que la masa microbiana dependente de la disponibilidad de las combinaciónes inestables de carbono.

No se pudo determinar una correlación fundamental entre la tasa de $C_{mic} : N_{mic}$ y la estructura de la masa microbiana como el determinado con el analisis de los acídos grasos de fosfato. Por eso, la tasa de $C_{mic} : N_{mic}$ no esta como un indicator acreditado por la composición de la masa microbiana.

El analisis de los acídos grasos de fosfato no demonstró un cambio de la estructura de la masa microbiana con la elevación de la altitud. En el Oi de 3 060 m se encontró altas occurencias de

hongos y tambien la estructura de la masa microbiana en el suelo mineral á 1 050 m metros fue muy diferente que en las muestras de los otros sitios de investigación. En comparación con otros tipos de uso y vegetación, los suelos del transecto mostraron occurencias bajas de actinomycetes y occurencias altas de hongos y bacterías Gram negativas. El estado fisiológico de la masa microbiana fue caracterizado por una reducción de la disponibilidad microbiana de carbono.

La declinación de los contenidos de nitrogeno total, mineralizable y mineral en las capas organicas con la elevación de la altitud en relación con el aumento de las capas organicas, permite la conclusión que la disponibilidad de nitrogeno limita la descomposición de la meteria organica en altitudes elevadas.

La correlación entre los contenidos altos del nitrogeno soluble en agua hirviendo (HWN) y nitrogeno extractable con KCl demonstraron, que las muestras investigados tienen un potenciál de mineralización muy alto que no esta realizado y por eso la disponibilidad de N por la masa microbiana y la absorción de la planta esta limitado. En este relación, las tasas de HWC : HWN, HWN : TN y SOC : TN son utiles para la evaluación de la descomposición organica por limitación de nitrogeno.

Los indices de mineralización neto de nitrogeno no fueron correlacionados uniformemente con la elevación de la altitud y parcialmente fueron relacionados positivamente con la altitud. Este resultado contrasta la conclusión que la descomposición organica esta limitada por la disponibilidad de nitrogeno en altitudes elevadas del transecto.

Al contrario, la declinación del índice de la mineralización neto del nitrógeno e inmovilización del amonio con la elevación de la altitud, subrayaron la reducción de la actividad microbiana debido al la limitación de la disponibilidad de nitrogeno.

A pesar de los argumentos presentados por la limitación de la transformación de la materia organica por disponibilidad de nitrogeno, hacen falta experimentos de abono para elucidar completamente la cuestión de la limitation de N en bosques tropicales montañosos.

La réspiración total del suelo fue caracterizada por una alta variabilidad espacial y temporal. En el nivel del sitio de investigación, el contenido del agua y la temperatura del suelo no fueron relacionado con la réspiración. En el transecto altitudinal completo la réspiración del suelo fue correlacionada significativamente con contenido del agua y temperatura del suelo, caida del residuo de las hojas e índice de área de la hoja.

Adémas, la respiración total del suelo fue relacionada con el contenido amonico del horizonte Oi. De este se concluye, que la disponibilidad de nitrogeno mineral es de alta importancía para la respiración. Por cuanto que el horizonte Oi casí no contiene raíces, en este horizonte la respiración total corresponde a la respiración microbiana y la relación observada subraya la conclusion que la actividad microbiana es dependiente de la disponibilidad del nitrogeno mineral. La respiración total fue correlacionada con el contenido de nitrogeno organico, que representa la parte de nitrogeno que esta mineralizado rapidamente. Este resultado también demonstró la importancía de nitrogeno para la actividad de la masa microbiana y de las raíces.

La cantidad de la masa microbiana no fue relacionada con la respiración total. Se razona este resultado principalmente por que la respiración total no solamente incluye la actividad de la masa microbiana, si no también de las raíces y de los organismos de la rizosfera.

Los resultados demonstraron la declinación del porcentaje de la respiración de las raíces con la elevación de la altitud. En condiciones de contenidos altos de agua y temperaturas bajas, la

actividad de raíces y en la rizosfera se reduce.

El metodo de “trenching” es aplicable solamente si se toma en consideración la distribución profunda de las raíces y el substrato suplemental por la mineralización, que se adiciona por el “trenching.” La declinación de la descomposición del residuo de las hojas con la elevación de la altitud esta reflejado en el aumento de las capas organicas.

En el transecto de este estudio, el metodo “litterbags” fue limitada por dos causas. Las raíces finas forman un enrejado denso y crecen dentro del “litterbag.” Adémas los hongos crecen en el “litterbag.” Este puede resultar en subestimación de los rangos de descomposición.

La tasa C : N de residuo de las hojas no fue correlacionado con el rango de descomposición del residuo de las hojas durante 44 semanas. Solamente durante las primeras cuatro semanas, la tasa C : N baja resultó en rangos de alta descomposición. En estudios futuros mas indicatores de la calidad de residuo de las hojas debe ser determinado y evaluado.

La comparación de los resultados de este estudio con la literatura actual demonstró la falta de estudios sobre capas organicas en bosques tropicales. Los resultados presentados demuestran la importancia de las capas organicas para el cyclo de carbono y nitrogeno el los suelos de bosques tropicales montañosos.

Debido a la variabilidad de los parámetros determinados el analisis estadistico fue limitado. En estudio futuros en la región de la investigación se necesita considerar con mas detalle la alta varibilidad.

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Appendix

Table 1: Spearman's rang correlation coefficients altitudinal gradient; significant correlations $p \leq 0.05$ are marked bold. I and II designate first and second sampling.

	Oi	**OeOa**	**0–10 cm**
pH	−0.07	**−0.52**	**−0.57**
SOC I	**0.45**	0.22	**0.55**
HWC I	−0.05	0.13	**0.74**
HWC II	0.40	−0.29	**0.66**
TOC_{KCl} I	−0.27	**−0.51**	0.32
TOC_{KCl} II	**−0.54**	**−0.88**	−0.04
C_{mic} I	**−0.49**	−0.08	−0.19
C_{mic} II	−0.08	0.14	0.26
TN I	**−0.86**	**−0.53**	0.35
HWN I	**−0.85**	**−0.62**	**0.39**
HWN II	**−0.58**	**−0.63**	**0.38**
TN_{KCl} I	**−0.88**	**−0.82**	−0.01
TN_{KCl} II	**−0.83**	**−0.86**	**−0.59**
$TN_{KCl(org)}$ I	**−0.55**	**−0.73**	0.21
$TN_{KCl(org)}$ II	**−0.75**	**−0.42**	**−0.45**
$TN_{KCl(inorg)}$ I	**−0.88**	**−0.73**	−0.18
$TN_{KCl(inorg)}$ II	**−0.76**	**−0.79**	**−0.60**
NH_4^+-N I	**−0.72**	**−0.48**	**0.80**
NH_4^+-N II	**−0.74**	**−0.63**	**0.45**
NO_3^--N I	**−0.88**	**−0.73**	**−0.53**
NO_3^--N II	**−0.81**	**−0.66**	**−0.75**
N_{mic} I	**−0.59**	−0.20	−0.15
N_{mic} II	−0.33	0.32	0.27
Gross Mineralisation	**−0.79**	−0.37	0.37
NH_4^+ consumption	**−0.74**	−0.05	0.42
Net ammonification	**0.90**	**0.90**	0.70
Net nitrification	−0.40	−0.60	0.00
Net mineralisation	**0.90**	−0.30	−0.30
SOC : TN	**0.82**	**0.63**	**0.61**
C_{mic} : N_{mic} I	0.15	0.09	−0.03
C_{mic} : N_{mic} II	**0.39**	**−0.45**	0.30
C_{mic} : SOC I	**−0.50**	−0.23	**−0.64**
HWC : SOC I	−0.16	−0.21	0.19
HWN : TN I	**−0.41**	**−0.56**	0.03
HWC : HWN I	**0.88**	**0.78**	**0.46**
HWC : HWN II	**0.84**	**0.62**	**0.72**
TOC_{KCl} : SOC I	−0.28	**−0.56**	−0.07

Table 2: Spearman's rang correlation coefficients profile gradient; significant correlations $p \leq 0.05$ are marked bold. I and II designate first and second sampling.

	1 050 m	**1 540 m**	**1 890 m**	**2 380 m**	**3 060 m**
pH	**−0.87**	**−0.50**	**−0.92**	**−0.92**	**−0.77**
SOC I	**−0.85**	**−0.94**	**−0.84**	**−0.77**	**−0.94**
HWC I	**−0.93**	**−0.98**	**−0.95**	**−0.94**	**−0.93**
HWC II	**−0.70**	**−0.89**	**−0.90**	**−0.88**	**−0.92**
TOC_{KCl} I	**−0.87**	**−0.94**	**−0.94**	**−0.94**	**−0.94**
TOC_{KCl} II	**−0.85**	**−0.94**	**−0.92**	**−0.94**	**−0.94**
C_{mic} I	**−0.84**	**−0.93**	**−0.93**	**−0.87**	**−0.76**
C_{mic} II	**−0.77**	**−0.84**	**−0.93**	**−0.68**	**−0.87**
TN I	**−0.75**	**−0.59**	**−0.54**	−0.39	**−0.47**
HWN I	**−0.91**	**−0.96**	**−0.92**	**−0.88**	**−0.86**
HWN II	**−0.58**	**−0.87**	**−0.87**	**−0.64**	**−0.77**
TN_{KCl} I	0.13	0.16	0.26	0.39	**0.72**
TN_{KCl} II	0.39	0.11	0.03	0.37	0.37
$TN_{KCl(org)}$ I	0.09	−0.08	−0.31	−0.34	**−0.60**
$TN_{KCl(org)}$ II	−0.16	**−0.47**	**−0.60**	−0.18	**−0.58**
$TN_{KCl(inorg)}$ I	0.10	0.05	0.42	**0.72**	**0.88**
$TN_{KCl(inorg)}$ II	0.29	0.34	0.31	**0.66**	**0.85**
NH_4^+-N I	**0.47**	0.03	**0.47**	**0.67**	**0.88**
NH_4^+-N II	0.24	0.31	0.37	**0.52**	**0.87**
NO_3^--N I	−0.10	**−0.50**	0.03	**0.63**	0.37
NO_3^--N II	0.16	0.31	0.37	0.31	0.23
N_{mic} I	**−0.75**	**−0.88**	**−0.89**	**−0.84**	**−0.62**
N_{mic} II	**−0.79**	**−0.81**	**−0.93**	**−0.55**	**−0.63**
Gross Mineralisation	**−0.90**		**−0.95**		−0.26
NH_4^+ consumption	**−0.74**		**−0.95**		−0.42
Net ammonification	0.50	0.50	0.50	−0.50	−0.50
Net nitrification	−0.50	0.50	−0.05	−0.05	1.00
Net mineralisation	0.50	0.50	0.50	−0.50	−0.50
SOC : TN I	**−0.80**	**−0.79**	**−0.88**	**−0.87**	**−0.94**
$C_{mic} : N_{mic}$ I	**−0.70**	**0.60**	**−0.44**	−0.37	**−0.64**
$C_{mic} : N_{mic}$ II	**−0.66**	**0.50**	**−0.67**	**−0.63**	−0.16
C_{mic} : SOC I	0.17	**0.58**	−0.39	0.45	−0.45
HWC : SOC I	**−0.64**	−0.39	**−0.54**	0.38	**−0.63**
HWN : TN I	**−0.58**	**−0.92**	**−0.72**	−0.05	**−0.80**
HWC : HWN I	**−0.70**	0.37	**−0.76**	**−0.89**	**−0.94**
HWC : HWN II	**−0.94**	**−0.55**	**−0.49**	**−0.75**	**−0.72**
TOC_{KCl} : SOC I	**−0,67**	**−0,68**	**−0,83**	**−0,93**	0,00

Table 3: Spearman's rang correlation coefficients remaining mass and exposure for stand and reference litter; significant correlations $p \leq 0.05$ are marked bold.

plot	stand litter	reference litter
1 050 m	**−0.922**	**−0.955**
1 540 m	**−0.867**	**−0.895**
1 890 m	**−0.655**	**−0.900**
2 380 m	**−0.633**	**−0.697**
3 060 m	**−0.677**	**−0.805**

Table 4: Spearman's rang correlation coefficients k values for the respective times of exposure, altitude and initial C : N ratio of the litter used. Significant correlations $p \leq 0.05$ are marked bold.

	altitude	C : N
altitude	1.000	0.900
C : N	**0.900**	1.000
k 4	−0.800	**−0.900**
k 8	**−0.900**	−0.800
k 16	**−0.900**	−0.800
k 28	−0.600	−0.800
k 44	**−0.900**	−0.800

Table 5: Spearman's rang correlation coefficients total soil respiration (TSR) with volumetric water content (VWC) and soil temperature (T_{soil}) for each measurement collar. Significant correlations $p \leq 0.05$ are marked bold.

	1 050 m		1 540 m		1 890 m		2 380 m		3 060 m	
TSR #	**VWC**	**T_{soil}**	**VWC**	**T_{soil}**	**VWC**	**T_{soil}**	**VWC**	**T_{soil}**	**VWC**	**T_{soil}**
1	0.11	−0.06	0.45	−0.37	0.21	0.09	−0.09	−0.09	−0.34	0.25
2	−0.14	−0.10	−0.44	0.04	**−0.47**	0.14	**0.49**	0.07	**−0.45**	0.03
3	−0.13	0.10	0.28	**−0.52**	−0.38	0.45	0.06	0.04	−0.16	0.38
4	0.07	−0.02	0.19	−0.02	−0.31	0.25	0.26	0.29	−0.27	**0.49**
5	−0.04	0.03	0.38	−0.13	−0.24	0.28	0.08	0.07	−0.15	−0.08
6	0.19	−0.03	−0.26	0.06	0.00	−0.03	0.26	0.25	−0.14	0.10
7	0.09	0.14	−0.26	−0.43	−0.20	0.36	**0.46**	−0.08	−0.18	**0.73**
8	0.31	−0.06	−0.05	−0.06	−0.08	0.03	0.05	−0.08	−0.31	**0.52**
9	0.17	0.29	−0.04	−0.14	−0.10	0.09	0.33	−0.16	0.19	**0.54**
10	−0.16	**0.47**	−0.30	−0.26	−0.09	0.37	−0.03	0.17	0.26	0.10
11	−0.30	−0.15	−0.05	−0.18	0.09	−0.19	0.07	0.08	−0.08	**0.55**
12	−0.02	−0.22	0.10	−0.40	0.13	0.17	−0.38	0.23	0.07	0.33
13	**−0.42**	−0.18	−0.02	−0.40	−0.27	−0.35	−0.06	0.01	−0.22	0.33
14	**−0.42**	−0.28	0.32	−0.07	−0.35	−0.13	−0.38	−0.15	−0.34	0.23
15	−0.07	−0.16	0.00	**−0.60**	−0.23	0.29	−0.42	−0.11	−0.23	−0.03
16	−0.16	0.12	0.41	−0.14	−0.10	0.10	0.03	−0.24	−0.38	0.20

Table 6: Spearman's rang correlation coefficients Oi horizon (first of three tables); significant correlations $p \leq 0.05$ are marked bold. I and II designate first and second sampling. Only correlations between the parameters for the same sampling should be regarded. Percentages of SOC were calculated for the first sampling only.

	altitude	T_{org}	T_{min}	VWC_{org}	VWC_{min}	TSR	RC%	SOC	TN
altitude									
T_{org}	**−1.00**								
T_{min}	**−1.00**	**1.00**							
VWC_{org}	**0.90**	**−0.90**	**−0.90**						
VWC_{min}	**1.00**	**−1.00**	**−1.00**	**0.90**					
TSR	−0.87	0.87	0.87	−0.67	−0.87				
RC%	−1.00	1.00	1.00	−1.00	−1.00	1.00			
SOC	0.70	−0.70	−0.70	**0.90**	0.70	−0.56	1.00		
TN	**−1.00**	**1.00**	**1.00**	**−0.90**	**−1.00**	0.87	−1.00	−0.70	
SOC : TN	**0.90**	**−0.90**	**−0.90**	**1.00**	**0.90**	−0.67	−0.50	**0.90**	**−0.90**
HWC I	**0.10**	−0.10	−0.10	0.00	0.10	0.15	1.00	−0.40	−0.10
HWN I	**−0.90**	**0.90**	**0.90**	**−1.00**	**−0.90**	0.67	−1.00	**−0.90**	**0.90**
HWC II	0.70	−0.70	−0.70	0.60	0.70	−0.36	1.00	0.30	−0.70
HWN II	**−0.90**	**0.90**	**0.90**	**−1.00**	**−0.90**	0.67	0.50	**−0.90**	**0.90**
HWC : SOC	−0.30	0.30	0.30	−0.40	−0.30	0.41	1.00	−0.70	0.30
HWN : TN	−0.80	0.80	0.80	**−0.90**	−0.80	0.67	1.00	−0.80	0.80
C_{mic} I	−0.80	0.80	0.80	**−0.90**	−0.80	0.67	0.50	−0.80	0.80
N_{mic} I	−0.60	0.60	0.60	−0.70	−0.60	0.67	−1.00	**−0.90**	0.60
$C_{mic} : N_{mic}$ I	0.30	−0.30	−0.30	0.10	0.30	−0.21	0.50	0.00	−0.30
C_{mic} II	−0.50	0.50	0.50	−0.60	−0.50	0.67	0.50	−0.80	0.50
N_{mic} II	−0.60	0.60	0.60	−0.80	−0.60	0.56	−1.00	**−0.90**	0.60
$C_{mic} : N_{mic}$ II	0.80	−0.80	−0.80	**0.90**	0.80	−0.67	1.00	0.80	−0.80
C_{mic} : SOC	−0.80	0.80	0.80	**−0.90**	−0.80	0.67	1.00	−0.80	0.80
gross min rate	**−1.00**	**1.00**	**1.00**	**−1.00**	**−1.00**	**1.00**	0.87	−0.50	**1.00**
GCR NH_4^+	−0.87	0.87	0.87	−0.87	−0.87	0.87	0.50	−0.87	0.87
TOC_{KCl} I	−0.10	0.10	0.10	−0.30	−0.10	0.05	1.00	−0.60	0.10
TN_{KCl} I	**−0.90**	**0.90**	**0.90**	**−1.00**	**−0.90**	0.67	0.50	**−0.90**	**0.90**
$TN_{KCl(org)}$ I	−0.60	0.60	0.60	−0.70	−0.60	0.67	1.00	**−0.90**	0.60
NH_4^+-N_{KCl} I	**−0.90**	**0.90**	**0.90**	**−0.70**	**−0.90**	**0.97**	1.00	−0.60	**0.90**
NO_3^--N_{KCl}	**−0.90**	**0.90**	**0.90**	**−1.00**	**−0.90**	0.67	0.50	**−0.90**	**0.90**
TOC_{KCl} II	−0.50	0.50	0.50	−0.60	−0.50	0.67	1.00	−0.80	0.50
TN_{KCl} II	**−1.00**	**1.00**	**1.00**	**−0.90**	**−1.00**	0.87	1.00	−0.70	**1.00**
$TN_{KCl(org)}$ II	**−0.90**	**0.90**	**0.90**	**−1.00**	**−0.90**	0.67	1.00	**−0.90**	**0.90**
NH_4^+-N_{KCl} II	**−0.90**	**0.90**	**0.90**	−0.70	**−0.90**	**0.97**	1.00	−0.60	**0.90**
NO_3^--N_{KCl} I	**−0.90**	**0.90**	**0.90**	**−1.00**	**−0.90**	0.67	−1.00	**−0.90**	**0.90**
Net Min rate	**0.90**	**-0.90**	**-0.90**	1.00	**0.90**	-0.67	-1.00	**0.90**	**-0.90**

GCR NH_4^+ = gross consumption rate of NH_4^+

Table 7: Spearman's rang correlation coefficients Oi horizon (second of three tables); significant correlations $p \leq 0.05$ are marked bold. I and II designate first and second sampling. Only correlations between the parameters for the same sampling should be regarded. Percentages of SOC were calculated for the first sampling only.

	SOC : TN	HWC I	HWN I	HWC II	HWN II	HWC : SOC	HWN : TN	C_{mic} I	N_{mic} I
SOC : TN									
HWC I	0.00								
HWN I	**−1.00**	0.00							
HWC II	0.60	0.40	−0.60						
HWN II	**−1.00**	0.00	**1.00**	−0.60					
HWC : SOC	−0.40	0.90	0.40	0.00	0.40				
HWN : TN	**−0.90**	−0.10	**0.90**	−0.30	**0.90**	0.20			
C_{mic} I	**−0.90**	−0.10	**0.90**	−0.30	**0.90**	0.20	**1.00**		
N_{mic} I	−0.70	0.70	0.70	−0.10	0.70	**0.90**	0.60	0.60	
C_{mic} : N_{mic} I	0.10	−0.10	−0.10	0.70	−0.10	−0.30	0.30	0.30	−0.10
C_{mic} II	−0.60	0.60	0.60	0.20	0.60	0.70	0.70	0.70	**0.90**
N_{mic} II	−0.80	0.30	0.80	0.00	0.80	0.50	**0.90**	**0.90**	0.80
C_{mic} : N_{mic} II	**0.90**	0.10	**−0.90**	0.30	**−0.90**	−0.20	**−1.00**	**−1.00**	−0.60
C_{mic} : SOC	**−0.90**	−0.10	**0.90**	−0.30	**0.90**	0.20	**1.00**	**1.00**	0.60
gross min rate	**−1.00**	−0.50	**1.00**	**−1.00**	**1.00**	0.50	**1.00**	**1.00**	0.50
GCR NH_4^+	−0.87	0.00	0.87	−0.87	0.87	0.87	0.87	0.87	0.87
TOC_{KCl} I	−0.30	0.80	0.30	−0.10	0.30	**0.90**	0.00	0.00	0.70
TN_{KCl} I	**−1.00**	0.00	**1.00**	−0.60	**1.00**	0.40	**0.90**	**0.90**	0.70
$TN_{KCl(org)}$ I	−0.70	0.70	0.70	−0.10	0.70	**0.90**	0.60	0.60	**1.00**
NH_4^+-N_{KCl} I	−0.70	0.20	0.70	−0.50	0.70	0.50	0.60	0.60	0.70
NO_3^--N_{KCl}	**−1.00**	0.00	**1.00**	−0.60	**1.00**	0.40	**0.90**	**0.90**	0.70
TOC_{KCl} II	−0.60	0.60	0.60	0.20	0.60	0.70	0.70	0.70	**0.90**
TN_{KCl} II	**−0.90**	−0.10	**0.90**	−0.70	**0.90**	0.30	0.80	0.80	0.60
$TN_{KCl(org)}$ II	**−1.00**	0.00	**1.00**	−0.60	**1.00**	0.40	**0.90**	**0.90**	0.70
NH_4^+-N_{KCl} II	−0.70	0.20	0.70	−0.50	0.70	0.50	0.60	0.60	0.70
NO_3^--N_{KCl} I	**−1.00**	0.00	**1.00**	−0.60	**1.00**	0.40	**0.90**	**0.90**	0.70
Net Min rate	1.00	0.00	−1.00	0.60	−1.00	−0.40	**−0.90**	**−0.90**	−0.70

GCR NH_4^+ = gross consumption rate of NH_4^+

Table 8: Spearman's rang correlation coefficients Oi horizon (third of three tables); significant correlations $p \leq 0.05$ are marked bold. I and II designate first and second sampling. Only correlations between the parameters for the same sampling should be regarded. Percentages of SOC were calculated for the first sampling only.

	$C_{mic}:N_{mic}$ I	C_{mic} II	N_{mic} II	$C_{mic}:N_{mic}$ II	$C_{mic}:SOC$	gross min rate	GCR NH_4^+	TOC_{KCl} I	TN_{KCl} I
$C_{mic}:N_{mic}$ I									
C_{mic} II	0.30								
N_{mic} II	0.40	**0.90**							
$C_{mic}:N_{mic}$ II	−0.30	−0.70	**−0.90**						
$C_{mic}:SOC$	0.30	0.70	0.90	**−1.00**					
gross min rate	**−1.00**	0.50	0.50	**−1.00**	**1.00**				
GCR NH_4^+	−0.87	0.87	0.87	−0.87	0.87	0.87			
TOC_{KCl} I	−0.40	0.40	0.30	0.00	0.00	0.50	0.87		
TN_{KCl} I	−0.10	0.60	0.80	**−0.90**	**0.90**	**1.00**	0.87	0.30	
$TN_{KCl(org)}$ I	−0.10	**0.90**	0.80	−0.60	0.60	0.50	0.87	0.70	0.70
NH_4^+-N_{KCl} I	−0.40	0.60	0.50	−0.60	0.60	**1.00**	0.87	0.20	0.70
NO_3^--N_{KCl}	−0.10	0.60	0.80	**−0.90**	**0.90**	**1.00**	0.87	0.30	**1.00**
TOC_{KCl} II	0.30	**1.00**	0.90	−0.70	0.70	0.50	0.87	0.40	0.60
TN_{KCl} II	−0.30	0.50	0.60	−0.80	0.80	**1.00**	0.87	0.10	**0.90**
$TN_{KCl(org)}$ II	−0.10	0.60	0.80	**−0.90**	**0.90**	**1.00**	0.87	0.30	**1.00**
NH_4^+-N_{KCl} II	−0.40	0.60	0.50	−0.60	0.60	**1.00**	0.87	0.20	0.70
NO_3^--N_{KCl} I	−0.10	0.60	0.80	**−0.90**	**0.90**	**1.00**	0.87	0.30	**1.00**
Net Min rate	0.10	−0.60	−0.80	**0.90**	**−0.90**	−1.00	−0.87	−0.30	−1.00

	$TN_{KCl(org)}$ I	NH_4^+-N_{KCl} I	NO_3^--N_{KCl}	TOC_{KCl} II	TN_{KCl} II	$TN_{KCl(org)}$ II	NH_4^+-N_{KCl} II	NO_3^--N_{KCl} I	
$TN_{KCl(org)}$ I									
NH_4^+-N_{KCl} I	0.70								
NO_3^--N_{KCl}	0.70	0.70							
TOC_{KCl} II	**0.90**	0.60	0.60						
TN_{KCl} II	0.60	**0.90**	**0.90**	0.50					
$TN_{KCl(org)}$ II	0.70	0.70	**1.00**	0.60	**0.90**				
NH_4^+-N_{KCl} II	0.70	**1.00**	0.70	0.60	**0.90**	0.70			
NO_3^--N_{KCl} I	0.70	0.70	1.00	0.60	**0.90**	**1.00**	0.70		
Net Min rate	-0.70	-0.70	-1.00	-0.60	**-0.90**	-1.00	-0.70	-1.00	

GCR NH_4^+ = gross consumption rate of NH_4^+

Table 9: Spearman's rang correlation coefficients OeOa horizon (first of three tables); significant correlations $p \leq 0.05$ are marked bold. I and II designate first and second sampling. Only correlations between the parameters for the same sampling should be regarded. Percentages of SOC were calculated for the first sampling only.

	altitude	T_{org}	T_{min}	VWC_{org}	VWC_{min}	TSR	RC%	SOC	TN
altitude									
T_{org}	**−1.00**								
T_{min}	**−1.00**	**1.00**							
VWC_{org}	**0.90**	**−0.90**	**−0.90**						
VWC_{min}	**1.00**	**−1.00**	−1.00	**0.90**					
TSR	−0.87	0.87	0.87	−0.67	−0.87				
RC%	−1.00	1.00	1.00	**−1.00**	−1.00	1.00			
SOC	0.10	−0.10	−0.10	0.20	0.10	−0.41	0.50		
TN	−0.70	0.70	0.70	−0.90	−0.70	0.31	1.00	0.10	
SOC : TN	**0.90**	**−0.90**	**−0.90**	**1.00**	**0.90**	−0.67	−1.00	0.20	**−0.90**
HWC I	0.10	−0.10	−0.10	0.20	0.10	−0.41	0.50	**1.00**	0.10
HWN I	−0.70	0.70	0.70	**−0.90**	−0.70	0.31	1.00	0.10	**1.00**
HWC II	−0.70	0.70	0.70	−0.40	−0.70	0.56	0.50	0.50	0.30
HWN II	−0.60	0.60	0.60	−0.70	−0.60	0.15	1.00	0.50	**0.90**
HWC : SOC	−0.70	0.70	0.70	**−0.90**	−0.70	0.31	1.00	0.10	**1.00**
HWN : TN	−0.70	0.70	0.70	**−0.90**	−0.70	0.31	1.00	0.10	**1.00**
C_{mic} I	−0.20	0.20	0.20	0.00	−0.20	−0.05	0.50	**0.90**	0.20
N_{mic} I	−0.40	0.40	0.40	−0.30	−0.40	0.10	1.00	0.70	0.50
$C_{mic} : N_{mic}$ I	0.40	−0.40	−0.40	0.30	0.40	−0.10	−1.00	−0.70	−0.50
C_{mic} II	0.50	−0.50	−0.50	0.60	0.50	−0.67	−0.50	**0.90**	−0.30
N_{mic} II	0.60	−0.60	−0.60	0.80	0.60	−0.56	−0.50	0.70	−0.60
$C_{mic} : N_{mic}$ II	−0.70	0.70	0.70	**−0.90**	−0.70	0.31	1.00	0.10	**1.00**
C_{mic} : SOC	**−0.90**	**0.90**	**0.90**	−0.70	**−0.90**	0.72	1.00	0.30	0.60
gross min rate	−0.50	0.50	0.50	−0.50	−0.50	0.50	0.50	1.00	0.50
GCR NH_4^+	−0.50	0.50	0.50	−0.50	−0.50	0.50	0.50	1.00	0.50
TOC_{KCl} I	−0.40	0.40	0.40	−0.70	−0.40	−0.05	1.00	0.20	**0.90**
TN_{KCl} I	**−0.90**	**0.90**	**0.90**	**−1.00**	**−0.90**	0.67	1.00	−0.20	**0.90**
$TN_{KCl(org)}$ I	**−0.90**	**0.90**	**0.90**	−0.70	**−0.90**	**0.97**	1.00	−0.30	0.40
NH_4^+-N_{KCl} I	−0.70	0.70	0.70	**−0.90**	−0.70	0.31	1.00	0.10	**1.00**
NO_3^--N_{KCl}	−0.70	0.70	0.70	**−0.90**	−0.70	0.31	1.00	0.10	**1.00**
TOC_{KCl} II	**−1.00**	**1.00**	**1.00**	**−0.90**	**−1.00**	0.87	1.00	−0.10	0.70
TN_{KCl} II	**−1.00**	**1.00**	**1.00**	**−0.90**	**−1.00**	0.87	1.00	−0.10	0.70
$TN_{KCl(org)}$ II	**−1.00**	**1.00**	**1.00**	**−0.90**	**−1.00**	0.87	1.00	−0.10	0.70
NH_4^+-N_{KCl} II	**−1.00**	**1.00**	**1.00**	**−0.90**	**−1.00**	0.87	1.00	−0.10	0.70
NO_3^--N_{KCl} I	**−0.90**	**0.90**	**0.90**	**−1.00**	**−0.90**	0.67	1.00	−0.20	**0.90**
Net N min rate	−0.30	0.30	0.30	−0.50	−0.30	−0.21	1.00	0.60	0.80

GCR NH_4^+ = gross consumption rate of NH_4^+

Table 10: Spearman's rang correlation coefficients OeOa horizon (second of three tables); significant correlations $p \leq 0.05$ are marked bold. I and II designate first and second sampling. Only correlations between the parameters for the same sampling should be regarded. Percentages of SOC were calculated for the first sampling only.

	SOC : TN	HWC I	HWN I	HWC II	HWN II	HWC : SOC	HWN : TN	C_{mic} I	N_{mic} I
SOC : TN									
HWC I	0.20								
HWN I	**−0.90**	0.10							
HWC II	−0.40	0.50	0.30						
HWN II	−0.70	0.50	**0.90**	0.50					
HWC : SOC	**−0.90**	0.10	**1.00**	0.30	**0.90**				
HWN : TN	**−0.90**	0.10	**1.00**	0.30	**0.90**	**1.00**			
C_{mic} I	0.00	**0.90**	0.20	0.70	0.60	0.20	0.20		
N_{mic} I	−0.30	0.70	0.50	0.60	0.80	0.50	0.50	**0.90**	
$C_{mic} : N_{mic}$ I	0.30	−0.70	−0.50	−0.60	−0.80	−0.50	−0.50	**−0.90**	**−1.00**
C_{mic} II	0.60	**0.90**	−0.30	0.20	0.10	−0.30	−0.30	0.70	0.40
N_{mic} II	0.80	0.70	−0.60	0.10	−0.20	−0.60	−0.60	0.60	0.30
$C_{mic} : N_{mic}$ II	**−0.90**	0.10	**1.00**	0.30	**0.90**	**1.00**	**1.00**	0.20	0.50
C_{mic} : SOC	−0.70	0.30	0.60	**0.90**	0.70	0.60	0.60	0.60	0.70
gross min rate	−0.50	1.00	0.50	1.00	0.50	0.50	0.50	1.00	0.50
GCR NH_4^+	−0.50	1.00	0.50	1.00	0.50	0.50	0.50	1.00	0.50
TOC_{KCl} I	−0.70	0.20	**0.90**	0.10	0.80	**0.90**	**0.90**	0.10	0.30
TN_{KCl} I	**−1.00**	−0.20	**0.90**	0.40	0.70	**0.90**	**0.90**	0.00	0.30
$TN_{KCl(org)}$ I	−0.70	−0.30	0.40	0.60	0.30	0.40	0.40	0.10	0.30
NH_4^+-N_{KCl} I	**−0.90**	0.10	**1.00**	0.30	**0.90**	**1.00**	**1.00**	0.20	0.50
NO_3^--N_{KCl}	**−0.90**	0.10	**1.00**	0.30	**0.90**	**1.00**	**1.00**	0.20	0.50
TOC_{KCl} II	**−0.90**	−0.10	0.70	0.70	0.60	0.70	0.70	0.20	0.40
TN_{KCl} II	**−0.90**	−0.10	0.70	0.70	0.60	0.70	0.70	0.20	0.40
$TN_{KCl(org)}$ II	**−0.90**	−0.10	0.70	0.70	0.60	0.70	0.70	0.20	0.40
NH_4^+-N_{KCl} II	**−0.90**	−0.10	0.70	0.70	0.60	0.70	0.70	0.20	0.40
NO_3^--N_{KCl} I	**−1.00**	−0.20	**0.90**	0.40	0.70	**0.90**	**0.90**	0.00	0.30
Net N min rate	−0.50	0.60	0.80	0.30	**0.90**	0.80	0.80	0.50	0.60

GCR NH_4^+ = gross consumption rate of NH_4^+

Table 11: Spearman's rang correlation coefficients OeOa horizon (third of three tables); significant correlations $p \leq 0.05$ are marked bold. I and II designate first and second sampling. Only correlations between the parameters for the same sampling should be regarded. Percentages of SOC were calculated for the first sampling only.

	$C_{mic}:N_{mic}$ I	C_{mic} II	N_{mic} II	$C_{mic}:N_{mic}$ II	$C_{mic}:SOC$	gross min rate	GCR NH_4^+	TOC_{KCl} I	TN_{KCl} I
$C_{mic}:N_{mic}$ I									
C_{mic} II	−0.40								
N_{mic} II	−0.30	**0.90**							
$C_{mic}:N_{mic}$ II	−0.50	−0.30	−0.60						
$C_{mic}:SOC$	−0.70	−0.10	−0.20	0.60					
gross min rate	−0.50	0.50	0.50	0.50	0.50				
GCR NH_4^+	−0.50	0.50	0.50	0.50	0.50	1.00			
TOC_{KCl} I	−0.30	−0.10	−0.50	**0.90**	0.30	0.50	0.50		
TN_{KCl} I	−0.30	−0.60	−0.80	**0.90**	0.70	0.50	0.50	0.70	
$TN_{KCl(org)}$ I	−0.30	−0.60	−0.50	0.40	0.80	0.50	0.50	0.00	0.70
NH_4^+-N_{KCl} I	−0.50	−0.30	−0.60	**1.00**	0.60	0.50	0.50	**0.90**	**0.90**
NO_3^--N_{KCl}	−0.50	−0.30	−0.60	**1.00**	0.60	0.50	0.50	**0.90**	**0.90**
TOC_{KCl} II	−0.40	−0.50	−0.60	0.70	**0.90**	0.50	0.50	0.40	**0.90**
TN_{KCl} II	−0.40	−0.50	−0.60	0.70	**0.90**	0.50	0.50	0.40	**0.90**
$TN_{KCl(org)}$ II	−0.40	−0.50	−0.60	0.70	**0.90**	0.50	0.50	0.40	**0.90**
NH_4^+-N_{KCl} II	−0.40	−0.50	−0.60	0.70	**0.90**	0.50	0.50	0.40	**0.90**
NO_3^--N_{KCl} I	−0.30	−0.60	−0.80	**0.90**	0.70	0.50	0.50	0.70	**1.00**
Net N min rate	−0.60	0.30	−0.10	0.80	0.40	0.50	0.50	**0.90**	0.50

	$TN_{KCl(org)}$ I	NH_4^+-N_{KCl} I	NO_3^--N_{KCl}	TOC_{KCl} II	TN_{KCl} II	$TN_{KCl(org)}$ II	NH_4^+-N_{KCl} II	NO_3^--N_{KCl} I
$TN_{KCl(org)}$ I								
NH_4^+-N_{KCl} I	0.40							
NO_3^--N_{KCl}	0.40	1.00						
TOC_{KCl} II	**0.90**	0.70	0.70					
TN_{KCl} II	**0.90**	0.70	0.70	**1.00**				
$TN_{KCl(org)}$ II	**0.90**	0.70	0.70	**1.00**	**1.00**			
NH_4^+-N_{KCl} II	**0.90**	0.70	0.70	**1.00**	**1.00**	**1.00**		
NO_3^--N_{KCl} I	0.70	**0.90**	**0.90**	**0.90**	**0.90**	**0.90**	**0.90**	
Net N min rate	−0.10	0.80	0.80	0.30	0.30	0.30	0.30	0.50000

GCR NH_4^+ = gross consumption rate of NH_4^+

Table 12: Spearman's rang correlation coefficients 0–10 cm horizon (first of three tables); significant correlations $p \leq 0.05$ are marked bold. I and II designate first and second sampling. Only correlations between the parameters for the same sampling should be regarded. Percentages of SOC were calculated for the first sampling only.

	altitude	T_{org}	T_{min}	VWC_{org}	VWC_{min}	TSR	RC%	SOC	TN
altitude									
T_{org}	**−1.00**								
T_{min}	**−1.00**	**1.00**							
VWC_{org}	**0.90**	**−0.90**	**−0.90**						
VWC_{min}	**1.00**	**−1.00**	**−1.00**	**0.90**					
TSR	−0.87	0.87	0.87	−0.67	−0.87				
RC%	−1.00	1.00	1.00	−1.00	−1.00	1.00			
SOC	0.40	−0.40	−0.40	0.30	0.40	−0.10	−1.00		
TN	0.50	−0.50	−0.50	0.20	0.50	−0.56	−1.00	0.70	
SOC : TN	0.70	−0.70	−0.70	**0.90**	0.70	−0.31	−1.00	0.50	0.10
HWC I	**0.90**	**−0.90**	**−0.90**	0.70	**0.90**	−0.72	−1.00	0.70	0.70
HWN I	0.30	−0.30	−0.30	−0.10	0.30	−0.41	−0.50	0.60	**0.90**
HWC II	0.70	−0.70	−0.70	0.60	0.70	−0.36	−1.00	**0.90**	0.60
HWN II	0.40	−0.40	−0.40	0.30	0.40	−0.10	−1.00	**1.00**	0.70
HWC : SOC	0.30	−0.30	−0.30	0.40	0.30	−0.15	−0.50	−0.40	−0.60
HWN : TN	−0.10	0.10	0.10	−0.30	−0.10	−0.21	0.50	−0.70	−0.30
C_{mic} I	−0.60	0.60	0.60	−0.30	−0.60	0.82	0.50	0.20	−0.30
N_{mic} I	−0.20	0.20	0.20	−0.10	−0.20	−0.15	0.50	−0.60	−0.10
$C_{mic} : N_{mic}$ I	0.10	−0.10	−0.10	0.20	0.10	0.36	−0.50	0.50	−0.20
C_{mic} II	0.30	−0.30	−0.30	0.50	0.30	0.21	−1.00	0.60	−0.10
N_{mic} II	0.30	−0.30	−0.30	−0.10	0.30	−0.41	−0.50	0.60	**0.90**
$C_{mic} : N_{mic}$ II	0.40	−0.40	−0.40	0.70	0.40	0.05	−1.00	0.30	−0.30
C_{mic} : SOC	−0.80	0.80	0.80	−0.50	−0.80	0.82	1.00	−0.60	**−0.90**
gross min rate	1.00	−1.00	−1.00	1.00	1.00	−1.00	−1.00	1.00	1.00
GCR NH_4^+	1.00	−1.00	−1.00	1.00	1.00	−1.00	−1.00	1.00	1.00
TOC_{KCl} I	0.40	−0.40	−0.40	0.30	0.40	−0.10	−1.00	**1.00**	0.70
TN_{KCl} I	0.30	−0.30	−0.30	−0.10	0.30	−0.41	−0.50	0.60	**0.90**
$TN_{KCl(org)}$ I	0.30	−0.30	−0.30	0.40	0.30	−0.41	−0.50	0.10	0.40
NH_4^+-N_{KCl} I	0.90	**−0.90**	**−0.90**	0.70	**0.90**	−0.72	−1.00	0.70	0.70
NO_3^--N_{KCl}	−0.50	0.50	0.50	−0.80	−0.50	0.21	0.50	−0.30	0.00
TOC_{KCl} II	0.30	−0.30	−0.30	0.40	0.30	0.10	−1.00	**0.90**	0.40
TN_{KCl} II	−0.60	0.60	0.60	−0.80	−0.60	0.56	0.50	0.30	0.20
$TN_{KCl(org)}$ II	−0.30	0.30	0.30	−0.60	−0.30	0.21	0.50	0.50	0.60
NH_4^+-N_{KCl} II	0.60	−0.60	−0.60	0.70	0.60	−0.15	−1.00	0.80	0.30
NO_3^--N_{KCl} I	**−0.90**	**0.90**	**0.90**	−1.00	**−0.90**	0.67	1.00	−0.30	−0.20
Net N min rate	−0.30	0.30	0.30	−0.40	−0.30	0.15	0.50	0.40	0.60

GCR NH_4^+ = gross consumption rate of NH_4^+

Table 13: Spearman's rang correlation coefficients 0–10 cm horizon (second of three tables); significant correlations $p \leq 0.05$ are marked bold. I and II designate first and second sampling. Only correlations between the parameters for the same sampling should be regarded. Percentages of SOC were calculated for the first sampling only.

	SOC : TN	HWC I	HWN I	HWC II	HWN II	HWC : SOC	HWN : TN	C_{mic} I	N_{mic} I
SOC : TN									
HWC I	0.60								
HWN I	−0.20	0.60							
HWC II	0.70	**0.90**	0.50						
HWN II	0.50	0.70	0.60	**0.90**					
HWC : SOC	0.30	0.10	−0.50	0.00	−0.40				
HWN : TN	−0.60	−0.20	0.00	−0.50	−0.70	0.50			
C_{mic} I	0.10	−0.50	−0.40	−0.10	0.20	−0.40	−0.70		
N_{mic} I	−0.30	−0.50	−0.30	−0.70	−0.60	−0.30	0.10	0.00	
$C_{mic} : N_{mic}$ I	0.50	0.30	−0.10	0.60	0.50	0.40	−0.30	0.30	**−0.90**
C_{mic} II	0.80	0.40	−0.20	0.70	0.60	0.30	−0.60	0.40	−0.70
N_{mic} II	−0.20	0.60	**1.00**	0.50	0.60	−0.50	0.00	−0.40	−0.30
$C_{mic} : N_{mic}$ II	**0.90**	0.30	−0.50	0.50	0.30	0.50	−0.50	0.30	−0.40
C_{mic} : SOC	−0.30	**−0.90**	−0.80	−0.70	−0.60	0.20	0.10	0.60	0.20
gross min rate	1.00	1.00	0.50	1.00	1.00	0.50	−0.50	−0.50	−0.50
GCR NH_4^+	1.00	1.00	0.50	1.00	1.00	0.50	−0.50	−0.50	−0.50
TOC_{KCl} I	0.50	0.70	0.60	**0.90**	**1.00**	−0.40	−0.70	0.20	−0.60
TN_{KCl} I	−0.20	0.60	**1.00**	0.50	0.60	−0.50	0.00	−0.40	−0.30
$TN_{KCl(org)}$ I	0.30	0.10	0.00	0.00	0.10	−0.50	−0.50	0.10	0.70
NH_4^+-N_{KCl} I	0.60	1.00	0.60	**0.90**	0.70	0.10	−0.20	−0.50	−0.50
NO_3^--N_{KCl}	**−0.90**	−0.30	0.40	−0.40	−0.30	−0.10	0.70	−0.30	−0.10
TOC_{KCl} II	0.70	0.50	0.20	0.80	**0.90**	−0.30	**−0.90**	0.50	−0.50
TN_{KCl} II	−0.60	−0.20	0.50	0.00	0.30	−0.50	0.00	0.30	−0.40
$TN_{KCl(org)}$ II	−0.50	0.10	0.80	0.20	0.50	−0.70	−0.10	0.10	−0.30
NH_4^+-N_{KCl} II	**0.90**	0.70	0.10	**0.90**	0.80	0.10	−0.70	0.20	−0.60
NO_3^--N_{KCl} I	**−0.90**	−0.70	0.10	−0.60	−0.30	−0.40	0.30	0.30	0.10
Net N min rate	−0.30	−0.10	0.50	0.00	0.40	**−1.00**	−0.50	0.40	0.30

GCR NH_4^+ = gross consumption rate of NH_4^+

Table 14: Spearman's rang correlation coefficients 0–10 cm horizon (third of three tables); significant correlations $p \leq 0.05$ are marked bold. I and II designate first and second sampling. Only correlations between the parameters for the same sampling should be regarded. Percentages of SOC were calculated for the first sampling only.

	$C_{mic} : N_{mic}$ I	C_{mic} II	N_{mic} II	$C_{mic} : N_{mic}$ II	$C_{mic} : SOC$	gross min rate	GCR NH_4^+	TOC_{KCl} I	TN_{KCl} I
$C_{mic} : N_{mic}$ I									
C_{mic} II	**0.90**								
N_{mic} II	−0.10	−0.20							
$C_{mic} : N_{mic}$ II	0.70	**0.90**	−0.50						
$C_{mic} : SOC$	0.10	0.00	−0.80	0.10					
gross min rate	0.50	1.00	0.50	1.00	−1.00				
GCR NH_4^+	0.50	1.00	0.50	1.00	−1.00	1.00			
TOC_{KCl} I	0.50	0.60	0.60	0.30	−0.60	1.00	1.00		
TN_{KCl} I	−0.10	−0.20	**1.00**	−0.50	−0.80	0.50	0.50	0.60	
$TN_{KCl(org)}$ I	−0.60	−0.20	0.00	0.00	−0.30	0.50	0.50	0.10	0.00
NH_4^+-N_{KCl} I	0.30	0.40	0.60	0.30	**−0.90**	1.00	1.00	0.70	0.60
NO_3^--N_{KCl}	−0.20	−0.60	0.40	−0.80	0.10	−0.50	−0.50	−0.30	0.40
TOC_{KCl} II	0.60	0.80	0.20	0.60	−0.30	1.00	1.00	**0.90**	0.20
TN_{KCl} II	0.20	−0.10	0.50	−0.50	0.10	−0.50	−0.50	0.30	0.50
$TN_{KCl(org)}$ II	0.00	−0.20	0.80	−0.60	−0.30	−0.50	−0.50	0.50	0.80
NH_4^+-N_{KCl} II	0.70	**0.90**	0.10	0.80	−0.40	1.00	1.00	0.80	0.10
NO_3^--N_{KCl} I	−0.20	−0.50	0.10	−0.70	0.50	−1.00	−1.00	−0.30	0.10
Net N min rate	−0.40	−0.30	0.50	−0.50	−0.20	−0.50	−0.50	0.40	0.50

	$TN_{KCl(org)}$ I	NH_4^+-N_{KCl} I	NO_3^--N_{KCl}	TOC_{KCl} II	TN_{KCl} II	$TN_{KCl(org)}$ II	NH_4^+-N_{KCl} II	NO_3^--N_{KCl} I
$TN_{KCl(org)}$ I								
NH_4^+-N_{KCl} I	0.10							
NO_3^--N_{KCl}	−0.60	−0.30						
TOC_{KCl} II	0.20	0.50	−0.60					
TN_{KCl} II	−0.50	−0.20	0.70	0.10				
$TN_{KCl(org)}$ II	−0.20	0.10	0.60	0.20	0.90			
NH_4^+-N_{KCl} II	0.10	0.70	−0.70	**0.90**	−0.20	−0.10		
NO_3^--N_{KCl} I	−0.40	−0.70	0.80	−0.40	0.80	0.60	−0.70	
Net N min rate	0.50	−0.10	0.10	0.30	0.50	0.70	−0.10	0.40

GCR NH_4^+ = gross consumption rate of NH_4^+

Table 15: p values of Mann-Whitney U Test for pairwise comparison of soil organic carbon (SOC) in the tested horizons for each plot. Significant differences at the level $p \leq 0.05$ are marked bold.

	1st sampling		2nd sampling	
SOC 1 050 m	Oi	OeOa	Oi	OeOa
OeOa	0.078		n/d	
0–10cm	**0.004**	**0.004**	n/d	n/d
SOC 1 540 m	Oi	OeOa	Oi	OeOa
OeOa	**0.004**		n/d	
0–10 cm	**0.004**	**0.004**	n/d	n/d
SOC 1 890 m	Oi	OeOa	Oi	OeOa
OeOa	0.109		n/d	
0–10 cm	**0.004**	**0.004**	n/d	n/d
SOC 2 380 m	Oi	OeOa	Oi	OeOa
OeOa	0.423		n/d	
0–10 cm	**0.004**	**0.004**	n/d	n/d
SOC 3 060 m	Oi	OeOa	Oi	OeOa
OeOa	**0.004**		n/d	
0–10 cm	**0.004**	**0.004**	n/d	n/d

Table 16: p values of Mann-Whitney U Test for pairwise comparison of total hot-water extractable organic carbon (HWC) in the tested horizons for each plot. Significant differences at the level $p \leq 0.05$ are marked bold.

	1st sampling		2nd sampling	
HWC 1 050 m	Oi	OeOa	Oi	OeOa
OeOa	0.873		0.873	
0–10cm	**0.004**	**0.004**	**0.004**	**0.004**
HWC 1 540 m	Oi	OeOa	Oi	OeOa
OeOa	**0.004**		**0.025**	
0–10 cm	**0.004**	**0.004**	**0.004**	**0.004**
HWC 1 890 m	Oi	OeOa	Oi	OeOa
OeOa	**0.025**		**0.010**	
0–10 cm	**0.004**	**0.004**	**0.004**	**0.004**
HWC 2 380 m	Oi	OeOa	Oi	OeOa
OeOa	0.631		**0.037**	
0–10 cm	**0.004**	**0.004**	**0.004**	**0.004**
HWC 3 060 m	Oi	OeOa	Oi	OeOa
OeOa	**0.025**		**0.010**	
0–10 cm	**0.004**	**0.004**	**0.004**	**0.004**

Table 17: p values of Mann-Whitney U Test for pairwise comparison of total KCl-extractable organic carbon (TOC_{KCl}) in the tested horizons for each plot. Significant differences at the level $p \leq 0.05$ are marked bold.

	1st sampling		**2nd sampling**	
TOC_{KCl} *1 050 m*	Oi	OeOa	Oi	OeOa
OeOa	**0.055**		**0.078**	
0–10 cm	**0.004**	**0.004**	**0.004**	**0.004**
TOC_{KCl} *1 540 m*	Oi	OeOa	Oi	OeOa
OeOa	**0.004**		**0.004**	
0–10 cm	**0.004**	**0.004**	**0.004**	**0.004**
TOC_{KCl} *1 890 m*	Oi	OeOa	Oi	OeOa
OeOa	**0.004**		**0.004**	
0–10 cm	**0.004**	**0.004**	**0.004**	**0.010**
TOC_{KCl} *2 380 m*	Oi	OeOa	Oi	OeOa
OeOa	**0.004**		**0.004**	
0–10 cm	**0.004**	**0.004**	**0.004**	**0.004**
TOC_{KCl} *3 060 m*	Oi	OeOa	Oi	OeOa
OeOa	**0.004**		**0.004**	
0–10 cm	**0.004**	**0.004**	**0.004**	**0.004**

Table 18: p values of Mann-Whitney U Test for pairwise comparison of microbial biomass carbon (C_{mic}) in the tested horizons for each plot. Significant differences at the level $p \leq 0.05$ are marked bold.

	1st sampling		**2nd sampling**	
C_{mic} *1 050 m*	Oi	OeOa	Oi	OeOa
OeOa	0.109		0.423	
0–10 cm	**0.004**	**0.004**	**0.004**	**0.004**
C_{mic} *1 540 m*	Oi	OeOa	Oi	OeOa
OeOa	**0.006**		0.109	
0–10 cm	**0.004**	**0.004**	**0.004**	**0.004**
C_{mic} *1 890 m*	Oi	OeOa	Oi	OeOa
OeOa	**0.006**		0.006	
0–10 cm	**0.002**	**0.002**	**0.004**	**0.004**
C_{mic} *2 380 m*	Oi	OeOa	Oi	OeOa
OeOa	0.150		0.749	
0–10 cm	**0.004**	**0.004**	**0.004**	**0.004**
C_{mic} *3 060 m*	Oi	OeOa	Oi	OeOa
OeOa	0.602		0.055	
0–10 cm	**0.009**	**0.009**	**0.004**	**0.004**

Table 19: p values of Mann-Whitney U Test for pairwise comparison of total nitrogen (TN) in the tested horizons for each plot. Significant differences at the level $p \leq 0.05$ are marked bold.

	1st sampling		**2nd sampling**	
TN 1 050 m	Oi	OeOa	Oi	OeOa
OeOa	0.631		n/d	
0–10cm	**0.004**	**0.004**	n/d	n/d
TN 1 540 m	Oi	OeOa	Oi	OeOa
OeOa	0.150		n/d	
0–10 cm	**0.004**	**0.004**	n/d	n/d
TN 1 890 m	Oi	OeOa	Oi	OeOa
OeOa	**0.037**		n/d	
0–10 cm	**0.004**	**0.004**	n/d	n/d
TN 2 380 m	Oi	OeOa	Oi	OeOa
OeOa	0.055		n/d	
0–10 cm	0.055	**0.004**	n/d	n/d
TN 3 060 m	Oi	OeOa	Oi	OeOa
OeOa	**0.004**		n/d	
0–10 cm	**0.004**	**0.004**	n/d	n/d

Table 20: p values of Mann-Whitney U Test for pairwise comparison of total hot-water extractable nitrogen (HWN) in the tested horizons for each plot. Significant differences at the level $p \leq 0.05$ are marked bold.

	1st sampling		**2nd sampling**	
HWN 1 050 m	Oi	OeOa	Oi	OeOa
OeOa	0.337		0.109	
0–10 cm	**0.004**	**0.004**	**0.004**	**0.004**
HWN 1 540 m	Oi	OeOa	Oi	OeOa
OeOa	**0.025**		0.055	
0–10 cm	**0.004**	**0.004**	**0.004**	**0.004**
HWN 1 890 m	Oi	OeOa	Oi	OeOa
OeOa	0.749		**0.037**	
0-10 cm	**0.004**	**0.004**	**0.004**	**0.004**
HWN 2 380 m	Oi	OeOa	Oi	OeOa
OeOa	**0.004**		0.423	
0–10 cm	**0.004**	**0.004**	**0.004**	**0.004**
HWN 3 060 m	Oi	OeOa	Oi	OeOa
OeOa	0.109		0.423	
0–10 cm	**0.004**	**0.004**	**0.004**	**0.004**

Table 21: p values of Mann-Whitney U Test for pairwise comparison of total KCl-extractable nitrogen (TN_{KCl}) in the tested horizons for each plot. Significant differences at the level $p \leq 0.05$ are marked bold.

	1st sampling		**2nd sampling**	
TN_{KCl} *1 050 m*	Oi	OeOa	Oi	OeOa
OeOa	0.423		0.016	
0–10 cm	**0.004**	**0.004**	**0.004**	**0.004**
TN_{KCl} *1 540 m*	Oi	OeOa	Oi	OeOa
OeOa	0.337		0.522	
0–10 cm	**0.004**	**0.004**	**0.004**	**0.004**
TN_{KCl} *1 890 m*	Oi	OeOa	Oi	OeOa
OeOa	0.109		0.873	
0–10 cm	**0.004**	**0.004**	**0.025**	**0.025**
TN_{KCl} *2 380 m*	Oi	OeOa	Oi	OeOa
OeOa	**0.016**		**0.025**	
0–10 cm	**0.004**	**0.004**	**0.004**	**0.004**
TN_{KCl} *3 060 m*	Oi	OeOa	Oi	OeOa
OeOa	**0.010**		0.068	
0–10 cm	0.055	0.078	0.200	**0.011**

Table 22: p values of Mann-Whitney U Test for pairwise comparison of total KCl-extractable organic nitrogen ($TN_{KCl(org)}$) in the tested horizons for each plot. Significant differences at the level $p \leq 0.05$ are marked bold.

	1st sampling		**2nd sampling**	
TN^{org}_{KCl} *1 050 m*	Oi	OeOa	Oi	OeOa
OeOa	0.522		1.000	
0–10 cm	**0.004**	**0.006**	**0.004**	0.336
TN^{org}_{KCl} *1 540 m*	Oi	OeOa	Oi	OeOa
OeOa	0.631		**0.004**	
0–10 cm	**0.004**	**0.004**	**0.004**	**0.004**
TN^{org}_{KCl} *1 890 m*	Oi	OeOa	Oi	OeOa
OeOa	0.055		**0.004**	
0–10 cm	**0.004**	**0.004**	**0.006**	0.262
TN^{org}_{KCl} *2 380 m*	Oi	OeOa	Oi	OeOa
OeOa	**0.037**		0.262	
0–10 cm	**0.004**	**0.004**	**0.004**	**0.004**
TN^{org}_{KCl} *3 060 m*	Oi	OeOa	Oi	OeOa
OeOa	**0.006**		**0.011**	
0–10 cm	0.749	**0.025**	**0.004**	0.144

Table 23: p values of Mann-Whitney U Test for pairwise comparison of total KCl-extractable inorganic nitrogen ($TN_{KCl(inorg)}$) in the tested horizons for each plot. Significant differences at the level $p \leq 0.05$ are marked bold.

	1st sampling		2nd sampling	
TN_{KCl}^{inorg} *1 050 m*	Oi	OeOa	Oi	OeOa
OeOa	0.522		0.078	
0–10 cm	**0.004**	**0.004**	**0.004**	**0.004**
TN_{KCl}^{inorg} *1 540 m*	Oi	OeOa	Oi	OeOa
OeOa	0.749		0.109	
0–10 cm	**0.004**	**0.004**	0.055	**0.004**
TN_{KCl}^{inorg} *1 890 m*	Oi	OeOa	Oi	OeOa
OeOa	0.078		0.200	
0–10 cm	0.200	**0.004**	0.150	**0.006**
TN_{KCl}^{inorg} *2 380 m*	Oi	OeOa	Oi	OeOa
OeOa	**0.004**		**0.004**	
0–10 cm	0.873	**0.004**	0.522	**0.004**
TN_{KCl}^{inorg} *3 060 m*	Oi	OeOa	Oi	OeOa
OeOa	**0.004**		**0.006**	
0–10 cm	**0.004**	**0.037**	**0.037**	**0.011**

Table 24: p values of Mann-Whitney U Test for pairwise comparison of NH_4^+-N in the tested horizons for each plot. Significant differences at the level $p \leq 0.05$ are marked bold.

	1st sampling		2nd sampling	
NH_4^+-*N 1 050 m*	Oi	OeOa	Oi	OeOa
OeOa	**0.004**		0.150	
0–10 cm	**0.004**	**0.004**	**0.004**	**0.004**
NH_4^+-*N 1 540 m*	Oi	OeOa	Oi	OeOa
OeOa	0.873		0.109	
0–10 cm	**0.004**	**0.004**	**0.025**	**0.004**
NH_4^+-*N 1 890 m*	Oi	OeOa	Oi	OeOa
OeOa	**0.004**		0.037	
0–10 cm	**0.004**	**0.004**	**0.010**	**0.004**
NH_4^+-*N 2 380 m*	Oi	OeOa	Oi	OeOa
OeOa	**0.006**		**0.004**	
0–10 cm	0.873	**0.004**	**0.025**	**0.004**
NH_4^+-*N 3 060 m*	Oi	OeOa	Oi	OeOa
OeOa	**0.004**		**0.006**	
0–10 cm	**0.004**	**0.037**	**0.025**	**0.011**

Table 25: p values of Mann-Whitney U Test for pairwise comparison of NO_3^--N in the tested horizons for each plot. Significant differences at the level $p \leq 0.05$ are marked bold.

	1st sampling		**2nd sampling**	
NO_3^--N 1 050 m	Oi	OeOa	Oi	OeOa
OeOa	0.522		0.337	
0–10 cm	**0.004**	**0.004**	**0.037**	**0.037**
NO_3^--N 1 540 m	Oi	OeOa	Oi	OeOa
OeOa	**0.025**		0.200	
0–10 cm	**0.010**	0.337	0.150	0.873
NO_3^--N 1 890 m	Oi	OeOa	Oi	OeOa
OeOa	0.749		0.262	
0–10 cm	0.337	0.055	0.262	0.262
NO_3^--N 2 380 m	Oi	OeOa	Oi	OeOa
OeOa	**0.010**		0.522	
0–10 cm	0.150	0.262	**0.004**	0.749
NO_3^--N 3 060 m	Oi	OeOa	Oi	OeOa
OeOa	0.055		0.357	
0–10 cm	**0.037**	0.150	0.872	0.234

Table 26: p values of Mann-Whitney U Test for pairwise comparison of microbial biomass nitrogen (N_{mic}) in the tested horizons for each plot. Significant differences at the level $p \leq 0.05$ are marked bold.

	1st sampling		**2nd sampling**	
N_{mic} 1 050 m	Oi	OeOa	Oi	OeOa
OeOa	0.631		0.337	
0–10 cm	**0.004**	**0.004**	**0.004**	**0.004**
N_{mic} 1 540 m	Oi	OeOa	Oi	OeOa
OeOa	**0.037**		0.200	
0–10 cm	**0.004**	**0.004**	**0.004**	**0.004**
N_{mic} 1 890 m	Oi	OeOa	Oi	OeOa
OeOa	0.084		**0.006**	
0–10 cm	**0.002**	**0.002**	**0.004**	**0.004**
N_{mic} 2 380 m	Oi	OeOa	Oi	OeOa
OeOa	**0.025**		0.055	
0–10 cm	**0.004**	**0.004**	**0.004**	**0.004**
N_{mic} 3 060 m	Oi	OeOa	Oi	OeOa
OeOa	0.347		0.337	
0–10 cm	**0.009**	**0.009**	**0.004**	**0.004**

Table 27: p values of Mann-Whitney U Test for pairwise comparison of soil organic carbon (SOC) : total nitrogen (TN) in the tested horizons for each plot. Significant differences at the level $p \leq 0.05$ are marked bold.

	1st sampling		2nd sampling	
SOC : TN 1 050 m	Oi	OeOa	Oi	OeOa
OeOa	0.262		n/d	
0–10cm	**0.004**	**0.004**	n/d	n/d
SOC : TN 1 540 m	Oi	OeOa	Oi	OeOa
OeOa	**0.004**		n/d	
0–10 cm	**0.004**	**0.337**	n/d	n/d
SOC : TN 1 890 m	Oi	OeOa	Oi	OeOa
OeOa	**0.004**		n/d	
0–10 cm	**0.004**	**0.037**	n/d	n/d
SOC : TN 2 380 m	Oi	OeOa	Oi	OeOa
OeOa	0.055		n/d	
0–10 cm	**0.004**	**0.004**	n/d	n/d
SOC : TN 3 060 m	Oi	OeOa	Oi	OeOa
OeOa	**0.004**		n/d	
0–10 cm	**0.004**	**0.004**	n/d	n/d

Table 28: p values of Mann-Whitney U Test for pairwise comparison of microbial biomass carbon (C_{mic}) : microbial biomass nitrogen (N_{mic}) in the tested horizons for each plot. Significant differences at $p \leq 0.05$ are marked bold.

	1st sampling		2nd sampling	
$C_{mic} : N_{mic}$ *1 050 m*	Oi	OeOa	Oi	OeOa
OeOa	0.150		0.631	
0–10 cm	**0.006**	0.109	**0.004**	**0.006**
$C_{mic} : N_{mic}$ *1 540 m*	Oi	OeOa	Oi	OeOa
OeOa	0.873		0.078	
0–10 cm	**0.016**	**0.016**	**0.010**	**0.006**
$C_{mic} : N_{mic}$ *1 890 m*	Oi	OeOa	Oi	OeOa
OeOa	0.110		0.423	
0–10 cm	0.064	0.564	**0.025**	**0.004**
$C_{mic} : N_{mic}$ *2 380 m*	Oi	OeOa	Oi	OeOa
OeOa	**0.037**		**0.004**	
0–10 cm	0.423	0.200	**0.006**	0.522
$C_{mic} : N_{mic}$ *3 060 m*	Oi	OeOa	Oi	OeOa
OeOa	0.076		**0.004**	
0–10 cm	**0.047**	0.175	0.631	0.055

Table 29: p values of Mann-Whitney U Test for pairwise comparison of total hot-water extractable organic carbon (HWC) : total hot-water extractable nitrogen (HWN) in the tested horizons for each plot. Significant differences at $p \leq 0.05$ are marked bold.

	1st sampling		**2nd sampling**	
HWC : HWN *1 050 m*	Oi	OeOa	Oi	OeOa
OeOa	0.150		**0.004**	
0–10 cm	**0.010**	0.055	**0.004**	**0.004**
HWC : HWN *1 540 m*	Oi	OeOa	Oi	OeOa
OeOa	0.522		0.262	
0–10 cm	0.150	**0.025**	**0.037**	0.150
HWC : HWN *1 890 m*	Oi	OeOa	Oi	OeOa
OeOa	**0.037**		0.522	
0–10 cm	**0.004**	0.150	0.055	0.150
HWC : HWN *2 380 m*	Oi	OeOa	Oi	OeOa
OeOa	**0.004**		**0.004**	
0–10 cm	**0.004**	**0.025**	**0.004**	0.631
HWC : HWN *3 060 m*	Oi	OeOa	Oi	OeOa
OeOa	**0.004**		**0.004**	
0–10 cm	**0.004**	**0.004**	**0.004**	0.873

Table 30: p values of Mann-Whitney U Test for pairwise comparison of soil organic carbon (SOC) in the respective plots for each horizon. Significant differences at the level $p \leq 0.05$ are marked bold.

	1st sampling				**2nd sampling**			
SOC Oi	1 540 m	1 890 m	2 380 m	3 060 m	1 540 m	1 890 m	2 380 m	3 060 m
1 050 m	0.262	0.337	0.631	**0.016**	n/d	n/d	n/d	n/d
1 540 m		0.078	0.631	**0.006**		n/d	n/d	n/d
1 890 m			0.150	**0.004**			n/d	n/d
2 380 m				0.055				n/d
SOC OeOa	1 540 m	1 890 m	2 380 m	3 060 m	1 540 m	1 890 m	2 380 m	3 060 m
1 050 m	0.200	0.150	0.200	0.873	n/d	n/d	n/d	n/d
1 540 m		0.873	**0.025**	0.150		n/d	n/d	n/d
1 890 m			**0.016**	0.150			n/d	n/d
2 380 m				0.200				n/d
SOC 0–10 cm	1 540 m	1 890 m	2 380 m	3 060 m	1 540 m	1 890 m	2 380 m	3 060 m
1 050 m	0.262	**0.004**	0.873	**0.004**	n/d	n/d	n/d	n/d
1 540 m		**0.016**	0.262	**0.004**		n/d	n/d	n/d
1 890 m			**0.004**	**0.004**			n/d	n/d
2 380 m				**0.004**				n/d

Table 31: p values of Mann-Whitney U Test for pairwise comparison of total hot-water extractable organic carbon (HWC) in the respective plots for each horizon. Significant differences at the level $p \leq 0.05$ are marked bold.

	1st sampling				**2nd sampling**			
HWC Oi	1 540 m	1 890 m	2 380 m	3 060 m	1 540 m	1 890 m	2 380 m	3 060 m
1 050 m	**0.016**	0.200	0.423	0.749	0.055	**0.037**	0.200	**0.025**
1 540 m		0.631	0.150	**0.037**		0.262	0.522	0.200
1 890 m			0.423	0.337			0.337	0.749
2 380 m				0.631				0.150
HWC OeOa	1 540 m	1 890 m	2 380 m	3 060 m	1 540 m	1 890 m	2 380 m	3 060 m
1 050 m	0.522	0.200	0.873	0.749	0.337	**0.078**	0.200	0.150
1 540 m		0.749	**0.010**	0.109		0.262	0.423	0.423
1 890 m			0.055	0.337			0.150	0.631
2 380 m				**0.037**				0.749
HWC 0–10 cm	1 540 m	1 890 m	2 380 m	3 060 m	1 540 m	1 890 m	2 380 m	3 060 m
1 050 m	**0.006**	**0.004**	**0.004**	**0.004**	**0.004**	**0.004**	**0.004**	**0.004**
1 540 m		0.150	0.631	**0.010**		1.000	0.055	**0.004**
1 890 m			0.055	0.055			0.078	0.055
2 380 m				**0.004**				**0.004**

Table 32: p values of Mann-Whitney U Test for pairwise comparison of total KCl-extractable organic carbon (TOC_{KCl}) in the respective plots for each horizon. Significant differences at the level $p \leq 0.05$ are marked bold.

	1st sampling				**2nd sampling**			
TOC_{KCl} *Oi*	1 540 m	1 890 m	2 380 m	3 060 m	1 540 m	1 890 m	2 380 m	3 060 m
1 050 m	0.337	0.109	0.200	**0.016**	0.522	0.150	**0.037**	**0.037**
1 540 m		0.522	0.749	**0.025**		0.150	**0.010**	**0.006**
1 890 m			0.262	**0.010**			**0.004**	**0.004**
2 380 m				**0.010**				1.000
TOC_{KCl} *OeOa*	1 540 m	1 890 m	2 380 m	3 060 m	1 540 m	1 890 m	2 380 m	3 060 m
1 050 m	0.109	0.200	0.423	**0.004**	**0.004**	**0.037**	**0.004**	**0.004**
1 540 m		0.078	0.055	**0.004**		0.150	**0.004**	**0.004**
1 890 m			1.000	**0.004**			0.200	**0.010**
2 380 m				**0.004**				**0.016**
TOC_{KCl} *0–10 cm*	1 540 m	1 890 m	2 380 m	3 060 m	1 540 m	1 890 m	2 380 m	3 060 m
1 050 m	0.631	0.055	**0.016**	**0.004**	**0.004**	0.522	**0.004**	0.055
1 540 m		0.262	**0.016**	**0.006**		0.150	**0.004**	0.749
1 890 m			**0.025**	**0.010**			**0.006**	0.262
2 380 m				**0.004**				**0.004**

Table 33: p values of Mann-Whitney U Test for pairwise comparison of microbial biomass carbon (C_{mic}) in the respective plots for each horizon. Significant differences at the level $p \leq 0.05$ are marked bold.

	1st sampling				**2nd sampling**			
C_{mic} *Oi*	1 540 m	1 890 m	2 380 m	3 060 m	1 540 m	1 890 m	2 380 m	3 060 m
1 050 m	0.522	0.775	**0.037**	0.068	0.631	0.109	0.522	1.000
1 540 m		0.568	**0.037**	**0.045**		0.522	0.337	0.423
1 890 m			0.063ref	0.088			0.200	0.200
2 380 m				0.465				0.337
C_{mic} *OeOa*	1 540 m	1 890 m	2 380 m	3 060 m	1 540 m	1 890 m	2 380 m	3 060 m
1 050 m	0.522	0.198	0.631	0.361	0.873	0.200	0.423	0.749
1 540 m		0.474	0.200	0.361		0.109	0.337	0.631
1 890 m			0.063	0.935			**0.016**	**0.037**
2 380 m				0.100				0.109
C_{mic} *0–10 cm*	1 540 m	1 890 m	2 380 m	3 060 m	1 540 m	1 890 m	2 380 m	3 060 m
1 050 m	0.150	0.317	0.150	1.000	**0.004**	**0.004**	0.262	**0.025**
1 540 m		**0.045**	**0.016**	0.465		0.262	**0.004**	0.749
1 890 m			0.668	0.122			**0.004**	0.109
2 380 m				**0.045**				0.037

Table 34: p values of Mann-Whitney U Test for pairwise comparison of total nitrogen (TN) in the respective plots for each horizon. Significant differences at the level $p \leq 0.05$ are marked bold.

	1st sampling				**2nd sampling**			
TN Oi	1 540 m	1 890 m	2 380 m	3 060 m	1 540 m	1 890 m	2 380 m	3 060 m
1 050 m	**0.010**	**0.004**	**0.016**	**0.004**	n/d	n/d	n/d	n/d
1 540 m		0.109	0.055	**0.004**		n/d	n/d	n/d
1 890 m			0.055	**0.004**			n/d	n/d
2 380 m				0.109				n/d
TN OeOa	1 540 m	1 890 m	2 380 m	3 060 m	1 540 m	1 890 m	2 380 m	3 060 m
1 050 m	0.150	0.337	0.200	**0.006**	n/d	n/d	n/d	n/d
1 540 m		0.423	0.522	**0.010**		n/d	n/d	n/d
1 890 m			0.749	**0.025**			n/d	n/d
2 380 m				**0.010**				n/d
TN 0–10 cm	1 540 m	1 890 m	2 380 m	3 060 m	1 540 m	1 890 m	2 380 m	3 060 m
1 050 m	**0.004**	**0.037**	**0.004**	**0.004**	n/d	n/d	n/d	n/d
1 540 m		**0.004**	1.000	**0.004**		n/d	n/d	n/d
1 890 m			**0.004**	**0.010**			n/d	n/d
2 380 m				**0.004**				n/d

Table 35: p values of Mann-Whitney U Test for pairwise comparison of total hot-water extractable nitrogen (HWN) in the respective plots for each horizon. Significant differences at the level $p \leq 0.05$ are marked bold.

	1st sampling				**2nd sampling**			
HWN Oi	1 540 m	1 890 m	2 380 m	3 060 m	1 540 m	1 890 m	2 380 m	3 060 m
1 050 m	0.055	0.078	**0.004**	**0.004**	0.200	0.873	**0.037**	**0.006**
1 540 m		0.749	**0.004**	**0.004**		0.109	0.200	**0.037**
1 890 m			**0.006**	**0.004**			**0.037**	**0.004**
2 380 m				0.109				0.423
HWN OeOa	1 540 m	1 890 m	2 380 m	3 060 m	1 540 m	1 890 m	2 380 m	3 060 m
1 050 m	**0.004**	**0.025**	**0.006**	**0.004**	**0.004**	**0.025**	**0.010**	**0.004**
1 540 m		0.078	**0.025**	**0.025**		0.262	0.631	**0.025**
1 890 m			0.337	**0.010**			1.000	0.078
2 380 m				**0.004**				**0.037**
HWN 0–10 cm	1 540 m	1 890 m	2 380 m	3 060 m	1 540 m	1 890 m	2 380 m	3 060 m
1 050 m	**0.004**	**0.037**	0.749	**0.037**	0.522	**0.004**	0.262	**0.004**
1 540 m		**0.004**	**0.016**	**0.004**		**0.037**	**0.078**	**0.010**
1 890 m			**0.025**	0.337			**0.004**	0.423
2 380 m				**0.037**				**0.004**

Table 36: p values of Mann-Whitney U Test for pairwise comparison of total KCl-extractable nitrogen (TN_{KCl}) in the respective plots for each horizon. Significant differences at the level $p \leq 0.05$ are marked bold.

	1st sampling				**2nd sampling**			
TN_{KCl} *Oi*	1 540 m	1 890 m	2 380 m	3 060 m	1 540 m	1 890 m	2 380 m	3 060 m
1 050 m	**0.025**	**0.016**	**0.004**	**0.004**	0.109	0.262	**0.004**	**0.004**
1 540 m		0.631	**0.025**	**0.004**		1.000	**0.006**	**0.004**
1 890 m			**0.016**	**0.004**			**0.004**	**0.004**
2 380 m				**0.006**				**0.025**
TN_{KCl} *OeOa*	1 540 m	1 890 m	2 380 m	3 060 m	1 540 m	1 890 m	2 380 m	3 060 m
1 050 m	**0.004**	**0.006**	**0.004**	**0.004**	**0.004**	**0.016**	**0.004**	**0.006**
1 540 m		0.150	0.423	**0.004**		0.423	0.055	**0.006**
1 890 m			**0.037**	**0.004**			0.078	**0.006**
2 380 m				**0.004**				**0.018**
TN_{KCl} *0–10 cm*	1 540 m	1 890 m	2 380 m	3 060 m	1 540 m	1 890 m	2 380 m	3 060 m
1 050 m	**0.004**	0.749	**0.010**	0.873	**0.006**	0.873	**0.004**	**0.006**
1 540 m		**0.004**	0.522	**0.004**		**0.006**	**0.004**	0.262
1 890 m			**0.010**	0.200			**0.004**	**0.004**
2 380 m				**0.010**				**0.016**

Table 37: p values of Mann-Whitney U Test for pairwise comparison of total KCl-extractable organic nitrogen ($TN_{KCl(org)}$) in the respective plots for each horizon. Significant differences at the level $p \leq 0.05$ are marked bold.

	1st sampling				**2nd sampling**			
TN^{org}_{KCl} *Oi*	1 540 m	1 890 m	2 380 m	3 060 m	1 540 m	1 890 m	2 380 m	3 060 m
1 050 m	0.200	0.109	0.337	**0.006**	**0.025**	0.522	**0.006**	**0.004**
1 540 m		0.631	0.055	**0.004**		**0.037**	**0.037**	**0.004**
1 890 m			**0.025**	**0.004**			**0.006**	**0.004**
2 380 m				**0.004**				0.055
TN^{org}_{KCl} *OeOa*	1 540 m	1 890 m	2 380 m	3 060 m	1 540 m	1 890 m	2 380 m	3 060 m
1 050 m	1.000	0.522	0.055	**0.004**	0.336	0.336	0.336	0.360
1 540 m		0.337	**0.025**	**0.004**		1.000	0.631	**0.006**
1 890 m			0.109	**0.004**			0.749	0.068
2 380 m				**0.004**				**0.018**
TN^{org}_{KCl} *0–10 cm*	1 540 m	1 890 m	2 380 m	3 060 m	1 540 m	1 890 m	2 380 m	3 060 m
1 050 m	0.150	**0.016**	0.150	**0.037**	0.004	0.423	**0.004**	**0.004**
1 540 m		0.054	0.631	**0.010**		**0.004**	0.109	0.631
1 890 m			0.054	**0.006**			**0.004**	**0.004**
2 380 m				**0.010**				**0.006**

Table 38: p values of Mann-Whitney U Test for pairwise comparison of total KCl-extractable inorganic nitrogen ($TN_{KCl(inorg)}$) in the respective plots for each horizon. Significant differences at the level $p \leq 0.05$ are marked bold.

	1st sampling				2nd sampling			
TN_{KCl}^{inorg} *Oi*	1 540 m	1 890 m	2 380 m	3 060 m	1 540 m	1 890 m	2 380 m	3 060 m
1 050 m	**0.016**	**0.016**	**0.004**	**0.004**	0.522	0.262	**0.004**	**0.004**
1 540 m		0.749	**0.016**	**0.004**		0.873	**0.025**	**0.010**
1 890 m			**0.016**	**0.004**			**0.016**	**0.006**
2 380 m				**0.016**				0.150
TN_{KCl}^{inorg} *OeOa*	1 540 m	1 890 m	2 380 m	3 060 m	1 540 m	1 890 m	2 380 m	3 060 m
1 050 m	**0.004**	**0.004**	**0.004**	**0.004**	0.150	0.200	**0.010**	**0.006**
1 540 m		**0.037**	0.631	**0.025**		0.337	**0.025**	**0.006**
1 890 m			0.078	**0.004**			**0.037**	**0.006**
2 380 m				**0.004**				**0.018**
TN_{KCl}^{inorg} *0–10 cm*	1 540 m	1 890 m	2 380 m	3 060 m	1 540 m	1 890 m	2 380 m	3 060 m
1 050 m	**0.004**	0.337	**0.010**	**0.037**	0.055	0.749	**0.004**	**0.016**
1 540 m		**0.004**	0.522	**0.016**		0.078	**0.004**	0.150
1 890 m			**0.010**	0.055			**0.004**	**0.025**
2 380 m				0.109				0.150

Table 39: p values of Mann-Whitney U Test for pairwise comparison of NH_4^+-N in the respective plots for each horizon. Significant differences at the level $p \leq 0.05$ are marked bold.

	1st sampling				2nd sampling			
NH_4^+-N *Oi*	1 540 m	1 890 m	2 380 m	3 060 m	1 540 m	1 890 m	2 380 m	3 060 m
1 050 m	**0.004**	0.337	0.055	**0.004**	0.337	0.262	**0.004**	**0.004**
1 540 m		**0.006**	**0.016**	**0.004**		0.150	**0.025**	**0.010**
1 890 m			0.055	**0.004**			0.055	**0.010**
2 380 m				**0.016**				0.109
NH_4^+-N *OeOa*	1 540 m	1 890 m	2 380 m	3 060 m	1 540 m	1 890 m	2 380 m	3 060 m
1 050 m	0.200	0.423	0.337	**0.025**	1.000	0.749	0.337	**0.011**
1 540 m		0.262	0.522	**0.037**		0.109	**0.004**	**0.006**
1 890 m			0.337	**0.004**			0.078	**0.006**
2 380 m				**0.004**				**0.018**
NH_4^+-N *0–10 cm*	1 540 m	1 890 m	2 380 m	3 060 m	1 540 m	1 890 m	2 380 m	3 060 m
1 050 m	**0.004**	**0.004**	**0.004**	**0.004**	**0.006**	0.078	0.078	**0.004**
1 540 m		0.109	0.423	**0.006**		0.200	0.055	0.423
1 890 m			1.000	**0.016**			0.522	0.055
2 380 m				**0.037**				**0.006**

Table 40: p values of Mann-Whitney U Test for pairwise comparison of NO_3^--N in the respective plots for each horizon. Significant differences at the level $p \leq 0.05$ are marked bold.

	1st sampling				**2nd sampling**			
NO_3^--N Oi	1 540 m	1 890 m	2 380 m	3 060 m	1 540 m	1 890 m	2 380 m	3 060 m
1 050 m	**0.004**	**0.016**	**0.004**	**0.004**	**0.006**	0.150	**0.004**	**0.004**
1 540 m		0.337	**0.004**	**0.004**		0.631	**0.004**	**0.010**
1 890 m			**0.006**	**0.006**			**0.004**	**0.006**
2 380 m				**0.037**				0.423
NO_3^--N OeOa	1 540 m	1 890 m	2 380 m	3 060 m	1 540 m	1 890 m	2 380 m	3 060 m
1 050 m	**0.004**	**0.004**	**0.004**	**0.004**	**0.004**	0.109	**0.006**	**0.006**
1 540 m		**0.010**	0.337	**0.010**		**0.004**	0.522	**0.018**
1 890 m			**0.025**	**0.004**			**0.025**	**0.006**
2 380 m				**0.006**				0.715
NO_3^--N 0–10 cm	1 540 m	1 890 m	2 380 m	3 060 m	1 540 m	1 890 m	2 380 m	3 060 m
1 050 m	**0.004**	0.631	**0.004**	**0.004**	**0.004**	0.522	**0.004**	**0.004**
1 540 m		**0.004**	0.873	0.337		**0.025**	0.337	**0.004**
1 890 m			**0.004**	**0.004**			**0.004**	**0.004**
2 380 m				0.631				**0.004**

Table 41: p values of Mann-Whitney U Test for pairwise comparison of microbial biomass nitrogen (N_{mic}) in the respective plots for each horizon. Significant differences at the level $p \leq 0.05$ are marked bold.

	1st sampling				**2nd sampling**			
N_{mic} Oi	1 540 m	1 890 m	2 380 m	3 060 m	1 540 m	1 890 m	2 380 m	3 060 m
1 050 m	0.749	1.000	0.055	**0.006**	0.873	0.337	0.109	0.262
1 540 m		0.568	**0.037**	**0.006**		0.262	0.109	0.150
1 890 m			0.063	0.019			0.055	**0.025**
2 380 m				0.144				0.337
N_{mic} OeOa	1 540 m	1 890 m	2 380 m	3 060 m	1 540 m	1 890 m	2 380 m	3 060 m
1 050 m	0.109	0.063	0.522	**0.028**	0.423	0.200	0.078	0.200
1 540 m		0.775	**0.016**	0.273		**0.037**	0.078	0.522
1 890 m			**0.015**	0.222			**0.004**	**0.010**
2 380 m				**0.006**				0.150
N_{mic} 0–10 cm	1 540 m	1 890 m	2 380 m	3 060 m	1 540 m	1 890 m	2 380 m	3 060 m
1 050 m	**0.016**	0.252	0.423	0.273	0.631	**0.006**	0.749	0.055
1 540 m		1.000	0.522	0.715		**0.010**	0.423	0.078
1 890 m			0.519	0.935			**0.006**	0.423
2 380 m				0.715				**0.037**

Table 42: p values of Mann-Whitney U Test for pairwise comparison of soil organic carbon (SOC) : total nitrogen (TN) in the respective plots for each horizon. Significant differences at the level $p \leq 0.05$ are marked bold.

	1st sampling				**2nd sampling**			
SOC : TN Oi	1 540 m	1 890 m	2 380 m	3 060 m	1 540 m	1 890 m	2 380 m	3 060 m
1 050 m	**0.010**	**0.016**	**0.010**	**0.004**	n/d	n/d	n/d	n/d
1 540 m		0.423	0.055	**0.004**		n/d	n/d	n/d
1 890 m			0.055	**0.004**			n/d	n/d
2 380 m				**0.025**				n/d
SOC : TN OeOa	1 540 m	1 890 m	2 380 m	3 060 m	1 540 m	1 890 m	2 380 m	3 060 m
1 050 m	0.337	0.631	0.200	**0.016**	n/d	n/d	n/d	n/d
1 540 m		**0.006**	**0.016**	**0.004**		n/d	n/d	n/d
1 890 m			**0.004**	**0.004**			n/d	n/d
2 380 m				**0.010**				n/d
SOC : TN 0–10 cm	1 540 m	1 890 m	2 380 m	3 060 m	1 540 m	1 890 m	2 380 m	3 060 m
1 050 m	**0.004**	**0.004**	**0.004**	**0.004**	n/d	n/d	n/d	n/d
1 540 m		**0.004**	**0.004**	**0.037**		n/d	n/d	n/d
1 890 m			0.522	**0.004**			n/d	n/d
2 380 m				**0.004**				n/d

Table 43: p values of Mann-Whitney U Test for pairwise comparison of microbial biomass carbon (C_{mic}) : microbial biomass nitrogen (N_{mic}) in the respective plots for each horizon. Significant differences at the level $p \leq 0.05$ are marked bold.

	1st sampling				**2nd sampling**			
$C_{mic} : N_{mic}$ *Oi*	1 540 m	1 890 m	2 380 m	3 060 m	1 540 m	1 890 m	2 380 m	3 060 m
1 050 m	0.423	0.775	0.109	0.100	0.262	0.631	0.078	0.109
1 540 m		0.568	0.522	**0.028**		0.522	0.150	0.262
1 890 m			0.116	0.167			0.078	0.200
2 380 m				**0.018**				0.522
$C_{mic} : N_{mic}$ *OeOa*	1 540 m	1 890 m	2 380 m	3 060 m	1 540 m	1 890 m	2 380 m	3 060 m
1 050 m	0.423	0.668	0.109	0.068	0.200	0.337	**0.037**	0.055
1 540 m		0.886	**0.037**	0.201		0.109	0.749	0.423
1 890 m			**0.022**	0.061			**0.004**	**0.010**
2 380 m				**0.006**				1.000
$C_{mic} : N_{mic}$ *0–10 cm*	1 540 m	1 890 m	2 380 m	3 060 m	1 540 m	1 890 m	2 380 m	3 060 m
1 050 m	**0.004**	0.252	0.631	0.100	**0.004**	**0.025**	**0.006**	**0.006**
1 540 m		**0.003**	**0.016**	**0.028**		**0.004**	**0.004**	**0.010**
1 890 m			0.567	0.935			0.078	0.055
2 380 m				0.273				0.078

Table 44: p values of Mann-Whitney U Test for pairwise comparison of total hot-water extractable organic carbon (HWC) : total hot-water extractable nitrogen (HWN) in the respective plots for each horizon. Significant differences at the level $p \leq 0.05$ are marked bold.

	1st sampling				**2nd sampling**			
HWC : HWN Oi	1 540 m	1 890 m	2 380 m	3 060 m	1 540 m	1 890 m	2 380 m	3 060 m
1 050 m	**0.006**	**0.010**	**0.004**	**0.004**	**0.004**	0.109	**0.004**	**0.004**
1 540 m		0.631	**0.006**	**0.004**		0.200	**0.025**	**0.004**
1 890 m			**0.010**	**0.004**			**0.004**	**0.004**
2 380 m				0.055				**0.006**
HWC : HWN OeOa	1 540 m	1 890 m	2 380 m	3 060 m	1 540 m	1 890 m	2 380 m	3 060 m
1 050 m	**0.004**	**0.006**	**0.004**	**0.004**	**0.004**	**0.004**	**0.025**	**0.004**
1 540 m		**0.016**	1.000	**0.004**		0.109	0.109	**0.025**
1 890 m			**0.010**	**0.004**			0.749	**0.025**
2 380 m				**0.004**				**0.004**
HWC : HWN 0–10 cm	1 540 m	1 890 m	2 380 m	3 060 m	1 540 m	1 890 m	2 380 m	3 060 m
1 050 m	**0.004**	**0.004**	**0.004**	**0.004**	**0.004**	**0.004**	**0.004**	**0.004**
1 540 m		**0.004**	**0.006**	**0.109**		**0.006**	0.150	**0.004**
1 890 m			**0.006**	**0.004**			0.055	**0.004**
2 380 m				**0.004**				**0.006**

Table 45: p values of Mann-Whitney U Test pairwise comparison of total soil respiration (TSR) at the studied plots. Significant differences at the level $p \leq 0.05$ are marked bold.

TSR	1 540 m	1 890 m	2 380 m	3 060 m
1 050 m	**0.000**	**0.000**	**0.000**	**0.000**
1 540 m		**0.000**	**0.000**	**0.000**
1 890 m			**0.000**	**0.000**
2 380 m				0.131

Table 46: p values of Mann-Whitney U Test pairwise comparison of stand and reference litter for each plot and time of exposure. Significant differences at the level $p \leq 0.05$ are marked bold.

plot	**weeks of exposure**				
	4	8	16	28	44
1 050 m	0.597	0.151	**0.002**	**0.010**	**0.001**
1 540 m	**0.002**	0.059	0.821	0.705	0.821
1 890 m	0.059	0.450	0.290	**0.004**	0.859
2 380 m	0.072	**0.049**	**0.000**	**0.004**	0.315
3 060 m	0.028	0.929	**0.041**	0.288	0.253

Table 47: p values of Wilkoxon Test for pairwise comparison of dependent samples: comparison of C fractions 1st and 2nd sampling. Significant differences at the level $p \leq 0.05$ are marked bold.

	plot	**Oi**	**OeOa**	**0–10 cm**
HWC	1 050 m	0.600	0.917	0.075
	1 540 m	0.753	0.753	0.173
	1 890 m	0.345	0.116	0.753
	2 380 m	0.753	**0.028**	0.600
	3 060 m	**0.046**	0.116	**0.028**
TOC_{KCl}	1 050 m	0.600	0.917	0.075
	1 540 m	0.753	0.753	0.173
	1 890 m	0.345	0.116	0.753
	2 380 m	0.753	**0.028**	0.600
	3 060 m	**0.046**	0.116	**0.028**

Table 48: p values Wilkoxon-Test for pairwise comparison of dependent samples: comparison of nitrogen fractions 1st and 2nd sampling. Significant differences at the level $p < 0.05$ are marked bold.

	plot	Oi	OeOa	0–10 cm
HWN	1 050 m	0.075	0.345	0.345
	1 540 m	0.173	**0.046**	**0.046**
	1 890 m	0.753	0.116	0.600
	2 380 m	0,075	0.075	0.173
	3 060 m	**0.028**	0.600	0.249
TN_{KCl}	1 050 m	**0.046**	0.116	**0.028**
	1 540 m	0.116	0.116	**0.028**
	1 890 m	0.917	0.173	0.345
	2 380 m	0.116	**0.046**	0.173
	3 060 m	**0.046**	0.225	**0.028**
TN^{org}_{KCl}	1 050 m	**0.028**	0.345	**0.028**
	1 540 m	0.600	**0.028**	0.075
	1 890 m	0.173	0.249	**0.028**
	2 380 m	0.249	0.753	**0.028**
	3 060 m	**0.028**	0.080	0.600
TN^{inorg}_{KCl}	1 050 m	**0.028**	**0.046**	0.463
	1 540 m	0.173	0.753	0.116
	1 890 m	0.600	0.249	0.753
	2 380 m	0.249	**0.028**	0.075
	3 060 m	0.917	0.080	**0.046**
NH^+_4-N	1 050 m	**0.028**	0.345	**0.046**
	1 540 m	0.173	0.600	0.345
	1 890 m	0.345	0.345	0.173
	2 380 m	0.249	**0.028**	**0.028**
	3 060 m	0.173	0.225	0.173
NO^-_3-N	1 050 m	**0.028**	**0.028**	0.463
	1 540 m	**0.028**	0.600	0.753
	1 890 m	0.345	0.116	0.753
	2 380 m	**0.028**	0.463	0.753
	3 060 m	0.345	0.500	**0.028**

Table 49: p values Wilkoxon-Test for pairwise comparison of dependent samples: comparison of microbial biomass carbon (C_{mic}), microbial biomass nitrogen (N_{mic}) and microbial biomass carbon (C_{mic}) : microbial biomass nitrogen (N_{mic}) 1st and 2nd sampling. Significant differences at the level $p < 0.05$ are marked bold.

	plot	Oi	OeOa	0–10 cm
C_{mic}	1 050 m	0.463	0.917	**0.028**
	1 540 m	0.753	0.917	0.600
	1 890 m	0.398	0.499	0.091
	2 380 m	0.600	0.173	0.600
	3 060 m	0.893	0.893	0.345
N_{mic}	1 050 m	0.600	0.116	**0.046**
	1 540 m	0.600	0.463	0.173
	1 890 m	0.866	0.735	**0.028**
	2 380 m	0.917	0.116	0.463
	3 060 m	**0.043**	**0.043**	0.225
$C_{mic} : N_{mic}$	1 050 m	**0.075**	**0.046**	**0.046**
	1 540 m	0.917	**0.046**	**0.028**
	1 890 m	**0.063**	0.176	**0.018**
	2 380 m	0.116	0.173	0.249
	3 060 m	0.138	0.500	0.080

Table 50: Descriptive statistics: total soil respiration (TSR) in g CO_2 $m^{-2}\,h^{-1}$, including data from all measurements.

plot	n	median	min	max	Q1	Q3	range	d_Q
		in g CO_2 $m^{-2}\,h^{-1}$						
1 050 m	862	0.56	0.06	2.61	0.41	0.71	2.55	0.30
1 540 m	448	0.72	0.07	2.68	0.49	0.99	2.61	0.50
1 890 m	872	0.39	0.00	1.53	0.27	0.56	0.18	1.53
2 380 m	464	0.15	0.01	1.40	0.11	0.22	1.39	0.11
3 060 m	991	0.15	0.00	1.12	0.10	0.21	1.12	0.11

Table 51: Descriptive statistics: total soil respiration (TSR) in g CO_2 $m^{-2}\,h^{-1}$ at $P_{1\,050\ m}$, separated for each measuring point.

point #	n	median	min	max	Q1	Q3	range	d_Q
		in g CO_2 $m^{-2}\,h^{-1}$						
1	56	0.54	0.10	0.80	0.45	0.60	0.70	0.15
2	54	0.55	0.12	1.04	0.45	0.64	0.92	0.19
3	56	0.44	0.13	1.86	0.37	0.59	1.73	0.22
4	56	0.67	0.16	1.09	0.55	0.75	0.93	0.20
5	56	0.45	0.06	1.33	0.36	0.59	1.27	0.23
6	56	0.54	0.24	2.15	0.45	0.65	1.91	0.20
7	58	0.77	0.21	2.02	0.61	0.93	1.81	0.32
8	42	0.74	0.25	1.73	0.58	0.86	1.48	0.28
9	42	0.63	0.08	1.53	0.43	0.81	1.45	0.38
10	40	0.35	0.11	0.86	0.26	0.40	0.75	0.14
11	55	0.47	0.16	0.83	0.37	0.57	0.67	0.20
12	56	0.54	0.23	1.61	0.42	0.73	1.38	0.31
13	56	0.41	0.16	0.78	0.30	0.52	0.62	0.22
14	56	0.64	0.21	1.03	0.55	0.81	0.82	0.26
15	56	0.54	0.18	1.51	0.41	0.65	1.33	0.25
16	54	0.97	0.47	2.61	0.71	1.29	2.14	0.58

Table 52: Descriptive statistics: total soil respiration (TSR) in g CO_2 $m^{-2}\,h^{-1}$ at $P_{1\,540\ m}$, separated for each measuring point.

point #	n	median	min	max	Q1	Q3	range	d_Q
		in g CO_2 $m^{-2}\,h^{-1}$						
1	28	0.60	0.13	1.54	0.50	0.94	1.41	0.44
2	28	1.07	0.25	2.41	0.77	1.32	2.16	0.55
3	28	0.66	0.14	1.73	0.37	0.98	1.59	0.61
4	28	1.06	0.18	2.06	0.76	1.41	1.88	0.65
5	28	0.73	0.42	1.13	0.56	0.90	0.71	0.35
6	28	0.81	0.29	1.80	0.62	0.91	1.51	0.30
7	28	0.68	0.19	1.65	0.50	0.92	1.46	0.42
8	28	0.84	0.21	2.06	0.69	1.06	1.85	0.38
9	28	0.72	0.18	1.62	0.54	0.86	1.44	0.32
10	28	1.07	0.26	2.47	0.82	1.37	2.21	0.55
11	28	0.52	0.09	1.15	0.32	0.74	1.06	0.42
12	28	0.51	0.10	0.94	0.42	0.68	0.84	0.27
13	28	0.72	0.13	1.70	0.51	0.90	1.57	0.39
14	28	0.60	0.19	1.45	0.36	0.80	1.26	0.44
15	28	0.78	0.29	2.68	0.50	1.21	2.39	0.71
16	28	0.37	0.07	0.79	0.20	0.54	0.72	0.35

Table 53: Descriptive statistics: total soil respiration (TSR) in g CO_2 $m^{-2}\,h^{-1}$ at $P_{1\,890\ m}$, separated for each measuring point.

point #	n	median	min	max	Q1	Q3	range	d_Q
		in g CO_2 $m^{-2}\,h^{-1}$						
1	55	0.42	0.13	0.88	0.31	0.57	0.75	0.26
2	55	0.45	0.12	0.95	0.38	0.67	0.83	0.29
3	55	0.35	0.01	1.12	0.27	0.56	1.11	0.29
4	55	0.53	0.07	1.05	0.32	0.70	0.98	0.38
5	54	0.20	0.00	0.72	0.15	0.24	0.72	0.09
6	56	0.54	0.02	1.45	0.29	0.72	1.43	0.44
7	55	0.24	0.01	0.62	0.18	0.34	0.61	0.16
8	55	0.28	0.04	0.63	0.20	0.44	0.59	0.24
9	55	0.44	0.09	0.84	0.34	0.50	0.75	0.16
10	55	0.46	0.08	1.18	0.39	0.57	1.10	0.18
11	53	0.40	0.18	0.73	0.31	0.52	0.55	0.21
12	55	0.38	0.06	0.90	0.30	0.62	0.84	0.32
13	55	0.53	0.12	0.94	0.36	0.68	0.82	0.32
14	54	0.63	0.11	1.53	0.49	0.81	1.42	0.32
15	55	0.33	0.06	1.27	0.26	0.43	1.21	0.17
16	55	0.30	0.02	0.80	0.23	0.37	0.78	0.14

Table 54: Descriptive statistics: total soil respiration (TSR) in g CO_2 $m^{-2}\,h^{-1}$ at $P_{2\,380\ m}$, separated for each measuring point.

point #	*n*	median	min	max	Q1	Q3	range	d_Q
		in g CO_2 $m^{-2}\,h^{-1}$						
1	29	0.13	0.04	0.40	0.10	0.17	0.36	0.07
2	29	0.09	0.04	0.70	0.07	0.12	0.66	0.05
3	29	0.21	0.06	0.64	0.15	0.30	0.58	0.15
4	29	0.13	0.04	0.42	0.10	0.15	0.38	0.05
5	29	0.13	0.02	0.61	0.09	0.19	0.59	0.10
6	29	0.10	0.03	0.49	0.06	0.12	0.46	0.06
7	29	0.14	0.02	0.62	0.10	0.20	0.60	0.10
8	29	0.13	0.04	0.50	0.11	0.20	0.46	0.09
9	29	0.18	0.07	0.69	0.13	0.30	0.62	0.17
10	29	0.18	0.07	0.58	0.12	0.24	0.51	0.12
11	29	0.17	0.07	0.45	0.13	0.21	0.38	0.08
12	29	0.18	0.03	1.40	0.14	0.21	1.37	0.07
13	29	0.14	0.01	0.57	0.09	0.25	0.56	0.16
14	29	0.21	0.11	0.42	0.17	0.26	0.31	0.09
15	29	0.16	0.08	0.53	0.12	0.17	0.45	0.05
16	29	0.22	0.07	0.67	0.19	0.28	0.60	0.09

Table 55: Descriptive statistics: total soil respiration (TSR) in g CO_2 $m^{-2}\,h^{-1}$ at $P_{3\,060\ m}$, separated for each measuring point.

point #	*n*	median	min	max	Q1	Q3	range	d_Q
		in g CO_2 $m^{-2}\,h^{-1}$						
1	62	0.19	0.00	0.54	0.15	0.24	0.54	0.09
2	62	0.20	0.02	1.12	0.12	0.39	1.10	0.27
3	62	0.18	0.00	0.42	0.14	0.21	0.42	0.07
4	62	0.14	0.02	0.44	0.09	0.19	0.42	0.10
5	62	0.13	0.01	0.63	0.10	0.20	0.62	0.10
6	59	0.16	0.01	0.46	0.13	0.21	0.45	0.08
7	62	0.16	0.00	0.43	0.10	0.20	0.43	0.10
8	63	0.10	0.00	0.39	0.08	0.14	0.39	0.06
9	62	0.10	0.02	0.25	0.08	0.13	0.23	0.05
10	62	0.20	0.00	0.68	0.14	0.25	0.68	0.11
11	62	0.08	0.01	0.47	0.05	0.11	0.46	0.06
12	62	0.15	0.02	0.61	0.12	0.21	0.59	0.09
13	62	0.29	0.07	0.82	0.16	0.38	0.75	0.22
14	62	0.16	0.01	1.04	0.13	0.24	1.03	0.11
15	62	0.19	0.05	0.56	0.16	0.26	0.51	0.10
16	62	0.11	0.00	0.82	0.09	0.14	0.82	0.05

Table 56: Descriptive statistics: soil organic carbon (SOC) in % for respective horizons and plots, April 2004.

SOC	horizon	*n*	median	min	max	Q1	Q3	range	d_Q
					in %				
1 050 m	Oi	6	48.21	35.23	51.47	47.13	49.09	16.24	1.96
	OeOa	6	43.13	35.22	48.44	40.27	46.56	13.22	6.29
	0–10 cm	6	3.27	3.03	3.75	3.20	3.33	0.72	0.14
1 540 m	Oi	6	49.04	48.26	50.82	48.33	49.49	2.56	1.16
	OeOa	6	40.45	31.81	43.37	35.52	42.26	11.56	6.74
	0–10 cm	6	4.09	2.64	5.23	3.11	4.26	2.58	1.15
1 890 m	Oi	6	44.96	32.94	49.62	40.78	48.52	16.68	7.74
	OeOa	6	37.59	24.19	44.67	32.06	43.96	20.49	11.89
	0–10 cm	6	5.71	4.32	7.26	4.42	6.75	2.94	2.34
2 380 m	Oi	6	50.28	32.65	51.42	45.32	50.78	18.77	5.46
	OeOa	6	46.77	38.81	51.47	45.10	49.11	12.66	4.01
	0–10 cm	6	3.25	2.16	3.98	2.71	3.96	1.81	1.25
3 060 m	Oi	6	51.50	49.77	52.55	51.22	52.41	2.78	1.19
	OeOa	6	42.77	38.54	48.83	40.99	45.90	10.28	4.91
	0–10 cm	6	11.55	9.06	14.87	9.45	14.10	5.81	4.65

Table 57: Descriptive statistics: total hot-water extractable organic carbon (HWC) in $\mu g\,g^{-1}$ soil for respective horizons and plots, April 2004.

HWC	horizon	*n*	median	min	max	Q1	Q3	range	d_Q
					in $\mu g\,g^{-1}$ soil				
1 050 m	Oi	6	20236.54	15571.19	21684.25	18713.56	21554.64	6113.06	2841.08
	OeOa	6	20373.49	14062.25	26485.05	14378.58	25286.19	12422.80	10907.62
	0–10 cm	6	853.40	754.00	1157.24	842.85	897.81	403.24	54.95
1 540 m	Oi	6	23255.27	20048.21	27987.20	22161.03	23645.62	7938.99	1484.60
	OeOa	6	16514.64	15387.86	18744.60	15998.11	18704.58	3356.73	2706.47
	0–10 cm	6	1599.34	992.03	2729.54	1201.07	1931.55	1737.52	730.48
1 890 m	Oi	6	25899.75	17406.16	28021.82	17811.68	26402.28	10615.66	8590.60
	OeOa	6	16275.33	13519.76	22080.55	13830.43	19480.30	8560.79	5649.86
	0–10 cm	6	2380.59	1180.17	2844.50	2297.01	2590.46	1664.34	293.46
2 380 m	Oi	6	21342.15	15269.25	26887.78	19076.81	22903.10	11618.52	3826.30
	OeOa	6	20419.45	18634.50	22631.47	19803.97	21352.90	3996.97	1548.93
	0–10 cm	6	1702.96	1231.08	2197.27	1299.80	2169.36	966.19	869.56
3 060 m	Oi	6	20388.59	81536.35	101918.94	122301.52	142684.11	3603.48	2028.22
	OeOa	6	18896.97	75569.90	94460.87	113351.84	132242.82	3553.68	3388.59
	0–10 cm	6	3381.43	13507.72	16883.15	20258.58	23634.00	2504.63	1253.16

Table 58: Descriptive statistics: total hot-water extractable organic carbon (HWC) in $\mu g\,g^{-1}$ soil for respective horizons and plots, November 2004.

HWC	horizon	*n*	median	min	max	Q1	Q3	range	d_Q
					in $\mu g\,g^{-1}$ soil				
1 050 m	Oi	6	19363.79	11757.23	22318.37	14573.74	20986.82	10561.13	6413.08
	OeOa	6	18091.51	14401.16	31275.52	15195.17	26422.75	16874.37	11227.57
	0–10 cm	6	830.64	679.68	963.58	747.17	888.35	283.90	141.18
1 540 m	Oi	6	24319.57	16111.15	31116.52	20339.67	26284.79	4109.346	15005.37
	OeOa	6	17511.88	13279.78	18340.16	15066.14	18093.44	1640.615	5060.38
	0–10 cm	6	2079.07	1611.89	3245.27	1697.46	2771.43	507.324	1633.38
1 890 m	Oi	6	28323.73	16352.61	35348.02	21930.73	31752.48	18995.42	9821.748
	OeOa	6	14739.94	8705.00	22746.41	11940.28	15536.96	14041.41	3596.676
	0–10 cm	6	2238.61	1311.98	10982.97	1924.39	2535.46	9670.99	611.066
2 380 m	Oi	6	21797.22	15591.31	40616.09	19140.74	22836.20	5662.099	25024.78
	OeOa	6	15805.48	13819.46	17693.76	15661.65	16216.25	779.142	3874.29
	0–10 cm	6	1492.34	1218.00	2193.30	1446.94	1759.14	250.584	975.30
3 060 m	Oi	6	29041.98	16642.91	44416.31	24430.09	31369.59	27773.40	6939.498
	OeOa	6	15422.63	10727.11	21359.59	14145.92	17583.55	10632.48	3437.632
	0–10 cm	6	4590.91	3512.54	5736.01	3716.12	5346.46	2223.47	1630.341

Table 59: Descriptive statistics: total KCl-extractable organic carbon (TOC_{KCl}) in $\mu g\,g^{-1}$ soil for respective horizons and plots, April 2004.

TOC_{KCl}	horizon	*n*	median	min	max	Q1	Q3	range	d_Q
					in $\mu g\,g^{-1}$ soil				
1 050 m	Oi	6	1774.73	1224.59	2289.46	1491.30	2261.06	1064.87	769.77
	OeOa	6	1207.77	451.71	1602.23	557.03	1544.26	1150.52	987.23
	0–10 cm	6	50.20	37.08	57.38	40.15	54.85	20.30	14.70
1 540 m	Oi	6	1811.06	1662.28	3170.76	1673.82	2795.95	1508.48	1122.13
	OeOa	6	513.02	460.16	658.67	480.15	630.57	198.51	150.42
	0–10 cm	6	51.18	37.06	103.11	39.32	67.26	66.05	27.94
1 890 m	Oi	6	2685.74	1385.74	3002.15	1817.72	2888.75	1616.42	1071.03
	OeOa	6	682.91	487.35	798.42	556.47	753.13	311.07	196.66
	0–10 cm	6	83.61	27.02	95.84	67.54	95.27	68.82	27.73
2 380 m	Oi	6	2171.92	1659.96	2398.16	1866.81	2377.43	738.20	510.62
	OeOa	6	636.73	604.02	913.03	605.06	683.98	309.01	78.92
	0–10 cm	6	31.95	20.07	41.23	22.75	38.62	21.16	15.86
3 060 m	Oi	6	785.39	590.00	1892.67	597.56	1140.63	1302.66	543.07
	OeOa	6	343.63	299.53	375.58	308.21	375.11	76.05	66.90
	0–10 cm	6	191.02	93.34	283.99	171.94	260.20	190.65	88.26

Table 60: Descriptive statistics: total KCl-extractable organic carbon (TOC_{KCl}) in $\mu g\,g^{-1}$ soil for respective horizons and plots, November 2004.

TOC_{KCl}	horizon	*n*	median	min	max	Q1	Q3	range	d_Q
					in $\mu g\,g^{-1}$ soil				
1 050 m	Oi	6	1661.89	1317.01	5367.07	1336.74	3031.71	4050.06	1694.97
	OeOa	6	901.07	562.31	3152.66	760.89	1350.43	2590.35	589.54
	0–10 cm	6	60.14	49.00	69.40	54.26	64.22	20.40	9.96
1 540 m	Oi	6	2482.34	1408.10	2771.30	1850.81	2708.29	1363.20	857.48
	OeOa	6	439.47	423.08	560.34	423.37	482.75	137.26	59.38
	0–10 cm	6	86.48	73.64	101.73	80.29	99.88	28.09	19.59
1 890 m	Oi	6	3140.36	1781.91	6851.71	2309.99	3494.01	5069.80	1184.02
	OeOa	6	364.44	160.08	1502.03	313.65	440.30	1341.96	126.65
	0–10 cm	6	67.99	22.34	344.45	50.53	81.76	322.10	31.23
2 380 m	Oi	6	1132.52	974.90	1593.78	1046.29	1470.04	618.88	423.76
	OeOa	6	256.92	190.51	407.71	233.92	344.31	217.20	110.39
	0–10 cm	6	15.93	3.88	24.26	9.85	22.33	20.38	12.49
3 060 m	Oi	6	1259.62	832.96	1737.10	918.35	1351.01	904.13	432.66
	OeOa	6	139.44	116.61	239.70	122.09	163.67	123.09	41.57
	0–10 cm	6	90.37	45.50	95.48	76.48	94.85	49.99	18.36

Table 61: Descriptive statistics: microbial biomass carbon (C_{mic}) in $\mu g\,g^{-1}$ soil for respective horizons and plots, April 2004.

C_{mic}	horizon	*n*	median	min	max	Q1	Q3	range	d_Q
					in $\mu g\,g^{-1}$ soil				
1 050 m	Oi	6	8405.32	5052.79	12641.27	5835.49	11082.57	7588.47	5247.08
	OeOa	6	5557.94	3796.65	10324.70	4227.76	6576.76	6528.05	2349.01
	0–10 cm	6	718.91	513.13	737.77	712.56	736.04	224.64	23.48
1 540 m	Oi	6	7363.61	5275.83	8133.23	6806.55	7945.49	2857.40	1138.94
	OeOa	6	4687.12	4299.05	5733.33	4404.63	5099.87	1434.28	695.24
	0–10 cm	6	1099.56	580.87	1568.99	717.42	1477.16	988.12	759.74
1 890 m	Oi	6	8210.85	4976.57	12926.78	5265.49	10661.31	7950.21	5395.82
	OeOa	6	4557.15	2992.20	6367.46	3435.49	4972.51	3375.25	1537.02
	0–10 cm	6	643.13	120.93	978.11	343.67	818.65	857.18	474.98
2 380 m	Oi	6	4560.09	2229.33	7125.20	3242.32	6076.03	1535.33	4895.87
	OeOa	6	5990.55	4238.33	8300.62	4601.65	7371.74	1317.05	4062.29
	0–10 cm	6	518.38	379.96	802.51	453.57	627.08	109.87	422.55
3 060 m	Oi	5	5066.18	3563.52	7557.44	3867.14	6461.39	3993.92	2594.25
	OeOa	5	4640.04	4053.66	4927.88	4237.10	4790.46	874.22	553.36
	0–10 cm	5	700.06	652.31	1620.21	674.20	752.03	967.90	77.82

Table 62: Descriptive statistics: microbial biomass carbon (C_{mic}) in $\mu g\, g^{-1}$ soil for respective horizons and plots, November 2004.

C_{mic}	horizon	*n*	median	min	max	Q1	Q3	range	d_Q
					in $\mu g\, g^{-1}$ soil				
1 050 m	Oi	6	5959.31	3736.67	8588.64	4170.57	8459.57	4851.97	4289.00
	OeOa	6	4604.51	3250.79	8518.33	4175.66	5215.72	5267.55	1040.06
	0–10 cm	6	443.27	389.62	615.05	402.79	561.86	225.43	159.07
1 540 m	Oi	6	6780.37	3869.17	10029.96	5126.06	7173.50	6160.79	2047.45
	OeOa	6	4412.92	4254.23	5506.60	4348.52	5414.62	1252.38	1066.10
	0–10 cm	6	1158.85	749.22	1926.86	754.84	1575.38	1177.64	820.54
1 890 m	Oi	6	8927.05	4654.91	9479.24	4999.32	9113.93	4824.32	4114.62
	OeOa	6	3964.92	1500.25	4712.97	3677.25	4559.91	3212.72	882.66
	0–10 cm	6	925.26	696.12	1187.48	798.32	959.00	491.36	160.67
2 380 m	Oi	6	5061.50	3265.40	11391.45	4446.64	5654.96	8126.05	1208.33
	OeOa	6	5106.42	3839.20	6852.43	4982.26	6481.81	3013.24	1499.55
	0–10 cm	6	580.25	365.65	665.75	472.57	650.43	300.10	177.85
3 060 m	Oi	6	5945.68	4489.67	7272.04	5037.79	6335.88	2782.37	1298.09
	OeOa	6	4798.63	3822.29	5444.18	4558.48	4844.54	1621.88	286.06
	0–10 cm	6	1094.27	421.94	1581.72	967.42	1514.69	1159.77	547.27

Table 63: Descriptive statistics: total nitrogen (TN) in % for respective horizons and plots, April 2004.

TN	horizon	*n*	median	min	max	Q1	Q3	range	d_Q
					in %				
1 050 m	Oi	6	2.13	1.85	2.45	1.88	2.39	0.60	0.51
	OeOa	6	2.23	1.47	2.63	1.83	2.35	1.16	0.52
	0–10 cm	6	0.25	0.24	0.29	0.25	0.26	0.05	0.02
1 540 m	Oi	6	1.64	1.54	1.88	1.62	1.78	0.34	0.16
	OeOa	6	1.83	1.58	2.00	1.69	1.93	0.42	0.24
	0–10 cm	6	0.19	0.14	0.22	0.16	0.21	0.09	0.05
1 890 m	Oi	6	1.55	1.19	1.72	1.39	1.64	0.53	0.24
	OeOa	6	1.97	1.40	2.50	1.67	2.15	1.10	0.48
	0–10 cm	6	0.33	0.25	0.43	0.28	0.38	0.17	0.11
2 380 m	Oi	6	1.09	0.06	2.08	1.04	1.15	2.02	0.11
	OeOa	6	1.91	1.68	2.07	1.69	2.07	0.39	0.38
	0–10 cm	6	0.20	0.14	0.22	0.15	0.21	0.08	0.06
3 060 m	Oi	6	0.83	0.63	1.10	0.72	0.93	0.47	0.21
	OeOa	6	1.40	1.29	1.73	1.31	1.43	0.44	0.11
	0–10 cm	6	0.45	0.39	0.60	0.39	0.55	0.21	0.15

Table 64: Descriptive statistics: total hot-water extractable nitrogen (HWN) in $\mu g\,g^{-1}$ soil for respective horizons and plots, April 2004.

HWN	horizon	*n*	median	min	max	Q1	Q3	range	d_Q
					in $\mu g\,g^{-1}$ soil				
1 050 m	Oi	6	1776.83	1179.55	2570.19	1679.01	2035.59	1390.63	356.58
	OeOa	6	2386.32	1231.27	3288.10	1630.70	2776.50	2056.83	1145.80
	0–10 cm	6	115.66	90.97	133.00	113.15	121.92	42.03	8.77
1 540 m	Oi	6	1169.72	898.57	1860.61	1019.73	1278.04	962.032	258.308
	OeOa	6	873.28	806.36	1093.02	860.30	972.41	286.657	112.112
	0–10 cm	6	71.14	44.12	89.25	61.38	87.98	45.122	26.603
1 890 m	Oi	6	1233.82	855.91	1943.24	1074.46	1291.22	1087.33	216.763
	OeOa	6	1200.75	758.55	1721.12	1034.79	1533.16	962.57	498.372
	0–10 cm	6	198.41	104.76	223.03	171.47	207.54	118.27	36.070
2 380 m	Oi	6	692.61	493.72	895.05	504.84	756.86	401.33	252.018
	OeOa	6	1095.05	943.43	1338.84	983.14	1150.58	395.41	167.441
	0–10 cm	6	113.32	72.36	146.07	90.85	128.83	73.71	37.981
3 060 m	Oi	6	537.94	370.82	639.36	470.70	589.35	268.544	118.654
	OeOa	6	605.16	537.01	876.80	572.86	795.21	339.790	222.355
	0–10 cm	6	175.29	115.72	220.94	120.08	189.72	105.225	69.634

Table 65: Descriptive statistics: total hot-water extractable nitrogen (HWN) in $\mu g\,g^{-1}$ soil for respective horizons and plots, November 2004.

HWN	horizon	*n*	median	min	max	Q1	Q3	range	d_Q
					in $\mu g\,g^{-1}$ soil				
1 050 m	Oi	6	1283.40	786.23	1538.04	1101.04	1471.81	751.81	370.77
	OeOa	6	1622.55	1196.92	2663.23	1205.35	2158.49	1466.31	953.14
	0–10 cm	6	98.78	88.66	135.11	92.24	125.30	46.45	33.05
1 540 m	Oi	6	1034.76	619.22	1402.62	907.98	1226.48	220.532	783.40
	OeOa	6	771.00	738.08	814.96	748.80	811.95	30.574	76.88
	0–10 cm	6	109.31	87.04	170.11	98.65	133.82	22.618	83.07
1 890 m	Oi	6	1262.94	1045.33	2075.29	1138.08	1422.65	1029.96	284.568
	OeOa	6	842.91	336.62	1736.35	763.10	905.32	1399.73	142.223
	0–10 cm	6	149.78	139.59	722.59	139.63	161.88	583.00	22.256
2 380 m	Oi	6	728.74	612.89	1460.07	661.25	789.48	209.959	847.18
	OeOa	6	883.57	676.22	1360.06	699.94	1038.69	215.121	683.84
	0–10 cm	6	93.79	74.01	103.40	88.62	100.43	7.350	29.40
3 060 m	Oi	6	674.46	550.92	894.41	653.51	730.92	343.48	77.408
	OeOa	6	637.17	460.88	803.70	485.62	690.56	342.81	204.938
	0–10 cm	6	185.51	136.29	252.17	153.82	212.56	115.88	58.739

Table 66: Descriptive statistics: total KCl-extractable organic nitrogen ($TN_{KCl(org)}$) in $\mu g\,g^{-1}$ soil for respective horizons and plots, April 2004.

TN^{org}_{KCl}	horizon	n	median	min	max	Q1	Q3	range	d_Q
			in $\mu g\,g^{-1}$ soil						
1 050 m	Oi	6	79.73	40.63	121.60	63.90	116.49	80.97	52.59
	OeOa	6	92.31	10.27	455.62	70.15	126.35	445.34	56.20
	0–10 cm	6	5.50	2.34	12.62	3.98	8.66	10.28	4.68
1 540 m	Oi	6	108.46	73.06	342.29	75.99	159.49	269.23	83.50
	OeOa	6	171.09	41.40	279.30	55.06	276.02	237.90	220.97
	0–10 cm	6	3.62	2.25	6.31	3.06	5.90	4.06	2.84
1 890 m	Oi	6	115.38	89.66	302.84	109.68	129.36	213.18	19.67
	OeOa	6	72.51	29.02	146.85	54.83	94.88	117.82	40.06
	0–10 cm	6	1.06	0.00	4.27	0.00	3.26	4.27	3.26
2 380 m	Oi	6	59.73	53.31	116.30	56.12	99.94	62.99	43.83
	OeOa	6	41.15	30.54	64.64	31.08	53.81	34.09	22.73
	0–10 cm	6	3.63	2.14	4.93	2.48	4.51	2.79	2.03
3 060 m	Oi	6	12.82	5.63	49.91	9.59	14.57	44.28	4.98
	OeOa	6	4.46	1.60	7.15	3.01	5.41	5.55	2.40
	0–10 cm	6	14.25	3.99	21.13	9.88	20.02	17.13	10.14

Table 67: Descriptive statistics: total KCl-extractable organic nitrogen ($TN_{KCl(org)}$) in $\mu g\,g^{-1}$ soil for respective horizons and plots, November 2004.

TN^{org}_{KCl}	horizon	n	median	min	max	Q1	Q3	range	d_Q
			in $\mu g\,g^{-1}$ soil						
1 050 m	Oi	6	227.51	125.51	577.00	134.84	429.26	451.49	294.42
	OeOa	6	384.75	0.00	1221.44	0.00	826.03	1221.44	826.03
	0–10 cm	6	22.21	18.02	34.50	20.58	29.36	16.48	8.78
1 540 m	Oi	6	111.18	79.56	180.14	95.44	130.05	100.58	34.60
	OeOa	6	52.95	25.48	60.04	34.37	58.99	34.55	24.61
	0–10 cm	6	10.36	0.00	14.68	7.51	13.11	14.68	5.60
1 890 m	Oi	6	192.77	105.24	426.14	146.24	271.34	320.91	125.10
	OeOa	6	52.39	2.76	71.57	47.86	57.09	68.82	9.22
	0–10 cm	6	25.23	18.91	123.39	24.67	25.47	104.49	0.80
2 380 m	Oi	6	50.43	40.11	132.20	47.63	61.31	92.09	13.68
	OeOa	6	33.61	19.23	90.19	20.66	79.09	70.96	58.43
	0–10 cm	6	5.22	3.65	8.12	4.25	7.54	4.47	3.29
3 060 m	Oi	6	35.18	21.90	51.42	26.79	43.49	29.52	16.71
	OeOa	5	16.12	4.61	22.46	13.87	18.57	17.85	4.69
	0–10 cm	6	11.94	7.78	15.98	9.02	13.01	8.21	3.98

Table 68: Descriptive statistics: total KCl-extractable inorganic nitrogen ($TN_{KCl(inorg)}$) in $\mu g\,g^{-1}$ soil for respective horizons and plots, April 2004.

TN^{inorg}_{KCl}	horizon	n	median	min	max	Q1	Q3	range	d_Q
			in $\mu g\,g^{-1}$ soil						
1 050 m	Oi	6	1179.56	329.16	2238.23	821.31	1826.91	1909.07	1005.60
	OeOa	6	1443.75	897.09	2088.46	1167.67	1993.45	1191.37	825.78
	0–10 cm	6	45.31	42.82	69.22	43.57	46.56	26.40	3.00
1 540 m	Oi	6	218.64	75.77	953.02	189.36	320.42	877.24	131.07
	OeOa	6	272.20	75.97	533.20	127.22	344.41	457.23	217.19
	0–10 cm	6	18.93	13.72	27.23	15.11	24.38	13.51	9.27
1 890 m	Oi	6	234.05	33.72	573.71	70.46	448.49	539.99	378.03
	OeOa	6	482.02	311.04	819.65	439.25	695.82	508.61	256.57
	0–10 cm	6	72.71	35.00	78.29	39.28	76.89	43.28	37.61
2 380 m	Oi	6	17.20	11.93	208.55	14.56	28.07	196.62	13.51
	OeOa	6	337.18	226.72	520.01	249.47	444.82	293.28	195.34
	0–10 cm	6	25.74	11.37	44.11	13.14	28.99	32.74	15.86
3 060 m	Oi	6	5.85	3.52	19.30	4.54	8.58	15.77	4.04
	OeOa	6	76.31	27.74	144.75	52.39	112.34	117.01	59.95
	0–10 cm	6	37.71	19.37	45.97	31.31	43.85	26.61	12.54

Table 69: Descriptive statistics: total KCl-extractable inorganic nitrogen ($TN_{KCl(inorg)}$) in $\mu g\,g^{-1}$ soil for respective horizons and plots, November 2004.

TN_{KCl}^{inorg}	horizon	*n*	median	min	max	Q1	Q3	range	d_Q
			in $\mu g\,g^{-1}$ soil						
1 050 m	Oi	6	256.19	91.65	420.00	191.45	288.66	328.35	97.21
	OeOa	6	490.49	197.22	1502.12	283.54	682.94	1304.90	399.41
	0–10 cm	6	42.81	32.42	67.94	39.80	59.68	35.52	19.88
1 540 m	Oi	6	183.58	12.57	526.42	139.28	265.37	513.84	126.09
	OeOa	6	285.18	245.78	362.10	258.76	308.87	116.32	50.11
	0–10 cm	6	28.75	20.00	53.69	20.26	33.21	33.69	12.95
1 890 m	Oi	6	125.87	15.19	580.71	76.89	269.13	565.52	192.24
	OeOa	6	241.50	140.19	1062.52	213.65	318.48	922.32	104.83
	0–10 cm	6	41.27	32.73	206.84	36.52	43.95	174.10	7.44
2 380 m	Oi	6	16.58	5.12	35.84	6.94	29.45	30.73	22.51
	OeOa	6	107.11	77.45	306.58	81.63	180.42	229.13	98.79
	0–10 cm	6	13.40	10.52	16.92	12.96	16.56	6.40	3.61
3 060 m	Oi	6	7.75	2.68	15.30	3.59	13.76	12.62	10.16
	OeOa	5	54.74	35.22	84.57	44.60	56.38	49.35	11.77
	0–10 cm	6	18.94	7.88	42.21	13.39	21.49	34.33	8.10

Table 70: Descriptive statistics: NH_4^+-N in $\mu g\,g^{-1}$ soil for respective horizons and plots, April 2004.

NH_4^+-N	horizon	*n*	median	min	max	Q1	Q3	range	d_Q
			in $\mu g\,g^{-1}$ soil						
1 050 m	Oi	6	40.61	35.07	50.58	37.64	42.74	15.52	5.09
	OeOa	6	593.23	53.07	926.35	179.55	799.97	873.28	620.42
	0–10 cm	6	1.82	1.48	2.15	1.67	1.89	0.67	0.21
1 540 m	Oi	6	190.89	66.15	736.21	161.65	288.62	670.07	126.97
	OeOa	6	256.71	65.77	521.69	119.71	327.28	455.92	207.57
	0–10 cm	6	8.21	7.53	14.23	7.66	10.40	6.70	2.74
1 890 m	Oi	6	28.00	24.09	90.15	25.76	57.77	66.07	32.01
	OeOa	6	353.41	232.86	571.03	251.45	481.91	338.17	230.46
	0–10 cm	6	13.83	3.27	18.68	11.36	15.06	15.41	3.70
2 380 m	Oi	6	11.14	6.51	201.91	8.68	18.47	195.40	9.79
	OeOa	6	306.88	182.65	436.75	219.52	425.56	254.09	206.04
	0–10 cm	6	13.53	2.35	27.99	7.50	17.76	25.65	10.26
3 060 m	Oi	6	3.41	1.83	11.58	2.61	4.00	9.75	1.39
	OeOa	6	70.39	23.83	136.78	47.44	106.97	112.95	59.53
	0–10 cm	6	28.14	13.32	37.92	25.10	35.46	24.60	10.36

Table 71: Descriptive statistics: NH_4^+-N in $\mu g\,g^{-1}$ soil for respective horizons and plots, November 2004.

NH_4^+-N	horizon	*n*	median	min	max	Q1	Q3	range	d_Q
			in $\mu g\,g^{-1}$ soil						
1 050 m	Oi	6	85.21	59.73	262.70	61.71	168.31	202.96	106.60
	OeOa	6	286.91	78.94	1242.54	85.52	649.08	1163.60	563.56
	0–10 cm	6	0.65	0.50	2.07	0.60	0.76	1.57	0.16
1 540 m	Oi	6	177.51	9.28	494.29	135.05	259.65	485.01	124.60
	OeOa	6	274.88	231.34	344.74	236.83	300.32	113.39	63.49
	0–10 cm	6	12.62	1.85	38.72	4.04	20.22	36.86	16.18
1 890 m	Oi	6	71.53	12.37	257.74	25.93	80.85	245.36	54.92
	OeOa	6	192.90	108.36	821.88	128.68	254.35	713.52	125.67
	0–10 cm	6	3.43	0.25	18.81	1.01	16.19	18.56	15.19
2 380 m	Oi	6	14.61	2.90	33.56	5.99	28.49	30.66	22.50
	OeOa	6	101.14	76.53	219.90	80.48	150.28	143.37	69.80
	0–10 cm	6	3.20	0.10	7.78	0.81	5.78	7.68	4.96
3 060 m	Oi	6	4.48	1.62	14.27	2.68	13.76	12.65	11.08
	OeOa	5	44.23	35.22	80.81	43.43	51.26	45.59	7.83
	0–10 cm	6	17.55	7.25	39.37	12.38	20.95	32.12	8.57

Table 72: Descriptive statistics: NO_3^--N in $\mu g\,g^{-1}$ soil for respective horizons and plots, April 2004.

NO_3^--N	horizon	n	median	min	max	Q1	Q3	range	d_Q
			in $\mu g\,g^{-1}$ soil						
1 050 m	Oi	6	1139.77	286.42	2187.65	786.25	1787.63	1901.22	1001.38
	OeOa	6	955.56	511.89	1358.47	818.82	1288.49	846.58	469.68
	0–10 cm	6	43.40	41.34	67.34	41.69	44.81	26.00	3.11
1 540 m	Oi	6	28.60	9.63	216.80	26.00	31.80	207.18	5.80
	OeOa	6	10.85	6.69	24.28	7.50	17.13	17.59	9.62
	0–10 cm	6	8.51	3.65	19.32	6.19	15.87	15.67	9.68
1 890 m	Oi	6	207.45	6.83	483.56	12.68	422.72	476.73	410.04
	OeOa	6	183.65	15.07	276.55	78.18	248.62	261.48	170.45
	0–10 cm	6	58.53	23.65	73.62	24.93	59.61	49.97	34.68
2 380 m	Oi	6	6.22	5.42	9.60	5.57	6.64	4.18	1.07
	OeOa	6	27.52	7.21	94.45	8.07	72.37	87.24	64.30
	0–10 cm	6	11.13	5.64	16.70	5.71	16.12	11.05	10.41
3 060 m	Oi	6	2.44	1.70	7.72	1.92	4.58	6.02	2.65
	OeOa	6	5.44	3.91	7.97	4.95	6.31	4.06	1.36
	0–10 cm	6	6.17	5.93	16.60	6.05	6.93	10.66	0.88

Table 73: Descriptive statistics: NO_3^--N in $\mu g\,g^{-1}$ soil for respective horizons and plots, November 2004.

NO_3^--N	horizon	n	median	min	max	Q1	Q3	range	d_Q
			in $\mu g\,g^{-1}$ soil						
1 050 m	Oi	6	130.37	31.92	226.95	92.74	168.93	195.03	76.19
	OeOa	6	175.03	33.86	261.71	111.70	259.58	227.85	147.88
	0–10 cm	6	42.18	31.82	67.26	39.18	57.61	35.44	18.43
1 540 m	Oi	6	5.84	3.29	32.12	4.23	6.18	28.83	1.95
	OeOa	6	15.52	3.99	21.93	8.55	17.37	17.94	8.82
	0–10 cm	6	15.60	4.35	31.07	7.48	20.48	26.72	13.00
1 890 m	Oi	6	8.56	2.81	499.87	5.58	148.36	497.05	142.79
	OeOa	6	54.27	31.83	240.64	38.19	99.57	208.81	61.37
	0–10 cm	6	38.75	13.93	190.65	33.69	43.70	176.72	10.02
2 380 m	Oi	6	1.94	0.95	2.28	0.96	2.27	1.33	1.31
	OeOa	6	5.98	0.92	86.68	1.13	30.15	85.76	29.01
	0–10 cm	6	10.23	8.78	12.86	9.64	11.14	4.07	1.50
3 060 m	Oi	6	1.35	0.00	4.89	0.00	1.97	4.89	1.97
	OeOa	5	3.48	0.00	12.15	1.18	3.76	12.15	2.58
	0–10 cm	6	1.28	0.00	2.85	0.63	1.75	2.85	1.12

Table 74: Descriptive statistics: microbial biomass nitrogen (N_{mic}) in $\mu g\,g^{-1}$ soil for respective horizons and plots, April 2004.

N_{mic}	horizon	n	median	min	max	Q1	Q3	range	d_Q
			in $\mu g\,g^{-1}$ soil						
1 050 m	Oi	6	1184.75	764.26	2253.05	827.35	1375.39	1488.79	548.04
	OeOa	6	1179.94	666.18	1572.69	763.33	1247.95	906.51	484.63
	0–10 cm	6	140.39	111.26	152.53	132.33	149.00	41.26	16.68
1 540 m	Oi	6	1233.98	780.35	1400.75	904.61	1272.89	620.40	368.28
	OeOa	6	791.22	576.16	935.86	672.01	926.97	359.69	254.96
	0–10 cm	6	108.35	69.84	124.36	100.25	119.67	54.53	19.42
1 890 m	Oi	6	1356.62	633.80	1983.60	694.02	1535.41	1349.80	841.39
	OeOa	6	744.39	419.98	1168.45	543.77	890.20	748.46	346.43
	0–10 cm	6	96.48	49.29	152.27	80.15	147.27	102.98	67.12
2 380 m	Oi	6	760.57	474.89	1147.65	633.41	919.02	184.82	672.76
	OeOa	6	1221.77	844.56	1819.75	965.36	1483.39	299.37	975.19
	0–10 cm	6	116.81	80.70	157.24	82.77	152.27	29.85	76.53
3 060 m	Oi	5	618.74	331.03	694.14	618.37	683.74	363.11	65.37
	OeOa	5	681.98	592.37	709.60	647.66	694.25	117.23	46.58
	0–10 cm	5	115.25	57.22	257.18	77.00	135.05	199.96	58.05

Table 75: Descriptive statistics: microbial biomass nitrogen (N_{mic}) in $\mu g\,g^{-1}$ soil for respective horizons and plots, November 2004.

N_{mic}	horizon	*n*	median	min	max	Q1	Q3	range	d_Q
			in $\mu g\,g^{-1}$ soil						
1 050 m	Oi	6	1085.99	656.07	1422.25	742.16	1328.12	766.18	585.96
	OeOa	6	804.07	623.80	1377.21	674.08	966.33	753.42	292.26
	0–10 cm	6	120.06	103.88	151.64	113.24	125.98	47.76	12.73
1 540 m	Oi	6	1048.89	687.99	1361.50	875.56	1172.74	673.51	297.19
	OeOa	6	886.45	670.04	1147.79	846.45	1004.61	477.75	158.16
	0–10 cm	6	115.58	92.82	143.60	106.67	140.35	50.79	33.68
1 890 m	Oi	6	1311.28	797.52	1916.99	1015.15	1328.69	1119.48	313.54
	OeOa	6	705.62	281.09	886.77	640.55	764.81	605.68	124.26
	0–10 cm	6	198.37	134.70	241.91	175.80	226.13	107.21	50.33
2 380 m	Oi	6	660.85	346.64	1386.82	551.31	818.83	1040.18	267.52
	OeOa	6	1001.57	941.72	1330.52	985.45	1295.97	388.81	310.52
	0–10 cm	6	116.85	63.53	136.33	90.16	130.80	72.80	40.64
3 060 m	Oi	6	848.14	671.39	1035.22	725.92	992.52	363.83	266.60
	OeOa	6	962.24	803.67	1085.84	884.84	1034.33	282.17	149.49
	0–10 cm	6	164.97	106.59	243.29	130.54	239.71	136.71	109.16

Table 76: Descriptive statistics: percentage total KCl-extractable nitrogen (TN_{KCl}) of total nitrogen (TN) for respective horizons and plots, April 2004.

TN_{KCl}	horizon	*n*	median	min	max	Q1	Q3	range	d_Q
			in %						
1 050 m	Oi	6	6.04	2.25	9.40	4.77	7.91	1.84	7.15
	OeOa	6	7.34	6.16	9.45	6.33	9.35	3.29	3.02
	0–10 cm	6	1.98	1.83	2.87	1.95	2.23	1.04	0.28
1 540 m	Oi	6	1.91	1.22	5.92	1.58	3.72	4.70	2.14
	OeOa	6	2.23	1.91	3.01	2.06	2.92	1.10	0.86
	0–10 cm	6	1.13	0.96	1.93	1.05	1.79	0.97	0.74
1 890 m	Oi	6	2.70	0.91	5.11	1.22	3.86	4.20	2.64
	OeOa	6	3.24	1.71	4.93	2.59	3.53	3.22	0.94
	0–10 cm	6	1.89	1.33	2.56	1.57	2.09	1.22	0.53
2 380 m	Oi	6	0.96	0.57	12.02	0.66	1.56	11.46	0.90
	OeOa	6	2.06	1.34	2.66	1.71	2.64	1.32	0.93
	0–10 cm	6	1.39	0.94	2.20	1.20	1.81	1.27	0.61
3 060 m	Oi	6	0.22	0.15	0.75	0.17	0.26	0.60	0.09
	OeOa	6	0.58	0.23	0.86	0.43	0.84	0.63	0.41
	0–10 cm	6	1.20	0.56	1.31	1.01	1.27	0.75	0.26

Table 77: Descriptive statistics: percentage total KCl-extractable organic nitrogen ($TN_{KCl(org)}$) of total nitrogen (TN) for respective horizons and plots, April 2004.

TN_{KCl}^{org}	horizon	*n*	median	min	max	Q1	Q3	range	d_Q
			in %						
1 050 m	Oi	6	0.42	0.17	0.65	0.26	0.51	0.14	0.48
	OeOa	6	0.44	0.07	1.99	0.32	0.48	1.92	0.16
	0–10 cm	6	0.22	0.09	0.44	0.15	0.35	0.35	0.20
1 540 m	Oi	6	0.69	0.44	1.92	0.47	0.85	1.48	0.38
	OeOa	6	0.90	0.26	1.51	0.33	1.50	1.24	1.17
	0–10 cm	6	0.21	0.15	0.28	0.16	0.28	0.13	0.12
1 890 m	Oi	6	0.79	0.64	1.77	0.70	0.92	1.12	0.22
	OeOa	6	0.39	0.15	0.75	0.28	0.51	0.60	0.23
	0–10 cm	6	0.03	0.00	0.17	0.00	0.08	0.29	0.12
2 380 m	Oi	6	0.57	0.46	9.63	0.53	0.90	9.17	0.38
	OeOa	6	0.24	0.15	0.31	0.16	0.29	0.16	0.13
	0–10 cm	6	0.19	0.10	0.27	0.17	0.27	0.17	0.10
3 060 m	Oi	6	0.14	0.09	0.54	0.13	0.16	0.45	0.02
	OeOa	6	0.03	0.01	0.05	0.02	0.04	0.04	0.02
	0–10 cm	6	0.30	0.10	0.43	0.23	0.39	0.32	0.16

Table 78: Descriptive statistics: percentage total KCl-extractable inorganic nitrogen ($TN_{KCl(inorg)}$) of total nitrogen (TN) for respective horizons and plots, April 2004.

TN_{KCl}^{inorg}	horizon	*n*	median	min	max	Q1	Q3	range	d_Q
					in %				
1 050 m	Oi	6	5.47	1.74	9.14	4.43	7.74	1.93	7.39
	OeOa	6	6.23	5.85	9.13	5.91	8.88	3.28	2.97
	0–10 cm	6	1.84	1.68	2.43	1.70	1.88	0.75	0.18
1 540 m	Oi	6	1.35	0.49	5.07	1.14	1.80	4.58	0.66
	OeOa	6	1.61	0.42	2.66	0.66	2.04	2.25	1.38
	0–10 cm	6	0.91	0.67	1.76	0.84	1.57	1.09	0.73
1 890 m	Oi	6	1.85	0.21	3.35	0.43	3.22	3.13	2.79
	OeOa	6	2.79	1.57	4.18	2.31	3.14	2.61	0.83
	0–10 cm	6	1.83	1.37	2.67	1.40	2.06	1.30	0.67
2 380 m	Oi	6	0.22	0.10	2.39	0.14	1.00	2.29	0.86
	OeOa	6	1.77	1.18	2.51	1.48	2.35	1.33	0.88
	0–10 cm	6	1.26	0.77	2.00	0.93	1.54	1.23	0.61
3 060 m	Oi	6	0.08	0.04	0.21	0.06	0.11	0.17	0.05
	OeOa	6	0.54	0.22	0.84	0.40	0.80	0.62	0.40
	0–10 cm	6	0.85	0.32	1.17	0.62	1.01	0.85	0.39

Table 79: Descriptive statistics: percentage NH_4^+-N of total nitrogen (TN) for respective horizons and plots, April 2004.

NH_4^+-N	horizon	*n*	median	min	max	Q1	Q3	range	d_Q
					in %				
1 050 m	Oi	6	0.20	0.16	0.23	0.17	0.22	0.02	0.07
	OeOa	6	2.86	0.36	4.24	0.68	3.58	3.88	2.90
	0–10 cm	6	0.07	0.06	0.09	0.06	0.08	0.03	0.01
1 540 m	Oi	6	1.18	0.43	3.91	0.98	1.62	3.49	0.65
	OeOa	6	1.52	0.36	2.61	0.62	1.94	2.24	1.32
	0–10 cm	6	0.48	0.34	0.68	0.46	0.62	0.33	0.16
1 890 m	Oi	6	0.20	0.17	0.53	0.18	0.35	0.35	0.17
	OeOa	6	1.87	1.17	2.91	1.51	2.24	1.74	0.73
	0–10 cm	6	0.47	0.08	0.54	0.31	0.50	0.46	0.19
2 380 m	Oi	6	0.15	0.06	1.40	0.08	0.97	1.34	0.88
	OeOa	6	1.61	1.08	2.31	1.14	2.05	1.23	0.91
	0–10 cm	6	0.70	0.16	1.27	0.53	0.85	1.11	0.32
3 060 m	Oi	6	0.04	0.02	0.13	0.03	0.06	0.10	0.03
	OeOa	6	0.50	0.18	0.79	0.36	0.76	0.61	0.40
	0–10 cm	6	0.70	0.22	0.87	0.49	0.75	0.65	0.26

Table 80: Descriptive statistics: percentage NO_3^--N of total nitrogen (TN) for respective horizons and plots, April 2004.

NO_3^--N	horizon	*n*	median	min	max	Q1	Q3	range	d_Q
					in %				
1 050 m	Oi	6	5.28	1.52	8.93	4.24	7.57	1.95	7.41
	OeOa	6	5.03	2.80	5.73	3.58	5.48	2.93	1.89
	0–10 cm	6	1.77	1.62	2.36	1.64	1.79	0.75	0.15
1 540 m	Oi	6	0.17	0.06	1.15	0.16	0.18	1.09	0.02
	OeOa	6	0.06	0.04	0.13	0.04	0.10	0.09	0.06
	0–10 cm	6	0.42	0.17	1.15	0.33	1.11	0.97	0.78
1 890 m	Oi	6	1.65	0.04	3.03	0.08	2.82	2.99	2.74
	OeOa	6	1.10	0.07	1.29	0.39	1.27	1.22	0.87
	0–10 cm	6	1.46	0.87	2.13	0.94	1.91	1.26	0.97
2 380 m	Oi	6	0.06	0.03	0.99	0.05	0.09	0.96	0.04
	OeOa	6	0.14	0.04	0.46	0.04	0.43	0.42	0.39
	0–10 cm	6	0.67	0.27	0.80	0.40	0.73	0.53	0.33
3 060 m	Oi	6	0.03	0.02	0.08	0.03	0.06	0.07	0.03
	OeOa	6	0.04	0.03	0.05	0.04	0.04	0.02	0.01
	0–10 cm	6	0.13	0.10	0.42	0.13	0.16	0.32	0.03

Table 81: Descriptive statistics: soil organic carbon (SOC) : total nitrogen (TN) for respective horizons and plots, April 2004.

SOC : TN	horizon	*n*	median	min	max	Q1	Q3	range	d_Q
1 050 m	Oi	6	20.22	18.76	27.25	19.71	25.75	8.49	6.04
	OeOa	6	17.70	16.13	31.61	16.90	26.46	15.48	9.55
	0–10 cm	6	12.93	12.32	13.46	12.65	13.16	1.14	0.51
1 540 m	Oi	6	30.47	25.70	31.24	27.42	30.67	5.54	3.25
	OeOa	6	21.22	20.10	23.76	21.01	21.63	3.67	0.62
	0–10 cm	6	19.79	19.08	24.35	19.11	23.33	5.28	4.22
1 890 m	Oi	6	29.11	23.63	35.96	26.76	30.33	12.33	3.57
	OeOa	6	18.63	17.30	20.79	17.59	20.06	3.49	2.47
	0–10 cm	6	17.30	15.52	17.78	16.60	17.61	2.27	1.00
2 380 m	Oi	6	46.33	21.75	52.96	44.76	48.49	31.21	3.73
	OeOa	6	24.09	21.77	29.16	21.80	27.25	7.39	5.45
	0–10 cm	6	17.74	15.36	19.06	15.93	18.36	3.70	2.43
3 060 m	Oi	6	62.62	45.37	83.36	55.34	71.69	37.99	16.34
	OeOa	6	30.80	27.34	33.31	28.26	32.41	5.97	4.15
	0–10 cm	6	24.22	23.06	27.25	23.65	27.12	4.19	3.47

Table 82: Descriptive statistics: microbial biomass carbon (C_{mic}) : microbial biomass nitrogen (N_{mic}) for respective horizons and plots, April 2004.

$C_{mic} : N_{mic}$	horizon	*n*	median	min	max	Q1	Q3	range	d_Q
1 050 m	Oi	6	6.83	5.54	9.35	5.61	7.76	3.80	2.15
	OeOa	6	5.59	3.10	8.27	5.23	5.70	5.18	0.47
	0–10 cm	6	5.00	4.61	5.58	4.67	5.19	0.96	0.51
1 540 m	Oi	6	5.99	5.51	8.78	5.56	6.76	3.27	1.20
	OeOa	6	6.23	4.88	8.85	5.13	6.81	3.97	1.68
	0–10 cm	6	10.33	7.16	13.18	7.35	12.62	6.02	5.27
1 890 m	Oi	6	7.51	4.14	8.42	5.37	8.31	4.28	2.93
	OeOa	6	6.65	4.83	7.12	5.12	6.68	2.30	1.56
	0–10 cm	6	6.42	1.51	6.97	3.42	6.67	5.46	3.25
2 380 m	Oi	6	5.89	4.69	6.61	5.12	6.34	0.63	1.92
	OeOa	6	4.83	4.39	5.45	4.40	5.37	0.43	1.06
	0–10 cm	6	5.13	4.70	9.10	4.71	5.48	1.13	4.39
3 060 m	Oi	5	10.44	6.25	11.05	7.30	10.77	4.80	3.47
	OeOa	5	6.94	5.94	7.16	6.90	7.15	1.22	0.25
	0–10 cm	5	5.66	4.99	9.77	5.13	6.30	4.77	1.17

Table 83: Descriptive statistics: microbial biomass carbon (C_{mic}) : microbial biomass nitrogen (N_{mic}) for respective horizons and plots, November 2004.

$C_{mic} : N_{mic}$	horizon	*n*	median	min	max	Q1	Q3	range	d_Q
1 050 m	Oi	6	5.90	5.03	6.37	5.26	6.36	1.33	1.09
	OeOa	6	5.98	4.20	6.69	5.40	6.52	2.50	1.12
	0–10 cm	6	3.77	3.37	4.88	3.71	3.80	1.52	0.09
1 540 m	Oi	6	6.29	5.05	7.48	5.62	7.37	2.43	1.74
	OeOa	6	5.10	4.70	6.62	4.80	5.39	1.92	0.59
	0–10 cm	6	9.41	6.52	13.66	8.07	13.42	7.14	5.35
1 890 m	Oi	6	6.29	4.75	7.13	4.92	6.88	2.38	1.96
	OeOa	6	5.59	5.31	5.96	5.34	5.82	0.65	0.48
	0–10 cm	6	4.70	4.20	5.17	4.54	4.91	0.97	0.37
2 380 m	Oi	6	7.86	5.59	12.83	5.92	9.71	7.24	3.78
	OeOa	6	5.10	3.90	5.29	5.00	5.15	1.39	0.15
	0–10 cm	6	5.17	4.47	5.76	5.04	5.26	1.28	0.22
3 060 m	Oi	6	6.83	5.65	8.73	6.07	7.52	3.08	1.45
	OeOa	6	4.94	4.46	5.39	4.64	5.26	0.93	0.63
	0–10 cm	6	6.41	3.96	7.62	5.65	7.51	3.66	1.86

Table 84: Descriptive statistics: microbial biomass carbon (C_{mic}) : soil organic carbon (SOC) in % for respective horizons and plots, April 2004.

$C_{mic} : SOC$	horizon	*n*	median	min	max	Q1	Q3	range	d_Q
					in %				
1 050 m	Oi	6	1.74	1.07	3.15	1.13	2.60	2.07	1.46
	OeOa	6	1.36	0.78	2.32	1.05	1.57	1.54	0.52
	0–10 cm	6	2.21	1.54	2.35	1.96	2.28	0.81	0.32
1 540 m	Oi	6	1.49	1.07	1.68	1.39	1.61	0.62	0.22
	OeOa	6	1.28	1.02	1.47	1.03	1.44	0.45	0.41
	0–10 cm	6	3.07	1.81	3.47	1.87	3.24	1.66	1.38
1 890 m	Oi	7	1.69	1.04	3.24	1.06	3.17	2.20	2.11
	OeOa	7	1.19	0.75	1.45	1.02	1.42	0.70	0.40
	0–10 cm	7	1.21	0.28	1.46	0.68	1.42	1.18	0.74
2 380 m	Oi	6	0.90	0.49	1.86	0.65	1.39	1.37	0.74
	OeOa	6	1.25	0.94	1.84	1.11	1.52	0.90	0.41
	0–10 cm	6	1.75	0.51	2.39	1.15	2.03	1.88	0.88
3 060 m	Oi	5	0.96	0.69	1.52	0.75	1.23	0.83	0.48
	OeOa	5	1.05	1.01	1.15	1.03	1.12	0.14	0.09
	0–10 cm	5	0.66	0.46	1.09	0.57	0.74	0.63	0.17

Table 85: Descriptive statistics: total hot-water extractable organic carbon (HWC) : soil organic carbon (SOC) in % for respective horizons and plots, April 2004.

$HWC : SOC$	horizon	*n*	median	min	max	Q1	Q3	range	d_Q
					in %				
1 050 m	Oi	6	4.08	3.30	6.12	3.75	4.54	2.81	0.79
	OeOa	6	5.28	2.97	6.58	3.02	5.69	3.61	2.67
	0–10 cm	6	2.70	2.26	3.08	2.60	2.81	0.82	0.21
1 540 m	Oi	6	4.71	3.94	5.79	4.59	4.85	1.85	0.26
	OeOa	6	4.32	3.92	5.03	4.26	4.44	1.11	0.18
	0–10 cm	6	4.37	3.19	5.22	3.57	4.57	2.04	0.99
1 890 m	Oi	6	5.43	4.16	6.29	5.28	5.78	2.13	0.49
	OeOa	6	4.83	3.47	5.59	4.36	5.02	2.12	0.66
	0–10 cm	6	3.99	2.35	5.55	3.50	5.20	3.20	1.70
2 380 m	Oi	6	4.56	3.02	5.84	4.36	5.23	2.82	0.87
	OeOa	6	4.53	4.05	4.80	4.07	4.73	0.75	0.66
	0–10 cm	6	5.15	4.53	6.54	4.76	6.02	2.01	1.26
3 060 m	Oi	6	3.99	3.61	4.37	3.76	4.16	0.76	0.41
	OeOa	6	4.22	3.56	4.91	3.99	4.67	1.35	0.68
	0–10 cm	6	3.15	1.74	3.39	2.60	3.27	1.65	0.67

Table 86: Descriptive statistics: total hot-water extractable nitrogen (HWN) : total nitrogen (TN) in % for respective horizons and plots, April 2004.

$HWN : TN$	horizon	*n*	median	min	max	Q1	Q3	range	d_Q
					in %				
1 050 m	Oi	6	8.84	6.24	10.49	7.22	9.73	4.25	2.50
	OeOa	6	10.36	8.36	13.98	8.91	11.23	5.62	2.32
	0–10 cm	6	4.56	3.67	5.11	4.37	4.67	1.44	0.29
1 540 m	Oi	6	6.86	5.82	9.89	6.15	7.91	4.08	1.76
	OeOa	6	5.13	4.45	5.46	4.78	5.31	1.00	0.52
	0–10 cm	6	4.08	2.71	4.85	3.00	4.33	2.15	1.33
1 890 m	Oi	6	8.46	5.44	11.33	7.89	9.03	5.90	1.14
	OeOa	6	6.94	3.82	7.82	5.76	7.40	4.00	1.64
	0–10 cm	6	5.38	3.66	6.94	5.24	6.84	3.29	1.60
2 380 m	Oi	6	6.26	4.30	81.43	4.73	6.84	77.13	2.11
	OeOa	6	5.71	5.50	6.46	5.56	5.99	0.95	0.43
	0–10 cm	6	6.04	4.89	6.62	5.73	6.46	1.73	0.73
3 060 m	Oi	6	6.40	4.97	7.41	5.52	7.28	2.44	1.76
	OeOa	6	4.65	3.86	5.64	4.01	5.07	1.78	1.06
	0–10 cm	6	4.04	1.94	4.27	3.06	4.25	2.33	1.19

Table 87: Descriptive statistics: total hot-water extractable organic carbon (HWC) : total hot-water extractable nitrogen (HWN) for respective horizons and plots, April 2004.

HWC : HWN	horizon	*n*	median	min	max	Q1	Q3	range	d_Q
1 050 m	Oi	6	10.50	8.23	16.38	9.02	12.91	8.15	3.90
	OeOa	6	8.96	7.47	11.42	8.05	9.66	3.95	1.61
	0–10 cm	6	7.64	6.99	8.70	7.33	8.29	1.71	0.96
1 540 m	Oi	6	19.10	15.04	24.66	18.17	21.90	9.62	3.73
	OeOa	6	18.33	17.12	21.42	17.15	19.84	4.30	2.69
	0–10 cm	6	22.77	17.90	30.58	20.28	25.69	12.68	5.41
1 890 m	Oi	6	18.38	14.42	30.54	14.55	20.45	16.12	5.90
	OeOa	6	13.14	11.20	18.23	12.83	15.73	7.03	2.90
	0–10 cm	6	12.44	11.27	13.40	11.62	12.75	2.13	1.14
2 380 m	Oi	6	31.65	22.97	39.67	29.23	37.79	16.70	8.56
	OeOa	6	18.72	15.95	21.40	17.21	21.10	5.45	3.89
	0–10 cm	6	15.57	12.93	18.41	14.15	17.01	5.48	2.86
3 060 m	Oi	6	38.08	33.34	51.16	36.33	42.82	17.82	6.49
	OeOa	6	29.49	22.51	32.32	23.79	31.78	9.81	7.99
	0–10 cm	6	19.86	18.76	21.98	19.27	21.26	3.22	1.98

Table 88: Descriptive statistics: total hot-water extractable organic carbon (HWC) : total hot-water extractable nitrogen (HWN) for respective horizons and plots, November 2004.

HWC : HWN	horizon	*n*	median	min	max	Q1	Q3	range	d_Q
1 050 m	Oi	6	15.06	12.66	15.75	13.24	15.59	3.09	2.36
	OeOa	6	11.89	10.84	12.61	11.47	12.24	1.76	0.77
	0–10 cm	6	7.62	7.07	8.99	7.09	8.52	1.92	1.43
1 540 m	Oi	6	22.63	18.32	28.44	22.18	26.02	10.13	3.83
	OeOa	6	21.53	17.72	24.85	19.01	24.16	7.13	5.16
	0–10 cm	6	19.27	16.34	20.71	18.62	19.50	4.37	0.88
1 890 m	Oi	6	21.27	14.23	25.03	14.37	24.85	10.79	10.48
	OeOa	6	16.70	13.10	25.86	14.84	19.88	12.76	5.04
	0–10 cm	6	14.40	9.40	18.16	12.30	15.72	8.76	3.42
2 380 m	Oi	6	28.62	25.44	31.65	27.82	28.95	6.21	1.13
	OeOa	6	18.74	11.53	22.76	15.94	20.90	11.23	4.96
	0–10 cm	6	16.61	15.28	21.21	16.14	17.52	5.93	1.38
3 060 m	Oi	6	40.15	30.21	64.71	31.67	44.92	34.50	13.24
	OeOa	6	25.35	23.28	29.13	23.30	26.58	5.85	3.28
	0–10 cm	6	24.97	21.20	26.99	23.31	26.42	5.78	3.11

Table 89: Descriptive statistics: total KCl-extractable organic carbon (TOC_{KCl}) : soil organic carbon (SOC) in % for respective horizons and plots, April 2004.

$TOC_{KCl} : SOC$	horizon	*n*	median	min	max	Q1	Q3	range	d_Q
						in %			
1 050 m	Oi	6	0.35	0.26	0.64	0.31	0.47	0.38	0.16
	OeOa	6	0.31	0.10	0.38	0.12	0.37	0.29	0.25
	0–10 cm	6	0.15	0.11	0.18	0.12	0.18	0.07	0.05
1 540 m	Oi	6	0.37	0.33	0.66	0.34	0.58	0.33	0.24
	OeOa	6	0.14	0.11	0.16	0.12	0.16	0.05	0.03
	0–10 cm	6	0.15	0.09	0.20	0.13	0.17	0.10	0.04
1 890 m	Oi	6	0.59	0.42	0.63	0.42	0.62	0.21	0.19
	OeOa	6	0.19	0.12	0.23	0.15	0.23	0.11	0.08
	0–10 cm	6	0.14	0.05	0.18	0.13	0.16	0.13	0.03
2 380 m	Oi	6	0.45	0.33	0.65	0.37	0.52	0.33	0.15
	OeOa	6	0.14	0.13	0.18	0.13	0.16	0.05	0.02
	0–10 cm	6	0.10	0.07	0.13	0.07	0.11	0.06	0.04
3 060 m	Oi	6	0.15	0.11	0.37	0.12	0.22	0.26	0.10
	OeOa	6	0.08	0.06	0.10	0.07	0.08	0.03	0.01
	0–10 cm	6	0.16	0.10	0.25	0.14	0.19	0.15	0.05

Table 90: Descriptive statistics: percentage of remaining leaf litter after incubation in the field.

plot	exposure	n	median	min	max	Q1	Q3	range	d_Q
	in weeks				in %				
1 050 m	4	10	90.94	87.69	91.66	89.48	91.48	3.97	2.00
	8	10	83.02	81.02	84.87	82.43	83.59	3.85	1.16
	16	10	84.42	75.17	87.17	79.34	86.15	12.00	6.81
	28	10	70.32	65.21	76.76	66.23	74.04	11.55	7.81
	44	10	49.75	45.83	56.33	48.24	52.07	10.49	3.83
1 540 m	4	10	89.94	85.05	94.69	88.52	91.78	9.64	3.26
	8	10	80.13	71.50	85.86	76.29	83.01	14.36	6.72
	16	10	81.12	75.86	84.53	79.87	83.97	8.66	4.10
	28	10	54.81	39.05	62.55	50.73	60.32	23.50	9.58
	44	10	55.88	48.95	65.88	52.95	59.30	16.94	6.35
1 890 m	4	10	92.45	91.55	95.86	92.16	93.72	4.31	1.56
	8	10	85.02	80.13	91.44	84.16	88.55	11.31	4.39
	16	10	86.98	77.52	92.86	85.27	90.27	15.34	5.00
	28	9	88.87	69.10	94.86	85.13	89.78	25.77	4.65
	44	8	54.20	48.80	58.53	51.04	56.77	9.73	5.74
2 380 m	4	9	94.29	91.26	95.99	94.02	95.23	4.73	1.21
	8	10	86.82	84.68	94.28	85.49	89.24	9.60	3.76
	16	10	90.56	88.23	92.22	88.70	91.54	4.00	2.84
	28	10	89.66	81.14	95.87	88.02	93.36	14.73	5.34
	44	10	63.69	59.93	68.64	61.52	65.33	8.72	3.80
3 060 m	4	10	93.36	87.18	104.10	91.75	94.59	16.92	2.84
	8	9	95.75	94.39	97.64	94.85	96.85	3.25	2.00
	16	10	90.85	76.34	95.77	76.52	92.67	19.44	16.15
	28	10	88.39	80.80	114.45	81.42	89.96	33.65	8.54
	44	10	71.29	60.90	80.01	69.63	76.63	19.11	7.01

Table 91: Result of the principal component analysis (PCA) of phospholipid fatty acids (PLFAs) from all plots and horizons.

PC	eigenvalue	% of total variation	cumulative eigenvalue	cumulated %
1	10.31	34.36	10.31	34.36
2	7.95	26.50	18.26	60.87
3	4.70	15.65	22.96	76.52
4	3.28	10.94	26.24	87.46
5	1.93	6.43	28.17	93.89
6	0.99	3.31	29.16	97.20
7	0.54	1.80	29.70	99.00
8	0.30	1.00	30.00	100.00

Table 92: Results of principal component analysis (PCA) of phospholipid fatty acids (PLFAs): factor loadings of the extracted PLFA for the principal components (PCs) 1–3.

PLFA	PC 1	PC 2	PC 3
14:0	−0.431	−0.537	0.388
14:1	−0.628	0.231	−0.270
15:0	−0.662	−0.058	−0.291
i15:0	0.826	0.027	−0.558
a15:0	0.549	0.104	−0.704
15:1n5c	−0.404	−0.008	0.050
16:0	0.056	−0.975	0.022
i16:0	−0.512	−0.095	−0.744
16:0 10Me	−0.096	0.662	−0.176
16:1n7c	−0.457	0.670	−0.112
17:0	−0.770	−0.479	−0.388
17:0 cy9.10	0.793	−0.118	−0.531
i17:0	0.794	−0.194	−0.527
17:1n7c	−0.642	0.658	−0.137
18:0	0.125	−0.399	−0.381
18:0 10Me	0.932	0.081	−0.321
18:1n9c	−0.566	0.799	0.004
18:1n7c	−0.271	0.932	0.192
18:2n6,9c	−0.596	−0.670	0.395
18:3n6,9,12c	−0.682	−0.122	−0.086
18:3n3,6,9c	−0.009	−0.651	0.639
19:0 cy9.10	0.873	0.375	−0.197
20:0	−0.661	−0.268	−0.660
20:1n9c	−0.355	0.858	0.036
20:2n6,9c	−0.696	−0.160	−0.660
20:3n3,6,9c	−0.491	−0.092	−0.555
20:4n6	−0.564	−0.474	−0.011
22:0	−0.567	−0.569	−0.166
22:1	0.148	0.813	0.347
24:0	0.765	−0.532	0.164

Table 93: k values for decomposition of stand and reference litter calculated separately for the different times of incubation in the field.

exposure	k **rate**		$\mathbf{t}_{0.5}$ in a	
in weeks	stand	reference	stand	reference
		1 050 m		
4	1.23	1.38	0.56	0.50
8	1.21	1.26	0.57	0.55
16	0.55	0.87	1.26	0.79
28	0.65	1.16	1.06	0.60
44	**0.83**	**1.05**	**0.84**	**0.66**
		1 540 m		
4	1.47	0.93	0.47	0.74
8	1.44	1.20	0.48	0.58
16	0.68	0.68	1.02	1.02
28	1.12	1.29	0.62	0.54
44	**0.69**	**0.70**	**1.01**	**0.99**
		1 890 m		
4	1.02	1.22	0.68	0.57
8	1.05	1.02	0.66	0.68
16	0.45	0.51	1.53	1.36
28	0.22	0.61	3.16	1.14
44	**0.72**	**0.71**	**0.96**	**0.98**
		2 380 m		
4	0.75	1.10	0.92	0.63
8	0.92	1.07	0.75	0.65
16	0.32	0.55	2.15	1.26
28	0.20	0.62	3.42	1.12
44	**0.55**	**0.40**	**1.26**	**1.72**
		3 060 m		
4	0.89	0.34	0.78	2.04
8	0.28	0.36	2.46	1.91
16	0.31	0.13	2.22	5.24
28	0.27	0.39	2.55	1.80
44	**0.41**	**0.38**	**1.69**	**1.83**

$t_{0.5}$ = half life period