Institute of Soil Science and Land Evaluation
University of Hohenheim
Soil Biology
Prof. Dr. Ellen Kandeler

Substrate Availability affects Abundance and Function of Soil Microorganisms in the Detritusphere

Dissertation

Submitted in fulfilment of the requirements for the degree "Doktor der Agrarwissenschaften"
(Dr. sc. agr. / Ph.D. in Agricultural Sciences)

to the
Faculty of Agricultural Sciences

presented by

Christian Poll
Hamburg
2007

This thesis was accepted as doctoral dissertation in fulfilment of requirements for the degree “Doktor der Agrarwissenschaften” by the Faculty of Agricultural Sciences at the University of Hohenheim. on: 18.09.2007

Date of oral examination: 12.10.2007

Examination Committee

Supervisor and Review:	Prof. Dr. E. Kandeler
Co-Reviewer:	Prof. Dr. G. Cadisch
Additional Examiner:	Prof. Dr. A. Fangmeier
Vice-Dean and Head of the Committee:	Prof. Dr. W. Bessei

This thesis was conducted at the Institute of Soil Science and Land Evaluation of the University of Hohenheim and funded by the Deutsche Forschungsgemeinschaft (DFG) priority program SPP 1090: „Böden als Quelle und Senke für CO_2- Mechanismen und Regulation der Stabilisierung organischer Substanz in Böden“.

Eidesstattliche Erklärung

Ich erkläre hiermit an Eides statt, dass ich die vorliegende Dissertation selbständig angefertigt, nur die angegebenen Quellen und Hilfsmittel benutzt und inhaltlich oder wörtlich übernommene Stellen als solche gekennzeichnet habe. Ich habe noch keinen weiteren Promotionsversuch unternommen.

Stuttgart, den 06.03.2008 Christian Poll

Contents

1 Summary

Plant litter is the major source of soil organic carbon (SOC). Its decomposition plays a pivotal role in nutrient recycling and influences ecosystem functioning and structure. Soil microorganisms are the main protagonists of litter decomposition. Among other factors, their activity is controlled by the physicochemical conditions of the soil. This interaction is strongly influenced by the soil structure, resulting in a heterogeneous distribution of microorganisms, substrates and physicochemical conditions at the small-scale. Due to this heterogeneity, microhabitats differ in their decomposition rate of organic C. Considering microhabitat diversity is therefore important for understanding C turnover. In the detritusphere, plant litter closely interacts with the soil by releasing soluble C into the adjacent soil and providing new sites for microorganisms. The abundant readily available substrates characterise the detritusphere as a hot spot of microbial activity and C turnover. Despite the important role of this microhabitat, the interaction of physicochemical conditions with soil microorganisms remains unclear. This thesis was designed to clarify the effect of litter C transport on the spatial and temporal availability of substrates and therefore on microbial abundance and activity in the detritusphere.

This goal was addressed in three studies. The first study focused on the influence of solute transport conditions on microbial activity and substrate utilisation by the microbial community. In two 2-week microcosm experiments, diffusion and convection were considered as transport mechanisms; both mechanisms were studied at two different water contents. The second study aimed to identify temporal patterns of diffusive solute transport and microbial activity at two water contents during an 84-day incubation. Both studies emphasised the important role of fungi in the detritusphere. The third study therefore identified fungi that benefit from freshly added litter.

The three studies combined classical soil biological methods and modern techniques. Analysis of microbial biomass, ergosterol content, CO_2 production, and enzyme activities provided general information on the mineralisation of litter C as well as on microbial activity and abundance. A convective-diffusive solute transport model with a first-order decay was used to interpret enzyme activity profiles. This allowed the underlying factors determining the spatial dimension of the detritusphere to be identified. By adding plant residues with a different ^{13}C signature than the SOC, it was possible to quantify the transport of litter C into different C pools. The incorporation litter C into different microbial groups, for example, was traced by coupling of phospholipid fatty acid (PLFA) extraction with ^{13}C analysis. Fungal species were identified by constructing clone libraries based on 18S rDNA and subsequent sequencing.

The results of the first study indicated that the transport rate of soluble substrates determines the spatial dimension of the detritusphere, with an enlarged detritusphere after convective versus diffusive transport. The isotopic ratios of bacterial and fungal PLFAs differed under both transport mechanisms, indicating different substrate utilisation strategies: bacteria relied on the small-scale transport of substrates, whereas fungi assimilated new C directly in the litter layer. Water content affected only diffusive C transport and modified the temporal pattern of microbial activity by enhancing transport at higher soil water content. The expected chronological order of C transport, microbial growth and enzyme release was verified in the second and third study. During the first two weeks, mainly easily available and soluble litter compounds were mineralised and transported into the adjacent soil. After this initial phase, depolymerisation of complex litter compounds started. During the initial phase, enhanced C transport induced greater microbial biomass and activity, and increased fungal diversity. During the later phase, however, substrate availability and microbial activity were reduced. Measurements of microbial biomass C and ergosterol indicated that the initial phase was dominated by bacterial *r* strategists, whereas fungal *K* strategists dominated the later phase. Sequencing of fungal 18S rDNA detected a shift in the fungal community during the initial phase, pointing to growth of pioneer colonisers, especially *Mortierellaceae*. These fungi do not produce ergosterol and therefore were not detected by the ergosterol measurements. Accordingly, the *r* strategists consist of both bacteria and fungi. During the later phase, the fungal community was dominated by the cellulose-degrading fungus *Trichocladium asperum*. Based on these results, the original concept was modified and a two-phase conceptual model of litter C turnover and microbial response in the detritusphere was developed.

In conclusion, this thesis yields new insight into litter decomposition at the small-scale. Combining classical methods with modern techniques enabled the development of a conceptual model of litter C turnover and microbial response in the detritusphere. This provides a useful basis for future studies addressing, for example, the impact of global change on the interaction of decomposition and soil microorganisms.

2 Zusammenfassung

Pflanzliche Biomasse ist die Hauptquelle organischer Bodensubstanz (OBS). Ihr Abbau ist von großer Bedeutung für die pflanzliche Nährstoffversorgung und beeinflusst somit die Funktion und Struktur von Ökosystemen. Hauptakteure in diesem Prozesses sind Bodenmikroorganismen, deren Aktivität u.a. durch die physikalisch-chemischen Eigenschaften des Bodens bestimmt wird. Ein weiterer Einflussfaktor ist die Bodenstruktur. Sie bedingt eine kleinräumige heterogene Verteilung von Bodenmikroorganismen, organischer Substanz und wechselnden physikalisch-chemischen Bodeneigenschaften. Diese Heterogenität des Bodens erzeugt eine Vielzahl an unterschiedlichen Mikrohabitaten, die sich u.a. in der Abbaurate organischer Substanz unterscheiden und somit von großer Bedeutung für den C-Umsatz im Boden sind. Die Detritussphäre umfasst die Streuschicht und den durch Transport von streubürtigem C beeinflussten Boden. Sie gehört wegen des großen Angebots an leichtverfügbaren Substraten zu den „hot spots" mikrobieller Aktivität und des C-Umsatzes. Trotz dieser wichtigen Eigenschaften bestehen große Wissenslücken in Bezug auf das Wirkungsgefüge zwischen physikalisch-chemischen Bodeneigenschaften und Bodenmikroorganismen. Ziel der vorliegenden Arbeit war es daher, den Einfluss des C-Transportes in der Detritussphäre auf die räumliche und zeitliche Variabilität der Substratverfügbarkeit und damit auf die mikrobiologische Abundanz und Aktivität zu untersuchen.

In der ersten Studie wurden zwei 2-wöchige Experimente etabliert, um den Einfluss unterschiedlicher Transportmechanismen auf die mikrobielle Substratnutzung und Aktivität zu untersuchen. Im ersten Experiment war der Transport auf Diffusion beschränkt, während im zweiten Konvektion dominierte. In beiden Experimenten wurden zusätzlich zwei Wassergehalte eingestellt. Aufbauend auf den Ergebnissen der ersten Studie wurde ein weiteres Experiment angesetzt, um den zeitlichen Verlauf des C-Transportes und der mikrobiellen Aktivität zu verfolgen. Das Experiment beschränkte sich auf Diffusion als Transportprozess und wurde mit denselben Wassergehalten über einen Zeitraum von 84 Tagen durchgeführt. Da die vorigen Experimente auf die große Bedeutung der Pilze hinwiesen, sollte in einer dritten Untersuchen festgestellt werden, welche Pilze von dem großen Nährstoffangebot in der Detritussphäre profitieren.

Für die Bearbeitung der Fragestellung wurde eine Kombination klassischer bodenbiologischer und moderner Methoden eingesetzt. Messungen der mikrobiellen Biomasse, des Ergosterolgehaltes, der CO_2 Produktion sowie von Enzymaktivitäten lieferten allgemeine Informationen über die Mineralisierung des Streukohlenstoffs und die mikrobielle Aktivität und Abundanz. Die Interpretation von Enzymaktivitäten mittels eines Konvektions-Diffusions-Models erlaubte es, Einflussfaktoren auf die räumliche Ausdehnung der Detritussphäre zu identifizieren. Die Verwendung von Streu und Boden mit unterschiedlicher ^{13}C Abundanz ermöglichte es, den Transport streubürtigen C in verschiedene Pools zu quantifizieren. Mit Hilfe des ^{13}C-Gehaltes von Phospholipidfettsäuren (PLFA) wurde zum Beispiel der Einbau streubürtigen C in verschiedene Mikroorganismengruppen verfolgt. Einzelne Pilzarten wurden durch die Klonierung und Sequenzierung von 18S rDNA bestimmt.

Konvektion erhöhte im Vergleich zur Diffusion die Transportrate streubürtigen C. Dies führte in der ersten Studie zu einer Ausdehnung der Detritussphäre. Außerdem deuteten die ^{13}C-Gehalte bakterieller und pilzlicher PLFAs unter diffusiven und konvektiven Transportbedingungen auf unterschiedliche Ernährungsstrategien hin: Bakterien sind auf kleinräumigen C-Transport angewiesen, während Pilze C direkt in der Streuschicht assimilieren können. Der Wassergehalt spielte nur bei Diffusion eine Rolle und veränderte durch eine erhöhte Transportrate das zeitliche Auftreten mikrobieller Aktivität. Die daraus abgeleitete Abfolge von diffusivem C-Transport, mikrobiellem Wachstum and der Produktion von extrazellularen Enzymen wurde in einem weiteren Experiment überprüft. Während der ersten 14 Tage wurden leicht verfügbare, lösliche Streukomponenten mineralisiert und in den Boden verlagert. Nach dieser Anfangsphase setzte der Abbau pflanzlicher Polymere ein. In der Anfangsphase wurden mikrobielle Biomasse und Aktivität sowie pilzliche Diversität durch einen erhöhten Wassergehalt gefördert. Dies reduzierte jedoch die Substratverfügbarkeit und verringerte dadurch die mikrobielle Aktivität am Ende des Experimentes. Mikrobielle Biomasse und Ergosterolgehalte deuteten auf eine anfängliche Dominanz bakterieller *r* Strategen hin, während pilzliche *K* Strategen erst in der späteren Phase auftraten. Die anfängliche bakterielle Dominanz wurde allerdings durch die DNA-Analysen widerlegt. Diese zeigten bereits während der Anfangsphase Wachstum von pilzlichen Pionierarten, insbesondere *Mortierellaceae*, an. Diese Pilze produzieren kein Ergosterol, so dass ihr Wachstum nicht durch die Messung des Ergosterolgehaltes detektiert wurde. Die anfangs dominierende Gruppe der *r* Strategen besteht daher vermutlich sowohl aus Bakterien als auch aus Pilzen. Am Ende des Experimentes wurde die pilzliche Gemeinschaft durch den Cellulose abbauenden Pilz *Trichocladium asperum* dominiert. Aufgrund der Ergebnisse wurde das ursprüngliche Konzept über den Prozessablauf in der Detritussphäre zu einem Zwei-Phasen-Model weiter entwickelt.

Zusammenfassend lässt sich festhalten, dass die vorliegende Arbeit das Verständnis über kleinräumige Prozesse des Streuabbaus vertieft hat. Die Kombination von klassischen sowie aktuellen bodenbiologischen Methoden hat hierbei wesentlich zu der Entwicklung eines konzeptionellen Models beigetragen. Solche Modelle sind grundlegend für zukünftige Studien, die zum Beispiel die Auswirkungen des Global Change auf den Streuabbau abschätzen wollen.

3 General Introduction

3.1 Carbon cycle

Soils are an important part of the global C cycle, with close interactions to other compartments like the biosphere and the atmosphere. Soil organic C (SOC) stocks are estimated to be 1500 Pg C, which is twice and threefold the amount present in the atmosphere and in plant biomass, respectively (IPCC, 2001). Most of the SOC is derived from the plant biomass and predominantly enters the soil as litter. Gross primary production is about 120 Pg C y^{-1}, of which 60 Pg C y^{-1} are released as CO_2 by autotrophic respiration and 60 Pg C y^{-1} by heterotrophic mineralisation after transfer into the soil. Mineralisation of the annual litter fall accounts for about 50 to 70% of the soil CO_2 production (Coûteaux et al., 1995; Aerts, 1997). Further processes contributing to C loss from soils are CH_4 emission, leaching of dissolved organic and inorganic C (DOC, DIC), and erosion (Lal, 2004). Whether soils accumulate or lose SOC depends on the balance between C input and output (Schulze and Freibauer, 2005). Soil organic C has several important functions, among them storing essential plant nutrients, providing substrate for soil organisms, improving water capacity and aggregating soil (Lal, 2004). Therefore, an altered SOC content has many implications for plant nutrition, soil stability, drinking water quality and the atmospheric CO_2 concentration. For example, Bellamy et al. (2005) estimated that the upper 15 cm of soils in the United Kingdom lose 13 million tonnes C per year, which is equivalent to 8% of the CO_2 emissions of the UK in 1990.

Whether SOC is stabilised or destabilised, however, depends on many factors and processes as well as their interactions, most of which remain poorly understood (Sollins et al., 1996). Soil organisms are among the important factors that control the stabilisation and destabilisation of SOC, because they can degrade almost any kind of organic substrates in soil (Schulze and Freibauer, 2005; Ekschmitt et al., 2008). The stability of SOC therefore depends strongly on the diversity and activity of soil organisms, which in turn are influenced by soil physical factors (Smith et al., 2003). One reason for the uncertainty about SOC stability might be the heterogeneity of the soil environment at different scales and the integration of processes over these scales. Recent methodological developments allowed small-scale studies of processes like sorption of SOC to mineral surfaces (Kaiser and Guggenberger, 2007) or litter decomposition (Gaillard et al., 1999; Kandeler et al., 1999). Studies on the interaction of the decomposer community with physicochemical conditions at the small-scale will therefore further improve our understanding of SOC stabilisation and destabilisation.

3.2 Litter decomposition

Litter decomposition has major impact on ecosystem functioning and structure due to its pivotal role in nutrient recycling and soil organic matter (SOM) formation (Swift et al., 1979). Plant growth and community structure, for example, depend heavily on nutrient availability (Hättenschwiler et al., 2005). Litter decomposition is mainly driven by the activity of soil organisms; it interacts with many processes like the transport of nutrients and substrates, competition between plants and soil organisms for nutrients, and sorption of substrates to mineral surfaces (Swift et al., 1979). This interaction determines which part and amount of the litter C is respired as CO_2, assimilated by soil microorganisms, transferred into SOC, leached as DOC, or remains in the litter fraction. The biotic activity and, in turn, the decomposition rate are controlled by many factors, which can be pooled into two categories: soil physicochemical conditions and litter quality (Aerts, 1997; Hättenschwiler et al., 2005). The importance of these factors depends on the scale of interest. At the global scale, climate is the best predictor for litter decomposition rates, whereas at the regional scale litter quality is more important (Aerts, 1997).

Soil physicochemical conditions include temperature, O_2 supply, soil moisture, soil texture, pH and inorganic nutrients (Sommers et al., 1981; Coûteaux et al., 1995). Soil moisture is known to influence litter decomposition (e.g. Virzo de Santo et al., 1993; Schimel et al., 1999). Carbon dioxide production of decomposing plant residues, for example, was reduced by a factor of 100 to 1000 when the soil water potential decreased from -0.001 to -10 MPa; maximum initial decomposition of corn residues occurred at a water potential of -0.005 MPa (Sommers et al., 1981). One explanation for this effect is an enhanced substrate diffusion rate at higher soil water contents. In a loamy soil, the diffusion rate was reduced by 50% at a matric potential of -0.1 MPa compared to saturation (Griffin, 1981). Generally, bacteria are more limited by extreme low water potentials than fungi; this might alter microbial community structure and, therefore, litter decomposition (Sommers et al., 1981). Water content closely interacts with temperature because both define soil respiration and decomposition processes over a wide range of soil moisture, but soil water content becomes the main factor as soils dry out (Donnelly et al., 1990; Smith et al., 2003). Aerobic conditions switch into anaerobic conditions if soil moisture approaches saturation. The degradation of aromatic substrates, for example, requires the direct incorporation of O_2 into the aromatic structure, which is inhibited under anaerobic conditions. As a consequence, great amounts of organic C accumulate in water-saturated peat soils because lignin degradation is suppressed (Sommers et al., 1981).

Litter quality includes leaf toughness, nutrient content and plant compounds (Hättenschwiler et al., 2005). Major plant compounds are either intracellular and include storage materials like proteins, starch and fructans, or cell wall compounds like cellulose, hemicellulose, lignin, polyphenols and lipids (Kögel-Knabner, 2002). They differ in their stability against degradation and, therefore, ratios of plant compounds and nutrients like C/N or lignin/N are often used as predictors for litter decomposition rates (Swift et al., 1979; Hättenschwiler et al., 2005). Litter quality closely interacts with other factors. The temperature sensitivity of litter decomposition, for example, is inversely related to litter quality (Fierer et al., 2005), with cellulose degradation being more sensitive to temperature increase than lignin degradation (Donnelly et al., 1990). In the same study, cellulose decomposition was more sensitive to changes in water content than lignin decomposition. Litter with high amounts of complex substrates like cellulose or lignin favour the fungal over the bacterial degradation pathway (de Boer et al., 2005). This, in turn, might influence the decomposition rate due to the different degradative capabilities of bacteria and fungi.

3.3 Soil organisms

Most soil organisms are involved in degrading organic matter (Hättenschwiler et al., 2005) and play the central role in the decomposition system (Swift et al., 1979). Soil microorganisms contribute approximately 85-90% to the biotic decomposition activity, whereas soil fauna contribute about 10-15% (Ekschmitt et al., 2008). The latter indirectly enhance litter decomposition by mixing plant residues with soil, improving soil structure, and grinding plant residues, which increases the surface area of the litter (Coûteaux et al., 1995). Soils contain 1-2 and 2-5 t ha^{-1} bacterial and fungal biomass, respectively. These organisms colonise only about 5% of the available pore space (Nannipieri et al., 2003). Microorganisms form an extremely diverse group, with approximately 6000 different bacterial genomes in 1 g soil. Among other factors, the short generation time and rapid growth of soil microorganisms might explain this great diversity. These abilities enable fast speciation of organisms in response to small environmental changes (Hättenschwiler et al., 2005), ensuring a more complete exploitation of microbial habitats and their resources (Ekschmitt et al., 2008). However, there is still uncertainty about the relationship between microbial diversity and ecosystem functioning (Hättenschwiler et al., 2005). The functional efficiency of a fungal community, for example, increased with diversity, but this effect was restricted to low species richness and came into saturation after more than 10 species were abundant (Setälä and McLean, 2004; Tiunov and Scheu, 2005). This agrees with the idea of functional redundancy of soil microorganisms, i.e. only a few species are essential for certain functions. A greater number of species, however, might be required to stabilize functions against disturbances like climate change (Nannipieri et al., 2003). Important factors controlling the size and structure of the soil microbial community are the quality and availability of C input (Brant et al., 2006). During litter decomposition, both the quality and availability of substrates vary due to differences in the decomposability of plant compounds. During the early stage of litter decomposition, mainly soluble litter compounds are degraded, whereas the final stages are dominated by lignin degradation (Berg and Matzner, 1997). Therefore, plant residues are decomposed by a succession of microorganisms (Coûteaux et al., 1995; McMahon et al., 2005).

Molecular techniques provided further insight into this microbial succession. Extracting microbial DNA from arable soils revealed that litter addition modified the microbial community structure by stimulating only a small part of the microbial population (Lejon et al., 2007; Nicolardot et al., 2007). This process is influenced by both soil properties and litter quality (Aneja et al., 2004), with an increased bacterial diversity during late stages of decomposition and in low-quality litter (Dilly et al., 2004). These studies, however, used fingerprinting methods, which provide general information on community structure and diversity but do not allow species identification. Lindahl et al. (2007) identified saprotrophic fungi associated with relatively young litter, whereas mycorrhizal species predominated in the more decomposed litter and humus. Analysing genes encoding laccase, an oxidative enzyme involved in lignin degradation, Luis et al. (2004) found a greater diversity of this functional gene among saprotrophic versus mycorrhizal fungi. Techniques such as stable isotope analysis provide further insight into the role of soil microorganisms in C cycling (Dijkstra et al., 2006). Combining the phospholipid fatty acid (PLFA) analysis with stable isotope techniques allows the identification of microbial groups involved in the utilization of certain substrates (Boschker and Middelburg, 2002).

Brant et al. (2006), for example, followed the incorporation of ^{13}C labelled phenol into fungal biomass by ^{13}C PLFA analysis. PLFA biomarker for gram-negative bacteria and fungi extracted from the rhizosphere of $^{13}CO_2$ pulse labelled plants showed the highest ^{13}C enrichment, indicating assimilation of root exudates by these two microbial groups (Treonis et al., 2004).

3.4 Enzymes

The functioning of microorganisms in terrestrial ecosystems relies mainly on the activity of extracellular enzymes, which break down complex organic polymers into soluble smaller compounds (Caldwell, 2005). Therefore, enzymes represent a direct link between substrate quality and the microbial community, which makes them a good estimator of microbial decomposition activity and functional diversity (Sinsabaugh et al., 2002). Important enzymes involved in C cycling are cellulolytic enzymes like endo-cellulase, cellobiohydrolase and β-glucosidase, and ligninolytic enzymes like phenol oxidase and peroxidase (Caldwell, 2005). Due to the central role in the microbial-substrate relationship, it is important to consider extracellular enzymes for understanding C cycling and the microbial response to substrate addition (Schimel and Weintraub, 2003). Extracellular enzyme activities explained the responses of litter decomposition to chronic N deposition, with increased cellulase activity and decreased activity of lignin-degrading phenol oxidase (Carreiro et al., 2000). This might affect the temporal pattern of litter decomposition because litter is degraded by a succession of enzymes (Sinsabaugh et al., 2002). Extracellular enzyme production is directly linked to the concentrations of substrates, products and nutrients in the soil. For example, enzyme production increases with increasing substrate concentration and decreases with increasing product concentration (Allison, 2005). However, enzyme production is nutrient intensive. Allison and Vitousek (2005) found higher β-glucosidase activity in the presence of cellulose together with N and C, but not when C was present in simple form or without additional N and C. Beside increased enzyme production in the presence of substrates, a basal level of extracellular enzyme activity in soils is maintained by constitutive microbial enzyme production and the activity of stabilized enzymes, which are attached to mineral surfaces or humic substances (Burns, 1982; Allison and Vitousek, 2005). Microorganisms probably use basal enzyme activities to detect new food sources (Vetter et al., 1998). Due to the spatial separation of microbes and substrates, the enzymatic degradation of organic polymers is subject to several restrictions. The degradation products, for example, might diffuse away from the cell or be captured by other organisms. These processes depend on physicochemical properties of the soil like pore size distribution, water content and aggregation (Allison, 2005). Therefore, the heterogeneous distribution of microorganisms and substrates is a key factor controlling microbial decomposition activity. Applying a new enzyme assay, which allows the simultaneous measurement of several enzyme activities in small sample sizes (Marx et al., 2001; Vepsäläinen et al., 2001), Marx et al. (2005), showed that the enzymes were heterogeneously distributed among particle-size fractions and that the substrate affinity depended on the location of the enzyme.

3.5 Soil heterogeneity

Soil heterogeneity is important for understanding below-ground processes (Young and Ritz, 1998). Spatial heterogeneity occurs at different spatial scales ranging from metres at the plot scale to centimetres or even millimetres at the small-scale. The controlling factors vary between scales as well. At the landscape-scale, for example, the distribution of organisms is influenced by gradients in SOC, land management, topography and soil texture (Ettema and Wardle, 2002). In contrast, the distribution of soil biota at the scale of centimetres to metres is mainly controlled by plant properties such as litter quality. At the small-scale, the physical structure of the soil, especially the pore system, determines the distribution of organisms and SOC. It also regulates the O_2 supply, water content, and diffusive transport of enzymes and solutes (Young and Ritz, 1998; Allison, 2005). Furthermore, small voids might protect substrates against microbial decay or microorganisms against predation (Young and Ritz, 1998). Morris (1999) and Stark et al. (2004) showed that biotic soil properties such as fungal and bacterial biomass and arginine deaminase activity were spatially autocorrelated at the 1-30 cm scale. In an arable soil the presence of bacteria was autocorrelated at scales of 1 mm, with bacterial densities being related to the nearest pore in subsoil but not in topsoil (Nunan et al., 2003). Water flow influences spatial heterogeneity, with regions of water flow having less SOC but more microbial biomass than regions without water flow (Gaston and Locke, 2002).

The heterogeneity of soil properties yields a diversity of microhabitats, each with a characteristic set of processes (e.g. competition, solute transport) acting at different rates.

This contributes to the coexistence of species and influences plant communities by distinct spatial patterns of decomposition processes and nutrient availability (Ettema and Wardle, 2002). Considering microhabitat diversity is important for modelling C turnover at the small-scale, which might further improve our understanding of C turnover. Microhabitats with abundant readily available substrates are characterized by great microbial activity and are referred to as hot spots (Beare et al., 1995). An example for such a hot spot is the detritusphere.

4 Outline of the Thesis

The detritusphere comprises the litter layer and the adjacent soil influenced by the litter. Plant-derived soluble substrates are transported into the soil, where they promote microbial activity within a distance of 1.1-4 mm from the litter layer (Gaillard et al., 1999; Kandeler et al., 1999). Depending on litter quality, 23-33% of the litter C is transported into the soil before mineralization (Gaillard et al., 2003). Despite the important role of the detritusphere as a hot spot of C turnover, the underlying physicochemical factors and their interactions with soil microorganisms remain unclear. This thesis therefore attempts to clarify the influence of transport processes on substrate availability and thus on the microbial community and its activity in the detritusphere. This aim was addressed in three different studies.

The first study focused on the translocation of litter C into the soil under different solute transport conditions. The hypothesis was that the volumetric water content as well as the mechanism of solute transport affect microbial activity and substrate utilisation by the microbial community. Therefore, two 2-week microcosms experiments that simulate the soil-litter interface were performed, with transport processes being restricted to diffusion in the first experiment and dominated by convection in the second. Stable isotope analysis (^{13}C) was used to follow the transport of litter C into the soil and its incorporation into phospholipid fatty acids (PLFA) of different microbial groups. Enzyme activities were interpreted using a mathematical convective-diffusive solute transport model with a first-order decay.

The first study indicated that soil moisture modifies the temporal pattern of microbial activity by enhancing diffusive litter C transport at higher soil water content. The second study therefore aimed to identify temporal patterns of litter C turnover in the detritusphere. The hypothesis was that processes/soil properties will peak in the following chronological order: transport of soluble litter C, microbial biomass and extracellular enzyme activity. Furthermore, this temporal pattern was expected to be modified by soil water content. Microcosms were incubated with ^{13}C labelled rye litter at two different water contents and sampled at six dates over 84 days. Ergosterol content was measured to test the response of fungi to litter addition; ^{13}C analyses were performed to calculate a balance of litter C for each sampling date.

Fungi play a central role in the transport and decomposition processes of the detritusphere. For example, they actively transport litter C and soil mineral N into the soil and litter layer, respectively (Frey et al., 2003). The first study of this thesis revealed different substrate utilisation strategies of bacteria and fungi. In the second study, ergosterol contents and microbial biomass C indicated different temporal patterns of bacterial and fungal growth. The third study therefore aimed to detect the response of the fungal community to litter addition. Fungal species were identified by constructing clone libraries based on the 18S rDNA and subsequent sequencing. Samples were taken before and after the ergosterol content indicated fungal growth.

5 Mechanisms of solute transport affect small-scale abundance and function of soil microorganisms in the detritusphere

European Journal of Soil Science 57 (2006): 583-595

C. Poll[a], J. Ingwersen[b], M. Stemmer[c], M. H. Gerzabek[d] & E. Kandeler[a]

[a]Institute of Soil Science and Land Evaluation, Soil Biology Section, University of Hohenheim, Emil-Wolff-Straße 27, 70599 Stuttgart, Germany,
[b]Institute of Soil Science and Land Evaluation, Biogeophysics Section, University of Hohenheim, Emil-Wolff-Straße 27, 70599 Stuttgart, Germany,
[c]Institute for Plant Protection, Products Evaluation and Authorisation, Austrian Agency for Health and Food Safety, Spargelfeldstraße 191, 1226 Vienna, Austria, and
[d]Institute of Soil Science, University of Natural Resources and Applied Life Sciences, Gregor-Mendel-Strasse 33, 1180 Vienna, Austria

Summary

In the detritusphere, particulate organic matter offers new sites for microorganisms, whereas soluble substrates are transported into the adjacent soil. We investigated how mechanisms of solute transport affect microbial abundance and function in the detritusphere. In a first experiment, transport was restricted to diffusion, whereas in a second experiment it was dominated by convection. Two soil moisture contents were established in each experiment. When diffusion was the exclusive transport mechanism, the addition of maize litter induced distinct gradients in enzyme activities, soil organic C content and microbial biomass to a depth of 1.5-2.8 mm. Convection enlarged these gradients to 2.5-3.0 mm. The moisture regime modified the temporal pattern of diffusive C transport, microbial growth and enzyme release by inducing faster transport at large water contents. Convective transport seemed to be unaffected by soil moisture content. Using a convective-diffusive transport model with first-order decay, it was possible to simulate the observed activity profiles. The results indicate that the spatial dimension of the detritusphere is governed by the ratio between decay rate of available substrates and transport rate. Bacteria and fungi showed differing utilization strategies as revealed by coupling phospholipids fatty acid (PLFA) analysis with stable isotope techniques. Fungi assimilated C directly in the litter, whereas bacteria took up the substrates in the soil and therefore depended more on transport processes than fungi. Our results demonstrate the impact of physicochemical conditions on the abundance and function of microorganisms in the detritusphere. Furthermore, the combination of enzymatic measurements and mathematical transport modelling may offer a new way to measure substrate decay rates in soil.

6 Dynamics of litter carbon turnover and microbial abundance in a rye detritusphere

Soil Biology and Biochemistry, doi:10.1016/j.soilbio.2007.04.002

C. Poll[a], S. Marhan[a], J. Ingwersen[b] & E. Kandeler[a]

[a]*Institute of Soil Science and Land Evaluation, Soil Biology Section, University of Hohenheim, Emil-Wolff-Straße 27, 70599 Stuttgart, Germany,*
[b]*Institute of Soil Science and Land Evaluation, Biogeophysics Section, University of Hohenheim, Emil-Wolff-Straße 27, 70599 Stuttgart, Germany*

Abstract

Factors determining C turnover and microbial succession at the small scale are crucial for understanding C cycling in soils. We performed a microcosm experiment to study how soil moisture affects temporal patterns of C turnover in the detritusphere. Four treatments were applied to small soil cores with two different water contents (matric potential of -0.0063 and -0.0316 MPa) and with or without addition of ^{13}C labelled rye residues ($\delta^{13}C$ = 299%), which were placed on top. Microcosms were sampled after 3, 7, 14, 28, 56 and 84 days and soil cores were separated into layers with increasing distance to the litter. Gradients in soil organic carbon, dissolved organic carbon, extracellular enzyme activity and microbial biomass were detected over a distance of 3mm from the litter layer. At the end of the incubation, 35.6% of litter C remained on the surface of soils at -0.0063 MPa, whereas 41.7% remained on soils at -0.0316 MPa. Most of the lost litter C was mineralised to CO_2, with 47.9% and 43.4% at -0.0063 and -0.0316 MPa, respectively. In both treatments about 6% were detected as newly formed soil organic carbon. During the initial phase of litter decomposition, bacteria dominated the mineralisation of easily available litter substrates. After 14 days fungi depolymerised more complex litter compounds, thereby producing new soluble substrates, which diffused into the soil. This pattern of differential substrate usage was paralleled by a lag phase of 3 days and a subsequent increase in enzyme activities. Increased soil water content accelerated the transport of soluble substrates, which influenced the temporal patterns of microbial growth and activity. Our results underline the importance of considering the interaction of soil microorganisms and physical processes at the small scale for the understanding of C cycling in soils.

7 Small-scale diversity and succession of fungi in the detritusphere of rye residues

Submitted to Microbial Ecology

C. Poll[a], T. Brune[a], D. Begerow[b] & E. Kandeler[a]

[a]*Institute of Soil Science and Land Evaluation, Soil Biology Section, University of Hohenheim, Emil-Wolff-Straße 27, 70599 Stuttgart, Germany*

[b]*Department of Evolution and Biodiversity of Plants, Geobotany Section, Ruhr-Universität Bochum, Universitätsstraße 150, 44780 Bochum, Germany*

Abstract

Transport of litter carbon in the detritusphere might determine fungal abundance and diversity at the small-scale. Rye residues were applied to the surface of soil cores with two different water contents and incubated at 10°C for two and twelve weeks. Fungal community structure was analysed by constructing clone libraries of 18S rDNA and subsequent sequencing. Litter addition decreased fungal diversity mainly due to the huge supply of substrates. Ergosterol content and N-acetyl-glucosaminidase activity indicated fungal growth after two weeks. Simultaneously, the structure of the fungal community changed, with *Mortierellaceae* proliferating during the initial phase of litter decomposition. Ergosterol measurements were unable to detect this early fungal growth because *Mortierellaceae* do not produce ergosterol. In the late phase during decomposition of polymeric substrates like cellulose and chitin, the fungal community was dominated by *Trichocladium asperum*. Water content influenced community composition only during the first two weeks due to its influence on transport processes in the detritusphere and on competition between fungal species. Our results underline the importance of species identification in understanding decomposition processes in soil.

8 Final Conclusions

The present thesis investigated the influence of transport processes on the microbial community and its activity in the detritusphere. This microhabitat provides high amounts of readily available substrates. Transport of soluble litter C induces gradients in microbial abundance and activity in the adjacent soil. This thesis showed that the formation of these gradients is affected by transport mechanisms and soil water conditions.

In the first study, a convective-diffusive transport model was used to interpret enzyme activity profiles. The model showed that the spatial dimension of the detritusphere is governed by the ratio between the decay rate and the transport rate. Therefore, convection versus diffusion enlarged the spatial dimension of the detritusphere by increasing the transport rate of soluble substrates. For the same reason, water content affected microbial activity when solute transport was restricted to diffusion. The different behaviour of enzyme activities and microbial biomass at the two applied water contents (Figure 5.1a,b; 5.3c) was explained by accelerated diffusive C transport, microbial growth and enzyme release from cells at the higher water content. Combining PLFA analysis with stable isotope techniques enabled the identification of different substrate utilisation strategies by bacteria and fungi (Figure 5.4). Bacteria relied on the small-scale transport of substrates, whereas fungi actively foraged for new substrates and assimilated new C directly in the litter layer.

Based on these results, a second study was designed to identify temporal patterns of litter C turnover in the detritusphere. The hypothesis was that different soil water contents will modify the expected temporal pattern of litter C transport, microbial growth and extracellular enzyme release (Figure 6.1a). The results showed an interaction between changing substrate quality during litter decomposition, microbial succession and soil moisture regime. The 84-day incubation revealed two phases: an initial phase dominated by mineralisation and diffusion of easily available and soluble litter compounds, and a later phase dominated by depolymerisation of complex litter compounds. Measurements of microbial biomass C and ergosterol indicated an early response of bacteria to litter addition, whereas fungi responded with a lag phase of two weeks (Figure 6.5). Therefore, the initial concept of one litter C pool and one microbial pool was extended (Figure 6.1b). The two-phase conceptual model of litter C turnover and microbial response in the detritusphere is based on the separation of litter C into a pool of soluble substrates, which is used by bacterial dominated *r* strategists, and a pool of complex substrates, which is mineralised by fungi dominated *K* strategists. Based on this concept and the results of the second study, a model was developed to simulate small-scale C turnover in the detritusphere (Ingwersen et al., 2008). Comparing the two water content treatments confirmed the hypothesis that an increased water content accelerates the transport of litter C. This induced greater initial microbial biomass and activity, but reduced substrate availability during the later phase (Figure 6.6d).

The first two studies emphasised the importance of fungi for litter decomposition in the detritusphere. The third study therefore investigated fungal community response to litter addition by identifying fungal species. There was a strong interaction between changing litter quality during litter decomposition and fungal succession; decomposition was accompanied by decreasing fungal diversity. Rapidly growing pioneer colonizers like *Motierellaceae* dominated the fungal community during the initial phase (Figure 7.5). However, the growth of these fungi was not detected by the ergosterol and N-acetyl-glucosaminidase measurements of the second study. This is because *Motierellaceae* do not produce ergosterol. Chitin, on the other hand, as a substrate for N-acetyl-glucosaminidase, probably accumulated after the death of pioneer colonizers and thereby induced delayed enzyme activity. The conceptual model was modified accordingly by assuming that the *r* strategists are not bacteria dominated but involve both bacteria and fungi. The later phase was dominated by *Trichocladium asperum*, which is capable of degrading polymeric substrates. Water content affected the fungal community during the initial phase by influencing both the competitiveness of fungal species and substrate transport (Figure 7.4).

Recent results suggest that endogeic earthworms influence microbial processes in the detritusphere. Grazing shifted the bacterial community towards Gram-negative bacteria and reduced fungal stabilisation of litter C in the soil (Butenschoen et al., 2007).

In conclusion, the results of the three studies provided new insight into litter decomposition at the small-scale by interpreting results of classical methods in a novel manner and applying modern techniques. Combining soil biological methods and mathematical modelling revealed the dependence of the spatial dimension of the detritusphere on transport processes. Increased diffusive transport rates at increased water content influenced several processes in the detritusphere, among them microbial growth, activity and succession. Stable isotope probing of PLFAs as well as phylogenetic analysis of the fungal community underlined the important role of fungi in litter decomposition. Based on the results of this thesis, it was possible to develop a conceptual model of litter C turnover and microbial response in the detritusphere. The identification of active microorganisms by stable isotope probing (SIP) of microbial DNA and the influence of global change on the interaction of decomposition and microbial community structure are interesting topics for future research in the detritusphere. Such studies will provide further information for models simulating C turnover.

9 References

Abraham, W.-R., Hesse, C., and Pelz, O. (1998) Ratios of carbon isotopes in microbial lipids as an indicator of substrate usage. Applied and Environmental Microbiology 64: 4202-4209.

Aerts, R. (1997) Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: a triangular relationship. Oikos 79: 439-449.

Allison, S.D. (2005) Cheaters, diffusion and nutrients constrain decomposition by microbial enzymes in spatially structured environments. Ecology Letters 8: 626-635.

Allison, S.D., and Vitousek, P.M. (2005) Responses of extracellular enzymes to simple and complex nutrient inputs. Soil Biology and Biochemistry 37: 937-944.

Altschul, S.F., Gish, W., Miller, W., Myers, E.W., and Lipman, D.J. (1990) Basic local alignment search tool. Journal of Molecular Biology 215:403-410.

Aneja, M.K., Sharma, S., Munch, J.C., and Schloter, M. (2004) RNA fingerprinting- a new method to screen for differences in plant litter degrading microbial communities. Journal of Microbiological Methods 59: 223-231.

Aon, M.A., and Colaneri, A.C. (2001) II. Temporal and spatial evolution of enzymatic activities and physico-chemical properties in an agricultural soil. Applied Soil Ecology 18: 255-270.

Balesdent, J., and Mariotti, A. (1996) Measurement of soil organic matter turnover using ^{13}C natural abundance. In: Button, T.W., and Yamasaki, S.I. (Eds.) Mass Spectrometry of Soils. Marcel Dekker, New York, pp. 83-111.

Bardgett, R.D., Hobbs, P.J., and Frostegaård, Å. (1996) Changes in soil fungal:bacterial biomass ratios following reductions in the intensity of management of an upland grass-land. Biology and Fertility of Soils 22: 261-264.

Beare, M.H., Coleman, D.C., Crossley, D.A. Jr, Hendrix, P.F., and Odum, E.P. 1995. A hierarchical approach to evaluating the significance of soil biodiversity to biogeochemical cycling. Plant and Soil 170: 5-22.

Bellamy, P.H., Loveland, P.J., Bradley, R.I., Lark, R.M., and Kirk, G.J.D. (2005) Carbon losses from all soils across England and Wales 1978-2003. Nature 437: 245-248.

Berg, B., and Matzner, E. (1997) Effect of N deposition on decomposition of plant litter and soil organic matter in forest systems. Environmental Review 5: 1-25.

Boschker, H.T.S., and Middelburg, J.J. (2002) Stable isotopes and biomarkers in microbial ecology. FEMD Microbiology Ecology 40: 85-95.

Boschker, H.T.S., Nold, S.C., Wellsbury, P., Bos, D., de Graaf, W., and Pel, R. et al. (1998) Direct linking of microbial populations to specific biogeochemical processes by ^{13}C- labelling of biomarkers. Nature 392: 801-805.

Brant, J.B., Sulzman, E.W., and Myrold, D.D. (2006) Microbial community utilization of added carbon substrates in response to long-term carbon input manipulation. Soil Biology and Biochemistry 38: 2219-2232.

Bridge, P., and Spooner, B. (2001) Soil fungi: diversity and detection. Plant and Soil 232: 147-154.

Burke, R.A., Molina, M., Cox, J.E., Osher, L.J., and Piccolo, M.C. (2003) Stable carbon isotope ratio and composition of microbial fatty acids in tropical soils. Journal of Environmental Quality 32: 198-206.

Burns, R.G. (1982) Enzyme activity in soil: location and a possible role in microbial ecology. Soil Biology and Biochemistry 14: 423-427.

Butenschoen, O., Poll, C., Langel, R., Kandeler, E., Marhan, S., and Scheu, S. (2007) Fungi and endogeic earthworms - antagonists in stabilization of litter carbon in soils. Soil Biology and Biochemistry 39: 2854-2864.

Butler, J.L., Williams, M.A., Bottomley, P.J., and Myrold, D.D. (2003) Microbial community dynamics associated with rhizosphere carbon flow. Applied and Environmental Microbiology 69: 6793-6800.

Caldwell, B.A. (2005) Enzyme activities as a component of soil biodiversity: a review. Pedobiologia 49: 637-644.

Carreiro, M.M., Sinsabaugh, R.L., Repert, D.A., and Parkhurst, D.F. (2000) Microbial enzyme shifts explain litter decay responses to simulated nitrogen deposition. Ecology 81: 2359-2365.

Colwell, R.K. (2006). EstimateS: statistical estimation of species richness and shared species from samples. Version 8.0. User's guide and application published at: http://purl.oclc.org/estimates.

Coppens, F., Merckx, R., and Recous, S. (2006) Impact of crop residue location on carbon and nitrogen distribution in soil and in water-stable aggregates. European Journal of Soil Science 57: 570-582.

Coûteaux, M.-M., Bottner, P., and Berg, B. (1995) Litter decomposition, climate and litter quality. Trends in Ecology and Evolution 10: 63-66.

Craig, H. (1957) Isotopic standards for carbon and oxygen and correction factors for mass-spectrometric analysis of carbon dioxide. Geochimica et Cosmochimica Acta 12: 133-149.

Darrah, P.R. (1991) Measuring the diffusion coefficient of rhizosphere exudates in soil. I. The diffusion of non-sorbing compounds. Journal of Soil Science 42: 413-420.

de Boer, W., Folman, L.B., Summerbell, R.C., and Boddy, L. (2005) Living in a fungal world: impact of fungi on soil bacterial niche development. FEMS Microbiology Reviews 29: 795-811.

Dijkstra, P., Ishizu, A., Doucett, R., Hart, S.C., Schwartz, E., Menyailo, O.V., and Hungate, B.A. (2006) ^{13}C and ^{15}N natural abundance of the soil microbial biomass. Soil Biology and Biochemistry 38: 3257-3266.

Dilly, O., Bloem, J., Vos, A., and Munch, J.C. (2004) Bacterial diversity in agricultural soils during litter decomposition. Applied and Environmental Microbiology 70: 468-474.

Dix, N.J., and Webster, J. (1995) Fungal Ecology. London, UK: Chapman & Hall, p. 549.

Djajakirana, G., Joergensen, R.G., and Meyer, B. (1996) Ergosterol and microbial biomass relationship in soil. Biology and Fertility of Soils 22: 299-304.

Domsch, K.H. (1960) Das Pilzspektrum einer Bodenprobe: II. Nachweis physiologischer Merkmale. Archiv für Mikrobiology 35: 229-247.

Donnelly, P.K., Entry, J.A., Crawford, D.L., and Cromack Jr., K. (1990) Cellulose and lignin degradation in forest soils: response to moisture, temperature, and acidity. Microbial Ecology 20: 289-295.

Ekschmitt, K., Kandeler, E., Poll, C., Brune, A., Buscot, F., Friedrich, M., Gleixner, G., Hartmann, A., Kästner, M., Marhan, S., Miltner, A., Scheu, S., and Wolters, V. (2008) Soil carbon preservation through habitat constraints and biological limitations on decomposer activity. Journal of Plant Nutrition and Soil Science 171: 27-35.

Ettema, C.H., and Wardle, D.A. (2002) Spatial soil ecology. Trends in Ecology and Evolution 17: 177-183.

Federle, T.W. (1986) Microbial distribution in soil – new techniques. In: Megusar, F., and Gantar, M. (Eds.) Perspectives in Microbial Ecology. Slovene Society of Microbiology, Ljubljana, pp. 493-498.

Fierer, N., Craine, J.M., McLauchlan, K., and Schimel, J.P. (2005) Litter quality and the temperatur sensitivity of decomposition. Ecology 86: 320-326.

Fontaine, S., Mariotti, A., and Abbadie, L. (2003) The priming effect of organic matter: a question of microbial competition? Soil Biology and Biochemistry 35: 837-843.

Frankland, J.C. (1998) Fungal succession- unravelling the unpredictable. Mycological Research 102: 1-15.

Frey, S.D., Six, J., and Elliott, E.T. (2003) Reciprocal transfer of carbon and nitrogen by decomposer fungi at the soil–litter interface. Soil Biology and Biochemistry 35: 1001-1004.

Frostegaård, Å., Bååth, E., and Tunlid, A. (1993) Shifts in the structure of soil microbial communities in limed forests as revealed by phospholipids fatty acid analysis. Soil Biology and Biochemistry 25: 723-730.

Gaillard, V., Chenu, C., Recous, S., and Richard, G. (1999) Carbon, nitrogen and microbial gradients induced by plant residues decomposing in soil. European Journal of Soil Science 50: 567-578.

Gaillard, V., Chenu, C., and Recous, S. (2003) Carbon mineralisation in soil adjacent to plant residues of contrasting biochemical quality. Soil Biology and Biochemistry 35: 93-99.

Gargas, A., and DePriest, P. T. (1996) A nomenclature for fungal PCR primers with examples from intron-containing SSU rDNA. Mycologia 88: 745-748.

Gaston, L.A., and Locke, M.A. (2002) Differences in microbial biomass, organic carbon, and dye sorption between flow and no-flow regions of unsaturated soil. Journal of Environmental Quality 31: 1406-1408.

Gleixner, G., Danier, H.-J., Werner, R.A., and Schmidt, H.-L. (1993) Correlations between the ^{13}C content of primary and secondary plant products in different cell compartments and that in decomposing basidiomycetes. Plant Physiology 102: 1287-1290.

Gleixner, G., Bol, R., and Balesdent, J. (1999) Molecular insight into soil carbon turnover. Rapid Communications in Mass Spectrometry 13: 1278-1283.

Gregorich, E.G., Beare, M.H., Stoklas, U., and St-Georges, P. (2003) Biodegradability of soluble organic matter in maize-cropped soils. Geoderma 113: 237-252.

Griffin, D.M. (1981) Water potential as a selective factor in the microbial ecology of soils. In: Parr, F., Gardner, W., and Elliot, L.F. (Eds.) Water Potential Relations in Soil Microbiology. Special publications No. 9, Soil Science Society of America, Madison, WI, pp. 141-151.

Hättenschwiler, S., Tiunov, A.V., and Scheu, S. (2005) Biodiversity and litter decomposition in terrestrial ecosystems. Annual Review of Ecology and Systematics 36: 191-218.

Hawksworth, D.L., and Mueller, G.M. (2005) Fungal communities: their diversity and distribution. In: Dighton, J., White, J.F., and Oudemans, P. (Eds.) The Fungal Community: its Organization and Role in the Ecosystem. CRC press, Boca Raton, pp. 27-37.

Henn, M.R., and Chapela, I.H. (2000) Differential C isotope discrimination by fungi during decomposition of C3- and C4-derived sucrose. Applied and Environmental Microbiology 66: 4180-4186.

Henriksen, T.M., and Breland, T.A. (1999) Nitrogen availability effects on carbon mineralization, fungal and bacterial growth, and enzyme activities during decomposition of wheat straw in soil. Soil Biology and Biochemistry 31: 1121-1134.

Henriksen, T.M., and Breland, T.A. (2002) Carbon mineralization, fungal and bacterial growth, and enzyme activities as affected by contact between crop residues and soil. Biology and Fertility of Soils 35: 41-48.

Hibbett, D.S., Binder, M., Bischoff, J.F., et al. (2007) A higher-level phylogenetic classification of the Fungi. Mycological Research 111: 509-547.

Hobbie, E.A., and Werner, R.A. (2004) Intramolecular, compound-specific, and bulk carbon isotope patterns in C3 and C4 plants: a review and synthesis. New Phytologist 161: 371-385.

Hobbie, E.A., and Horton, T.R. (2007) Evidence that saprotrophic fungi mobilise carbon and mycorrhizal fungi mobilise nitrogen during litter decomposition. New Phytologist 173: 447-449.

Hughes, J.B., Hellmann, J.J., Ricketts, T.H., and Bohannan, B.J.M. (2001) Counting the uncountable: statistical approaches to estimating microbial diversity. Applied and Environmental Microbiology 67: 4399-4406.

Hunt, J., Boddy, L., Randerson, P.F., and Rogers, H.J. (2004) An evaluation of 18S rDNA approaches for the study of fungal diversity in grassland soils. Microbial Ecology 47: 385-395.

Ingwersen, J., Poll, C., Streck, T., and Kandeler, E. (2008) Micro-scale modelling of carbon turnover at a biogeochemical interface. Soil Biology and Biochemistry 40: 872-886.

IPCC (2001) Climate Change 2001: The Scientific Basis. Cambridge University Press, Cambridge, UK.

Joergensen, R.G. (1996) The fumigation-extraction method to estimate soil microbial biomass: calibration of the *k*(EC) value. Soil Biology and Biochemistry 28: 25-31.

John, B., Ludwig, B., and Flessa, H. (2003) Carbon dynamics determined by natural ^{13}C abundance in microcosm experiments with soils from long-term maize and rye monocultures. Soil Biology and Biochemistry 35: 1193-1202.

Jumpponen, A., and Johnson, L.C. (2005) Can rDNA analyses of diverse fungal communities in soil and roots detect effects of environmental manipulations - a case study from tallgrass prairie. Mycologia 97: 1177-1194.

Jury, W.A., Gardner, W., and Gardner, W. (1991) Soil Physics. John Wiley & Sons, New York.

Kaiser, K., and Guggenberger, G. (2007) Sorptive stabilization of organic matter by microporous goethite: sorption into small pores vs. surface complexation. European Journal of Soil Science 58: 45-59.

Kandeler, E. (1990) Characterization of free and adsorbed phosphatases in soils. Biology and Fertility of Soils 9: 199-202.

Kandeler, E., Luxhøi, J., Tscherko, D., and Magid, J. (1999) Xylanase, invertase and protease at the soil-litter interface of a loamy sand. Soil Biology and Biochemistry 31: 1171-1179.

Katoh K., Misawa K., Kuma K., and Miyata T. (2002) MAFFT: a novel method for rapid multiple sequence alignment based on fast Fourier transform. Nucleic Acids Research 30: 3059-3066.

Kjøller, A.H., and Struwe, S. (2002) Fungal communities, succession, enzymes, and decomposition. In: Burns, R.G., and Dick, R.P. (Eds.) Enzymes in the Environment - Activity, Ecology and Applications. Marcel Dekker, New York, pp. 267-284.

Kögel-Knabner, I. (2002) The macromolecular organic composition of plant and microbial residues as inputs to soil organic matter. Soil Biology and Biochemistry 34: 139-162.

Lal, R. (2004) Soil carbon sequestration to mitigate climate change. Geoderma 123: 1-22.

Lang, E., Kleeberg, I., and Zadrazil, F. (2000) Extractable organic carbon and counts of bacteria near the lignocellulose–soil interface during the interaction of soil microbiota and white rot fungi. Bioresource Technology 75: 57-65.

Lax, E. 1967. Taschenbuch für Chemiker und Physiker. 1. Band. Springer-Verlag, Berlin.

Lejon, D.P.H., Sebastia, J., Lamy, I., Chaussod, R., and Ranjard, L. (2007) Relationships between soil organic status and microbial community density and genetic structure in two agricultural soils submitted to various types of organic management. Microbial Ecology 53: 650-663.

Lindahl, B.D., Ihrmark, K., Boberg, J., Trumbore, S.E., Högberg, P., Stenlid, J., and Finlay, R.D. (2007) Spatial separation of litter decomposition and mycorrhizal nitrogen uptake in a boreal forest. New Phytologist 173: 611-620.

Loague, K., and Green, R.E. (1991) Statistical and graphical methods for evaluating solute transport models: overview and application. Journal of Contaminant Hydrology 7: 51-73.

Luis, P., Walther, G., Kellner, K., Martin, F., and Buscot, F. (2004) Diversity of laccase genes from Basidiomycetes in a forest soil. Soil Biology and Biochemistry 36: 1025-1036.

Macey, R., Oster, G., and Zahnley, T. (2000) Berkeley Madonna User's Guide 8.0. University of Berkeley, Berkeley.

Marx, M.-C., Wood, M., and Jarvis, S.C. (2001) A microplate fluorimetric assay for the study of enzyme diversity in soils. Soil Biology and Biochemistry 33: 1633-1640.

Marx, M.-C., Kandeler, E., Wood, M., Wermbter, N., and Jarvis, S.C. (2005) Exploring the enzymatic landscape: distribution and kinetics of hydrolytic enzymes in soil particle-size fractions. Soil Biology and Biochemistry 37: 35-48.

McLean, M.A., and Huhta, V. (2000) Temporal and spatial fluctuations in moisture affect humus microfungal community structure in microcosms. Biology and Fertility of Soils 32: 114-119.

McMahon, S.K., Williams, M.A., Bottomley, P.J., and Myrold, D.D. (2005) Dynamics of microbial communities during decomposition of carbon-13 labeled ryegrass fractions in soil. Soil Science Society of America Journal 69: 1238-1247.

Miller, M., Palojärvi, A., Rangger, A., Reeslev, M., and Kjøller, A. (1998) The use of fluorogenic substrates to measure fungal presence and activity in soil. Applied and Environmental Microbiology 64: 613-617.

Millington, R.J., and Quirk, J.P. (1961) Permeability of porous solids. Transactions of the Faraday Society 57: 1200-1207.

Morris, S.J. (1999) Spatial distribution of fungal and bacterial biomass in southern Ohio hardwood forest soils: fine scale variability and microscale patterns. Soil Biology and Biochemistry 31: 1375-1386.

Morris, S.J., and Robertson, G.P. (2005) Linking function between scales of resolution. In: Dighton, J., White, J.F., and Oudemans, P. (Eds.) The Fungal Community: its Organization and Role in the Ecosystem. CRC press, Boca Raton, pp. 13-26.

Nannipieri, P., Asher, J., Ceccherini, M.T., Landi, L., Pietramellara, G., and Renella, G. (2003) Microbial diversity and soil functions. European Journal of Soil Science 54: 655-670.

Nes, W.D., and Nichols, S.D. (2006) Phytosterol biosynthesis pathway in *Mortierella alpine*. Phytochemistry 67: 1716-1721.

Nicolardot, B., Bouziri, L., Bastian, F., and Ranjard, L. (2007) A microcosm experiment to evaluate the influence of location and quality of plant residues on residue decomposition and genetic structure of soil microbial communities. Soil Biology and Biochemistry 39: 1631-1644.

Nunan, N., Wu, K., Young, I.M., Crawford, J.W., and Ritz, K. (2003) Spatial distribution of bacterial communities and their relationships with the micro-architecture of soil. FEMS Microbiology Ecology 44: 203-215.

O'Brien, H.E., Parrent, J.L., Jackson, J.A., Moncalvo, J.-M., and Vilgalys, R. (2005) Fungal community analysis by large-scale sequencing of environmental samples. Applied and Environmental Microbiology 71: 5544-5550.

Poll, C., Ingwersen, J., Stemmer, M., Gerzabek, M.H., and Kandeler, E. (2006) Mechanisms of solute transport affect small-scale abundance and function of soil microorganisms in the detritusphere. European Journal of Soil Science 57: 583-595.

Poll, C., Marhan, S., Ingwersen, J., and Kandeler, E. (2008) Dynamics of litter carbon turnover and microbial abundance in a rye detritusphere. Soil Biology and Biochemistry, doi:10.1016/j.soilbio.2007.04.002.

Potthoff, M., Loftfield, N., Buegger, F., Wick, B., John, B., Joergensen, R.G., and Flessa, H. (2003) The determination of $\delta^{13}C$ in soil microbial biomass using fumigation-extraction. Soil Biology and Biochemistry 35: 947-954.

Rai, B., and Srivastava, A.K. (1983) Decomposition and competitive colonization of leaf litter by fungi. Soil Biology and Biochemistry 15: 115-117.

Schimel, J.P., and Weintraub, M.N. (2003) The implications of exoenzyme activity on microbial carbon and nitrogen limitation on soil: a theoretical model. Soil Biology and Biochemistry 35: 549-563.

Schimel, J.P., Gulledge, J.M., Clein-Curley, J.S., Lindstrom, J.E., and Braddock, J.F. (1999) Moisture effects on microbial activity and community structure in decomposing birch litter in the Alaskan taiga. Soil Biology and Biochemistry 31: 831-838.

Schulze, E.D., and Freibauer, A. (2005) Carbon unlocked from soils. Nature 437: 205-206.

Scott, N.A., Cole, C.V., Elliott, E.T., and Huffman, S.A. (1996) Soil textural control on decomposition and soil organic matter dynamics. Soil Science Society of America Journal 60: 1102-1109.

Sengeløv, G., Kowalchuk, G.A., and Sørensen, S.J. (2000) Influence of fungal–bacterial interactions on bacterial conjugation in the residuesphere. FEMS Microbiology Ecology 31: 39-45.

Setälä, H., and McLean, M.A. (2004) Decomposition rate of organic substrates in relation to the species diversity of soil saprophytic fungi. Oecologia 139: 98-107.

Sinsabaugh, R.L., Carreiro, M.M., and Alvarez, S. (2002) Enzyme and microbial dynamics of litter decomposition. In: Burns, R.G., and Dick, R.P. (Eds.) Enzymes in the Environment: Activity, Ecology and Application. Marcel Dekker, New York, pp. 249-265.

Six, J., Frey, S.D., Thiet, R.K., and Batten, K.M. (2006) Bacterial and fungal contributions to carbon sequestration in agroecosystems. Soil Science Society of America Journal 70: 555-569.

Smith, K.A., Ball, T., Conen, F., Dobbie, K.E., Massheder, J., and Rey, A. (2003) Exchange of greenhouse gases between soil and atmosphere: interactions of soil physical factors and biological processes. European Journal of Soil Science 54: 779-791.

Sollins, P., Homann, P., and Caldwell, B.A. (1996) Stabilization and destabilization of soil organic matter: mechanisms and controls. Geoderma 74: 65-105.

Sommers, L.E., Gilmour, C.M., Wildung, R.E., and Beck, S.M. (1981) The effect of water potential on decomposition processes in soils. In: Parr, F., Gardner, W., and Elliot, L.F. (Eds.) Water Potential Relations in Soil Microbiology. Special publications No. 9, Soil Science Society of America, Madison, WI, pp. 97-117.

Stark, C.H.E., Condron, L.M., Stewart, A., Di, H.J., and O'Callaghan, M. (2004) Small-scale spatial variability of selected soil biological properties. Soil Biology and Biochemistry 36: 601-608.

Strong, D.T., de Wever, H., Merckx, R., and Recous, S. (2004) Spatial location of carbon decomposition in the soil pore system. European Journal of Soil Science 55: 739-750.

Swift, M.J., Heal, O.W., and Anderson, J.M. (1979) Decomposition in Terrestrial Ecosystems. Blackwell, Oxford.

Swofford, D.L. (2002) PAUP* Phylogenetic Analysis Using Parsimony (*and Other Methods). Version 4. Sinauer Associates, Sunderland, Massachusetts.

Tester, C.F. (1988) Role of soil and residue microorganisms in determining the extent of residue decomposition in soil. Soil Biology and Biochemistry 20: 915-919.

Thomsen, I.K., Schjønning, P., Jensen, B., Kristensen, K., and Christensen, B.T. (1999) Turnover of organic matter in differently textured soils- II. Microbial activity as influenced by soil water regimes. Geoderma 89: 199-218.

Tiunov, A.V., and Scheu, S. (2000) Microfungal communities in soil, litter and casts of *Lumbricus terrestris* L. (Lumbricidae): a laboratory experiment. Applied Soil Ecology 14: 17-26.

Tiunov, A.V., and Scheu, S. (2005) Facilitative interactions rather than resource partitioning drive diversity-functioning relationships in laboratory fungal communities. Ecology Letters 8: 618-625.

Treonis, A.M., Ostle, N.J., Stott, A.W., Primrose, R., Grayston, S.J., and Ineson, P. (2004) Identification of groups of metabolically-active rhizosphere microorganisms by stable isotope probing of PLFAs. Soil Biology and Biochemistry 36: 533-537.

Vance, E.D., Brookes, P.C., and Jenkinson, D.S. (1987) An extraction method for measuring soil microbial C. Soil Biology and Biochemistry 19: 703-708.

van der Wal, A., van Veen, J.A., Pijl, A.S., Summerbell, R.C., and de Boer, W. (2006) Constraints on development of fungal biomass and decomposition processes during restoration of arable sandy soils. Soil Biology and Biochemistry 38: 2890-2902.

Van Noordwijk, M., de Ruiter, P.C., Zwart, K.B., Bloem, J., Moore, J.C., van Faassen, H.G., and Burgers, S.L.G.E. (1993) Synlocation of biological activity, roots, cracks and recent organic inputs in a sugar beet field. Geoderma 56: 265-276.

Vepsäläinen, M., Kukkonen, S., Vestberg, M., Sirviö, H., and Niemi, R.M. (2001) Application of soil enzyme activity test kit in a field experiment. Soil Biology and Biochemistry 33: 1665-1672.

Vetter, Y.A, Deming, J.W., Jumars, P.A., and Krieger-Brockett, B.B. (1998) A predictive model of bacterial foraging by means of freely released extracellular enzymes. Microbial Ecology 36: 75-92.

Virzo de Santo, A., Berg, B., Rutigliano, F.A., Alfani, A., and Fioretto, A. (1993) Factors regulating early-stage decomposition of needle litters in five different coniferous forests. Soil Biology and Biochemistry 25: 1423-1433.

Waldrop, M.P., Zak, D.R., Blackwood, C.B., Curtis, C.D., and Tilman, D. (2006) Resource availability controls fungal diversity across a plant diversity gradient. Ecology Letters 9: 1127-1135.

Wallenstein, M.D., McMahon, S., and Schimel, J. (2007) Bacterial and fungal community structure in arctic tundra tussock and shrub soils. FEMS Microbiology Ecology 59: 428-435.

Weete, J.D., and Gandhi, S.R. (1999) Sterols and fatty acids of the Mortierellaceae: taxonomic implications. Mycologia 91: 642-649.

Wu, T., Chellemi, D.O., Martin, K.J., Graham, J.H., and Rosskopf, E.N. (2007) Discriminating the effect of agricultural land management practices on soil fungal communities. Soil Biology and Biochemistry 39: 1139-1155.

Young, I.M., and Ritz, K. (1998) Can there be a contemporary ecological dimension to soil biology without a habitat? Soil Biology and Biochemistry 30: 1229-1232.

Curriculum vitae

Name:	*Christian Poll*
Date of birth:	*19.11.1974*
Place of birth:	*Hamburg, Germany*
Marital status:	*married, one child*

School education

1981-1985	Primary school in Bargteheide/Schleswig-Holstein
1985-1994	Grammar school in Bargteheide/Schleswig-Holstein
1994	General qualification for university entrance (*Abitur*)

Civilian service

1994-1995	Community care for psychiatric patients

Studies

1995-2002	Studies of physical geography with focus on soil science and geobotany at the University of Trier/Rhineland-Palatinate
2002-2007	PhD student at the Institute of Soil Science and Land Evaluation, University of Hohenheim/Baden-Württemberg, funding by the Deutsche Forschungsgemeinschaft (DFG) priority program 1090 “Böden als Quelle und Senke für CO_2- Mechanismen und Regulation der Stabilisierung organischer Substanz in Böden”.
since 11/2007	Postdoc at the Institute of Soil Science and Land Evaluation, University of Hohenheim/Baden-Württemberg, funding by the DFG priority program 1315 “Biogeochemical Interfaces in Soil” and the DFG project “Impact of modified temperature and precipitation regime on soil microorganisms and carbon cycling in arable soils”.

Other activities

1997-2001	Student assistant at the Institute of Soil Science, University of Trier/Rhineland-Palatinate
07/2000-10/2000 and	Soil mapping and evaluation for rainwater infiltration, ARK

09/2001-10/2001	Umweltplanung und –consulting, Saarbrücken/Saarland
2000-2002	Vice-chairman of the local group of BUND e.V. in Trier, an organization active in environmental protection and nature conservation

Stuttgart, den 06.03.2008 Christian Poll

Publications and Presentations

Parts of the PhD thesis and other projects were published or presented on conferences as follows:

Poster Presentations

Poll, C., Ingwersen, J., Stemmer, M., and Kandeler, E. (2003) Effect of Water Supply on the Soil-Litter Interface as a Microbial Habitat. Annual Meeting of the DBG, Frankfurt/Oder, Germany.

Poll, C., Ingwersen, J., Stemmer, M., and Kandeler, E. (2003) Effect of Water Supply on the Soil-Litter Interface as a Microbial Habitat. International Conference on Mechanisms and Regulation of Organic Matter Stabilisation in Soils, Hohenkammer, Germany.

Poll, C., Marhan, S., Ingwersen, J., and Kandeler, E. (2005) Abundanz und Funktion von Mikroorganismen in der Detritussphäre. Annual Meeting of the DBG, Marburg, Germany.

Poll, C., Ingwersen, J., Stemmer, M., Gerzabek, M.H., and Kandeler, E. (2005) Mechanisms of Solute Transport affect Small-Scale Abundance and Function of Soil Microorganisms in the Detritusphere. 2nd International Conference on Mechanisms of Organic Matter Stabilisation and Destabilisation in Soils, Asilomar, USA.

Poll, C., Ingwersen, J., and Kandeler, E (2006) Mechanisms of Solute Transport affect Small-Scale Abundance and Function of Soil Microorganisms in the Detritusphere. International Conference of SPP 1090 “Soils as source and sink for CO_2 - Mechanisms and regulation of organic matter stabilization in soils", Thurnau, Germany.

Poll, C., Ingwersen, J., Stemmer, M., Gerzabek, M.H., and Kandeler, E. (2006) Mechanisms of Solute Transport affect Small-Scale Abundance and Function of Soil Microorganisms in the Detritusphere. Workshop of DBG Working Group “Bodenökologie” Upscaling: Soil organisms and soil ecological processes up to the landscape scale, Vechta, Germany.

Kandeler, E., Poll, C., Ingwersen, J., Streck, T., Enowashu, E., and Marhan, S. (2006) Mechanisms of Solute Transport modify Small-Scale Abundance and Function of Microorganisms in Soil. World Congress of Soil Science, Philadelphia, USA.

Poll, C., Ingwersen, J., and Kandeler, E. (2007) Enzymes in the Detritusphere – Measurement and Modelling. 3RD International Conference “Enzymes in the Environment – Ecology, Activity, Applications”, Viterbo, Italy.

Oral Presentations

Poll, C., Ingwersen, J., Stemmer, M., Gerzabek, M.H., and Kandeler, E. (2004) Small-Scale Abundance and Function of Soil Microorganisms at the Soil-Litter Interface. Eurosoil, Freiburg, Germany.

Butenschoen, O., Marhan, S., Poll, C., Kandeler, E., and Scheu, S. (2005) Einfluss endogäischer Regenwürmer auf die Translokation von Kohlenstoff an der Grenzfläche Streu-Boden. Annual Meeting of the DBG, Marburg, Germany.

Poll, C., Ingwersen, J., Stemmer, M., Gerzabek, M.H., and Kandeler, E. (2005) Abundanz und Funktion von Mikroorganismen in der Detritussphäre - Einfluss der Bodenfeuchte. Soil Science Colloquium TU Berlin, Germany, 29.11.2005.

Poll, C., Marhan, S., Ingwersen, J., and Kandeler, E. (2006) Abundanz und Funktion von Mikroorganismen in der Detritussphäre. Meeting of Commission III (Soil Biology) and Commission VIII (Soil Protection) of the DBG, Braunschweig, Germany.

Marhan, S., Poll, C., Haase, S., Bisharat, R., Erbs, M., Fangmeier, A., and Kandeler, E. (2006) Einfluss von erhöhter atmosphärischer CO_2-Konzentration auf die mikrobielle Besiedlung und den Abbau zweier Streuarten (Sommerweizen und Kornblume) in einem Ackerboden. Meeting of Commission III (Soil Biology) and Commission VIII (Soil Protection) of the DBG, Braunschweig, Germany.

Poll, C. (2007) Abundanz und Funktion von Mikroorganismen in der Detritussphäre. Colloquium of the Institute of Soil Science and Land Evaluation, University of Hohhenheim, Germany, 29.01.2007.

Poll, C., Brune, T., Begerow, D., and Kandeler, E. (2007) Abundanz und Diversität von Pilzen in der Detritusphäre. Annual Meeting of the DBG, Dresden, Germany.

Poll, C. (2008) Abundanz und Funktion von Mikroorganismen in der Detritussphäre. Colloquium of the Department of Evolution and Biodiversity of Plants, Ruhr-Universität Bochum, Germany, 09.01.2008.

Peer-Reviewed Journals

Poll, C., Thiede, A., Wermbter, N., Sessitsch, A., and Kandeler, E. (2003) Micro-scale distribution of microorganisms and microbial enzyme activities in a soil with long-term organic amendment. European Journal of Soil Science, 54, 715-724.

Poll, C., Ingwersen, J., Stemmer, M., Gerzabek, M.H., and Kandeler, E. (2006) Mechanisms of solute transport affect small-scale abundance and function of soil microorganisms in the detritusphere. European Journal of Soil Science, 57, 583-595.

Rasche, F., Hödl, V., Poll, C., Kandeler, E., Gerzabek, M.H., van Elsas, J.D., and Sessitsch, A. (2006) Rhizosphere bacteria affected by transgenic potatoes with antibacterial activities compared with the effects of soil, wild-type potatoes, vegetation stage and pathogen exposure. FEMS Microbiology Ecology, 56, 219-235.

Butenschoen, O., Poll, C., Langel, R., Kandeler, E., Marhan, S., and Scheu, S., (2007) Endogeic earthworms alter carbon translocation by fungi at the soil–litter interface. Soil Biology and Biochemistry, 39, 2854-2864.

Ekschmitt, K., Kandeler, E., Poll, C., Brune, A., Buscot, F., Friedrich, M., Gleixner, G., Hartmann, A., Kästner, M., Marhan, S., Miltner, A., Scheu, S., and Wolters, V. (2008) Soil-carbon preservation through habitat constraints and biological limitations on decomposer activity. Journal of Plant Nutrition and Soil Science, 171, 27-35.

Ingwersen, J., Poll, C., Streck, T., and Kandeler, E. (2008) Micro-scale modelling of carbon turnover driven by microbial succession at a biogeochemical interface. Soil Biology and Biochemistry, 40, 872-886.

Poll, C., Marhan, S., Ingwersen, J., and Kandeler, E. (2008) Dynamics of litter carbon turnover and microbial abundance in a rye detritusphere. Soil Biology and Biochemistry, doi:10.1016/j.soilbio.2007.04.002.

Poll, C., Brune, T., Begerow, D., and Kandeler, E. (2008) Small-scale diversity and succession of fungi in the detritusphere of rye residues. Microbial Ecology, submitted.

Acknowledgements

First, I would like to thank Prof. Kandeler, who greatly supported my work. She gave me freedom to find my own scientific way, but always found time for helpful and motivating discussions if needed.

For taking the part of the co-supervisor of my thesis, I would like to thank Prof. Cadisch. I thank Prof. Fangmeier for being the third examiner during the oral examination.

Special thanks to Joachim Ingwersen for the very good cooperation and for supporting me in establishing the lab experiments. He also found, if needed, words of encouragement like:" Well, that's science."

For performing the ^{13}C analysis of PLFAs and visiting a "Heuriger" near Vienna I thank Michael Stemmer (Institute for Plant Protection, Products Evaluation and Authorisation, Austrian Agency for Health and Food Safety, Vienna, Austria). Thanks also to Thomas Brune and Dominik Begerow, who did a great job in performing the molecular analyses.

Daniel Diehl, Nicole Schmid and Erhard Strohm helped me a lot with the experiments and sample preparation, Many thanks for this.

Sven Marhan is currently sharing the office with me, which is a great pleasure. I hope, there will be a lot more time for me to ask him many questions ("Sveeeen,…?") and to make some projects together. Thanks to him and to Michael Stachowitsch for critically reading the manuscript of this thesis.

I would like to thank Nicola and Klaus Lorenz and Diana Ebersberger, who helped me to have a good start in Hohenheim.

Oliver Koch spent the first years with me in our office, which I very much enjoyed (especially the long discussions with Günther Scholich about everything).

Thanks also to Marc Lamers for giving me hope that St. Pauli will come back and to Susan Haase for being the "weltbeste Kollegin". I apologise for not drinking coffee or tea.

Many thanks to all members of the Soil Biology group (Doreen Benter, Stephanie Bihlmayer, Thomas Brune, Esther Enowashu, Mingrelia Espaňa, Susan Haase, Heike Haslwimmer, Ellen Kandeler, Oliver Koch, Sven Marhan, Sabine Rudolph, Liliane Rueß, Dagmar Tscherko). You make our institute a happy place to work in.

Thanks to several colleagues (e.g. Olaf Butenschoen, Frank Rasche), who spent small rooms or tents with me during conferences. I apologise for going several times to the toilet during the nights.

I am most grateful to my family. My parents always supported me and always trusted in me and my plans. Thank you for giving me a lovely home. Thank you to Julia for being such a wonderful wife and mother, and giving new motivation when needed. Thanks to Malte for being such a wonderful baby and allowing me to sleep during most of the nights.