THE ROLE OF FINE ROOT LITTER FOR ORGANIC MATTER STORAGE IN SOILS

DISSERTATION

(kumulativ)

zur Erlangung des akademischen Grades doctor rerum naturalium

(Dr. rer. nat.)

vorgelegt dem Rat der Chemisch-Geowissenschaftlichen Fakultät der
Friedrich-Schiller-Universität Jena

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Tag der Verteidigung: 10 Dezember 2014

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Acknowledgments

There are many people who have helped me during the course of my PhD time spent in Jena, Germany, at the Biogeochemical Processes Department, in the Max Planck Institute for Biogeochemistry. I do not only refer to the process of writing this thesis, but to all the support during the 3 years which it took to get here. The time I spent in this research group has shaped me in many ways as a scientist and has convinced me of the importance of understanding and quantifying the role of ecosystem processes for biogeochemical cycles.

First, I would like to thank my supervisors: Dr. Marion Schrumpf, Dr. Ingo Schöning, Prof. Dr. Susan Trumbore, and Prof. Dr. Beate Michalzik. Thank you for giving me the opportunity to conduct my PhD under your supervision, for your encouragement and support during the dissertation work, for your advice in many meetings and for your thorough manuscript reviews. I hope that we will continue to collaborate together in the future.

The funding from the DFG Priority Program 1374 "Infrastructure-Biodiversity-Exploratories" (SCHR 1181/2-1), and the collaborative research centre AquaDiva (CRC 1076) is gratefully acknowledged.

I thank the managers of the Biodiversity Exploratories for their help with the field work and technical organization; Iris Kuhlmann and Theresa Klötzing, for their support in many ways in the laboratory and for teaching me how to do soil organic matter density fractionations; Ines Hilke, Birgit Fröhlich for the large number of C and N measurements and Axel Steinhof for radiocarbon analyses; Marco Pöhlmann for the help with the field work. A big thank you goes to all of the students who have helped me with my experiments, it was fun to work with you during the long hours passed together sorting out roots and in the field.

Professor Dr. Chris Field is acknowledged for the valuable discussions during my research stay at the Department for Global Ecology, Carnegie Institution for Science, in Stanford, USA.

I will never forget the cooperation and the friendship of all the members at the Max Planck Institute for Biogeochemistry in Jena, especially that of Ashish Malik, Sadat Maghani, Martin Novak, Ronny Thoms, Caroline Thoms, Theresa Klötzing, Bernhard Ahrens, Roman Witt, Gabriela Pereyra, Enrico Weber, Lenka Forkelova, Carlos Sierra, Shaun Levick, Mirco Migliavacca and Nuno Carvalhais. Thank you for the scientific discussions, the days spent together and the laughs during our lunch breaks. Your pleasant company always made me feel at home.

I thank the friends who I have met in Jena for their good friendship, and my friends in Italy for still making me feel as part of the group.

I also wish to thank all the co-authors of the papers for good collaboration and valuable input and comments on the manuscripts. Thank you Bernhard Ahrens, for the help with the German Summary.

My dearest "grazie" are reserved for my family: my parents Martin Solly and Nellise Alloa, and my sister Alys Solly. Thank you for your endless support and encouragement, unconditional faith and for always being there for me, even when I was far away. Our skype calls have been a continuous source of moral support. I hope that soon we will again have more chances to spend time all together. Martin, thank you for always being interested in my scientific research and for always reading my manuscripts. Nellise, thank you for your great hospitality every time I came back to Torino, and also... for teaching me how to use a sewing machine! This skill has been essential during the time of my PhD. Alys, I miss you a lot.

Jakob, thank you for your love and encouragement, and for supporting me, particularly in the last weeks of the PhD. I was lucky to meet you...

1 Introduction

1.1 Motivation

The levels of atmospheric carbon dioxide (CO_2) and other greenhouse gases are continuing to increase in the atmosphere, perturbing the climate system and the global carbon (C) cycle, primarily due to human activities such as fossil fuel combustion and land management (NOAA, 2014). In recent decades the quantification and characterization of these perturbations have been substantially improved thanks to advanced monitoring capabilities and new data set efforts (IPCC, 2013). However, the precise impacts of these changes remain highly uncertain mainly due to the lack of understanding of the Earth as a dynamic system. A major source of uncertainty arises from poorly understood long-term feedbacks between the global C cycle and the climate system (Cox et al., 2000; Friedlingstein et al., 2006; Heimann and Reichstein, 2008). A further challenge is given by the difficulty in predicting responses of C stocks to changes in land use and management intensification (Houghton et al., 2012).

The global C cycle is of central interest for the Earth system as C is one of the main constituents of living tissue and of two important greenhouse gases: CO_2 and methane (CH_4). Improving our knowledge about C exchanges between the atmosphere, the oceans and the terrestrial biosphere is essential, given that the terrestrial and marine environments are absorbing a large part of the CO_2 which is emitted by fossil-fuel burning (Schimel et al., 2001; Le Quéré et al., 2013). It is important to quantify the length and extent of this net CO_2 absorption in different ecosystem types (Reichstein et al., 2013). Scientific research is constantly being carried out to understand the C exchanges between the different C pools and how variations in these fluxes, in different ecosystems, can potentially mitigate or enhance climate change. The focus of this study lies on a large, yet potentially vulnerable C pool of the terrestrial biosphere: the soil.

At the global scale the amount of C stored in soils represents the largest terrestrial C reservoir in rapid exchange with atmospheric CO_2. Soil C includes about 1500 Pg

(1 Pg=10^{15}g) of soil organic C and 950 Pg of soil inorganic C (Jobbágy and Jackson, 2000; Lal, 2004; Scharlemann et al., 2014). This is more than three times the amount of C present in either the atmosphere or the terrestrial vegetation. Most of the concern associated with soil C responses to global change is mainly about the short and long term changes of organic C stocks. Yet, until now the predicted responses still largely differ in their magnitude (Jones and Falloon, 2009). This variability mainly reflects uncertainties in how models parameterize i) the influence of climate and land use changes on decomposition rates; and ii) the changes in the rate of soil organic C accumulation due to variations in vegetation productivity (Friedlingstein et al., 2006). To improve our predictions of changes in soil organic C, a better knowledge is required on the interacting and complex environmental factors (such as climate, land management, plant species composition and biodiversity) that allow organic matter to be formed, stabilized and lost in the soil environment (Trumbore, 2009). Although much of the C present in soil is derived from fine roots, the allocation and residence time of fine root C in soils is one of the least understood aspects of the global C cycle (Rasse et al., 2005; Strand et al., 2008). Hence, this thesis is specifically aimed to improve the current knowledge of the factors controlling these processes.

1.2 State of the art

1.2.1 Soil organic matter

Soil organic matter is an important human resource which plays a key role in determining most of the physical, chemical and biological properties of soils. For instance, it improves soil fertility and soil structure, serves as an energy source for heterotrophic soil organisms, increases soil water holding capacity, and is the largest terrestrial C reservoir (Ontl and Schulte, 2012). While traditionally the focus of research on soil C has been on the influence that organic matter has in determining soil fertility, during the past decades several studies on soil organic matter have clarified the mechanisms involved in the persistence of organic C in soils. Yet we are still lacking knowledge about the vulnerability of soil organic C to climatic and environmental change across a range of differently managed ecosystems and soil types (Trumbore, 2009; Scharlemann et al., 2014).

Soil organic matter is defined as the ensemble of all dead organic compounds in soil at all stages of decomposition, derived from plant, animal, and microbial biomass (Trumbore, 1997; Trumbore and Czimczik, 2008). While for decades it has been as-

sumed that soil organic matter was mainly composed of complex and relatively recalcitrant humic substances, we now understand that these large and complex components represent a small fraction of the total organic matter and that most of the molecular structures are broken down to simpler metabolic products which can organize through interactions with mineral surfaces and with each other (Lehmann et al., 2008; Kleber and Johnson, 2010; Schmidt et al., 2011; Kögel-Knabner, 2002).

1.2.2 The soil C cycle

The C stored in soils is commonly found in both organic and inorganic forms. This thesis focuses on organic C, although the exchanges between the inorganic components of the soil and the atmospheric CO_2, control atmospheric CO_2 concentrations over long time scales ($> 10^3$ years) (Berner et al., 1983; Chadwick et al., 1994; IPCC, 2013).

An overall scheme of organic C cycling in soil is shown in Figure 1.1. The major source of soil organic C is derived from plants which produce organic material by fixing atmospheric CO_2 by photosynthesis (Trumbore, 1997). A large part of this material enters the organic layers and the mineral soil in the form of plant litter (including dead roots, leaves and stems), as well as root exudates and symbiotic fungi. These inputs are then metabolized and transformed by the decomposer community, including soil fauna and microbes. During these processes a part of C is incorporated into the decomposer biomass and another part is respired as CO_2 or converted in soluble metabolites (dissolved organic matter) or microbial by-products. A portion of the C converted into microbial biomass and by-products can be also "recycled" into new microbial biomass (Gleixner et al., 2002). Lastly, a fraction of organic compounds is stabilized in the soil for a longer time (see paragraph 1.2.7).

Dissolved organic matter is a fraction of the total organic matter in soil, important in various biogeochemical processes due to its movement through soil pores and interactions with the mineral phase (Malik and Gleixner, 2013; Kindler et al., 2011). The current understanding of the sources of dissolved organic matter indicates that it is mainly derived by recent plant litter and soil organic matter, or produced anew by soil microorganisms (Kalbitz et al., 2000; Malik and Gleixner, 2013). Dissolved organic matter is also input of throughfall (Michalzik et al., 2001), and root exudation (Neff and Asner, 2001).

While most studies and models on soil C cycling have been focusing on the top 10-20 cm of the soil, a large part of organic C is found at deeper depths in a wide range of ecosystems (Jobbágy and Jackson, 2000; Rumpel et al., 2012). Hence, increasing

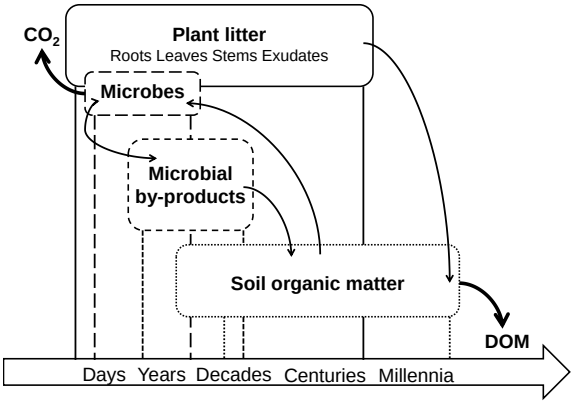

FIGURE 1.1: Organic C transformation pathways in the soil (adapted from Trumbore and Czimczik, 2008). The bottom arrow indicates the mean turnover times of each pool.

interest has been given to the organic matter stored in subsoil horizons, despite organic C is usually observed to decrease in its concentration with soil depth (Jobbágy and Jackson, 2000). Another property of subsoil C is that it has an older radiocarbon age compared to topsoil C (Trumbore, 2000, 2009; Schrumpf et al., 2013), suggesting that a high proportion of "deep" soil C is stable for a longer time. Although the mechanisms controlling the vertical distribution and age of subsoil organic C are poorly understood, the decline of microbial activities and organic substrates with soil depth, as well as changes in soil abiotic conditions (such as temperature and moisture variability and more frequent anaerobic conditions) are presumed to contribute to these patterns (Rumpel and Kögel-Knabner, 2011). In the frame of global change and soil organic C as a sink for atmospheric CO_2, it is crucial to better understand the processes which lead to to the build up and loss of big quantities of old C in subsoils (Trumbore, 2009; Rumpel and Kögel-Knabner, 2011).

1.2.3 Belowground C allocation

Determining the size of C inputs to the soil quantitatively or relative to the size of C losses due to leaching and mineralization is essential to predict how and why ecosystem C storage will vary due to global change (Bolinder et al., 2007; Trumbore, 2009). Belowground C allocation of plant litter and root exudation commonly equals or ex-

ceeds aboveground litterfall C, making it one of the main yet least well quantified C fluxes at the global scale (Davidson et al., 2002). This is because C allocation and root distributions belowground are difficult to estimate due to our low ability to observe and quantify root and mycorrhizal processes in situ (Trumbore and Gaudinski, 2003).

Measuring root primary production and root biomass, for instance, require the manual analysis of many root samples from a known volume of soil, and to account for large spatial and temporal variation (Nadelhoffer, 2000). By comparing minirhizotron data with measurements from horizontal in-situ root screens, Tierney and Fahey (2001) estimated that the productivity rate of fine roots is about 303 g m^{-2} yr^{-1} in the forest floor of a temperate broadleaf forest in North America. Estimates of fine root biomass (living + dead roots) from different age-class forest stands in Central Europe range between 119 and 636 g m^{-2} in the upper 30 cm of the soil (Claus and George, 2005). Commonly, fine root densities are greater in the top soil layers and gradually decrease with depth (Schmid, 2002).

1.2.4 Definition of fine roots

Plant fine roots allocate C into the soil, and they are the most dynamic part of the root system aquiring soil resources. Hence, fine roots have a key role in biogeochemical cycling (Strand et al., 2008; Lukac, 2011). Fine roots are also the primary site of infection by mycorrhizal fungi.

In this thesis we define fine roots as the roots with a diameter smaller than 2 mm. This definition has been commonly adopted in previous studies on root production, decomposition and turnover. Although it is easier to include all roots below a certain diameter in one size class, rather than sorting them into root branching orders, it is important to underline that this classification may cover up differences in tissue chemistry between roots with different biological function (Goebel et al., 2011). Roots belonging to different branching orders perform different functions, with higher orders (e.g. fourth and fifth) mainly used for structural support, transport and reserve storage, and lower orders used for acquiring nutrients and water from the soil (Guo et al., 2008; Valenzuela-Estrada et al., 2008; Goebel et al., 2011). Previous studies indicate that root tissue chemical properties such as C:N ratios, lignin and Ca concentrations vary between different root branching orders (Pregitzer et al., 2002; Guo et al., 2004; Fan and Guo, 2010).

1.2.5 Root turnover

Fine roots are an interface between plants and soil, therefore studying their turnover (growth and dieback), is important for quantifying the C input of fine roots to soil organic matter (Lukac, 2011). Unfortunately, measuring fine root turnover still represents a challenge in ecology due to the lack of reliable methods for measuring fine root lifespans (Lukac, 2011). The main drawback is that root growth and dieback usually happen simultaneously.

Traditionally, fine root turnover times have been directly determined by dividing the amount of living root biomass by the annual production rate of fine roots estimated with root in-growth cores, sequential coring or root screens; typically yielding values ranging from $<$1 to 3 years (Trumbore and Gaudinski, 2003). These methods all deal with big uncertainties due to large spatial and temporal variability in root distributions and most have significant disturbance effects (Lukac, 2011). In order to minimize labor-intensive and time-consuming methods, other methods have been developed to quantify root turnover times, including tracing the radiocarbon (^{14}C) bomb peak in fine roots (see Box 1), ^{13}C-^{14}C labeling, and following root growth and dieback in situ with cameras (minirhizotrons). Whereas minirhizotron observations suggest an even more dynamic picture of fine roots than the traditional methods, the isotopic measurements indicate that most root C is several years old (Gaudinski et al., 2001; Trumbore and Gaudinski, 2003; Matamala et al., 2003; Fröberg, 2012). These varying observations can be reconciled by assuming that different techniques collect information about roots with different function and lifespan, and hence that roots are not a single homogeneous pool (Trumbore and Gaudinski, 2003; Gaudinski et al., 2010). The C inputs from plants to soil depend on the turnover time of plant tissues, including fine roots, hence it is important that ecosystem C models incorporate findings on root turnover times for different ecosystem types and different plant species.

1.2.6 Litter decomposition

The decomposition of plant litter is the chemical and physical process which transforms litter to its chemical and elemental components (Aerts, 1997). Therefore decomposition dynamics largely control nutrient cycling in terrestrial ecosystems. The decomposition of plant litter can be divided in two stages. First, the litter is broken down by detritivores to small fragments. Second, bacteria and fungi further reduce and mineralize these fragments to inorganic molecules (Aerts, 1997). During these pro-

cesses the mass of the decomposing material decreases over time as it is metabolized, transformed and respired by the soil fauna (Bocock and Gilbert, 1957; Parton et al., 2007).

Decomposition rates (k) can be estimated from the rate of mass loss of fresh plant litter assuming first order kinetics:

$$\frac{dM}{dt} = -kM; \quad k = -t^{-1} \ln \frac{M_t}{M_0} \tag{1.1}$$

where M_0 is the initial mass and M_t is the mass at time t after deployment (Torn et al., 2009). Commonly, plant litter mass loss is studied with litterbag experiments, consisting of enclosing a known mass of litter in a number of screened containers and disposing it either in or above the mineral soil for a certain period of time (Bocock and Gilbert, 1957). This method is complicated, as a large number of litterbags is needed to account for spatial and temporal variability. Although most litterbag studies have focused on the decomposition of leaf litter and few of them have been published on root litter decomposition, similar decomposition patterns may or may not occur for the two litter types (Silver and Miya, 2001). For instance, there are differences in the chemical composition of organic compounds of above- and belowground litter types and in the factors affecting their decomposition rates (Kögel-Knabner, 2002; Hobbie et al., 2010).

Box 1

Radiocarbon (^{14}C) is a useful tool for investigating the dynamics of organic C in soils. ^{14}C is an unstable isotope of C which decays with a half-life of 5,730 years. It is constantly created by interactions of high energy cosmic rays with the upper atmosphere. The ^{14}C is oxidized to $^{14}CO_2$ and it is mixed into the troposphere (the lower part of the atmosphere), where it can be taken up by plants during photosynthesis or it can dissolve in the oceans or surface waters. The equilibrium between cosmogenic production, radioactive decay and mixing with the terrestrial biosphere and oceans, determines the natural abundance of ^{14}C (one every 10^{12} C atoms). Thermonuclear weapons testing, which peaked in 1963, nearly doubled the amount of ^{14}C in the atmosphere of the Northern Hemisphere (see Figure 1.2). After 1963, the amount of ^{14}C in the atmosphere decreased due to mixing with the atmosphere of the Southern Hemisphere, incorporation into terrestrial and oceanic C, and dilution due to fossil fuel burning. Hence, the "bomb" ^{14}C can be used as a global isotopic tracer for the C cycle. The principle of the radiocarbon method is that the age of organic material containing C can be estimated by measuring its ^{14}C concentrations, considering the background concentrations of $^{14}CO_2$ in the atmosphere at the time of fixation by photosynthesis and the rate of ^{14}C decay (Trumbore, 2009). Radiocarbon can be also used to estimate the mean age of carbon in plant tissues (Gaudinski et al., 2001). It can further be adopted to determine the relative stability of the soil organic C reservoirs (Torn et al., 2009; Trumbore, 2009).

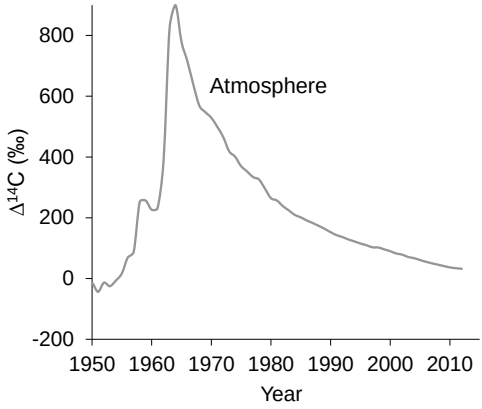

FIGURE 1.2: Atmospheric radiocarbon concentrations in the Northern Hemisphere from 1950 to date.

1.2.7 Organic C stabilization in soils

The persistence of organic matter in soil has been for decades related to its intrinsic chemical quality. However, more recent investigations have proved that soil organic matter quality alone does not control its stability: also, physicochemical and biological influences from the surrounding environment control the rate of decomposition of organic matter (Schmidt et al., 2011). Soil organic matter may be stabilized (protected from microbial respiration) by different mechanisms including:

I Physicochemical stabilization: as a result of the binding between soil organic matter and soil minerals (i.e. silt and clay particles) or other organic surfaces (Sørensen, 1972; von Lützow et al., 2006).

II Physical protection in aggregates: location of organic compounds in aggregates creates barriers to the interaction of organic substances and their contact to microbes and enzymes (Six et al., 2002).

III Chemical recalcitrance: although all organic C is ultimately potentially degradable, some precursor material may be difficult to decompose because of molecular level characteristics which might retard its degradation by microbes (i.e. pyrolized carbon formed in fire or some lipid compounds) (Preston et al., 2006; Mikutta et al., 2006).

IV Climatic stabilization: soil organic matter can be preserved by freezing temperature, high moisture content and low O_2 content (Torn et al., 2009).

An important mechanism for organic C stabilization is also the adsorption of dissolved organic matter to the mineral phase (Kalbitz and Kaiser, 2008). All of these mechanisms contribute to long term soil organic matter stabilization, but their relative importance is poorly known and varies between soil texture and mineralogy as well as local environmental conditions (von Lützow et al., 2006). Soil organic matter can be destabilized when the environmental and biological factors which control these processes are modified due to disturbance, erosion and changes in land management or plant species composition (Sollins et al., 1996; Torn et al., 2009).

Isotopically labeled C plant litter (enriched or depleted in ^{13}C or ^{14}C) may be added to soils to follow specific decomposition pathways, and finally determine how much of the litter-derived soil organic matter is decomposed rapidly or persists in the soil for

many years. These estimations are possible because soil organic matter can be separated into fractions with different density, namely: the organic debris residing inside and outside aggregates (light fraction) and the organic matter bound to minerals (heavy fraction) (Golchin et al., 1994; Sohi et al., 2001). The light fraction mainly consists of plant and animal litter at different stages of decomposition (Gregorich et al., 2006), while the heavy fraction contains higher amounts of microbial residues in comparison to the light fraction (Golchin et al., 1994). The organic compounds forming the heavy fraction can originate from decomposition products of the light fraction or from dissolved organic C in the percolating soil solution (Kalbitz and Kaiser, 2008; Sanaullah et al., 2011). The availability of binding sites on mineral surfaces controls organic C storage in the heavy fraction (Schrumpf et al., 2013). Evidences of radiocarbon and stable isotopic (δ^{13}C) measurements show that the heavy fraction usually contains older organic C in comparison to the light fraction (Schöning and Kögel-Knabner, 2006; Trumbore, 2009; Schrumpf et al., 2013; Herold et al., 2014a).

The formation of stable soil organic matter from fine root biomass is poorly known. Analytical and experimental advances suggest that root C might be stabilized preferentially in comparison to leaf or shoot C, contributing in high quantities to soil organic C (Rasse et al., 2005; Sanaullah et al., 2011). Some of the reasons are that fine roots can be more easily physically protected in soil aggregates, and that root decomposition products might be better incorporated on mineral surfaces due to their close proximity; roots are more recalcitrant compared to the above plant tissues because of higher lignin:N ratios and higher alkyl C content (Abiven et al., 2005; Rasse et al., 2005; Bird and Torn, 2006; Sanaullah et al., 2011).

1.2.8 Possible predictors of soil organic matter feedbacks to environmental change

Changes in climate, differences in soil parent material, variations in land management and plant species composition can affect organic C cycling in soil (Trumbore, 2000). However, a process understanding of soil organic matter responses to these factors is still insufficient for predictive models (Heimann and Reichstein, 2008; Trumbore and Czimczik, 2008).

Climate

It is complicated to separate climate and plant species composition controls on soil organic matter dynamics, as plant communities respond rapidly to changes in climate and as well influence the local microclimate (Trumbore, 2009). Studies on litter decomposition indicate that climate variables such as temperature and moisture, together with the chemical composition of plant litter, play a key role in influencing the initial stages of decomposition (Aerts, 1997; Silver and Miya, 2001). Decomposition is usually positively correlated with temperature due to associated increases in microbial activity and diffusion of substrates (Dioumaeva et al., 2002; Mikan et al., 2002). Moisture retention stimulates decomposer activity (Chen et al., 2000), as long as the conditions remain aerobic. If soil moisture contents are very high, oxygen diffusion is limited and may lead to anaerobic respiration and CH_4 production. Temperature, soil moisture and precipitation events also control seasonal changes in concentrations and fluxes of dissolved organic matter in soils (Kalbitz et al., 2000). Dissolved organic C concentrations commonly increase following rewetting after dry periods (Mcdowell and Wood, 1984). Likely as a result of reduced rates of decomposition in dry soils which drive the accumulation of microbial products leading to high dissolved organic C concentrations in the soil leachate (Kalbitz et al., 2000). Anaerobic conditions, caused by saturation, have also been observed to increase the release of dissolved organic matter from soils (Sedell and Dahm, 1990).

Soil parent material

Soil parent material, the mineral substrate from which soils develop, largely controls soil organic matter storage and turnover through its influence on soil texture and mineralogy. Soil texture (in particular clay and silt particles) has been observed to be positively correlated to soil organic C stocks in many sites (Sørensen, 1972; Hassink, 1997). Moreover, there is evidence that soil organic matter in clay and fine silt fractions turns over on longer timescales than organic matter in coarser fractions (Anderson and Paul, 1984; Eusterhues et al., 2003). Soil texture further controls the formation of aggregates in which organic matter can be protected from access by microbes, as well as biological activity and physical-chemical conditions (Six et al., 2002; von Lützow et al., 2006; Torn et al., 2009). Mineralogy, and in particular mineral surface area and surface charge, also contributes to directly control the stability of soil organic matter

via inter-molecular interactions between organic matter and mineral surfaces (Eusterhues et al., 2003).

Land management

Land management practices such as fertilization, mowing and grazing in grasslands, and thinning and harvesting in forests, are considered to decrease species diversity and alter biomass production, as well as its decomposition (Dickinson and Polwart, 1982; Hobbie, 2005; Semmartin et al., 2008; Berthrong et al., 2009; Liao et al., 2010; Socher et al., 2012). In intensively managed grasslands with overall high-nutrient contents, that is, high fertilization regimes, the need to mineralize organic matter may be lower than in extensively managed grasslands with low-nutrient contents (Fog, 1988). Hence, decomposition rates may be slowed down in these ecosystems. Moreover, plants from high-nutrient ecosystems might have different resource acquisition or conservation strategies and allocation to belowground parts than plants from low-nutrient grasslands. One hypothesis is that in less fertile sites plants may invest more energy in the formation and maintenance of new root tissues than plants in more fertile sites (Chapin III et al., 2002); consequently their roots might have longer turnover times. Field and laboratory experiments have shown that organic fertilization increases the release of dissolved organic matter due to stimulated mineralization and addition of water-soluble organic matter (Gregorich et al., 1998). Grazing and mowing activities may additionally alter decomposition rates through changes in soil properties such as soil moisture and bulk density (Taboada and Lavado, 1988; Sankaran and Augustine, 2004). Thinning and harvesting of trees in forest ecosystems may also lead to changes in soil C and nutrient concentrations due to a reduction in litter input and changes in local climatic conditions driving soil microbial processes (Nave et al., 2010). These results indicate that soil C is a potentially manageable resource. Nonetheless, it is not easy to generalize land use effects on soil organic C dynamics, due to the numerous interactions and feedbacks between vegetation composition and productivity, decomposer communities, and soil properties (Birkhofer et al., 2012).

Plant species composition and biodiversity

Plant species composition largely influences the amount of C stored in soils and its decomposability, as it determines the rate and the chemical quality of organic matter inputs. Hobbie (1996) showed that plant species belonging to the same func-

tional type were more similar in their effects on aboveground litter decomposition than were species belonging to different growth forms. Further, Hobbie (1996) found that graminoid litter had the fastest decomposition rate in comparison to woody species which decompose more slowly. Generally, leaf litter decomposition is inversely related to the C:N and lignin:N ratios and directly related to the N content of the litter (Hobbie, 1992). For instance, in temperate hardwood forests the foliar decomposition is directly related to its lignin:N ratio (Melillo et al., 1982). Due to the low number of studies on belowground decomposition it is still unclear whether root decomposition is similarly controlled by changes in plant species composition, and its related variations in root litter quality. Nevertheless, the results of a global meta-analysis by Silver and Miya (2001) indicate that fine root decomposition rates were closely linked to changes in root litter chemistry, in particular to lignin:N, C:N ratios, as well as Ca and N concentrations.

Recent results from field experiments across terrestrial ecosystems ranging from the subarctic to the tropics indicate that a reduction of functional diversity of decomposers and plant litter types slows down the cycling of litter C and other nutrients. Overall, this suggests that species diversity loss, related to changes in land management and climate, has large effects on litter decomposition and the cycling of C on broad spatial scales (Handa et al., 2014).

1.3 Aims and objectives

Considering the above-mentioned research gaps, the main aim of this thesis is to improve our understanding of the potential factors that can affect root derived C allocation, storage and loss in a range of soils in temperate forests and grasslands. Specific attention is given to fine root turnover times, decomposition rates of fine roots and stabilization of root-derived C in relation to different climate, soil parent material, land management, plant species composition and biodiversity at the regional scale. In particular, the thesis aims to accomplish the following objectives:

I To estimate the mean C age of fine roots with the bomb-radiocarbon technique in a range of grasslands and forests with diverse plant species diversity, land management and soil properties.

II To quantify root litter decomposition in the topsoil of differently managed temperate grasslands and forests; and to understand whether environmental site con-

ditions or differences in root litter quality (due to changes in plant species composition) have a stronger influence on decomposition at the regional scale.

III To determine the depth-dependence of the decomposition of fine roots for a range of beech forest soils differing in climate and parent material.

IV To quantify how much root C is stabilized long-term in the mineral associated organic matter in temperate grassland soils which differ in their texture.

The activities of this thesis are included in the framework of the Biodiversity Exploratories project (Fischer et al., 2010) funded by the German research foundation (DFG). The Biodiversity Exploratories provide the scientific infrastructure to study the effects of forest and grassland management on biodiversity and ecosystem processes in the long term and on a large scale. They comprise a hierarchical set of standardized field plots in three different regions of Germany: the Biosphere Reserve Schorfheide-Chorin in the State of Brandenburg, the National Park Hainich and its surroundings in the State of Thüringen, and the Biosphere Reserve Schwäbische Alb in the State of Baden-Württemberg (Figure 1.3). Each region consists of 50 experimental grassland plots and 50 experimental forest plots with different land use types and intensities and has a size bigger than 400 km^2. These regions are disposed along a climate gradient and differ in their parent material. In Schorfheide-Chorin, the dominant parent material is glacial till. The glacial till is often covered by aeolian and fluvial sand in depressions. In Hainich-Dün, the parent material is loess over Triassic shell lime-stone. The soils of the Schwäbische Alb formed on Jurassic limestone. Mean annual temperatures range from 8-8.5 °C in Schorfheide-Chorin, 6.5-8 °C in Hainich-Dün and 6-7 °C in the Schwäbische Alb. Mean annual precipitation is highest in the Schwäbische Alb, followed by Hainich-Dün and Schorfheide-Chorin, ranging from 500 to 1000 mm.

FIGURE 1.3: Geographic location of the three Biodiversity Exploratories in Germany (source: University of Münster, Institute of Landscape Ecology).

1.4 Outline of the thesis

Including the introduction, this thesis comprises six main chapters. Chapters 2 - 5 are thematically aligned with the four main research objectives described above. An evaluation of the long-term effects of land management and soil properties on estimated fine root C ages in temperate grasslands and forests is provided in Chapter 2. Fine root C ages are estimated from radiocarbon measurements associated with a steady state model implemented by Gaudinski et al. (2001). In Chapter 3, fine root decomposition rates between temperate grasslands and forests are compared at large spatial scale using the litterbag method during the first 12 months of decomposition. Moreover, the effects of litter quality and environmental site effects on fine root decomposition are quantified using a partition of variation analysis. Chapter 4 presents a study to test whether decomposition rates of fine root litter vary with depth for a range of soils in temperate beech forests. The initial decomposition rates are calculated from the mass loss of fine root litter buried in litterbags at 3 different soil depths (5, 20 and 35 cm). In Chapter 5 the amount of root-derived C transfered to the mineral associated soil or-

ganic matter of soils with different texture is estimated, after incubating ^{14}C depleted grass root litter in sieved subsoil in the field for 18 months. Finally, Chapter 6 discusses the main findings of the thesis and provides an outlook on their potential future implications.

2 Mean age of carbon in fine roots from temperate forests and grasslands with different management[1]

Abstract

Fine roots are the most dynamic portion of a plant's root system and a major source of soil organic matter. By altering plant species diversity and composition, soil conditions and nutrient availability, and consequently belowground allocation and dynamics of root carbon (C) inputs, land-use and management changes may influence organic C storage in terrestrial ecosystems. In three German regions, we measured fine root radiocarbon (^{14}C) content to estimate the mean time since C in root tissues was fixed from the atmosphere in 54 grassland and forest plots with different management and soil conditions. Although root biomass was on average greater in grasslands 5.1 ± 0.8 *g (mean±SE, n=27) than in forests* 3.1 ± 0.5 *g (n=27) ($p < 0.05$), the mean age of C in fine roots in forests averaged* 11.3 ± 1.8 *yr and was older and more variable compared to grasslands* 1.7 ± 0.4 *yr ($p < 0.001$). We further found that management affects the mean age of fine root C in temperate grasslands mediated by changes in plant species diversity and composition. Fine root mean C age is positively correlated with plant diversity ($r = 0.65$) and with the number of perennial species ($r = 0.77$). Fine root mean C age in grasslands was also affected by study region with averages of* 0.7 ± 0.1 *yr (n=9) on mostly organic soils in northern Germany and of* 1.8 ± 0.3 *yr (n=9) and* 2.6 ± 0.3 *(n=9) in central and southern Germany ($p < 0.05$). This was probably due to differences in soil nutrient contents and soil moisture conditions between study regions, which affected plant species diversity and the presence of perennial species. Our results indicate more long-lived roots or internal redistribution of C in perennial species and suggest linkages between fine root C age and management in grasslands. These findings improve our ability to predict and model belowground C fluxes across broader spatial scales.*

[1] This chapter is published as Solly, E., I. Schöning, S. Boch, J. Müller, S. A. Socher. S. E. Trumbore, and M Schrumpf, 2013. *Biogeosciences* **10**, 4833–4843.

2.1 Introduction

In terrestrial ecosystems, plant fine roots (defined here as < 2 mm in diameter) play an important role in biogeochemical cycling (Brunner and Godbold, 2007). The flux of C from plants to soil includes allocation to grow and maintain roots, and to support supply of C to the rhizosphere. Fine roots are considered to be the most dynamic part of the root system and to control the acquisition of water and nutrients from the soil (Lukac, 2011). However, estimating the amount of C allocated in fine roots and the turnover times of root systems are still challenges in ecology. Furthermore, our ability to observe directly and quantify roots in situ is limited (Majdi et al., 2005; Trumbore and Gaudinski, 2003).

Estimates of C allocation to root growth and maintenance have been based on the assumption that fine roots turn over approximately annually (Jackson et al., 1997). However, measurements of isotopes in fine roots demonstrated that both the ^{14}C age (Gaudinski et al., 2001) and the incorporation rate of a continuous ^{13}C label (Matamala et al., 2003) in fine root C were inconsistent with an annual turnover. The various observations can be reconciled by assuming that fine roots are not a single homogeneous pool (Gaudinski et al., 2010; Guo et al., 2008; Strand et al., 2008; Tierney and Fahey, 2002; Trumbore, 2009). To date, published fine root radiocarbon ^{14}C data are mostly from forest ecosystems and little is known of how these observations apply to non-forested ecosystems, or a range of forest types (Fröberg, 2012; Gaudinski et al., 2010; Riley et al., 2009). Identifying predictors of fine root C age is of specific importance to develop indices of root dynamics and modelling efforts given the pressing need to improve our knowledge about belowground C fluxes (Ostle et al., 2009).

Management intensification and land-use changes are considered to be the main processes eroding species diversity (Laliberté et al., 2010). Changes in plant species can influence ecosystem nutrient dynamics by a variety of mechanisms including biomass production, decomposition and nutrient cycling (Hättenschwiler et al., 2005; Hobbie, 1992; Tilman et al., 1996). However, the mechanisms by which management-driven alterations of plant species diversity, and soil conditions including moisture, pH and nutrient availability can affect mean ages of fine root C and belowground C cycling remain unclear (Schmidt et al., 2011). For example, older roots may occur in less fertile sites because plants invest less in new tissues than plants in nutrient-rich sites (Chapin III et al., 2002). Thus, differences in the mean age of root C between trees and grasses, or perennial and annual plants, could reflect differences in plant resource con-

servation and acquisition strategies between species or functional types. These in turn can reflect differences in root anatomy, chemistry and architecture, and the capacity for internal recycling of C in perennial root systems. Predicting ecosystem responses to environmental change requires understanding of root dynamics from a range of vegetation covers representing forests and grasslands across a large spatial scale and over a range of managements and soil types. To address some of these questions, plant species may be classified according to their ecological behaviour (i.e. Ellenberg's ecological indicator values; (Ellenberg et al., 2001), to summarize environmental factors like soil moisture and available nitrogen (N) content. However, those factors such as moisture and the available N content in the soil can be altered by management and climate during the growing season.

Radiocarbon measurements of roots are a useful measure for understanding belowground carbon fluxes, if the root carbon pools of interests are defined appropriately (Majdi et al., 2005). ^{14}C is a radioactive isotope (half-life 5730 yr) which is naturally present in the atmosphere. Thermonuclear weapon explosions in the atmosphere also produce radiocarbon and during the 1950s and early 1960s nearly doubled the amount in the Northern Hemisphere atmosphere. Since the nuclear test ban treaty in 1963, atmospheric ^{14}C values have been declining through atmospheric mixing, incorporation into terrestrial and aquatic C pools and dilution by combustion of ^{14}C free fossil fuels. The documented time history of atmospheric "bomb" ^{14}C provides a global isotope tracer of the carbon cycle (Naegler and Levin, 2006; Randerson et al., 2002). Plants fixing atmospheric CO2 record its ^{14}C signature, once data are corrected for mass-dependent isotopic fractionation (Stuiver and Polach, 1977). The precision of ^{14}C measurements using accelerator mass spectroscopy (AMS; $\pm$ 2-3 ‰) combined with the recent rate of ^{14}C decline of $\sim$ 4-5 ‰ per year (Levin et al., 2010) enables us to use radiocarbon as a tool for determining the average time elapsed between C fixation and its incorporation into root tissues (Gaudinski et al., 2001). Accordingly, ^{14}C investigations can be used to estimate average fine root C ages rather than the direct turnover time of root systems.

Here we use ^{14}C to estimate root C age of fine roots samples in 27 grasslands and 27 forest plots with different management in three regions in Germany, with a steady-state model implemented by Gaudinski et al. (2001). Because part of the overall C age might reflect plant allocation of older carbon to the root system, we use the term "fine root C age" instead of fine root age. Our main objective is to evaluate the differences in the mean age of the standing stock of C in root biomass in grassland and forest sites

under diverse management, plant species diversity and soil properties. We are also interested in understanding if the mean age of C in fine roots is related to fine root nutrient concentration and root biomass. We hypothesize that (i) in forest ecosystems the age of root carbon is older than in grasslands due to the greater ability of trees to use storage compounds and recycle C internally; (ii) in grasslands the management effect is reflected in the mean age of fine root C and is mediated by the total number of perennial species present; (iii) ^{14}C of fine roots differs between study regions mainly driven by differences in soil characteristics (e.g. nutrient contents) and climate.

2.2 Materials and methods

2.2.1 Study regions

The research was carried out in 54 plots distributed in three German regions, the so-called Biodiversity Exploratories (Fischer et al., 2010), which comprise a variety of forests and grasslands managed with different intensities. The Schwäbische Alb (ALB) is situated in south-western Germany, the Hainich-Dün (HAI) in central Germany and the Schorfheide-Chorin (SCH) in north-eastern Germany. The three study regions differ in climate, altitude and soil characteristics (Table 2.1; for details, see Fischer et al. (2010).

	ALB	HAI	SCH
Location	SW Germany	Central Germany	NE Germany
Coordinates	48 °26'N, 9 °23'E	51 °9'N, 10 °28'E	53 °0'N, 13 °46'E
Area	$\sim$ 422km^2	$\sim$ 1300km^2	$\sim$ 1300km^2
Soil type forest	Cambisol (Eutric)	Luvisol	Cambisol (Dystric)
Soil type grassland	Leptosol/Cambisol	Cambisol/Stagnosol	Histosol/Gleysol
Altitude a.s.l.	$460 - 860$m	$285 - 550$m	$3 - 140$m
Annual mean temperature	$6.0 - 7.0\,^{\circ}$C	$6.5 - 8.0\,^{\circ}$C	$8.0 - 8.5\,^{\circ}$C
Annual mean precipitation	$700 - 1000$mm	$500 - 800$mm	$500 - 600$mm

TABLE 2.1: Main geographical and environmental characteristics of the three study regions.

In each region we selected 9 grassland an d 9 forest plots to span a range of land-use intensities. In grasslands of the ALB and SCH, we selected three plots of different land uses: unfertilized pastures, fertilized meadows and mown pastures. The mown pastures were unfertilized in SCH and fertilized in ALB. In forests of the ALB and SCH, we selected three European beech (*Fagus sylvatica* L.) dominated unmanaged stands, three European beech dominated age-class managed forests and three conifer plantations (Norway spruce (*Picea abies* (L.) H. Karst) in the ALB and Scots pine

(*Pinus sylvestris* L.) in the SCH). For the HAI we followed a different plot-selection scheme, and selected 9 grassland and 9 forest plots following gradients of soil texture and land-use intensity. Land-use intensity in HAI grasslands was quantified as a land-use intensity index (LUI) summarizing the individual land uses by summing up values for fertilization (kgN per hectare per year), mowing (times mown per year), and grazing intensities livestock units per hectare per year), which have been normalized by the mean of the appropriate land-use type in order to standardize the scales (Blüthgen et al., 2012).

To evaluate land-use and disturbance intensity in the forests, we used an index called LUDI. This index was established Luyssaert et al. (2011) by combining values of stand density and diameter at breast height for a relatively unmanaged forest and different management schemes, in conjunction with self-thinning values. The LUDI is calculated as the sum of two components: the "planning intensity", which relates to the potential stand density and the associated changes in diameter, and the "operational intensity", which relates to the standing biomass (or diameter) at a given stand density. Thus, the LUDI distinguishes between the long and short timescales which are associated with management and disturbance.

2.2.2 Soil and root sampling

Root sampling took place in early May 2011. On each plot we collected 14 mineral soil cores using a split tube sampler with a diameter of 5 cm. In the forest sites organic layers were collected and removed before coring; in grasslands, aboveground portions of plants were removed. Cores were taken along two transects which were always selected in the same relationship to the overall plot. The two transects were 20 m long in grasslands and 40 m long in forests; the soil cores were evenly collected at a distance of 7m in the forests and of 3 m in the grasslands. We then opened the core and cut a section representing a fixed sampling depth of 0 to 10 cm for further analysis.We prepared composite samples by mixing the material collected from the 14 cores. Roots were then removed from the composite sample, refrigerated at $4\,^{\circ}\mathrm{C}$ and transported to the laboratory. Then, we removed the soil particles attached to the roots by cleaning them with distilled water in a 500 μm sieve and collected the fine roots with a diameter < 2 mm. Dead roots were removed from the < 2 mm samples based on qualitative visual characteristics, including colour and breakability. Fine root samples were dried at $40\,^{\circ}\mathrm{C}$ to constant weight in a force-air oven. The roots were stored in plastic bags at room temperature until analysis.

2.2.3 Biomass, C and N concentrations and C and N stocks of fine roots

We weighed the dry biomass of the fine roots after drying. Total C and N concentrations of ground fine root material were analysed using an elemental analyser "Vario EL" (Elementar Analysensysteme GmbH, Hanau, Germany). Spruce needles (CRM 101 with 51.44% C; 1.889% N) were used as reference material. Root samples collected in the grasslands, which in our plots are characterized by higher pH values (5 to 7.5) than forests (3.0 to 6.0), were decalcified in order to avoid carbonate contamination. Carbon and nitrogen stocks of fine roots (0-10 cm depth) were calculated from the total carbon and nitrogen concentrations in the roots and from the dry biomass values of each sample.

2.2.4 Management data, vegetation survey and soil characteristics

In forests, land use was verified with a systematic inventory of a circular sampling area of 500 m^2 (Fischer et al., 2010). In grasslands, land-use intensity data were obtained from a questionnaire for all land users. Forests were not fertilized. In 2008, we recorded the vegetation in forests in spring and again in summer, and in grasslands only once in summer. Plots in grasslands were 4 m x 4 m and in forests 20 m x 20 m. We identified all vascular plant species and estimated their percentage cover. To assess the diversity of the vascular plant species in the forest plots, we combined the spring and summer records in order to consider early and late emerging plants. We calculated the "Shannon index" as a measure of plant species diversity. This index is based on an expression elaborated by Shannon for his mathematical theory of communication, where H corresponds to the entropy (Shannon, 1948) (Eq. 2.1):

$$H = -\sum_{i=1}^{n} p_i \ln p_i \tag{2.1}$$

pi is the percentage of the individuals represented by species i and is assessed by the quotient of number of individuals of species i (N_i) and the total number of individuals (N). Thus, the maximum diversity possible for *N* individuals occurs when each individual belongs to a different species. We further calculated the total number of annual and perennial species per plot. We used Ellenberg indicator values for "moisture" and "nitrogen" for each plot. These indicator values represent a measure of the real-

ized ecological niche on an ordinal scale from 1 to 9 (Ellenberg et al., 2001) and are considered to be a valuable tool that can perform well (Schaffers and Sỳkora, 2000).

We also measured soil pH of the same combined mineral soil samples from which we collected the roots. Soil samples were air-dried and sieved to < 2 mm. Then, we calculated the mean of two pH measurements per soil sample, which were analysed in a 0.01 $MCaCl_2$ solution with a soil solution ratio of 1 : 2.5.

2.2.5 Radiocarbon measurements and root C mean age

We measured the ^{14}C content of the ground fine root samples at the accelerator mass spectrometry (AMS) facility in Jena, Germany (Steinhof et al., 2004). After combusting the samples, the resulting CO_2 was catalytically reduced to graphite at $625\,^{\circ}C$ by H_2 reduction. An aliquot of the CO_2 was used to determine the $\delta^{13}C$ of the sample. We express radiocarbon data as $\Delta^{14}C$, which is defined as the difference in parts per thousand (‰) between the ^{14}C / ^{12}C ratio in the sample, corrected for mass-dependent isotope fractionation to a common $\delta^{13}C$ value of -25‰ , in comparison to an oxalic acid universal standard (Trumbore, 2009) (Eq. 2.2). The standard is corrected for decay between 1950 and the year of the measurement y, which for the present work was 2011.

$$\Delta^{14}C = \left[\frac{\frac{^{14}C}{^{12}C}]_{sample,-25}}{0.95\frac{^{14}C}{^{12}C}]_{Oxl,-19} \times e^{(y-1950)/8267}} - 1 \right] \cdot 1000 \qquad (2.2)$$

We further derived the mean C age of fine roots, which represents the time C was stored in the plant before being allocated for root growth, plus the root average lifespan. For our composite root samples, we chose a steady-state model implemented by Gaudinski et al. (2001). This method includes the ^{14}C concentration of atmospheric CO_2 over the past n years, where n represents the average age of the root composite sample assuming that any variation in ages of the root mixture is normally distributed around the mean (Gaudinski et al., 2001). The equation we used is (Eq. 2.3):

$$C_{(t)} \times R_{root(t)} = I \times R_{atm(t)} + C_{(t-1)} \times R_{root(t-1)} \times (1 - k - \lambda) \qquad (2.3)$$

In this method C is the carbon stock of fine roots expressed in g Cm^{-2}, I the input of C by new production of fine roots in g Cm^{-2} yr^{-1}, k the multiplicative inverse of the

mean age of fine root C age in yr^{-1}, and *t* equals the time (yr) for which the calculation is being performed. R_{root} is calculated as [$\Delta^{14}C_{root}$/1000+1] (Torn et al., 2009); *k* is the radioactive decay constant for ^{14}C (1/8267 yr). For the time history of radiocarbon (R_{atm}) at the three sites, we used (Levin et al., 2010), updated to 2012 (personal communication). An example of the method for using ^{13}C values to estimate the mean age of C in fine roots is illustrated in Fig. 2.1. The atmospheric $^{14}C_2$ (R_{atm}) value for spring 2011 is equal to (1.034, or 34‰/1000+1). The model assumes a constant input and output of C to the root fraction every year. Thus, significantly large variations of storage capacities and fluxes between years (for instance, a greater root production in dry years rather than wet years, or a larger consumption of old storage compounds in dry years) might bias the results of the model. Further, the model assumes a homogeneous pool of roots. Therefore, it is possible that by using this method we are averaging more than one pool, i.e. short-lived roots and long-lived roots (Gaudinski et al., 2010). Local release of fossil C can impact the mean ^{14}C signature at any or all of our sites, which would tend to reduce the Ratm, and can potentially lead to $\Delta^{14}C$ root values lower than 34‰ (i.e. contemporary roots were formed in 2011 from freshly fixed photosynthetic products). The presence of fossil C signatures would serve to underestimate systematically the age of root C; since we did not encounter many samples with $\Delta^{14}C$ below the current atmosphere, and mostly in the SCH grasslands, we do not think there is a large systematic bias in our results.

2.2.6 Statistics

We conducted all analyses with the (R Core Team, 2012) version 2.15.2 (R). To examine statistical differences of biomass, C and N concentrations and stocks, ^{14}C content and mean C age of fine roots across the three study regions and between grasslands and forests, we used twoway analysis of variance (ANOVA) accompanied by Holm's test. To detect statistical differences of plant diversity and perennial species present on plot among study regions in the grasslands, we used one-way ANOVA. We present data as means$\pm$standard error. We used linear least-squares to compare correlations among all variables. For the grassland sites, we determined the Cox proportional hazards test (Cox, 1972) to identify the risk ratio of different variables on fine root C mean age. We used linear regression to assess the effect of plant diversity, number of perennial species, root nutrient concentrations, Ellenberg indicator values for soil moisture and available N content on the mean age of fine roots. Prior to analysis we transformed

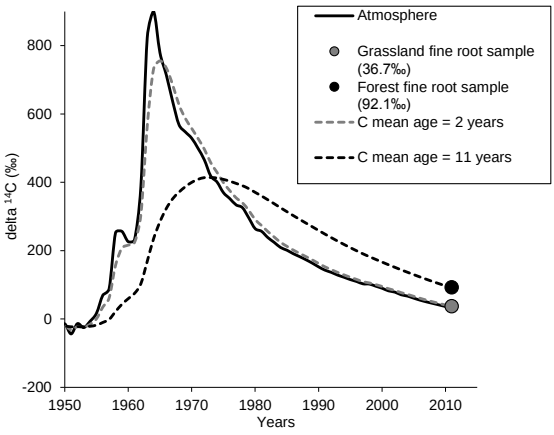

FIGURE 2.1: Example of the model we used to determine the mean age of fine root C from the ^{14}C signature of the fine roots (Gaudinski et al., 2001).

data if necessary to meet assumptions of normality. For all statistical tests, we use a significance level of 0.05.

2.3 Results

2.3.1 Fine root biomass and C and N stocks

Fine root biomass was greater in grasslands than in the forests of the SCH ($p < 0.001$), although this pattern was not observed to be significant in the HAI and ALB study regions (Table 2.2). In grasslands, fine root biomass was greater in SCH and HAI than in the ALB, while in the forests HAI had the highest biomass, followed by ALB and SCH (Table 2.1). Carbon concentrations of roots were higher in the forest sites compared to the grassland sites for all study regions ($p < 0.05$). Further, total C concentrations were observed to be significantly higher in SCH and ALB than in HAI for both grasslands and forests. Total fine root N concentrations did not differ significantly among forests and grasslands (Table 2.3), although in grasslands higher N concentrations were observed in the SCH, followed by HAI and ALB (Table 2.2). C and N stocks of roots reflected patterns of biomass (Table 2.2).

2.3.2 Fine root radiocarbon in grasslands and forests

Most ^{14}C values exceeded the contemporary atmospheric mean (34‰ in spring 2011), indicating that the fine root samples analysed in this study contained a detectable proportion of "bomb" carbon fixed from the atmosphere after 1964. In the forests, fine root mean ^{14}C values exceeded the contemporary atmospheric average in all study regions by 53 to 58‰. In the grasslands, mean fine root ^{14}C values also exceeded the contemporary atmospheric mean by 6‰ in ALB and 2‰ in HAI, while in SCH the average root ^{14}C values were lower than atmospheric ^{14}C values for 2011 by 2‰.

Overall, the greatest difference in fine root $\Delta^{14}C$ values was between forests and grasslands (Table 2.4), with significantly higher and more variable $\Delta^{14}C$ in the forest sites, ranging from 135‰ to 50 ‰, than in grasslands with fine root ^{14}C values ranging from 49‰ to 26‰. Due to the major variation of fine root ^{14}C values, we did not encounter any significant effects of changes in plant diversity, management and root quality on the fine root carbon age in forests.

The ^{14}C values of fine roots collected in the forest sites did not differ significantly between study regions, although the variability in ALB was higher 88$\pm$12‰ than in HAI 94$\pm$6‰ and SCH 87$\pm$7 ‰. This corresponds to mean ages of 5 to 30 yr in the ALB, 8 to 16 yr in the HAI and 6 to 16 yr in the SCH. In contrast, root ^{14}C values were less variable in grasslands, and significant variations among the three study regions were detected (Table 4, Fig. 2.2). The ^{14}C content of bulk live fine roots in the ALB grasslands had a mean value of 40$\pm$2‰ indicating mean ages overall ranging from 1 to 5 yr, whereas the root samples from the HAI grasslands showed mean ^{14}C values of 36$\pm$2‰ with ages ranging from 0 to 3 yr, and the SCH grasslands had the lowest ^{14}C values 32$\pm$1‰ with ages of 0 to 1 yr.

2.3.3 Effect of plant diversity and number of perennial species on fine root C mean age in grasslands

In grasslands, plant species diversity (Shannon diversity) was positively correlated with the total number of perennial species (Table 2.5). Further, across all study regions the mean age of fine roots in grasslands increases with species diversity and with the number of perennial species ($p < 0.001$, Fig. 2.3). The unit risk ratios indicated that higher plant diversity and greater presence of perennial species significantly increased the mean age of C in roots (Table 2.6).

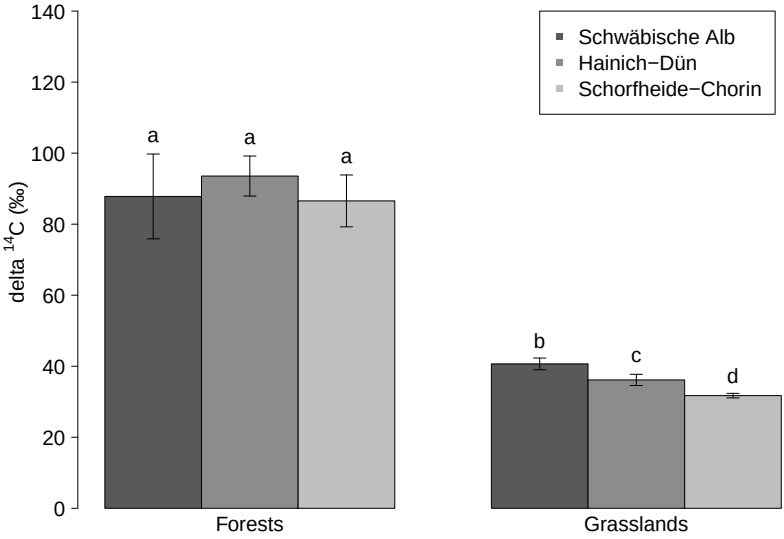

FIGURE 2.2: Comparison of mean Δ^{14}C values of fine roots between grassland and forest sites across study regions ($p < 0.001$). The columns denoted with different letters are significantly different ($p < 0.05$). Error bars represent SE of means (n = 9).

Mean plant diversity was largest in ALB (2.3±0.1), followed by HAI 2±0.1 and SCH 1.6±0.1 ($p < 0.05$) according to one-way ANOVA analysis. Also the average number of perennial species was observed to be higher in ALB 29±4 followed by HAI 22±3 and SCH 15±1 (p < 0.05) according to oneway ANOVA analysis. Plant diversity ranged from 1.0 to 2.9 (mean: 2.0±0.1) and declined significantly for increasing values of soil available N and soil moisture according to the Ellenberg indicator values (p <0.05, Table 5). The absolute number of perennial species present on plots ranged from 11 on plots characterized by higher soil available N content to 47 on plots characterized by lower soil available N content (mean: 22±2), and also decreased significantly for increasing Ellenberg indicator values for soil moisture content and root N concentrations ($p < 0.05$, Table 5). We found no strong relation between pH and root biomass and the ^{14}C age of fine roots for our grassland study sites. Fertilization, grazing and mowing activities as well as the LUI index did not directly influence fine root C mean age significantly.

2.4 Discussion

2.4.1 Root ^{14}C age difference between grasslands and forests

Our findings of higher ^{14}C contents in the forest fine roots than in the grassland fine roots by 9 yr support our hypothesis that in forest ecosystems the age of root C is older than in grasslands (Table 4). We used radiocarbon contents to infer the mean C age in roots rather than root longevity. Overall the ages of fine root C were broadly consistent with earlier radiocarbon studies in forest mineral soils and in pastures (Gaudinski et al., 2001, 2010; Sah et al., 2013; Strand et al., 2008; Veldkamp, 1994). Older root C age in the forest sites may be due to higher contents of perennial root tissues or to the ability of tree species to use storage compounds and recycle C internally on a longer term compared to annual and perennial species in grasslands. Sah et al. (2013) recently concluded from their results that new live tree roots may use old carbon reserves for cellulose formation.

We further found a greater variability in ^{14}C of fine roots in forests than in grasslands. This could be attributed to major differences in root-branching and chemistry in fine tree roots compared to fine roots of herbaceous species growing in grasslands (Waisel et al., 2002). Guo et al. (2004) suggested that root age might be related to cellulose content in different root branching orders in trees. Cellulose was observed to increase from the most distal parts of the fine root system (first and second root orders) to the more proximal portions (fifth order roots) (Guo et al., 2004). An inclusion of various root orders with different functions in the selected diameter size class of $<$ 2mm is also possible. It might be that forests species produced more variable amounts of short-lived, absorptive roots vs. long-lived, transport/storage roots.

Negative relations between fine root N concentrations and fine root lifespans have also been previously reported (Tjoelker et al., 2005). Furthermore, patterns of higher N and P concentrations in roots of lower order rather than higher order were observed in four tree species of temperate forests by Goebel et al. (2011). However, we did not see significant differences in N content between roots of forests and grasslands (Table 3), even though they differed markedly in age. Under the assumption that older mean ages of forests are due to longer turnover times rather than internal recycling of C, our observation of less root biomass in forests compared to grasslands suggests overall smaller root litter input to forest than grassland topsoils. We can however only refer to the upper 10 cm of the mineral soil, and it is possible that in forests litter input to subsoils is larger than in grasslands (Jobbágy and Jackson, 2000).

2.4.2 Root ^{14}C age in grassland ecosystems

We confirmed our hypothesis that in grasslands the management effect is reflected in the mean age of fine root C and is mediated by the total number of perennial species present, by observing that the age of C in fine roots was significantly greater on sites characterized by a higher plant diversity and total number of perennial species. This relates to the results from a number of ^{14}C pulse labelling studies by (Veldkamp, 1994) and (Milchunas et al., 1985), which demonstrated that C is recycled in perennial grass roots over a period of years. In contrast, annual plants are constructed almost entirely of contemporary atmospheric-derived C except what is inherited from their seed.

Although the number of fertilized plots was limited to 12 plots, our results suggest a negative relation between the amount of fertilizer and the total number of perennial species present on the plots (Table 5, $p = 0.06$). This in turn can reflect in variations of mean age of C in fine roots. Previous studies have already demonstrated the negative effects of fertilization on species richness (Socher et al., 2012; Stewart and Pullin, 2008; Zechmeister et al., 2003). Recently, a study by Socher et al. (2012) conducted in the same study regions has shown a loss of 19% of the total number of vascular plant species on a grassland site with an annual fertilization input of 35 kg of N per hectare. Given the limited amount of grazed and mowed sites in our dataset, we did not find any significant effect of these management practices on root C age. We also did not find any significant correlation with soil pH, which was surprising because we expected that soil pH would vary according to different management schemes (Falkengren-Grerup et al., 2006; Birkhofer et al., 2012)

Addressing our third hypothesis that the ^{14}C content of fine roots differs between study regions due to differences in soil characteristics and climate, we found that in grasslands the variation of ^{14}C age of fine roots among study regions is considerable, with older root C in ALB followed by HAI and SCH. We assume that the annual plant roots with lower than ^{14}C atmospheric values, which we mainly found in the SCH grasslands, might define the local atmospheric ^{14}C. As this effect was not great (2‰), we did not correct for the calculated ages. We further believe that regional differences are not due to different levels of contamination because there was no such trend in the adjacent forests. Nevertheless, we cannot exclude the possibility that these roots may have taken up extremely old carbon which was stored in the organic soils, i.e. amino acid C. The ability of herbaceous plant species to take up amino acids was demonstrated by Näsholm et al. (2000).

We did not find the same pattern in the forests, where the larger variability may overprint similar effects and induce management dissimilarities. We relate differences among study regions to variations in climate and soil properties like moisture and nutrient content, which may lead to changes in species diversity and total number of perennial species. Nutrient-poor sites (i.e. ALB) could for example favour perennial species over annual species, reflecting a trade-off between rapid acquisition of resources and conservation ofresources (Tjoelker et al., 2005). Older root C age in nutrientpoor sites may be explained by the necessity of plants to optimize the uptake of nutrients (Sah et al., 2013), for example by reducing carbon and nutrient expenses in fine root production.

The climate gradient across the three study regions could also reflect differences in fine root C mean age. As the mean temperatures are higher in SCH than in ALB and we collected samples in spring, plants in northern Germany may have grown a larger amount of newly grown roots than plants in southern Germany at the time of sampling. This might have resulted in a relatively larger contribution of young roots in SCH.

Furthermore, variations in perennial root tissue may also occur as a result of plant functional types or phenotypical variation in plants in reaction to different nutrient and energy limitations in the study regions, resulting in root mean C age changes. The negative correlation between root mean C age and root N content (Table 5), which we found in grasslands for example, suggests that larger N contents of roots with faster turnover could be due to a greater contribution of lower order roots. We also found that root biomass and related C stocks were greater in more fertile sites characterized by lower ^{14}C content in roots, indicating faster root turnover (i.e in SCH, HAI) than in less fertile sites showing higher ^{14}C content in roots (ALB). The largest fine root litter input to the soil therefore probably occurs in the more fertile sites with a large biomass of young roots. Whether this leads to larger soil organic carbon stocks depends on the decomposition rates.

2.5 Conclusion

Our observations of the mean age of fine root C from forest and grassland sites in Germany indicate that variations in the mean age of fine root C between tree vs. herbaceous grassland species and annual vs. perennial herbaceous species in grasslands can be associated with differences in root tissue lifetime or in resource acquisition and resource conservation strategies. Differences in plant resource acquisition and mainte-

nance strategies are in turn reflected by the ability of recycling C internally. The mean age of root C in grasslands is affected by changes in plant species diversity and in the number of perennial species due to changes in soil moisture and available nutrients in the soil, which in turn may be influenced by different management practices. Therefore, plant diversity indices or other easy to measure parameters like the Ellenberg indicator values for “nitrogen” or “moisture” are potentially applicable by grassland ecologists and modellers to make some first speculations about the turnover time of root C in their field sites. They are therefore of particular importance for further understanding and descriptions of management influences on belowground processes to be included in climate and landscape models.

We suggest additional efforts to improve our knowledge of how the internal redistribution dynamics of C occurs in perennial plant species and in roots with different roles (absorbtion, transport and storage) belonging to different species and plant functional types. This would enable separation of the age of C into a recycling component and a newly grown component and allow estimation of the root lifetimes from ^{14}C data.

Land use	Study region	n	Root biomass (g)	C conc. (%)	N conc. (%)	C stocks (g Cm^{-2})	N stocks (g Cm^{-2})
Forest	All plots	27	3.1 ± 0.5^{A}	47.2 ± 0.8^{A}	1.1 ± 0.03^{A}	51.1 ± 7.7^{A}	1.2 ± 0.2^{A}
	ALB	9	2.8 ± 0.7^{a}	48.8 ± 0.74^{a}	1.2 ± 0.1^{a}	39.7 ± 9.7^{a}	0.9 ± 0.2^{a}
	HAI	9	4.9 ± 1^{b}	42.8 ± 1.1^{b}	1.1 ± 0.04^{a}	79.9 ± 16.4^{b}	2.0 ± 0.4^{b}
	SCH	9	1.7 ± 0.4^{a}	49.9 ± 0.8^{a}	1.1 ± 0.1^{a}	33.8 ± 7.6^{a}	0.7 ± 7.6^{a}
Grasslands	All plots	27	5.1 ± 0.8^{B}	41.8 ± 0.5^{B}	1.2 ± 0.1^{A}	80.24 ± 13.4^{B}	2.4 ± 0.5^{B}
	ALB	9	1.7 ± 0.6^{a}	41.7 ± 0.7^{b}	$0.9 \pm 0.5^{a,b}$	20.4 ± 3.4^{a}	0.4 ± 0.1^{a}
	HAI	9	6.2 ± 0.7^{b}	39.9 ± 1.1^{c}	$1.1 \pm 0.1^{a,c}$	92.04 ± 11.9^{b}	2.4 ± 0.8^{b}
	SCH	9	7.4 ± 1.7^{b}	43.8 ± 0.4^{b}	1.6 ± 0.1^{d}	128.2 ± 29.2^{b}	4.5 ± 2.92^{b}

TABLE 2.2: Root biomass, C and N concentrations and C and N stocks in fine roots ($<$ 2mm) among different land uses and study regions (mean$\pm$SE). Significant differences between study regions are indicated by lowercase letters and between land-use types by capital letters, according to Holm's test ($p < 0.05$).

Dependent variable	Study region			Land use			Study region × Land use		
	df	F	P	df	F	P	df	F	P
Root biomass	2	9.67	<0.001	1	6.77	0.012	2	6.44	0.003
C concentrations	2	24.05	<0.001	1	63.94	<0.001	2	3.65	0.034
N concentrations	2	7.91	<0.001	1	1.42	0.240	2	11.47	<0.001
C stocks	2	13.42	<0.001	1	3.52	0.001	2	6.80	0.002
N stocks	2	9.52	<0.001	1	10.73	0.001	2	11.75	<0.001

TABLE 2.3: ANOVA results of fine root biomass, C and N concentrations and stocks, to compare variance between study regions and differences between grasslands and forests (defined here as land use).

Land use	Study region	n	Fine root Δ^{14}C ‰	Fine root mean age
Forest	All plots	27	90 ± 5^{A}	11.3 ± 1.8^{A}
	ALB	9	88 ± 12^{a}	11.9 ± 3.0^{a}
	HAI	9	94 ± 6^{a}	10.6 ± 0.9^{a}
	SCH	9	87 ± 7^{a}	10.5 ± 1.1^{a}
Grasslands	All plots	27	36 ± 1^{B}	1.7 ± 0.4^{B}
	ALB	9	40 ± 2^{b}	2.6 ± 0.3^{b}
	HAI	9	36 ± 2^{c}	1.8 ± 0.3^{c}
	SCH	9	32 ± 1^{d}	0.7 ± 0.1^{d}

TABLE 2.4: Mean values of ^{14}C content and mean age of fine roots (< 2 mm) among land-use types and study regions (mean±SE). Two-way ANOVA results are presented with Holm's test ($p < 0.05$). Significant differences between study regions are indicated by lowercase letters and between land-use types by capital letters.

Trait	Plant diver--sity (S.I)	Perennial species	Nitrogen (E.I.)	pH	Moisture (E.I.)	Ferti--lization	Root biomass	N conc. roots	C conc. roots
Root C mean age	**0.65**	**0.77**	**-0.72**	-0.20	**-0.73**	-0.33	-0.30	**-0.63**	**-0.26**
Plant diversity (S.I.)		**0.71**	**-0.51**	-0.19	**-0.72**	-0.25	**-0.42**	**-0.59**	-0.11
Perennial species			**-0.88**	-0.02	**-0.79**	-0.41	-0.16	**-0.64**	-0.06
Nitrogen (E.I.)				-0.06	**0.69**	0.31	-0.01	**0.54**	-0.06
pH					-0.09	0.28	**0.45**	0.24	-0.11
Moisture (E.I)						0.29	0.28	**0.60**	**0.38**
Fertilization							-0.18	0.07	-0.38
Root biomass								0.14	0.13
N conc. roots									0.24
C conc. roots									

TABLE 2.5: Pearson's correlation matrix between variables in grasslands. Numbers in bold indicate a significant correlation ($p < 0.05$). E.I.=Ellenberg indicator values, S.I.=Shannon index (n=27).

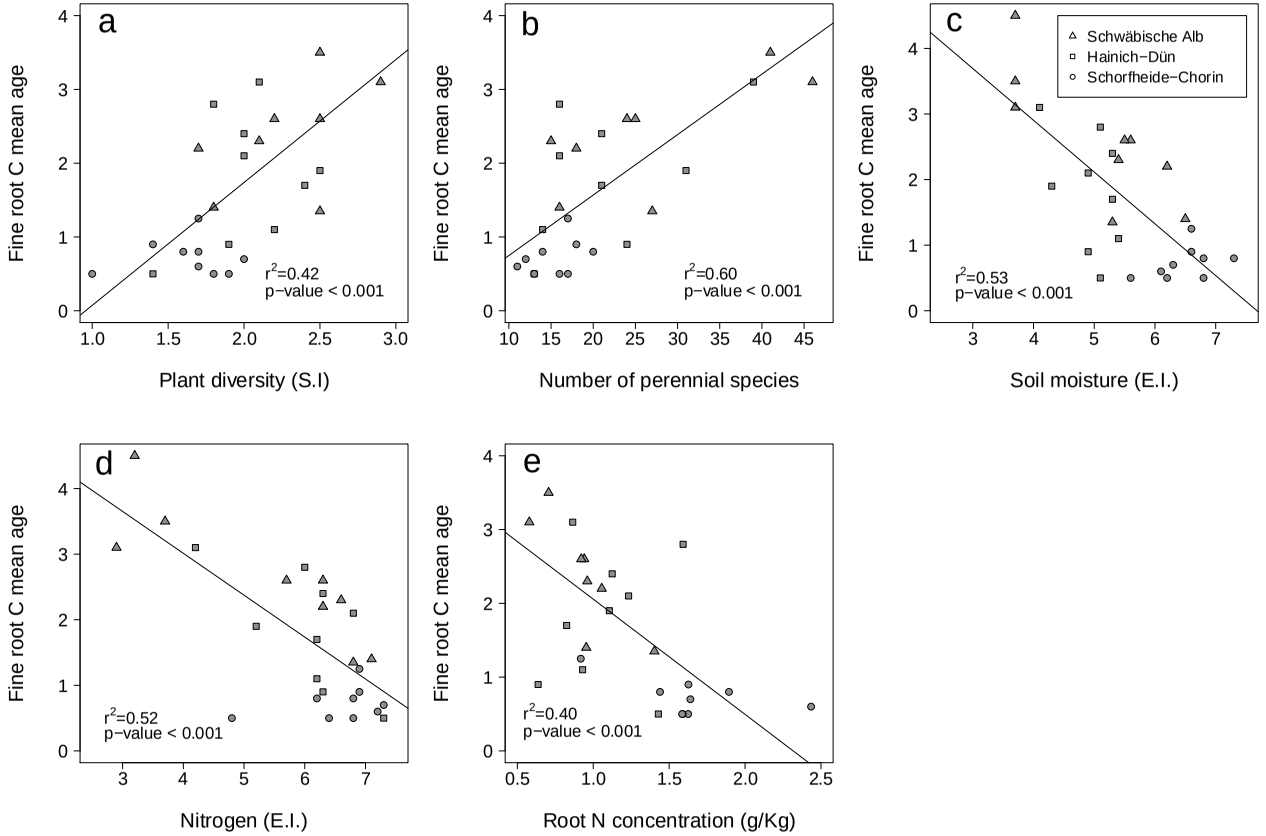

FIGURE 2.3: Relationships between the mean age of fine roots and (a) plant diversity, (b) total number of perennial species, (c) Ellenberg indicator for moisture, (d) Ellenberg indicator for nitrogen, and (e) fine root nitrogen concentration in the grasslands (n=27).

Factor	X2	P >X2	Risk ratio
Plant diversity (S.I.)	15.1	**< 0.001**	0.088
Perennial species	20.8	**< 0.001**	0.88
Nitrogen (E.I.)	23.1	**< 0.001**	3.99
pH	0.78	0.38	-
Moisture (E.I.)	19.1	**< 0.001**	3.11
Fertilization	1.34	0.24	-
Root biomass	2.1	0.14	-
N conc. roots	13.8	**< 0.001**	7.3
C conc. roots	1.4	0.24	-

TABLE 2.6: Summary of proportional hazards fits in grasslands (n=27). Risk ratios <1.0 represent a positive effect on fine root mean age, and risk ratios >1.0 represent a negative effect. Results in bold indicate significant results (p <0.05). E.I.=Ellenberg indicator values, S.I.=Shannon Index.

3 Factors controlling decomposition rates of fine root litter in temperate forests and grasslands [1]

Abstract

Fine root decomposition contributes significantly to element cycling in terrestrial ecosystems. However, studies on root decomposition rates and on the factors that potentially influence them are fewer than those on leaf litter decomposition. To study the effects of region and land use intensity on fine root decomposition, we established a large scale study in three German regions with different climate regimes and soil properties. In 150 forest and 150 grassland sites we deployed litterbags (100 μm mesh size) with standardized litter consisting of fine roots from European beech in forests and from a lowland mesophilous hay meadow in grasslands. In the central study region, we compared decomposition rates of this standardized litter with root litter collected on-site to separate the effect of litter quality from environmental factors. Standardized herbaceous roots in grassland soils decomposed on average significantly faster ($24 \pm 6\%$ mass loss after 12 months, mean $\pm$ SD) than beech roots in forest soils ($12 \pm 4\%$; $p < 0.001$). Fine root decomposition varied among the three study regions. Land use intensity, in particular N addition, decreased fine root decomposition in grasslands. The initial lignin:N ratio explained 15% of the variance in grasslands and 11% in forests. Soil moisture, soil temperature, and C:N ratios of soils together explained 34% of the variance of the fine root mass loss in grasslands, and 24% in forests. Grasslands, which have higher fine root biomass and root turnover compared to forests, also have higher rates of root decomposition. Our results further show that at the regional scale fine root decomposition is influenced by environmental variables such as soil moisture, soil temperature and soil nutrient content. Additional variation is explained by root litter quality.

[1] This chapter is published as Solly, E. F., I. Schöning, S. Boch, E. Kandeler, S. Marhan, B. Michalzik, J. Müller, J. Zscheischler, S. E. Trumbore, and M. Schrumpf, 2014. *Plant and Soil*, **382**, 203–218.

3.1 Introduction

Decomposition of plant litter is one of the main processes driving nutrient and carbon (C) cycling in terrestrial ecosystems and constitutes a major source of atmospheric CO_2 (Hobbie, 1992). While most of the previous studies on decomposition have focused on aboveground plant litter, recent isotopic analyses and assessments of root and shoot biomarkers indicate that root-derived C is retained more efficiently in soils and microorganisms than are C inputs from above ground plant litter (Kramer et al., 2010; Mendez-Millan et al., 2010). Due to the close proximity, root decomposition products are generally better incorporated into soil aggregates and more easily adsorbed to mineral surfaces than the ones of aboveground litter (Rasse et al., 2005; Sanaullah et al., 2011). Thus, plant litter, consisting of dead roots, is a major source of soil organic matter, the largest terrestrial pool of C (Schmidt et al., 2011).

Fine root decomposition rates do not mirror those of aboveground plant litter in temperate ecosystems (Bird and Torn, 2006; Hobbie et al., 2010; Silver and Miya, 2001), due to differences in the chemical composition of both litter types (Kögel-Knabner, 2002), and because aboveground litter experiences different environmental conditions compared to belowground litter (Hobbie et al., 2010). Yet, only few experimental studies have been designed to identify predictors of fine root decomposition (Chen et al., 2002; Cusack et al., 2009; Fahey et al., 1988; Ostertag and Hobbie, 1999), and ever fewer extend beyond a single ecosystem (e.g. Long-term Intersite Decomposition Experiment (LIDET), Harmon et al., 2009). Previous studies have shown that root litter quality (mainly lignin, nitrogen (N), C and calcium (Ca) content) and climate factors such as temperature and precipitation are the primary controls of root decomposition (Chen et al., 2002; Hobbie, 2005; Silver and Miya, 2001). However, little is known about how the direct and indirect effects of land use and management may influence fine root decomposition.

In grasslands, management practices such as fertilization, mowing and grazing can alter plant community structure, litter inputs and soil properties (Dickinson and Polwart, 1982; Hobbie, 2005; Semmartin et al., 2008). Some studies found that fertilization increases the decomposition of plant litter, due to higher N availability (Carreiro et al., 2000; Hobbie and Vitousek, 2000). In contrast, other studies observed either no significant change or a suppression of decomposition rates as a response to higher fertilization regimes (Bryant et al., 1998). The contrasting responses to N additions across studies may be partly explained by differences in site-specific atmospheric N

deposition and by litter quality (Knorr et al., 2005). However, it is unclear how N fertilization alters root decomposition. Long-term grazing and mowing activities may affect root decomposition directly by altering the plant species composition and soil decomposer communities (Bardgett et al., 1998), or indirectly through changes in soil properties such as bulk density and soil moisture (e.g. through trampling, Sankaran and Augustine, 2004; Taboada and Lavado, 1988).

In forests, thinning and harvesting can lead to soil degradation via soil compaction (Berthrong et al., 2009; Liao et al., 2010), which in turn might alter fine root decomposition rates due to changes in the aeration of the soil and the volumetric soil moisture content. Further, these practices as well as tree species selection may lead to variations in soil C and nutrient contents which may result in changes of the decomposer community. Higher temperature and moisture in more heavily thinned forests can further result in faster root decomposition although responses may vary among forests of different dominant tree species (Cortina and Vallejo, 1994; Prescott et al., 2000). The goal of this study was to quantify root litter decomposition rates in differently managed temperate grasslands and forests, and to disentangle the effects of litter quality from environmental site effects.

In terrestrial ecosystems, decomposition of plant litter is commonly assessed using the litterbag method, which consists of enclosing plant tissue of known mass and chemical composition in a screened container (Bocock and Gilbert, 1957) that is placed in or on top of the soil. When adopting the litterbag approach some artifacts need to be considered, such as microclimate alterations and exclusion of specific fauna size classes due to the selection of small mesh sizes. Nevertheless, the litterbag method is helpful to study decomposition especially if comparing decomposition rates occurring in different ecosystems and regions in a consistent way (Kurz-Besson et al., 2005). Meta-analyses have been used in previous studies to synthesize root decomposition (for example Silver and Miya, 2001). The main caveat of the meta-analysis approach is that it compares decomposition rates derived from smaller scale root decomposition studies which adopted different methodologies (i.e diverse litterbag mesh sizes, enclosure of root litter with diverse quality, and deployment at different soil depth). To study fine root decomposition at a large spatial scale in a comparative way, we used a standardized methodology for a range of ecosystems with different soil types, land uses and climate.

Our main objective was to quantify root litter decomposition after 12 months in differently managed temperate grasslands and forests. We were further interested in

understanding whether environmental site conditions (including the microbial decomposer abundance) have a stronger impact on decomposition than differences in root litter quality between grasslands and forests. We deployed litterbags containing standardized herbaceous fine roots in 150 grassland plots and European beech roots in 150 forest plots in three German study regions managed with different land use intensities. Moreover, we compared the mass loss rates of standardized root litter with the rates for root litter collected on-site for one of the three regions (50 forest and 50 grassland plots). We hypothesized that root decomposition rates of standardized root litter would vary between the three study regions, reflecting differences in climate and soil properties. We also hypothesized that decomposition of on-site collected root litter would be affected by management practices, specifically fertilization, grazing and mowing activities in grasslands, and by different disturbance intensity and tree species selection in forests.

3.2 Material and methods

3.2.1 Study regions, management data, vegetation survey

Our study was carried out in the Biodiversity Exploratories (Fischer et al., 2010) which comprise a variety of forests and grasslands under different land use intensities in three regions within Germany. The Schwäbische Alb (ALB) is situated in south-western Germany, the Hainich-Dün (HAI) in central Germany, and the Schorfheide-Chorin (SCH) in north-eastern Germany. Each study region includes 50 forest plots and 50 grassland plots. In SCH 27 grassland plots have been established on organic soils (Histosols and Gleysols) and 23 on mineral soils. The three study regions differ in climate, altitude, and soil characteristics (Table 3.1).

In grasslands a land use intensity index (LUI) was calculated using landowner surveys. The LUI summarizes the individual land uses by summing up values for fertilization (kg N per hectare per year), mowing (number of cuts per hectare per year), and grazing intensities (livestock units per hectare per year) which have been normalized by the mean of the region (Blüthgen et al., 2012). To evaluate land use and disturbance intensity in the forests we used the LUDI index (Luyssaert et al., 2011). This index combines values of stand density and diameter at breast height for a relatively unmanaged forest and different management schemes, in conjunction with self-thinning values.

	Schwäbische Alb	Hainich-Dün	Schorfheide-Chorin
Location	SW Germany	Central Germany	NE Germany
Coordinates	N 48° 26' E 9° 23'	N 51° 9' E 10° 28'	N 53° 0' E 13° 46'
Area [km^2]	≈422	≈ 1,300	≈ 1,300
Soil type forest	Cambisol (eutric)-Leptosol	Luvisol	Cambisol (dystric)
Soil type grassland	Leptosol-Cambisol	Cambisol-Stagnosol-Vertisol	Histosol-Gleysol-Cambisol-Luvisol-Albeluvisol
Altitude a.s.l [m]	460–860	285–550	3–140
Mean annual temperature (MAT) [°C]	6.0–7.0	6.5–8.0	8.0–8.5
Mean annual precipitation [mm]	700–1,000	500–800	500–600

TABLE 3.1: Main geographical and environmental characteristics of the three study regions: Schwäbische Alb, Hainich-Dün, Schorfheide-Chorin.

In 2009, we recorded vegetation data in 20 m × 20 m forest plots in spring and summer (for details see Boch et al., 2013), and in 4 m × 4 m grassland plots only once in summer (for details see Socher et al., 2013). We identified all vascular plant species and estimated their percentage cover. To assess the diversity of the vascular plant species in forest plots, we combined the spring and summer records to consider early and late emerging plants. For both, grassland and forest sites, we calculated the "Shannon Index" as a measure of plant species diversity (Shannon, 1948):

$$H = -\sum_{i=1}^{n} p_i \ln p_i \,, \tag{3.1}$$

where H corresponds to entropy in this case equivalent to the Shannon Index, p_i is the percentage cover of individuals in the sampling area represented by species i and is assessed by the quotient of number of individuals of species i (N_i) and the total number of individuals (N). Thus, the maximum diversity possible for N individuals occurs when all species have the same percentage cover when each individual belongs to a different species. We further distinguished annual and perennial species and calculated their number per plot.

3.2.2 Soil temperature and moisture

Soil temperature and soil moisture were measured continuously in each plot every 10 minutes with ground surface temperature sensors (Meier NT Type 2021, Zwönitz, Germany) and soil humidity probes (DeltaT ML2X, Cambridge, UK) at a soil depth

of 10 cm. In this study, we used the 6 and 12 months averages of soil temperature and volumetric soil moisture. We also calculated the number of days during which the soil was frozen ($< 0°C$) for each plot. Due to gap periods during the measurements complete data on soil temperature was only available for 187 and soil moisture for 274 of the 300 plots.

3.2.3 Root collection, abiotic soil properties and microbial biomass

In each of the 300 plots we collected 14 mineral soil cores with a split tube sampler (diameter of 5 cm) along two 20 m transects in grasslands and 40 m transects in forests in May 2011. Organic layers in forests and aboveground plant parts in grasslands were removed before coring. We then prepared a composite sample from the 14 mineral soil cores by mixing the upper 10 cm of the mineral soil. Roots were removed from the composite sample, cooled to 4 °C for soil analysis (root biomass, texture, pH and C and N concentrations,) and frozen to -20 °C for microbial biomass measurements, and transported to the laboratory. Soil samples were all sieved to < 2 mm.

Microbial biomass C was estimated by chloroform-fumigation-extraction (Vance et al., 1987). In brief, 10 g soil (fresh weight) of a homogeneous subsample of each plot was fumigated under vacuum with ethanol-free chloroform in a desiccator for 24 h. After removing the chloroform, samples were extracted by adding 40 ml of a 0.5 M K_2SO_4 solution (1:4 w/v soil / extractant ratio), shaken for 30 min at 250 rev min^{-1} on a horizontal shaker and centrifuged for 30 min at 4422 g. A second subsample of 10 g was treated similarly but without fumigation for the estimation of 0.5 M K_2SO_4 solution extractable organic C. Organic C in the supernatants was measured with a DOC / TN-analyser (Multi N/C 2100S, Analytik Jena, Jena, Germany). Extractable organic C content of the non-fumigated samples was subtracted from C content of the fumigated samples and resulted in extractable microbial biomass. For estimation of total microbial biomass a kec-factor of 0.45 was used (Joergensen, 1996).

Soil samples were air dried. The dry biomass of the washed fine roots was weighed after oven-drying the root samples at 40 °C. To evaluate the soil texture we determined the percentage of sand (2-0.063 mm), silt (0.063-0.002 mm) and clay (< 0.002 mm) in the soil samples. We separated soil particles and size classes by sieving and sedimentation procedures (DIN-ISO 11277). We determined the pH values of our composite soil samples in duplicate using a 0.01 M $CaCl_2$ solution. The soil solution ratio was 1:2.5.

Soil subsamples were ground in a ball mill (RETSCH MM200, Retsch, Haan, Germany). Total C and N concentrations were determined by dry combustion in an elemental analyser (VarioMax, Hanau, Germany). To evaluate the concentration of organic C in each soil sample we determined the amount of inorganic C by removing all organic carbon at a temperature of 450 °C for 16 hours, and subtracted this value from the total C concentration.

3.2.4 Chemical composition of fine roots

To identify the initial quality, subsamples of the root litter were ground in a ball mill (RETSCH MM200, Retsch, Haan, Germany). Total C and N concentrations were determined using an elemental analyzer (Vario EL, Elementar, Hanau, Germany). Concentrations of Ca, magnesium (Mg), aluminium (Al) and phosphorus (P) were measured using inductively coupled plasma - optical emission spectrometry (ICP-OES, Optima 3300 DV, Perkin Elmer, Norwalk, USA), after 50 mg of root material were diluted in 3 ml of HNO_3 65%, (Merck, Darmstadt, Germany) and microwave digested at high pressure (Multiwave, Anton Paar, Graz, Austria) (Raessler et al., 2005). Lignin and holocellulose content (ideally composed by cellulose and hemicellulose) were estimated from thermogravimetric analysis in Argon atmosphere (TGA / SDTA851e Mettler Toledo, GmbH, Giessen, Germany) (Yang et al., 2005). Temperature programming consisted of an initial isothermal phase at a temperature of 100 °C for 5 minutes, a dynamic phase with a heating rate of 40 °C min^{-1} from 100 °C to 1000 °C, and a second isothermal phase for 10 minutes at a temperature of 1000 °C. To prevent heat and mass transfer limitations, small samples (5 to 10 mg) were used. Weight loss and heating rate were continuously recorded. We calculated the amounts of lignin and holocellulose by dividing the biomass pyrolysis in the following ranges: < 220 °C, moisture evolution; 220 - 400 °C, holocellulose decomposition; > 400 °C, lignin decomposition as indicated by Yang et al. (2005). As reference materials we used pure lignin (alkali, low sulfonate content) and cellulose powder.

3.2.5 Root litter decomposition experiments

We conducted two litterbag decomposition experiments using two different litter types: 1) we studied decomposition of standardized root litter at all 300 plots in forests and grasslands of the three regions, and 2) we used on-site collected material only in plots of the HAI region. As standard material for the forest sites we used fine roots collected

from 2 year old European beech saplings (*Fagus sylvatica* L.) grown in sand. As standard material for the grassland sites, we used fine roots which we collected from a 16 m^2 area in a lowland mesophilous hay meadow belonging to the alliance Arrhenatherion elatoris W. Koch (Isserstedt, Thuringia, Germany, 50° 57' 30.3" N 11° 31' 20.5" E).

We removed the mineral-soil particles attached to the roots, by carefully washing the roots with distilled water in a 63 μm sieve. In addition, we suspended the root material in a tray containing distilled water to remove the more adherent mineral particles. We separated the fine roots ($<$ 2 mm diameter) from the coarse roots and dried all samples at 40 °C to constant weight in a force-air oven. We put 0.5 g of dry fine root litter (mass selected according to average local root biomass distributions in top-soils) into a 10 cm $\times$ 10 cm litterbag made of a 100 μm polyester mesh screening to allow microfaunal decomposition (Schwegmann Filtrations-Technik GmbH, Grafschaft-Gelsdorf, Germany). The variation of the initial weight was (0.508 ± 0.006 g). We individually labelled each litterbag with a stainless steel label which was placed inside the enclosure and measured the total mass of each litterbag.

For each of the two experimental set-ups we tied together three litterbags, representing replicates containing the same material type (standard litter and on-site collected litter) for every collection time. In October 2011, we placed them approximately 3 m apart from meteorological stations. The litterbags were distributed vertically into a 10 cm deep slit in the mineral soil. After 6 months (in April 2012) and after 12 months (October 2012) respectively we collected three litterbags at each site containing standardized material. In addition, we sampled three litterbags containing on-site collected material in all of the 100 HAI plots in October 2012. The collected litterbags were transported to the laboratory where we gently removed the ingrown material and cleaned the fine root-litter from adherent soil particles. After drying at 40 °C we calculated the fine root decomposition rates (mass loss in %) for each plot as the mean mass loss of the three litterbags collected at each collection date (standard deviations for the three replicates ranged between 0.1 and 3.5 % after 6 months of decomposition and between 0.1 and 8.2 % after 12 months of decomposition). We further used the negative exponential single-pool decomposition model (Olson, 1963) to estimate the root litter decomposition rates (k), though we recognize that this represents only initial decomposition rates (12 months) and that these slow over time in most decomposition experiments (e.g. Sun et al., 2013).

3.2.6 Statistics

We conducted statistical analyses with R, version 3.0.2 (R Development Core Team 2013). Throughout the manuscript we present data as means ± standard error. Two way analysis of variance (ANOVA) accompanied by Holm's test was used to examine statistical differences between the mass loss of standardized fine root litter (after 6 and 12 months), soil moisture, soil temperature, soil properties, land use and root biomass, in grassland and forest plots among the regions (in the SCH study region we additionally distinguished between organic soils (Histosols and Gleysols) and mineral soils). Significant differences between fine root litter chemistry of grasslands and forests, and between standardized and on-site collected root material were tested with Student's t-test.

To detect the environmental predictors of fine root decomposition in grasslands and forests, we applied general linear models (GLM). In grasslands we conducted three separate GLMs, one grouping all three study regions, one for the mineral soils in the three study regions and one for SCH to evaluate the difference between organic and mineral soils. To check whether complex interactions between explanatory variables were present and to select which variables should be included in the GLM and in which order, before conducting each GLM we fitted a tree model (Crawley, 2007). In the tree model analysis we included the following variables: soil properties (pH, organic C content, C:N ratio and texture, microbial biomass), climate (soil temperature and moisture), land use (LUI and LUDI), plant diversity (Shannon index) and number of perennial species. We calculated the variance inflation factor (VIF) between the variables selected from the fitting of the tree models to prevent multicollinearity. We manually simplified all GLMs to the minimum adequate model by using stepwise selection of variables until all terms contained in the model were significant (Crawley, 2007). We then checked the model assumptions using the diagnostic plot function in R (Crawley, 2007).

To assess whether environmental variables have a stronger impact on decomposition than root litter chemistry differences within grassland and forest sites, we used multiple regression analysis. As for the GLMs, we fitted a tree model (one for grasslands and one for forests) before conducting multiple regressions. Root litter chemistry (content of C, N, Ca, Mg, Al, P, holocellulose, C:N and lignin:N ratio) was included in the tree models in addition to the environmental variables. Quadratic terms of each variable were included in the model to check for non-linear responses.

Land use	Study region	Soil moisture		Soil temperature	
		6 months %	12 months %	6 months °C	12 months °C
Forests	All plots	26 ± 10^{A}	26 ± 10^{A}	7 ± 5^{A}	9 ± 4^{A}
	Schwäbische Alb	34 ± 7^{a}	34 ± 7^{a}	5 ± 3^{a}	7 ± 2^{a}
	Hainich-Dün	29 ± 6^{b}	29 ± 6^{b}	5 ± 1^{a}	9 ± 2^{ab}
	Schorfheide-Chorin	15 ± 3^{c}	15 ± 4^{c}	10 ± 5^{b}	10 ± 4^{b}
Grasslands	All plots	37 ± 9^{B}	34 ± 9^{B}	7 ± 4^{A}	11 ± 4^{A}
	Schwäbische Alb	41 ± 4^{e}	40 ± 4^{d}	5 ± 2^{a}	8 ± 2^{a}
	Hainich-Dün	33 ± 6^{a}	29 ± 4^{b}	6 ± 2^{a}	11 ± 3^{b}
	Schorfheide-Chorin	34 ± 11^{a}	29 ± 10^{b}	12 ± 6^{c}	14 ± 4^{c}

TABLE 3.2: Soil moisture and temperature over 6 and 12 months, in all study regions (mean $\pm$ SD). Soil temperature is expressed in °C and soil moisture is expressed in percentage of volumetric water content (%VWC). Significant differences between study regions are indicated by lowercase letters, and between land use types by capital letters according to Holm's test ($p < 0.05$) ($n = 274$ for soil moisture, $n = 187$ for soil temperature).

We used partial linear regression to determine the amounts of variations explained by land use and the other environmental variables on decomposition of standardized fine root litter in grasslands Legendre (2008). We used this method also to distinguish between the variation explained by environmental and root-litter chemistry variables on fine root decomposition in grasslands and forests of the HAI region. The variables we adopted in the partial linear regression were the ones which were selected from the minimum adequate GLM and the multiple regressions.

3.3 Results

3.3.1 Soil characteristics and root biomass

The soils of the ALB study region showed higher volumetric soil moisture content than the ones in HAI and SCH for both grasslands and forests during 6 and 12 months of decomposition. Soil temperatures were higher in SCH than in the ALB and HAI regions (Table 3.2). The soils in the HAI study region were on average frozen for more days during the 12 months period (7 days) than ALB (5 days) and SCH (4 days).

In grassland soils, we found on average higher clay contents, pH values, C:N ratios and microbial biomass than in forest soils (Table 3.3). Soil properties also differed between study regions (Table 3.3). Organic C and microbial C were positively related to clay contents ($r = 0.68$, $r = 0.70$) in mineral soils. Microbial biomass was also positively correlated with the soil organic C content ($r = 0.65$). The organic soils

of the SCH contained higher soil organic C and microbial biomass compared to the mineral soils of the study region. In grasslands, fine root biomass was highest in the mineral soils of the SCH followed by HAI, the organic soils in SCH, and then ALB, whereas in the forests root biomass was greater in the HAI study region than in SCH and ALB.

3.3.2 Fine root initial chemical composition

C concentrations, estimated lignin content and lignin:N ratios were lower, and P and holocellulose content were higher in root samples collected in grasslands than those collected in the forest sites (Table 3.4). Variability in the chemical quality of roots was greater for root material collected across 50 plots (both for forest and grassland) compared to standard material derived from a single site (grassland) or species (forest). The standardized grassland root litter differed significantly from fine root litter collected in the HAI grassland plots, with lower N ($p < 0.05$) and holocellulose content ($p < 0.001$). The higher N content and variability for the roots collected on-site compared to the standardized material in grasslands probably results from the wide range of fertilization regimes. The Ca and Al concentrations were lower in the standardized compared to on-site collected root material (Table 3.4). The standardized root material used in forests differed from the average of the fine root litter collected on the HAI forest sites, with higher C ($p < 0.001$) and lignin ($p < 0.05$) content, possibly due to variable contributions of understory roots in on-site collected samples. In addition, standardized beech roots had lower Mg, Ca and Al content than the root material collected on site in the HAI forest plots ($p < 0.05$).

3.3.3 Fine root mass loss in the standardized litter across three regions

Herbaceous standardized fine root litter deployed in grasslands lost more mass ($p < 0.01$) after 12 months ($24 \pm 6\%$ mass loss) compared to the mass loss of tree standardized fine root litter in forests ($12 \pm 4\%$). The mass loss of fine root litter in both land uses nearly doubled from the first collection (6 months, over winter) to the second (a full year, including summer; Table 3.5). The mass loss of fine root litter was significantly faster in the SCH study region followed by ALB and HAI for both collection times (Table 3.5). Mass loss of standardized fine root material after 6 and 12 months of decomposition was correlated in grasslands ($r = 0.51$) and forests ($r = 0.64$) (Fig. 3.1). These not so high correlations may be related to the comparison of different

Land use	Study region	n	Sand g kg^{-1}	Clay g kg^{-1}	pH	Total N g kg^{-1}	Organic C g kg^{-1}	C:N	Microbial biomass μg g^{-1}	Root biomass g m^{-2}
Forests	All plots	150	329 ± 387^{A}	281 ± 203^{A}	4 ± 1^{A}	3 ± 2^{A}	40 ± 20^{A}	15 ± 3^{A}	436 ± 308^{A}	98 ± 90^{A}
	Schwäbische Alb	50	60 ± 46^{a}	496 ± 105^{a}	5 ± 1^{a}	5 ± 1^{a}	53 ± 14^{a}	13 ± 1^{a}	737 ± 220^{a}	67 ± 56^{a}
	Hainich-Dün	50	58 ± 18^{a}	301 ± 99^{b}	5 ± 1^{b}	3 ± 1^{b}	36 ± 10^{ab}	13 ± 1^{a}	449 ± 214^{b}	155 ± 120^{b}
	Schorfheide-Chorin	50	871 ± 61^{b}	45 ± 19^{c}	3 ± 0.1^{c}	1 ± 0.2^{b}	21 ± 5^{b}	19 ± 3^{b}	123 ± 38^{c}	73 ± 45^{a}
Grasslands	All plots	150	190 ± 228^{B}	378 ± 192^{B}	7 ± 1^{B}	7 ± 5^{B}	72 ± 64^{B}	10 ± 1^{B}	656 ± 291^{B}	175 ± 149^{B}
	Schwäbische Alb	50	57 ± 45^{a}	536 ± 134^{d}	6 ± 1^{d}	6 ± 1^{a}	65 ± 14^{a}	10 ± 1^{c}	748 ± 210^{a}	35 ± 30^{d}
	Hainich-Dün	50	58 ± 23^{a}	423 ± 130^{e}	7 ± 1^{e}	4 ± 1^{ab}	46 ± 12^{a}	10 ± 1^{c}	594 ± 169^{d}	215 ± 87^{e}
	Schorfheide-Chorin									
	mineral soils	23	643 ± 101^{c}	137 ± 93^{f}	6 ± 1^{d}	2 ± 1^{b}	21 ± 4^{b}	10 ± 1^{c}	236 ± 62^{e}	246 ± 122^{f}
	organic soils	27	324 ± 179^{d}	216 ± 119^{g}	7 ± 1^{e}	15 ± 2^{d}	170 ± 102^{c}	11 ± 2^{c}	906 ± 338^{f}	180 ± 127^{e}

TABLE 3.3: Soil properties and dry root biomass among different land uses and study regions (mean $\pm$ SD). Significant differences between study regions are indicated by lowercase letters and between forests and grasslands by capital letters according to Holm's test ($p < 0.05$).

Fine root material	Land use	n	C mg g^{-1}	N mg g^{-1}	P mg g^{-1}	Ca mg g^{-1}	Mg mg g^{-1}	Al mg g^{-1}	Holocellulose mg g^{-1}	Lignin mg g^{-1}	C:N mg g^{-1}	Lignin:N mg g^{-1}
Standardized	Forests	20	470 ± 13^{a}	11 ± 2^{a}	1^{a}	5^{a}	1^{a}	6 ± 0^{a}	418 ± 6^{a}	433 ± 7^{a}	49 ± 6^{a}	40 ± 1^{a}
	Grasslands	20	433 ± 17^{b}	8 ± 1^{b}	2^{b}	6 ± 1^{a}	3^{b}	5^{a}	585 ± 7^{b}	251 ± 5^{b}	53 ± 3^{b}	31 ± 1^{b}
Collected	Forest	50	448 ± 32^{c}	11 ± 2^{a}	1^{a}	10 ± 5^{b}	2 ± 2^{b}	7 ± 3^{b}	424 ± 40^{a}	361 ± 35^{c}	41 ± 7^{c}	34 ± 6^{c}
on-site	Grasslands	50	400 ± 24^{d}	11 ± 3^{a}	2 ± 1^{b}	9 ± 4^{b}	2 ± 3^{b}	8 ± 3^{b}	510 ± 32^{b}	259 ± 13^{b}	38 ± 9^{d}	24 ± 5^{b}

TABLE 3.4: Chemical quality of the standardized fine root litter and the fine root litter collected on site in the Hainich-Dün and used in this study (mean $\pm$ SD). For the standardized material 20 replicates of fine root material were analyzed. Significant differences between fine roots collected on-site and standardized material for grasslands and forests are indicated by lowercase letters according to Holm's test ($p < 0.05$).

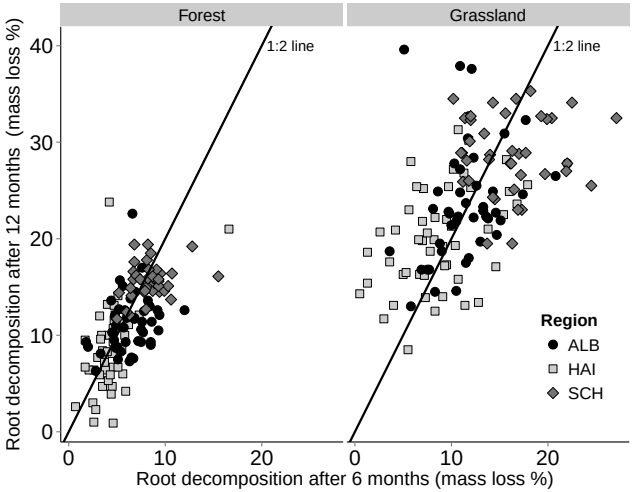

FIGURE 3.1: Comparison between the mass loss of standardized fine root litter after 6 and 12 months of decomposition across all study regions, for both grasslands and forests.

root litterbags collected at different times in the same plots. We based our subsequent analyses on the mass loss of fine roots after 12 months decomposition.

3.3.4 Predictors of fine root mass loss (standardized litter)

Differences between study regions influenced fine root decomposition in grasslands and forests (Table 3.6b, 3.6d). Within all grasslands, the mass loss of the standardized fine root material was further influenced by the total organic C content present in the soil, the soil moisture and the LUI (adjusted $r^2 = 0.39$) (Table 3.6a). Partial linear regression analysis showed that the LUI explained 4% of the variation while organic C, study region, and soil moisture together explained 24% of the variation. The effect of organic C and soil moisture was not observed in the model including only the mineral soils of the three study regions (Table 3.6b). In fact, when excluding the organic soils present in the SCH, fine root mass loss was explained by differences in study regions and LUI. The separation between organic and mineral soils in the SCH explained most of the variance of fine root mass loss in this study region followed by the LUI index (Table 3.6c). We checked the effect of fertilization, grazing and mowing intensities on fine root mass loss within the grasslands of all three study regions. The standardized

Fine root litter	Land use	Study region	n	Mass loss after 6 months (%)	Mass loss after 12 months (%)	k-values (year^{-1})
Standardized	Forests	All plots	150	6 ± 3^{A}	12 ± 4^{A}	0.12 ± 0.5^{A}
		Schwäbische Alb	50	6 ± 2^{a}	11 ± 3^{a}	0.12 ± 0.03^{a}
		Hainich-Dün	50	4 ± 2^{b}	8 ± 5^{b}	0.09 ± 0.05^{b}
		Schorfheide-Chorin	50	8 ± 2^{c}	16 ± 2^{c}	0.17 ± 0.02^{c}
	Grasslands	All plots	150	12 ± 5^{B}	24 ± 6^{B}	0.27 ± 0.8^{B}
		Schwäbische Alb	50	12 ± 4^{d}	23 ± 7^{d}	0.27 ± 0.07^{d}
		Hainich-Dün	50	9 ± 4^{c}	20 ± 5^{e}	0.22 ± 0.06^{e}
		Schorfheide-Chorin				
		mineral soils	23	15 ± 3^{e}	26 ± 3^{f}	0.32 ± 0.04^{f}
		organic soils	27	17 ± 4^{e}	31 ± 3^{g}	0.37 ± 0.04^{g}
Collected on site	Forest	Hainich-Dün	50	-	8 ± 4^{Cb}	0.09 ± 0.05^{Cb}
	Grassland	Hainich-Dün	50	-	19 ± 7^{De}	0.21 ± 0.06^{De}

TABLE 3.5: Mass loss of standard fine root litter and of the fine root litter collected on-site after 6 and 12 months of decomposition (mean $\pm$ SD). Significant differences between study regions are indicated by lowercase letters, and between forests and grasslands by capital letters according to Holm's test ($p < 0.05$).

Coefficients	Df	Mean Sq	F value
a) Mass loss (standardized material, grasslands)			
Organic C	1	119.6	4.9^{*}
Study region	2	742.7	30.4^{***}
Soil Moisture	1	140.3	5.7^{*}
LUI	1	191.1	7.8^{**}
Residuals	109	24.5	
b) Mineral soils Schwäbische Alb, Hainich-Dün, Schorfheide-Chorin. Mass loss (standardized material, grasslands)			
Study region	2	330.42	12.30^{**}
LUI	1	176.9	0.01^{*}
Residuals	92	30.2	
c) Schorfheide-Chorin. Mass loss (standardized material, grasslands)			
Mineral vs Organic soil	1	236.7	26.27^{***}
LUI	1	50.2	5.57^{**}
Residuals	38	9.1	
d) Mass loss (standardized material, forests)			
Study region	2	563.5	53.35^{***}
Residuals	132	10.6	

TABLE 3.6: Result of the best predictive model on decomposition rates (mass loss %) of standardized fine root litter a) in all grasslands (mineral and organic soils, 150 plots) b) in the mineral soil of the grasslands c) in the grasslands of the Schorfheide-Chorin (mineral and organic soils, 50 plots) d) forests (150 plots), according to ANCOVA analysis. $^{***} = p < 0.001$, $^{**} = p < 0.01$, $^{*} = p < 0.05$.

fine roots decomposed faster in unfertilized plots than fertilized plots both after six months (unfertilized grasslands: $12 \pm 4\%$; fertilized grasslands: $10 \pm 4\%$, $p < 0.01$) and after 12 months (unfertilized grasslands: $25 \pm 6\%$; fertilized grasslands: $22 \pm 6\%$, $p < 0.01$). Fine root mass loss did not differ significantly between grazed and not grazed plots and mowed and not mowed plots. In forests we did not observe an effect of land use on fine root decomposition.

3.3.5 Fine root mass loss for on-site collected litter in the Hainich-Dün region

Despite differences in the initial fine root litter quality, the average mass loss of fine roots during the first 12 months of decomposition was similar between on-site collected root litter and the standardized root material in the HAI study region both for grasslands ($\approx 20\%$ mass loss) and forests ($\approx 8\%$ mass loss) (Table 3.5). Overall, the correlation between mass lost by on-site collected root litter versus standardized root litter was poor ($r = 0.44$ in grasslands and $r = 0.10$ in forests) (Fig. 3.2).

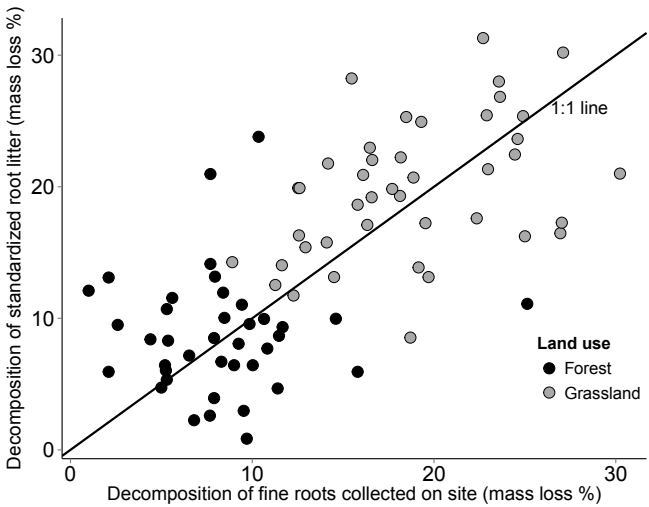

FIGURE 3.2: Relationship between the mass loss of fine roots collected on-site and fine roots used as standardized material in the Hainich-Dün study region after 12 months of decomposition

3.3.6 Predictors of fine root mass loss (on-site collected litter)

According to our analysis fine root decomposition in grasslands was primarily positively related to the lignin:N ratio of roots and to soil C:N ratios (Table 3.7a). We further observed a relation between fine root decomposition and soil moisture and soil temperature. The best linear model for predicting fine root mass loss in grasslands was highly significant ($p < 0.001$) with an adjusted r^2 value of 0.55. We observed that in the grasslands the lignin:N ratio of fine roots was negatively correlated to the LUI index ($r = -0.64$) (Fig. 3.3). In grasslands the lignin:N ratio explained 15% of the variation of fine root decomposition; while the sum of the environmental variables explained 34% of the variation (Fig. 3.4a).

In forests, fine root decomposition was negatively related to the lignin:N ratio of roots, followed by soil moisture and temperature (Table 3.7b). The best linear model for predicting fine root decomposition in grasslands was highly significant ($p < 0.001$) with an adjusted r^2 value of 0.42. We further observed a decline in the lignin:N ratio with the number of tree species present on site ($r = -0.31$, $p < 0.05$). Root lignin:N ratios explained 11% of the decomposition of fine roots, while the sum of the environmental variables explained 24% of the variance (Fig.. 3.4b).

Coefficients	Estimate	Std. Error	t value
a) Mass loss (on-site collected material, grasslands)			
Intercept	-233.80	95.83	-2.44^{*}
Lignin/N ratio	49.40	15.90	3.11^{**}
C/N ratio soil	25.26	9.83	2.57^{*}
Soil Moisture	8.60	3.08	2.79^{**}
(Soil Temperature)^2	0.18	0.7	2.5^{*}
C:N ratio soil : Soil Moisture	-0.97	0.32	-3.05^{**}
Soil moisture : Soil temperature	0.14	0.05	2.68^{*}
Residual standard error: 3.262 on 25 degrees of freedom			
b) Mass loss (on-site collected material, forests)			
Intercept	84.88	17.87	4.75^{***}
Lignin/N ratio	-0.18	0.06	-2.89^{**}
Soil Moisture	-1.44	0.37	-3.94^{***}
Soil Temperature	-10.04	2.82	-3.57^{**}
(Soil Temperature)^2	0.27	0.09	2.72^{*}
Soil moisture : Soil temperature	0.16	0.04	3.9^{***}
Residual standard error: 2.431 on 35 degrees of freedom			

TABLE 3.7: Result of the best predictive model on decomposition rates (mass loss %) of fine roots collected on-site in the a) Hainich-Dün grasslands and b) Hainich-Dün forests, according to multiple regression analysis. $^{***} = p < 0.001$, $^{**} = p < 0.01$, $^{*} = p < 0.05$.

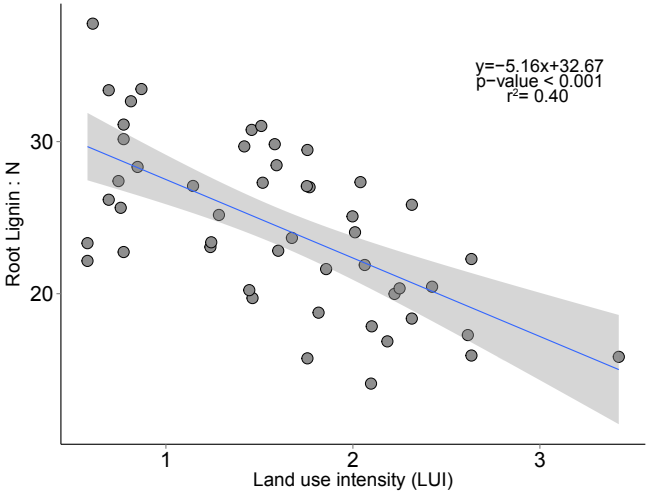

FIGURE 3.3: Regression between the lignin:N ratio and the land use intensity index (LUI) in the Hainich-Dün study region

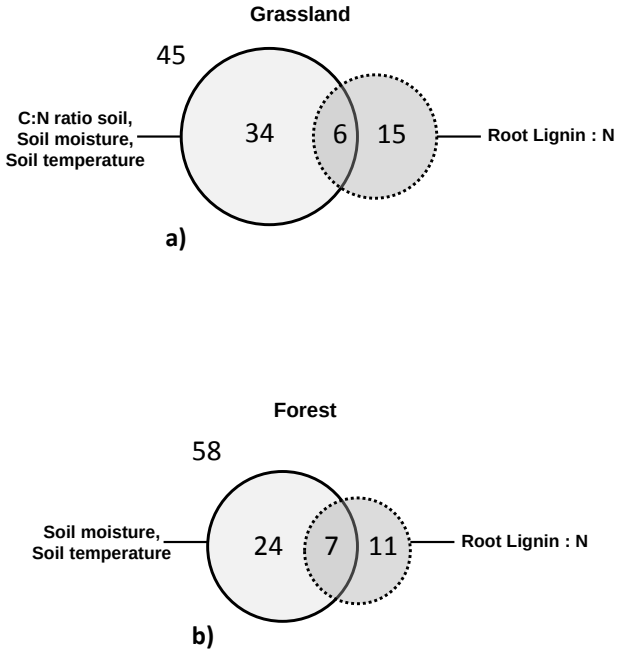

FIGURE 3.4: Venn diagrams representing the partition of the variation of decomposition in response to environmental variables (continuous line) and litter chemistry (dashed line) for grassland (a) and forest ecosystems (b) in the Hainich-Dün region. The total variation for each diagram is 100. The intersection represents the amounts of variation explained by two different linear models we used for the analysis (the first model only including root litter quality and the second only including the environmental variables). The unexplained variation (residual variation) is represented by the number outside the circles. Partition of variation is expressed in %. Adapted from Legendre (2008).

3.4 Discussion

Our root decomposition study shows, in accordance with other experiments using the litterbag method, that substantial decomposition can occur in litterbags in grasslands and forests, even in the absence of mechanical breakdown by macrofauna. Overall we observed relatively low rates of mass loss during the first year of decomposition. One factor to explain this is the relatively cold and dry conditions in temperate ecosystems. Parton et al. (2007) observed that leaf and root decomposition were slowest in cold dry regions such as tundra and boreal forests and fastest in tropical regions. We cannot exclude that absolute values might be affected by the experimental set-up (i.e. mesh size), but as all litterbags were the same, our discussion will focus on relative differences between study sites and root litter quality. In any case, with this work in three large regions in Germany we mostly provide an indication of the initial decomposition rates of fine roots and the factors which control this process in central European temperate grasslands and forests.

In comparison to previous studies on aboveground litter decomposition in temperate ecosystems (Butenschön et al., 2011; Heim and Frey, 2004), fine roots seem to lose mass at lower rates than leaves. Other studies also found that roots decompose more slowly than leaf litter of different species or ecosystem types (Vivanco and Austin, 2006). Lower decomposition rates of root litter in comparison to aboveground litter may be a result of different nutritional requirements of decomposers above versus belowground. Environmental differences above and belowground could also overcome litter chemistry effects on decomposition (Hobbie et al., 2010).

3.4.1 Fine root decomposition rates in grasslands and forests

Overall, herbaceous roots (deployed in grasslands) decomposed twice as fast than roots from forests (deployed in forests) in all study regions (Table 3.5). This was true for both standardized and on-site collected litter. No common material was incubated in both grasslands and forests so this result can be related to differences in environmental conditions or in litter quality. We observed for instance, higher soil moisture in grasslands than in forests (Table 3.3). Direct influences of moisture contents on fine root respiration, for unsaturated soils, have been previously observed by Chen et al. (2000) for unsaturated soils. In grasslands, we further observed higher microbial biomass contents and higher pH values.

We also observed differences in fine root litter quality between herbaceous plants and trees (Table 3.4). For example greater lignin content in tree roots can control mass loss rates during the first stages of decomposition by its high resistance to enzymatic attack, as well as through physical interference with the decomposition of other cell wall fractions (Alexander, 1977). Results of the global meta-analysis on fine root decomposition performed by Silver and Miya (2001) have also shown that decomposition rates of roots belonging to tree species were lower than those of graminoid roots due to lower Ca content and higher lignin:N ratios in tree roots.

Overall, we found up to 2 times higher stocks of fine roots and roughly 2 times faster decomposition rates in grasslands than in forests. These observations together with the results of recent studies in the same regions which have shown younger C in fine roots (Chapter 2), and in the labile fraction of the soil organic matter (Herold et al., 2014a) in grasslands, indicate faster fine root derived C cycling in grasslands than in forests. Interestingly these differences do not extent to the mineral associated fraction of the soil organic matter.

3.4.2 Site effects on fine root decomposition rates

As hypothesized, standardized root decomposition varied among the three study regions, with the highest rates (in grassland and forest) in the SCH study region, followed by ALB and HAI (Table 3.5). The decomposition patterns were the same for herbaceous and beech standardized root material deployments, indicating that the trends were not related to litter quality, but to differences in the soil decomposition environment between the study regions. HAI is intermediate in average climate and most soil properties (Table 3.2, Table 3.3), but has the lowest overall decomposition rates. The only factor we found that might explain this is that the soils in HAI were frozen for a longer number of days compared to ALB and SCH. It has been shown that in soils with temperatures below 0 °C the microbial activity is slowed down. This is due to the rapid decline of unfrozen water content which can decrease the diffusion of substrates, nutrients, and waste products (Dioumaeva et al., 2002; Mikan et al., 2002; Ostroumov and Siegert, 1996). Thus, also the degradation of fine roots may be slowed down, especially during the winter season in temperate ecosystems. In grasslands, we further observed considerably higher fine root decomposition in organic soils (Histosols and Gleysols present in the SCH study region) than in mineral soils in the SCH study region. This was probably related to the different soil properties, such as soil moisture and nutrient

contents, which may in turn influence the soil biota which directly degrades the root litter.

After the removal of variance specific of the study regions and differences in organic and mineral soils, we observed that the decomposition of standardized fine root litter in grasslands decreased with increasing land use intensity. However, in comparison to other environmental properties which explained together 24% of fine root decomposition, land use intensity explained only a small proportion of variation (4%). The negative relation observed between root decomposition and land use intensity is in our study mainly affected by the addition of N by fertilization. The lower need to mineralize organic N might slow down decomposition rates (Fog, 1988). Knorr et al. (2005) reported that litter decomposition is inhibited by N additions when fertilization rates exceed by 2 to 20 times the atmospheric N deposition level. Since our fertilized plots received a maximum of 140 kg N ha^{-1} yr^{-1} and the average bulk N deposition levels for our study regions are on average 10 kg N ha^{-1} yr^{-1} (Schwarz et al., 2014), it is possible that the amount of added fertilizer inhibited the rates of root decomposition in fertilized ecosystems. In forests we did not observe land use effects on fine root decomposition.

3.4.3 Relevance of environmental site conditions and root litter chemistry on fine root decomposition

The lignin:N ratio explained the largest amount of variability (15% in grasslands and 11% in forests) of the mass loss of on-site collected fine root-litter in the grasslands and forests of the HAI region (Fig. 3.4). The remaining variability was explained by the sum of other environmental factors such as soil moisture and soil temperature, but also by the soil C:N ratios in grasslands (all environmental variables explained 34% of the variance in grasslands and 24% in forests) (Fig. 3.4). Although the lignin:N ratio itself merely describes the proportions of lignin to N without providing information about how lignin and N are distributed in plant organs, previous studies have shown that it is a valuable predictor for root decomposition (Bardgett et al., 1998; Hobbie, 2005; Scheffer and Aerts, 2000). Berg (1984) also concluded that the dominant factors for initial mass loss rates of root litter in a Scots pine forest are the relative amount of nutrients together with the initial lignin content. In particular, plant litter with higher N concentrations decomposes faster than its lower nitrogen counterpart, while plant litter with high levels of lignin decomposes slower (Berg, 1984; Janssens et al., 2010). While in forest ecosystems we observed a decline of the decomposition rates for in-

creasing lignin:N ratio of the litter, in grasslands we found the opposite relationship. The detected patterns may reflect the variation in the initial root chemistry among the fine roots collected on-site in grasslands and forests (Hobbie et al., 2010; Silver and Miya, 2001). For instance we observed high variability of N concentration in fine roots of grasslands (Table 3.4). The lignin concentrations were instead relatively constant. On the other hand in forest sites the lignin concentrations in tree roots encompassed a relatively large variability. In the grasslands of the HAI region we observed a negative relation between the LUI index and the lignin:N ratio of fine roots collected on-site (Fig. 3.2). This indicates that land use can affect fine root decomposition through its influence on litter quality. In forests, we observed a negative correlation between the lignin:N ratio and the number of tree species per plot. However, this may be a function of our study design, as most of our plots are covered by pure European beech or mixed forests with more than one species and only a small number are pure Norway spruce (*Picea abies* (L.) H.Karst.) or Scots pine (*Pinus sylvestris* L.) forests. Therefore, higher lignin:N ratio in plots with a smaller number of tree species may be due to the higher amounts of lignin contained in European beech fine roots in comparison to, for example, coniferous tree species (Hobbie et al., 2010).

3.5 Conclusions

We observed that fine root decomposition in temperate grasslands is two times faster than in temperate forests within the range of measured values. This finding together with other observations of older C in fine roots and in the labile fractions of soil organic matter in forests overall indicate slower C turnover in forests compared to grasslands. In both grasslands and forests the decomposition patterns of standardized fine root litter were different for the three study regions, indicating that the trends are influenced by differences in environmental properties such as the soil biota and the soil microclimate. Land use intensity in grasslands, in particular N additions, also had an influence on fine root decomposition, though this amount of variation was small compared to the other abiotic factors. Within one study region, environmental variables explained the decomposition of both standardized and on-site collected litter. Additional variation for the on-site collected litter was explained by root lignin:N ratio, which in our study was influenced by land use; for example N addition in grasslands and tree species composition in forests.

4 No depth-dependence of fine root litter decomposition in temperate beech forest soils[1]

Abstract

Subsoil organic carbon (OC) tends to be older and is presumed to be more stable than topsoil OC, but the reasons for this are not yet resolved. One hypothesis is that decomposition rates decrease with increasing soil depth. We tested whether decomposition rates of beech fine root litter varied with depth for a range of soils using a litterbag experiment in German beech forest plots. In three study regions (Schorfheide-Chorin, Hainich-Dün and Schwäbische-Alb), we buried 432 litterbags containing 0.5 g of standardized beech root material (fine roots with a similar chemical composition collected from two year old Fagus sylvatica L. saplings, root diameter < 2 mm) at three different soil depths (5, 20 and 35 cm). The decomposition rates as well as the changes in the carbon (C) and nitrogen (N) concentrations of the decomposing fine root litter were determined at a six months interval during a two year field experiment. The amount of root litter remaining after two years of field incubation differed between the study regions ($76 \pm 2\%$ in Schorfheide-Chorin, $85 \pm 2\%$ in Schwäbische-Alb, and $88 \pm 2\%$ in Hainich-Dün) but did not vary with soil depth. Our results indicate that the initial fine root decomposition rates are more influenced by regional scale differences in environmental conditions including climate and soil parent material, than by changes in microbial activities with soil depth. Moreover, they suggest that a similar potential to decompose new resources in the form of root litter exists in both surface and deep soils.

4.1 Introduction

Forests cover approximately 30% of the global land surface and forest soils contain up to 40% of the total belowground terrestrial C, including soil organic matter, litter

[1] This chapter is in press as Solly, E. F., I. Schöning, N. Herold, S. E. Trumbore, and M. Schrumpf, 2015. *Plant and Soil*, doi:10.1007/s11104-015-2492-7

and living roots (Brunner and Godbold, 2007; Dixon et al., 1994). Roots are a major source supplying C to soil organic matter, the largest reservoir of the terrestrial C cycle (Schlesinger, 1997; Rasse et al., 2005; Mendez-Millan et al., 2010). The organic compounds contained in dead roots are transformed by decomposition and are partly converted to stable forms of soil organic matter or are being mineralized (Trumbore, 2009). Root decomposition controls on the dynamics of soil OC storage involve complex interactions between plants and the soil biota as well as their reactions to changes in local environmental conditions such as climate, soil parent material, pH and nutrient availability (Chen et al., 2000; Thoms et al., 2010; Handa et al., 2014)(Chapter 3). Although edaphic conditions vary with depth in a soil profile and more than half of total soil OC is found in subsoils (Jobbágy and Jackson, 2000; Rumpel and Kögel-Knabner, 2011), the majority of the studies on root litter decomposition and C dynamics have focused on topsoils (Heim and Frey, 2004; Hobbie et al., 2010; Sun et al., 2013; van Huysen et al., 2013). Accordingly, the pattern of root decomposition in the deeper soil layers and its controlling factors remain poorly understood (Gill and Burke, 2002; Rumpel and Kögel-Knabner, 2011). Moreover, the lack of large scale studies on root decomposition at different soil depths inhibits our ability to determine how soil OC storage will respond to short and long term environmental changes in different regions. Even small variations of decomposition rates of plant litter in forest ecosystems could influence the OC concentrations and storage of the large soil C reservoir (Trumbore, 2009).

While OC concentrations are higher in the topsoil, due to higher plant inputs, root densities, microbial biomass and substrate input through litter leaching, the age of soil OC increases with depth in most ecosystems (Paul et al., 1997; Trumbore, 2000). One possible explanation for older subsoil OC is a reduction in OC turnover with depth, which is supported by increasing portions of mineral-protected OC, changes in the quantity and quality of plant litter input and lower seasonal variations in soil water content and soil temperature in deeper compared to surface soil, all altering microbial activity and root decomposition rates (Rovira and Ramón Vallejo, 2002; Fierer et al., 2003a; Fontaine et al., 2007; Rumpel and Kögel-Knabner, 2011). Interestingly, the age of the free light fraction of soil organic matter, representing the C not protected inside aggregates or associated with minerals, does not show a consistent increase with depth (Schöning and Kögel-Knabner, 2006; Schrumpf et al., 2013). This suggests that C mineral protection is more important for decreasing subsoil OC turnover than an overall reduced potential for microbial decomposition. However, until now little

effort was done to determine whether greater C stability and reduced microbial activity with soil depth influence organic matter decomposition rates (Gill and Burke, 2002; Sanaullah et al., 2011).

In temperate forest topsoils, fine root decomposition rates have been observed to vary regionally and with changes in environmental conditions such as soil temperature and moisture (Chapter 3), which in turn influence the relative activities of the decomposer community (Chen et al., 2000). But it is still unclear whether the same pattern will be observed in deeper soil layers and whether decomposition shows a similar dependence on depth in different soil types. The vast majority of decomposition studies have until now been conducted at small scales and using on-site specific litter, complicating site and regional inter-comparison (Parton et al., 2007). Hence, here we used a standardized fine root litter, with similar chemical quality, to determine controls of fine root decomposition in twelve beech (*Fagus sylvatica* L.) forest plots.

The main objective of this study is to assess the depth-dependence of fine root litter decomposition for a range of forest soils distributed over three German study regions that differ in climate and soil parent material. We used the litterbag method to estimate decomposition rates of standardized beech fine root litter. Our hypotheses are that i) the rate of root decomposition decreases with increasing soil depth, reflecting changes in soil abiotic and biotic conditions; and that ii) the decomposition rates differ between the three study regions for all studied depths, mainly due to diverse and site-specific climate and soil biota, with faster decomposition in warmer and moister not waterlogged sites.

4.2 Material and methods

4.2.1 Study sites

We conducted this study in twelve forest plots dominated by European beech (*Fagus sylvatica* L.,) and distributed in three German regions of the "Biodiversity Exploratories" (Fischer et al. 2010). The Schwäbische Alb is situated in south-western Germany, the Hainich-Dün in central Germany and the Schorfheide-Chorin in north-eastern Germany. These three study regions differ in climate and soil parent material (Table 3.1; for details see Fischer et al., 2010). For each region we selected four forest plots (100m x 100m) with similar age class management. All forests were harvested at 80-120 year intervals and were in an old timber development stage.

	ALB	HAI	SCH
Location	SW Germany	Central Germany	NE Germany
Coordinates	N 48° 26' E 9° 23'	N 51° 9' E 10° 28'	N 53° 0' E 13° 46'
Area [km^2]	≈422	≈ 1, 300	≈ 1, 300
Soil type forest	Cambisol (eutric)-Leptosol	Luvisol	Cambisol (dystric)
Altitude a.s.l [m]	460–860	285–550	3–140
Mean annual temperature [°C]	6.0–7.0	6.5–8.0	8.0–8.5
Mean annual precipitation [mm]	700–1, 000	500–800	500–600
Parent material	Jurassic limestone	Triassic shell limestone and loess	Glacial till and aeolian–fluvial sand in depressions

TABLE 4.1: Main geographical and environmental characteristics of the three study regions: Schwäbische Alb (ALB), Hainich-Dün (HAI), Schorfheide-Chorin (SCH).

4.2.2 Soil properties

To evaluate the soil OC and total N concentrations and stocks, we collected one mineral soil core in each of the forest plots (for more details see: Grüneberg et al., 2010). We used a soil corer with an inner diameter of 8.3 and a length of 110 cm (Eijkelkamp Agrisearch Equipment BV, Giesbeek, The Netherlands). The core was driven into the soil with a motor hammer (Atlas Copco AB, Nacka, Sweden). Organic layers were removed before coring. We sectioned the soil cores into increments (0-10, 10-30 and 30-50 cm) for analysis. Prior to processing, the soil samples were air dried at 20°C to constant weight and sieved to < 2 mm. Roots were air dried and their weight was determined.

Sieved soil subsamples were ground in a ball mill (RETSCH MM300, Retsch, Haan, Germany). Total C and N concentrations were determined by dry combustion in an elemental analyser (VarioMax, Hanau, Germany). To calculate the concentration of OC in each soil sample we determined the amount of inorganic C by removing all OC at a temperature of 550°C for five hours (Heiri et al., 2001), and subtracted this value from the total C concentrations. C and N stocks of the soil samples were calculated from the OC and total N concentrations of the soils and the dry weight of the sieved soil samples.

Soil temperature and soil moisture were measured continuously from 10 meteorological stations in the same study region every 30 minutes with ground surface temperature sensors (Meier NT Type 2021, Zwönitz, Germany, installed at 10, 20 and 50 cm belowground) and soil humidity probes (DeltaT ML2X, Cambridge, UK, installed at 10 and 20 cm). In this study, we used the yearly averages of soil temperature and volumetric soil moisture for the two consecutive years of root decomposition. We also calculated the number of days during which the soil was frozen (≤ 0°C).

4.2.3 Chemical composition of fine roots

To determine the homogeneity of the initial quality of the standardized root litter (fine roots with a similar chemical composition collected from two year old *Fagus sylvatica* L. saplings, root diameter < 2 mm), subsamples were ground in a ball mill (RETSCH MM200, Retsch, Haan, Germany). Total C and N concentrations were determined using the elemental analyzer (Vario EL, Elementar, Hanau, Germany). Concentrations of calcium (Ca), magnesium (Mg), aluminium (Al) and phosphorous (P) were measured using inductively coupled plasma - optical emission spectrometry (ICP-OES, Optima

3300 DV, Perkin Elmer, Norwalk, USA) (for details on the method see Raessler et al., 2005). Lignin and cellulose content were estimated from thermogravimetric analysis in Argon atmosphere (TGA / SDTA851e Mettler Toledo, GmbH, Giessen, Germany) (Yang et al. (2005), method described in Chapter 3).

4.2.4 Root decomposition

We assessed the decomposition rates of beech fine root litter buried at three depths. To provide a nearly homogeneous substrate for decomposition, we used fine roots collected from two year old beech saplings grown in sand. While there may be some chemical differences between deep and shallow fine roots, as well as between roots of different diameter size and age, our aim was to focus on the effect of soil depth on fine root decomposition rather than on the differences triggered by plant allocation patterns.

After removing the mineral soil particles attached to the fine roots of the saplings, by carefully cleaning the roots with distilled water in a 63 μm sieve, we separated the fine roots ($<$ 2 mm diameter) from the coarse roots and dried all samples at 40°C to constant weight in a forced-air oven. For details on the method see Chapter 3.

We prepared 432 litterbags by placing 0.5 ± 0.01 g of dry fine root litter into a 10 cm x 10 cm litterbag made of a 100 μm polyester mesh screening to allow microfaunal decomposition (Schwegmann Filtrations-Technik GmbH, Grafschaft-Gelsdorf, Germany). We individually labelled each litterbag with a stainless steel label that was placed inside the enclosure and measured the total mass of each litterbag. We buried 36 litterbags (n=12 at three depths) in each of the twelve forest plots in October 2011. After extracting twelve intact soil cores (48 mm diameter, 40 cm depth) from each forest plot, we placed the litterbags vertically, adhering to the lateral surface of the soil core hole, at average soil depths of 5, 20 and 35 cm. To backfill the space between the litterbags we used the soil extracted from the core, which we cut at the specific depths. In April 2012, October 2012, April 2013 and October 2013 we collected three litterbags from each soil depth in every forest plot (n=9 per collection date in each site). The collected litterbags were transported to the laboratory where we gently removed the fine roots and hyphae grown around the litterbags as well as soil particles adhering to the fine root-litter. After drying at 40°C we calculated the fine root decomposition rates (mass recovery in $\%$) for each forest plot as the average amount of mass recovered in the three litterbags collected at each collection date. We further estimated the fine

root litter decomposition rates (*k-values*) for every soil depth in all forest plots by fitting the exponential function.

$$X_t = X_0 e^{-kt} \tag{4.1}$$

to the decomposition values of the whole time series (Olson 1963). Where X_t is the amount of fine root remaining at time t and X_0 is the initial root mass at time 0 (Olson, 1963). After two years of decomposition, three replicates per soil depth were analyzed for total C and N concentrations.

4.2.5 Statistics

We conducted statistical analyses with R, version 3.0.2 (R Development Core Team 2013). Throughout the manuscript we present data as means $\pm$ standard deviation. Analysis of variance (ANOVA) accompanied by Tukey-Kramer HSD test was used to examine statistical differences of the fine root mass remaining, the root biomass, the OC and total N concentrations and stocks in the different study regions and at the different soil depths. ANOVA analysis was also used to detect significant differences between the C:N ratio, C and N concentrations of the decomposing fine root litter at different soil depths. Significant changes in the C:N ratio, C and N concentrations between the initial standardized fine root litter and the root litter after two years of decomposition (averaged at all soil depths) were tested with Studentt's t test. Normal distribution of residuals and homogenous variances were checked before statistical analysis. The chosen p-value for detecting statistical differences was $p < 0.05$.

4.3 Results

4.3.1 Soil C N concentrations and stocks and root biomass

OC concentrations ranged between 12 and 42 g kg^{-1} in the soil sampled at 0-10 cm depth. These were significantly higher than the concentrations found at 30-50 cm belowground, which ranged between 2 and 11 g kg^{-1}. Total N concentrations also declined significantly with depth (Table 4.2). OC and total N concentrations were highest in the Schwäbische-Alb, followed by Hainich-Dün and Schorfheide-Chorin. The amount of root biomass (dead and live) extracted from soils as well as OC and total N stocks decreased with depth in all study regions (Table 2a). Variability in the

chemical quality of roots (C, N, Ca, Mg, Al, P, lignin and cellulose) found in the beech fine root biomass that we used for our decomposition experiment was minor (Table 2b). The variability of soil moisture and soil temperature declined with depth for all study regions (Table 4.4). The soils of the Schwäbische-Alb study region had a similar volumetric soil water content (ranging between 20 and 38%) to the ones in the Hainich-Dün (ranging between 22 and 31%) and a higher volumetric soil water content than the soils in the Schorfheide-Chorin (ranging between 9 and 20%). The topsoil in the Hainich-Dün was frozen for the longest period (8 days per year) in comparison to the Schwäbische-Alb (6 days) and the Schorfheide-Chorin (4 days).

4.3.2 Mass recovery and decay rates

After two years of decomposition on average for all depths $76 \pm 2\%$ in Schorfheide-Chorin, $85 \pm 2\%$ in Schwäbische-Alb, and $88 \pm 2\%$ in Hainich-Dün of initial mass of beech fine root litter remained. The mass remaining did not differ significantly for the three depths sampled in the three regions for the majority of the collection times (Fig. 4.1), and thus our calculated decomposition rate-constants also did not vary with depth (Table 4.5). Only in the Hainich-Dün the mass remaining differed significantly between depths after twelve and eighteen months of decomposition, and in the Schwäbische-Alb the amount of mass remaining differed among the three depths after six months of decomposition but not for the subsequent decomposition times (Fig. 4.1). Regional differences in the amount of fine root litter remaining after two years of decomposition were consistent over the three soil depths (Fig. 4.1;Fig. 4.2). Decomposition significantly increased the C:N ratio of the fine root litter from 46 to 54 on average after two years (Fig. 4.3). The increase was similar across different soil depths (Fig. 4.3), and primarily driven by N loss as no major changes in the C concentrations were detected. After two years the C and N concentrations as well as the C:N ratio of the decomposing fine roots were nearly constant throughout the soil profile, however the C concentrations of the roots decomposing at 20 and 35 cm soil depths were higher compared to the roots decomposing at 5 cm ($p<0.05$) (Fig. 4.3).

4.4 Discussion

4.4.1 Similar fine root decomposition at different soil depths

Previous research proposed that litter decomposition rates would be highest in the topsoil and decrease in deeper soil horizons because microbial activities and substrate

availability as well as relative variations in soil moisture and soil temperature decline with soil depth (e.g. more pronounced maximum temperature in the topsoil may increase decomposition in comparison to subsoil) (Fierer et al. 2003a; Jobbágy and Jackson 2000; Trumbore 2000; Weaver et al. 1935). In the studied forest plots the variability of both soil moisture and soil temperature slightly declined throughout the soil profile (Table 4.4), together with OC and N concentrations (Table 4.2). Herold et al. (2014b) showed that extracellular enzyme activities significantly declined with soil depth in forest plots of the same study regions (Table 4.6). Although these variables declined with soil depth we found that fine root decomposition was nearly uniform through the forest soil horizons, except after twelve and eighteen months in the Hainich-Dün and after six months in the Schwäbische-Alb (Fig. 4.1). One reason explaining the similarity of the decomposition rates with soil depth, could be that while we observed that the variation of temperature and moisture declined with soil depth, their means were similar. Accordingly, lower winter temperatures in topsoils might balance lower summer temperatures of forest subsoils, leading to comparable decomposition rates in the topsoil and the subsoil. The same could be true for soil moisture, where greater variation in the topsoil (too dry or too wet) can be detrimental for decomposition Chen et al. (2000).

The similarity of root decomposition at the three depths agreed with a study by Sanaullah et al. (2011). Sanaullah et al. (2011) showed that the amount of wheat root derived C and N remaining in the soil was similar in top- and subsoil horizons of a temporary grassland managed with a ley cropping system in southern France after 3 years of decomposition. Weaver (1947) also concluded that the rate of root decomposition did not show consistent differences at different soil depths throughout a prairie soil profile in North America. The recently published study by Li et al. (2015) also indicates no changes in the decomposition rates between the organic horizon and the mineral horizon in a pine forest ecosystem, for roots decomposing both in situ and in litterbags. These observations together with our finding of similar C:N ratios of the decomposing fine root litter at different soil depths, suggest that fine root decomposition is not strongly affected by the overall changes in soil abiotic and biotic conditions with depth. We assume that the higher biological activity in topsoil than in subsoil is probably promoted by larger amounts of root litter in topsoil (Table 4.2), and additional nutrient and organic substrate input via throughfall and from litter leaching (Qualls and Haines, 1992). Declining enzyme activities with soil depth are therefore likely to be a consequence of reduced resource availability and thus less microbial activity in deeper

soil horizons (Fierer et al., 2003b; Herold et al., 2014b), which we also observed in our study with decreased root biomass and nitrogen and OC concentrations with soil depth (Table 4.2). When inputs are increased, for example by adding a litterbag with new resources, microbial activity can also be stimulated in subsoils to achieve comparable decomposition to that in topsoils. Studies on lignin decomposition indicate that it depends on a continuous input of available energy and C sources, which enable the production of lignin degrading enzymes, and that it is hampered when bioavailable C becomes limited, i.e. during late decomposition stages (Klotzbücher et al., 2011). Hence, it is possible that in later decomposition phases (after two years), the lower substrate inputs and nutrient resources in subsoils may hamper subsoil decomposition rates relative to topsoils. Longer-term decomposition experiments would be necessary to test this hypothesis.

It has been shown that the radiocarbon age of the more active, physicochemically unprotected C in the free light fraction only slightly increases with soil depth, while the less active fractions (C occluded in aggregates or in association with minerals) become older along the vertical soil profile (Schöning and Kögel-Knabner, 2006; Schrumpf et al., 2013). Together with our results, this indicates that in both surface and deep soils the free light fraction, presumably derived from the breakdown of fine root litter -and aboveground litter in the topsoil, is preferentially decomposed at all soil depths.

Although after 2 years of decomposition the estimated decomposition rates (*k-values*) for the whole time series were similar for all studied soil depths in all three study regions, in the Schwäbische-Alb study region the mass remaining after 6 months was highest in the topsoil. This may be related to colder temperatures in the topsoil during the winter months. Moreover, in the Hainich-Dün study region the decomposition of fine roots was observed to decline across the soil profile. An explanation for this is that the studied soils in this area (Luvisols) are characterized by a rich clay accumulation in the subsurface horizons, where soil water may stagnate for a longer time during wet periods, or dry out during the summer months. Hence, these conditions may reduce root decomposition across the soil profile. These exceptions indicate that the length of an experiment could lead to different outcomes of the influence of depth gradients on root decomposition rates within one study region.

After 2 years, the mass of the standardized beech fine root litter remaining was slightly higher than averages reported for other temperate tree species (Parton et al., 2007; Sun et al., 2013). These slower decomposition rates may reflect the higher amounts of lignin in *Fagus sylvatica* L. roots compared to roots of other tree species

(Hobbie et al., 2010). More lignified roots have a higher resistance to enzymatic attack and therefore tend to have slower decomposition rates than the less lignified counterparts (Berg, 1984). In our experiment we used a litterbag mesh size of 100 μm, which enabled us to account only for microfaunal decomposition and excluded the larger soil decomposer community, which contributes to the mechanical breakdown of plant litter especially in topsoil layers. We cannot exclude that the decomposition absolute values might be different for roots decomposing in situ with different diameter sizes or ages (i.e. fine roots of two year-old samplings vs fine roots of adult trees or roots found at different soil depths), as was suggested by earlier studies (Dornbush et al., 2002; Hishi, 2007; Goebel et al., 2011; Li et al., 2015). Therefore, the absolute amount of root mass that we recovered at different soil depths might be influenced by the set-up of the experiment. However, as litterbags and fine root litter were standardized, we can still compare the effects of soil properties on decomposition rates at different soil depths and in different regions.

4.4.2 Site effects on decomposition of fine roots

Although we observed no general trend with soil depth, the recovered fine root masses varied over all soil depths between the three regions (Fig. 4.2), supporting our second hypothesis. The same pattern of higher decomposition rates in the Schorfheide-Chorin followed by Schwäbische-Alb and Hainich-Dün was also found in a larger study aimed at investigating the factors controlling root decomposition in the topsoil of the same regions (Chapter 3). In this larger scale experiment, exploring decomposition of standardized fine root litter in a range of forest types, soil temperature and moisture explained most of the regional variability of root decomposition in temperate forests. Although the Hainich-Dün study region has intermediate soil properties and climate, it has on average the lowest root decomposition rates. One explanation could be that in the Hainich-Dün the soils are on average frozen for a higher number of days in comparison to the other study regions (Chapter 3). Previous studies have already shown that in soils with temperatures below 0 °C microbial activity declines (Dioumaeva et al., 2002; Mikan et al., 2002). Moreover, higher root decomposition rates in the Schorfheide-Chorin may result from a greater vertical water movement through the sand in this study region, which can increase the leaching of the soluble organic matter derived from the decomposing roots. Regional differences in the diversity of the soil biota, adapted to diverse edaphic factors including climate, soil texture

and pH may also have played a role in determining the regional variability in fine root decomposition (Birkhofer et al., 2012; Thoms et al., 2010).

4.5 Conclusions

Our results show that fine root decomposition in litterbags has a larger variability across regions than at different soil depths within a given site. Thus, a similar potential to decompose root derived C exists in both, surface and deep soils. Biological activity in different soil horizon would then be mainly limited by root litter input and thus the input of new substrates. Overall, rapid decomposition of litter along the soil profile is supported by the consistent young ages of C in unprotected fractions observed for different soil horizons in other studies. The increase in the age of bulk soil C with depth is likely to be more related to the mineral-stabilized C, but further studies are required to test this hypothesis. Macroclimatic or other large-scale differences like parent material seem to be more important for initial stages of litter decomposition than changing conditions with soil depth, as regional differences in decomposition persisted for all studied soil depths.

Study region	Soil depth [cm]	OC conc. [g kg^{-1}]	TN conc. [g kg^{-1}]	OC stocks [[g m^{-2}]	TN stocks [[g m^{-2}]	Root biomass [g]
Schwäbische	0-10	33.0 ± 16.7^{Aa}	3.0 ± 1.4^{Aa}	3.4 ± 0.7^{Aa}	0.29 ± 0.07^{Aa}	3.6 ± 2.1^{Aa}
Alb	10-30	17.7 ± 6.7^{Aab}	1.7 ± 0.6^{Aab}	3.0 ± 0.6^{Aa}	0.28 ± 0.05^{Aa}	4.3 ± 0.1^{Aa}
	30-50	9.72 ± 2.18^{Ab}	0.9 ± 0.3^{Ab}	1.2 ± 0.6^{ABb}	0.11 ± 0.06^{ACb}	0.1 ± 0.1^{Ab}
Hainich-Dün	0-10	32.2 ± 4.5^{Aa}	2.5 ± 0.5^{Aa}	2.8 ± 0.7^{Aa}	0.22 ± 0.03^{ABa}	6.9 ± 7.4^{Aa}
	10-30	10.9 ± 2.2^{ABb}	1.0 ± 0.2^{Ab}	3.1 ± 0.5^{Aa}	0.30 ± 0.05^{Aa}	4.3 ± 3.2^{Aa}
	30-50	7.73 ± 1.4^{Ac}	0.8 ± 2.3^{Ab}	1.9 ± 0.5^{Ab}	0.21 ± 0.06^{Bb}	1.5 ± 2.4^{Ab}
Schorfheide-	0-10	23.6 ± 5.9^{Aa}	1.3 ± 0.6^{Ba}	2.7 ± 0.8^{Aa}	0.17 ± 0.06^{Ba}	3.3 ± 1.1^{Aa}
Chorin	10-30	7.4 ± 2.9^{Bb}	0.4 ± 0.2^{Bb}	2.2 ± 0.9^{Aa}	0.31 ± 0.05^{Ba}	4.9 ± 3.3^{Aa}
	30-50	2.8 ± 1.4^{Bc}	0.1 ± 0.25^{Bc}	1.0 ± 0.5^{Bb}	0.04 ± 0.02^{Cb}	0.2 ± 3.4^{Ab}

TABLE 4.2: Organic carbon (OC) and nitrogen (N) concentrations, OC and N stocks, and root biomass in three different soil increments of beech forests in the studied regions. Data are presented as average $\pm$ SD. Significant differences between study regions are indicated by capital letters and between soil depths by lowercase letters according to Tukey HSD test ($p < 0.05$).

Fagus sylvatica fine root characteristics	C	N	P	Ca	Mg	Al	Cellulose	Lignin
	[mg g^{-1}]							
	470 ± 13	11 ± 2	1	5	1	6	418 ± 6	433 ± 7

TABLE 4.3: Chemical quality of the *Fagus sylvatica* fine root litter used in this study ($n = 20$). Data are presented as average $\pm$ SD.

Study region	Soil depth [cm]	Soil temperature [°C]	Soil moisture [%]
Schwäbische Alb	10	6.3 ± 3.8	31 ± 9
	20	6.3 ± 3.6	30 ± 7
	50	6.6 ± 3.2	-
Hainich-Dün	10	7.2 ± 4.6	29 ± 5
	20	7.4 ± 4.4	28 ± 4
	50	7.6 ± 3.8	-
Schorfheide-Chorin	10	6.6 ± 5.2	16 ± 3
	20	9.0 ± 5.3	12 ± 2
	50	7.6 ± 4.7	-

TABLE 4.4: Soil moisture and temperature over two years of decomposition, in all study regions at different soil depths (mean $\pm$ SD). Soil temperature is expressed in °C and soil moisture is expressed in percentage of volumetric water content (%VWC). n = 10.

Soil depth [cm]	ALB	HAI	SCH
	k values [year^{-1}]		
5	0.09 ± 0.02	0.07 ± 0.01	0.13 ± 0.01
20	0.07 ± 0.02	0.06 ± 0.01	0.13 ± 0.04
35	0.08 ± 0.01	0.05 ± 0.01	0.12 ± 0.02

TABLE 4.5: Estimates of the decomposition rate constant (k) of fine roots at three different soil depths in beech forests of the Schwäbische-Alb, Hainich-Dün and Schorfheide-Chorin regions. Data are presented as average $\pm$ SD.

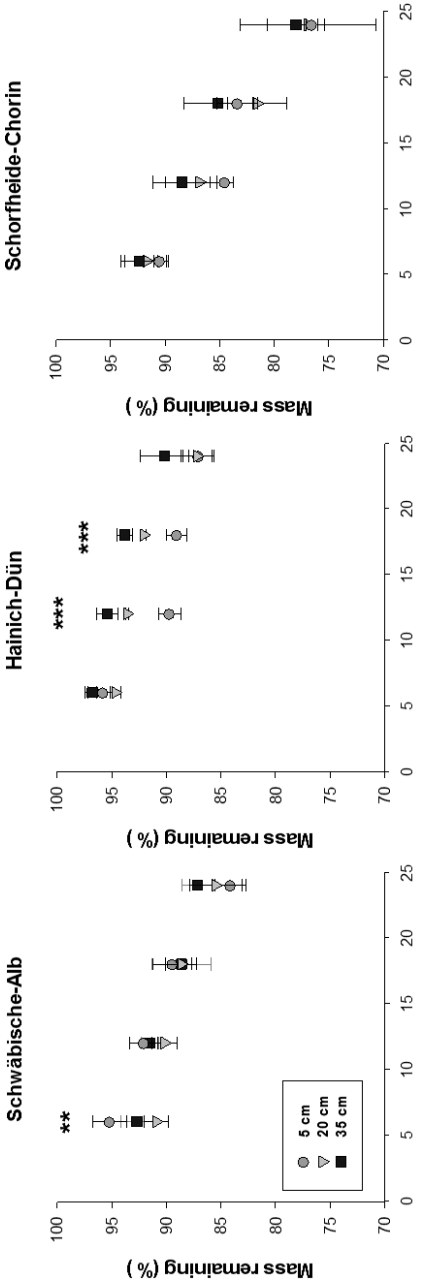

FIGURE 4.1: Remaining fine root litter at different soil depths in beech forest plots of the a) Schwäbische-Alb, b) Hainich-Dün and c) Schorfheide-Chorin study regions. Beech fine roots were distributed in litterbags at three different soil depths (5, 20 and 35 cm) and harvested four times in the first two years of decomposition. Data is presented as mean ± SD. Statistical differences according to ANOVA and Tukey-Kramer HSD test results are presented as: * ($p < 0.05$), ** ($p < 0.01$) and *** ($p < 0.001$).

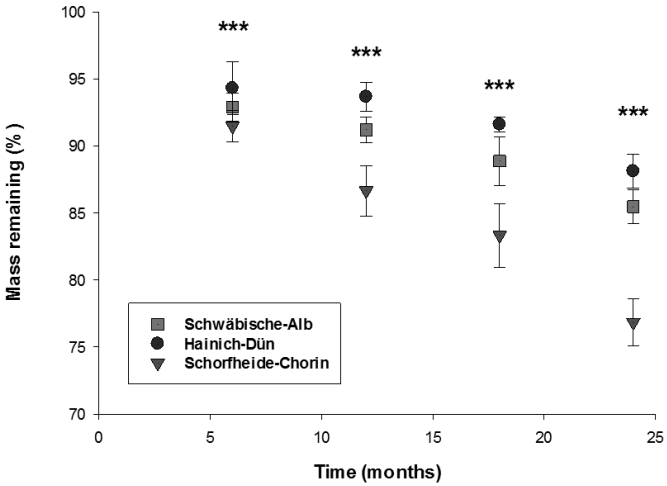

FIGURE 4.2: Remaining fine root litter in beech forest plots of the Schwäbische-Alb Hainich-Dün and Schorfheide-Chorin study regions during two years of decomposition. Data is presented as mean $\pm$ SD calculated for all samples of one study region collected over the three soil depths for each sampling time. Statistical differences according ANOVA results and Tukey-Kramer HSD test are presented as: * ($p < 0.05$), ** ($p < 0.01$) and *** ($p < 0.001$).

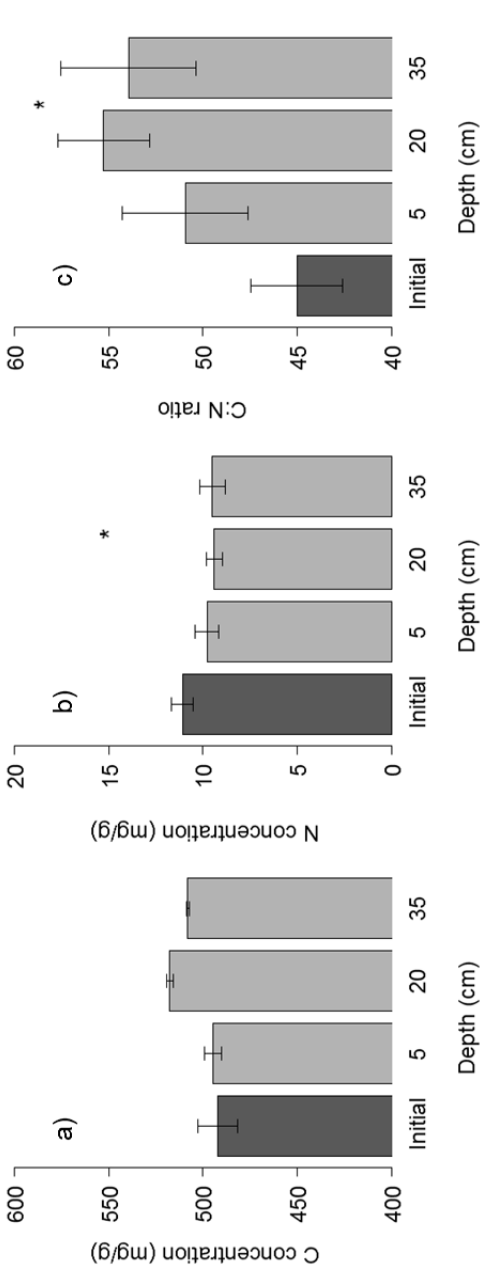

FIGURE 4.3: Comparison of a) C concentrations, b) N concentrations and c) C:N ratio of the initial standardized fine roots with the fine root litter after two years of decomposition at 5, 10 and 35 cm soil depth. Statistical differences between the initial fine root litter (darkgrey) and the mean of the decomposing roots over all depths (grey) are indicated as: * ($p < 0.05$), ** ($p < 0.01$) and *** ($p < 0.001$).

Study region	Soil horizon	Thickness [cm]	n.	pH	Sand	Clay	BG	NAG	PHOS
					[g kg^{-1}]		[nmol MUF g^{-1} dw h^{-1}]		
Schwäbische Alb	A	9.0 ± 4.4^{Aa}	9	4.2 ± 1.0^{Aa}	61 ± 30^{Aa}	448 ± 116^{Aa}	1388 ± 754^{Aa}	1265 ± 841^{Aa}	6026 ± 1980^{Aa}
	B1	13.4 ± 3.4^{Ab}	8	4.6 ± 1.0^{Aa}	80 ± 39^{Aa}	402 ± 141^{Aa}	436 ± 199^{Ab}	339 ± 196^{Ab}	1557 ± 769^{Ab}
Hainich-Dün	A	8.7 ± 2.7^{Ba}	9	4.3 ± 0.5^{Aa}	45 ± 21^{Ba}	295 ± 102^{Aa}	1244 ± 746^{Ba}	752 ± 228^{Ba}	4735 ± 1820^{Ba}
	B1	17.6 ± 5.5^{Bb}	9	4.2 ± 0.4^{Aa}	45 ± 26^{Ba}	299 ± 97^{Aa}	183 ± 123^{Bb}	163 ± 83^{Bb}	1092 ± 613^{Bb}
	B2	18.1 ± 5.2^{Bb}	9	5.3 ± 0.7^{Ab}	28 ± 10^{Ba}	565 ± 104^{Ab}	149 ± 102^{Bb}	137 ± 98^{Bb}	510 ± 150^{Bc}
Schorfheide-Chorin	A	9.2 ± 3.4^{Ba}	7	3.2 ± 0.2^{Ba}	914 ± 36^{Ca}	17 ± 11^{Ba}	205 ± 8.1^{Ca}	298 ± 167^{Ca}	2146 ± 896^{Ca}
	B1	18.3 ± 9.0^{Bb}	7	3.7 ± 0.2^{Bb}	939 ± 32^{Ca}	6 ± 7^{Ba}	32 ± 15^{Cb}	53 ± 27^{Cb}	281 ± 152^{Cb}
	B2	21.4 ± 4.7^{Bb}	6	3.9 ± 0.1^{Bb}	943 ± 33^{Ca}	9 ± 13^{Ba}	15 ± 9^{Cb}	28 ± 23^{Cb}	122 ± 66^{Cc}

TABLE 4.6: Mean $\pm$ SD of soil pH, soil texture and enzyme activities in three different soil horizons in the three study regions (data from Herold et al. (2014b)). Significant differences between study regions are indicated by capital letters and between soil depths by lowercase letters according to Tukey HSD test ($p < 0.05$). Abbreviations: BG= β-glucosidase activity, NAG=N-acetylglucosidase activity, PHOS=phosphatase activity.

5 Formation of new mineral associated organic matter from roots [1]

Abstract

Fine root litter inputs contribute significantly to the formation of soil organic matter. Part of the carbon (C) contained in dead roots is respired as CO_2 or dissolved in the perculating soil solution, and part of it is converted to stable forms of soil organic matter. To better understand and model belowground C processes it is important to assess how much root C resides and is long-term stabilized in the soil. In three German grasslands with similar land management (mown pastures) but contrasting soil texture (sandy loam, silty loam and clay), we incubated: i) homogeneously ^{14}C depleted; and ii) unlabeled -control- Arrhenatherum elatius root litter, in mesocosms containing sieved subsoil. After 18 months of incubation in the field, soil samples were recovered from the mesocosms and subjected to soil organic matter density fractionation. Bulk soil samples and mineral associated soil organic matter fractions, before and after the incubation in the field, as well as initial fine root samples, were analyzed for organic C and $\Delta^{14}C$ concentrations. The total amount of root C recovered in the bulk mineral soil was higher in clayey ($45 \pm 7\%$, average $\pm$ SD) than in silty loam ($34 \pm 5\%$) and sandy soils ($31 \pm 6\%$). In contrast, more root C was found to be stabilized by mineral association in sandy loam soils ($26 \pm 3\%$, average $\pm$ SD) in comparison to silty loam ($23 \pm 4\%$) and clayey soils ($16 \pm 5\%$). These results confirm differences in the protection mechanisms and stabilization rates in organo-mineral complexes of organic C between soils with diverse texture.

5.1 Introduction

Soil organic matter dynamics are crucial in the global carbon (C) cycle, as soil organic C represents the largest terrestrial C pool and the main source of energy for many bio-

[1] This chapter is in preparation for submission.

geochemical processes which regulate plant productivity (Schlesinger, 1997). Plant litter in the form of dead roots is a major source of soil organic C (Rasse et al., 2005; Mendez-Millan et al., 2010), yet only a few studies have attempted to quantify the amount and long term stability of root C stored in soils. A large part of root C may reside in the soil (protected from microbial respiration), due to the physical isolation of fine roots in soil aggregates, the close proximity of root decomposition products to mineral surfaces, and the recalcitrant nature of fine root tissues (Abiven et al., 2005; Rasse et al., 2005; Bird and Torn, 2006). Accordingly, a better understanding of the contribution of root C to the soil is required to improve our knowledge about belowground C processes and ecosystem scale C models.

Density fractionation is a useful method to separate organic matter into components that differ in chemistry and C turnover time (Sollins et al., 2006; Schöning et al., 2013; Schrumpf et al., 2013). Low density soil organic matter (light fraction, LF) consists of plant litter at different stages of decomposition which is not strongly associated with mineral surfaces, while high density organic matter (heavy fraction, HF) consists of the decomposition products associated to soil minerals and contains larger amounts of microbial residues than the LF (Golchin et al., 1994; Gregorich et al., 2006; Cerli et al., 2012; Schrumpf et al., 2013). The compounds forming the HF can be derived from decomposition products of the LF or from dissolved organic matter contained in the percolating soil solution (Sanaullah et al., 2011; Kalbitz and Kaiser, 2008). Stable isotope (^{13}C) and radiocarbon analyses (^{14}C) on organic C stored in different density fractions indicate that the HF usually contains more old C components than the LF, hence C in the HF is more stable and turns over longer timescales (Trumbore et al., 1989; Schöning and Kögel-Knabner, 2006; Schrumpf et al., 2013; Herold et al., 2014a).

Density fractionation of soil organic matter in conjunction with isotopic tracers (such as depletion or enrichment of ^{14}C, ^{13}C and ^{15}N) can be used to estimate the transfer rates of specific substrates among different soil fractions (Gale and Cambardella, 2000; Bird et al., 2008). Most experimental studies which have dealt with these quantifications have focused on aboveground litter, showing limited transfer rates of leaf derived C to the mineral soil (less than 10 -15%) during the first 10 -18 months of decomposition in forests or arable land (Kölbl et al., 2007; Langenbruch et al., 2014). However, root C seems to be more easily retained in the mineral soil in comparison to leaf litter (Bird and Torn, 2006), due to the higher lignin:N ratios and alkyl C contents in root tissues (Rasse et al., 2005; von Lützow et al., 2006), and their direct allocation

and decomposition within the soil system. To date, the few published studies on root C dynamics in different fractions of soil organic matter, are mostly from forest ecosystems and arable land (Gale and Cambardella, 2000; Bird et al., 2008; Sanaullah et al., 2011), and little is known about how these observations might be applicable across range of soil types in grassland ecosystems.

While there is abundant evidence that soil texture and mineralogy largely control soil organic matter storage and turnover rates (Anderson and Paul, 1984; Eusterhues et al., 2003), it is still unclear whether the protection mechanisms and stabilization rates of root derived C differ between diverse soil types. The main objective of this study is to estimate the portion of "freshly added" root C residing in the soil, as well as the contribution of root C stabilized in the HF of three temperate grasslands with very different soil texture.

To achieve this, we incubated for 18 months differently labelled *Arrhenatherum elatius* root material, i) homogeneously ^{14}C depleted root litter, and ii) control root litter not depleted in ^{14}C, in mesocosms containing sieved subsoil. By comparing the results of these two treatments we were able to assess the total portion of root C residing in the bulk soil, and to trace how much ^{14}C ended up in the HF. We were further able to estimate the portion of root C which remained as LF. Our hypothesis were: i) that an important portion of root C would reside in the soil and be transferred to the HF of all three soil types; and ii) that the portion of root C recovered in the HF would be higher in soils containing larger amounts of clay, due to the high availability of binding sites on clay mineral surfaces (Wattel-Koekkoek et al., 2001).

5.2 Material and methods

5.2.1 Sites description

The experimental sites were located in three temperate grasslands in Germany. We selected the grasslands to account for distinct soil types: 1) a Cambisol with a sandy loam texture; 2) a Stagnosol with a silty loam texture; and 3) a Stagnosol with a clayey texture. The grassland with a sandy loam texture is located in north-eastern Germany (N 53° 0' E 13° 46') has a mean annual temperature ranging between 8-8.5°C and receives a mean annual precipitation of 500-600 mm. The grasslands with a silty loam and a clayey texture are located in central Germany (N 51° 9' E 10° 28'), have a mean annual temperature ranging between 6.5-8°C and a mean annual precipitation of around 500-800 mm. The grasslands are all mowed once a year, grazed by cattle

and fertilized. More details on soil characteristics are given in Table 5.1, Table 5.3 and Table 5.4.

	Sand [%]	Silt [%]	Clay [%]	Bulk density [g cm^{-3}]
Cambisol (Sandy loam)	53.8	23.7	22.5	1.37
Stagnosol (Silty loam)	4.5	69.8	25.7	0.92
Stagnosol (Clayey soil)	7.5	41.4	51.1	0.70

TABLE 5.1: Percentages of sand, silt and clay in the three studied soils .

	C concentration [%]	N concentration [%]	^{14}C [% Modern]
^{14}C depleted grass roots	44.5 ± 0.6	1.1 ± 0.3	7 ± 1
Unlabeled grass roots (control)	42.7 ± 0.9	0.9 ± 0.1	102 ± 1

TABLE 5.2: Total C and N concentrations, ^{14}C % Modern concentrations of depleted and control fine roots. Data are presented as average $\pm$ standard deviation.

5.2.2 Experimental layout

In June 2012, we installed a field mesocosm experiment consisting of two treatments. For the first treatment we added ^{14}C depleted fine root litter to sieved subsoil; and for the second treatment we added unlabeled fine root litter to sieved subsoil. In total we deployed 6 mesocosms (3 for each treatment) in each of the three grasslands. In order to obtain fine root litter with very different ^{14}C concentrations, two different batches of the perennial grass *Arrhenatherum elatius* (L.) P. Beauv were grown in growth chambers at the Max Planck Institute for Biogeochemistry in Jena, Germany. In one chamber the grasses were grown with a $^{14}CO_2$ depleted atmosphere (the ^{14}C concentration of the gas was smaller than $0.25 \pm 0.07^{14}C$ (% Modern)), while in the other chamber the grasses were grown in natural atmosphere. This produced root litter, with similar C and N concentrations but very different ^{14}C signatures (Table 5.2). From each of the grasslands, mineral subsoil was collected at a depth of 10-20 cm. This soil was then transported to the laboratory where it was sieved to < 2 mm. We carefully removed the fine roots remaining in the sieved soil by hand. We then mixed the fresh soil free of roots, with 1 g of *Arrhenaterhum elatius* fine root litter and put it into a PVC cylinder with a diameter of 7 cm and a height of 10 cm. The weight of each soil type was adjusted so as to approximate the in-situ bulk density for each site.

We brought the mesocosms to the field and carefully placed them in the top 10 cm of the mineral soil, at least 0.5 m apart from each other. Finally, we closed the mesocosms with a 0.5 mm mesh on top, to keep other plants from growing in. Each mesocom was individually marked with a plastic label which we positioned in the surrounding soil. The mesocosms were collected after 18 months after they experienced 2 summers and 1 winter, and subsequently analyzed in the laboratory.

5.2.3 Soil density fractionation

Soil samples were dried at 40 °C and subjected to density fractionation. The fractionation was performed using sodium polytungstate (SPT, C and N poor, Tungsten Compounds, Grub am Forst, Germany) solution of 1.6 g cm^{-3} density (Golchin et al., 1994; Sohi et al., 2001; Cerli et al., 2012). 15 g of soil were placed into 250 ml centrifugation glasses and 100 ml of SPT solution was added. Samples were treated with ultrasonic sound to break aggregates. We used a stepwise increase of sonication energy, for each soil type, to determine the sonication energy needed for complete disruption of soil aggregates (as described in Cerli et al. (2012); Schrumpf et al. (2013)). To estimate the energy applied by the sonicator (Branson GmbH, Hannover, Germany), we used calorimetrical calibration (Schmidt et al., 1999). For the sandy loam and silty loam soil an energy input of 450 J ml^{-1} was enough to disrupt aggregates, while the clayey soil required 900 J ml^{-1} (Schrumpf et al., 2013). After sonication the samples were horizontally shaken for 10 minutes and then centrifuged for 30 minutes at 3500 g. The supernatant was decanted onto glass fibre filters (GF/A 100 Circles 5.0, Whatman GmbH, Dassel, Germany). The settled HF was washed with Millipore water (1000 ml) to remove the SPT. The HF was then freeze-dried and ground with a ball mill (Retsch MM200, Retsch, Haan, Germany).

5.2.4 Elemental and ^{14}C analysis

We determined the total C and N concentrations of the bulk soil samples, the HF and fine root litter, before and after the incubation in the field, by dry combustion in an elemental analyser. To evaluate the concentration of organic C in each soil sample, we determined the amount of inorganic C by removing all organic C at a temperature of 450 °C for 16 hours, and subtracting this value from the total C concentration. C and N stocks in the bulk soil, the HF and the fine roots were calculated based on the mass per area for each sample (Schrumpf et al., 2011).

All bulk soil samples and HF fraction before and after the incubation in the field, as well as initial fine root samples, were analyzed for ^{14}C concentrations. Sample preparation and analyses were performed at the ^{14}C laboratory in Jena, Germany (Steinhof et al., 2004). After combusting the samples, the resulting CO_2 was catalytically reduced to graphite at 625 °C by H_2 reduction. The graphite was analyzed by ^{14}C AMS (3MV Tandetron 4130 AMS ^{14}C system: High Voltage Engeneering Europe, HVEE, the Netherlands). We express radiocarbon data as percent modern (pM) or ^{14}C (% Modern) (Stuiver and Polach, 1977).

5.2.5 Calculations and statistical analysis

We estimated the fraction (f) of ^{14}C depleted fine root C residing in the bulk soil or transferred to the HF with the following equation:

$$f = \frac{s_l - s_c}{r_l - r_c} p \,, \tag{5.1}$$

where s_l, s_c, r_l and r_c denote the ^{14}C (% Modern) concentrations in the bulk soil or HF exposed to ^{14}C depleted roots (s_l), the control bulk soil or HF exposed to control roots (s_c), the ^{14}C depleted root litter (r_l) and the control root litter respectively (r_c), and p is the organic C stock (g C m^{-2}) contained in the bulk soil or HF. We then calculated the recovery of ^{14}C depleted root derived C in the bulk soil (rdBS) and in the HF (rdHF) by

$$rdBS, rdHF = \frac{f}{d} 100 \,, \tag{5.2}$$

where d is the amount of root C added to the volume of soil. rdBS and rdHF are considered as the portion of root derived C recovered in the bulk soil and HF after 18 months of field incubation. As the amount of LF recovered was too small to account for ^{14}C measurements, we estimated the root C residing in the LF (rdLF) by subtracting the percentages of rdHF from the percentages of rdBS.

For statistical analysis, we used one way analysis of variance accompanied by Holm's test to examine differences between the portion of ^{14}C root C recovered in the rdBS, rdHF and estimated rdLF of the three soil types. Throughout the chapter we present data as means ± standard deviation. The level of significance of statistical tests

used for this study is $p < 0.05$. We conducted statistical analysis with R, version 3.0.2 (R Development Core Team 2013).

5.3 Results

5.3.1 Mass and organic C losses during density fractionation

The average mass recovery during density fractionation was $96 \pm 3\%$ across all samples. The smallest losses occurred for the sandy loam soil ($2 \pm 1\%$), and the largest losses for the clayey soil ($6 \pm 3\%$). The recovery of organic C was on average less than the mass recovery. The largest recoveries were for the silty loam soil ($84 \pm 1\%$) followed by the sandy loam soil ($82 \pm 2\%$) and the clayey soil ($74 \pm 4\%$). The mass and OC recoveries are in the range of values reported by other studies (Grünewald et al., 2006; Castanha et al., 2008; Schrumpf et al., 2013).

5.3.2 Recovery of root derived C in the bulk soil and in the heavy fraction

After 18 months of incubation, the addition of ^{14}C depleted fine root litter decreased the ^{14}C values of the bulk soil and HF in relation to the initial values, for all of the three soil types (Table 5.3). On average, the addition of fine root litter slightly increased the initial C concentrations and C stocks of the bulk soil and HF (Table 5.4, Table 5.5). After 18 months of incubation, the added ^{14}C depleted and unlabeled roots to the soil lead to similar C concentrations and C stocks in the bulk soil and HF of the two treatments (Table 5.4, Table 5.5). The total amount of rdBS was higher in the clayey soil, followed by the silty loam soil and the sandy loam soil (Fig. 5.1). On the other hand, the rdHF in the sandy soil ($26 \pm 3\%$) was on average higher than in the silty loam ($23 \pm 4\%$) and clayey soil ($16 \pm 5\%$) (Fig. 5.1). The estimated rdLF was therefore on average lower in the sandy soil ($5 \pm 5\%$) than in the silty soil ($11 \pm 6\%$) and clayey soil ($29 \pm 8\%$), reflecting the differences between the percentages of rdBS soil and the respective rdHF.

Soil type	^{14}C % Modern concentrations in the bulk soil			^{14}C % Modern concentrations in the heavy fraction of SOM		
	before incubation with roots	after incubation with depleted roots	after incubation with control roots	before incubation with roots	after incubation with depleted roots	after incubation with control roots
Sandy loam soil	105 ± 1	101 ± 1	105 ± 0	105 ± 2	101 ± 1	105 ± 0
Silty loam soil	104 ± 1	101 ± 2	103 ± 1	104 ± 1	99 ± 2	103 ± 1
Clayey soil	109 ± 1	106 ± 1	108 ± 0	109 ± 1	106 ± 1	107 ± 1

TABLE 5.3: ^{14}C % Modern concentrations in the bulk soil and in the heavy fractions of soil organic matter (SOM) in the three studied soils. Data are presented as average $\pm$ standard deviation (n=3).

Soil type	C concentration in the bulk soil (%)			C stocks in the bulk soil (g C m^{-1})		
	before incubation with roots	after incubation with depleted roots	after incubation with control roots	before incubation with roots	after incubation with depleted roots	after incubation with control roots (n=3)
Sandy loam soil	1.04 ± 0.09	1.15 ± 0.16	1.21 ± 0.09	1098 ± 152	1241 ± 197	1262 ± 144
Silty loam soil	1.00 ± 0.02	1.05 ± 0.03	1.04 ± 0.30	589 ± 36	685 ± 41	670 ± 46
Clayey soil	3.08 ± 0.58	3.21 ± 0.70	3.14 ± 0.48	1156 ± 102	1367 ± 139	1346 ± 141

TABLE 5.4: C concentrations and C stocks in the bulk soil in the three studied soils. Data are presented as average $\pm$ standard deviation

Soil type	C concentrations in the heavy fractions of SOM (%)			C stocks in the heavy fractions of SOM (g C m^{-2})		
	before incubation with roots	after incubation with depleted roots	after incubation with control roots	before incubation with roots	after incubation with depleted roots	after incubation with control roots
Sandy loam soil	0.80 ± 0.08	0.89 ± 0.11	0.86 ± 0.09	959 ± 78	1124 ± 159	1077 ± 90
Silty loam soil	0.78 ± 0.02	0.88 ± 0.20	0.81 ± 0.08	556 ± 62	640 ± 49	612 ± 299
Clayey soil	2.42 ± 0.45	2.83 ± 0.56	2.57 ± 0.45	1003 ± 81	1121 ± 175	1041 ± 85

TABLE 5.5: C concentrations and C stocks in the heavy fractions of soil organic matter in the three studied soils. Data are presented as average $\pm$ standard deviation (n=3)

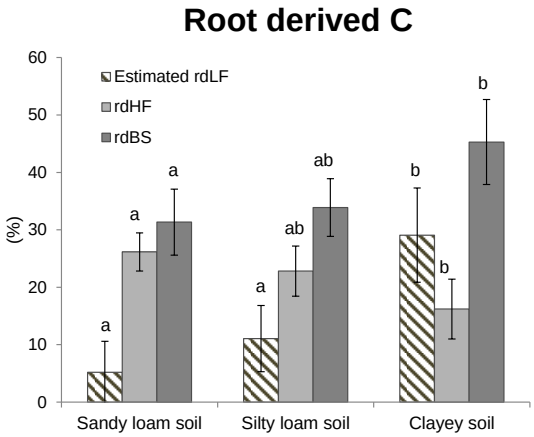

FIGURE 5.1: Percentage of root derived C in the estimated light fraction (rdLF), in the HF (rdHF) and in the bulk soil (rdBS), in temperate grasslands with different soil types, after 18 months of incubation in mesocosms. Significant differences between the rdLF, rdHF and rdBS of the three soil types are indicated by lowercase letters, according to Holm's test ($p < 0.05$).

5.4 Discussion

After 18 months of incubation in mesocosms, the total amount of *Arrhenaterhum elatius* fine root C which was recovered in the mineral soil ranged between slightly less than half and one third of the initial input, depending on the soil type (Fig. 5.1). These values are similar to the ones observed by Sanaullah et al. (2011) who studied the decomposition and stabilization of wheat roots in an arable grassland in Southern France (Cambisol with a loamy texture). Slightly lower values were instead recovered by Bird and Torn (2006) in a pine forest in California (sandy soil). The average portion of root derived C transferred to the HF that we observed in our study was again comparable to the observations of Sanaullah et al. (2011) but higher than that observed by Bird et al. (2008). Bird et al. (2008) on the other hand observed more root C residing in the LF. The differences observed in the portions of root derived C recovered in forested vs non forested ecosystems, for similar incubation times, can be explained by diverse types of litter substrates used in the experiments (i.e. grasses vs pine tree roots) (Rasse et al., 2005; von Lützow et al., 2006). Other studies have already shown that the decomposition rates of fine root litter are influenced by litter quality and vary

between roots of herbaceous plant species and roots of tree species (Silver and Miya, 2001). For instance, Silver and Miya (2001) observed that conifer roots had the lowest levels of Ca and N, the highest C:N and lignin:N ratios, and decomposed at slower rates than graminoid herbaceous species. Litter quality effects were also observed in Chapter 3 of this thesis. Moreover, the varying amounts of root C residing in the soil and transferred to the HF in diverse ecosystem types are probably related to differences in environmental conditions controlling the stabilization of soil organic matter, such as climate and soil mineralogy.

The estimated mass loss of *Arrhenaterhum elatius* fine root litter in mesocosms was approximately 30% higher than the mass loss of grass fine root litter from a lowland mesophilous hay meadow, studied in litterbags in the same study sites for the same period of time (Chapter 3). This disparity is probably related to differences in the chemical quality between the two root litter types or due to the enclosure of root litter in a screened container with a small mesh size which excluded the breakdown of root litter from macrofauna.

Previous studies, which focused on the the storage of aboveground plant litter in soils, showed that around 80 to 90% of litter C is respired as CO_2 or leached on an annual basis (Ngao et al., 2005; Kölbl et al., 2007); and only a smaller portion is accumulated as soil organic C (Kölbl et al., 2007; Kammer and Hagedorn, 2011). In relation to these results, our study suggests that less root C is mineralized or leached, and approximately 10 to 35% more to reside in the bulk mineral soil. Different decomposition / stabilization rates between aboveground and belowground plant tissues are likely to be related to differences in the chemical recalcitrance of the two litter types. For instance, root tissues are commonly more recalcitrant than aerial plant tissues, containing higher lignin : N ratios and higher alkyl contents (Rasse et al., 2005). The direct interaction of root decomposition products with the soil minerals may further play a role in protection pathway for root C in soils (Balesdent and Balabane, 1996).

In topsoils of temperate ecosystems, it was observed that the soil organic C in the HF can contain a detectable portion of "bomb" C fixed from the atmosphere since 1963, indicating that a significant portion of physicochemically protected C in the HF may be prone to steady replacement by freshly produced reactive organic compunds (Schöning et al., 2013). Together with our results, this suggests that a portion of mineral associated organic C may be of a more transient nature and cycling on relatively fast timescales.

Our results further indicate that the initial amount of root ^{14}C transferred to the HF is lower in soils containing larger amounts of clay (Fig. 5.1), despite the probably higher availability of binding sites of clay minerals (Wattel-Koekkoek et al., 2001). Possible reasons for this are slower decomposition rates of fine root litter (breakdown to smaller compounds more easily bound to minerals) and smaller amounts of C leached as dissolved organic matter in clayey soil, in comparison to silty and sandy loam soils. The lower decomposition rates / leaching of fine root organic matter in clayey soils compared to silty and sandy loam soils are deduced from the lower amounts of root C recovered in the bulk mineral soils (Fig. 5.1). Another reason could be that root C might be better protected in soils containing more clay, due to its higher probability to be occluded in aggregates inaccessible by microbes (Sørensen, 1981; von Lützow et al., 2006). Slower decomposition rates of fine root litter and larger amounts of fine root C occluded in aggregates could, for example, hinder the potential amount of root stabilized by mineral association in the HF.

Although previous studies have shown that less CO_2 is produced, and smaller portions of organic C are leached in soils containing higher amounts of clay (Schimel et al., 1985; Brown et al., 1995; McInerney and Bolger, 2000), we cannot exclude some experimental drawbacks. For instance, the clayey and silty loam soils may have been subjected to a more heavy compaction or formation of physical soil crusts than the sandy loam soils, which may have reduced the biological activity. In any case the mesocosms were all covered with a 0.5 mesh on the top which limited these drawbacks. Moreover, in Northern Germany, where the mesocosms containing sandy loam soil were placed, the mean annual temperature is slightly warmer than in central Germany where the other mesocosms have been incubated. These factors could have slowed down the in situ aerobic decomposition rates of the clayey soils and silty soils in comparison to the sandy soils, where the conditions may have been more favourable for decomposition. Nonetheless, slower decomposition rates of root litter and assumed higher protection of root C in aggregates of clayey soils, together with the larger provision of surface area on which organic matter can be sorbed by clay minerals, may, over longer time scales ($>$ 18 months), result in a more efficient persistence of root C in comparison to sandy soils. This is supported by the evidence of apparent slower turnover times of finer texture soil fractions (Anderson and Paul, 1984; Eusterhues et al., 2003).

5.5 Conclusions

Our results show that the portion of root litter C transferred to the mineral associated organic matter in temperate grasslands, after 18 months of incubation in mesocosms, ranged between 16% and 26% of the initial amount of added root litter C. This indicates that a significant amount of mineral-stabilized C is formed by 'fresh' organic compounds produced from the breakdown of fine root tissues. The variability of these quantifications depends on the different decomposition rates and conversion efficiencies of root C to mineral associated organic matter in soil with different texture. Hence, this confirms that soil physical properties, such as texture, can play a role in influencing the mineral-stabilization of root C and its persistence in the soil.

6 General discussion and conclusion

6.1 Fine root C ages

This thesis provides new insights on the environmental factors that can affect fine root (diameter < 2 mm) C dynamics in soils in a wide range of temperate forests and grasslands. Estimating the root mean C ages, from radiocarbon (^{14}C) measurements, Chapter 2 finds that the ^{14}C in grasslands ($36 \pm 1‰$, mean $\pm$ SD) is generally much closer to the atmospheric ^{14}C curve than fine root ^{14}C in forests ($90 \pm 5‰$). This is reflected in a mean root C age difference of about 9 years between the two ecosystem types (11 ± 2 years in forests and 2 ± 0.4 years in grasslands, mean $\pm$ SD). The question arises whether the differences in root mean C ages observed between the two ecosystems are related to higher contents of perennial root tissues in tree species compared to herbaceous species, or to a higher ability of tree species to use old C reserves to produce new roots. Gaining knowledge on the reasons driving these differences can significantly improve our ability to model and predict belowground C fluxes.

Previous studies which measured and modelled the spectrum of fine root turnover times (Tierney and Fahey, 2002; Strand et al., 2008; Gaudinski et al., 2010), have suggested that fine roots of trees may be cycling on different time scales. A reason for different time scales of C cycling in fine roots is that trees may produce variable amounts of short-lived, absorptive fine roots and longer lived, transport or storage fine roots (Guo et al., 2008; Goebel et al., 2011). Xia et al. (2010) suggested that fine root mortality and production may occur in clusters of low order roots with diverse structure and function. Yet a portion of the fine roots turnover rapidly (Guo et al., 2008), while a large fraction of C in fine roots remains for several years (Gaudinski et al., 2010). Hence, the use of two-pool survival functions is best suited to represent fine-root turnover in models for forest ecosystems rather than steady state models (Ahrens et al., 2014; Lynch et al., 2013).

As we cannot rule out that perennial species may use old C reserves to produce new roots (Trumbore and Gaudinski, 2003; Gaudinski et al., 2010), in this thesis the radio-

carbon contents were used to estimate fine root C ages rather than the direct turnover time of fine roots. A recent study by Sah et al. (2013) concluded that trees may use old carbon reserves for the production of new live tree roots in mature boreal forests. This finding is supported by the studies by Vargas et al. (2009, 2010) which showed that plants in tropical forests can allocate old stored carbon to form new fine roots and mycorrhizae following hurricane disturbance. On the other hand, Lynch et al. (2013) found that most of the fine roots produced in a sweetgum plantation in Tennessee, USA, were mainly produced from current photosynthates. The lack of consistency may be related to to the different resource aquisition and conservation strategies of the studied plant species or to different methods of investigation.

Till now the mechanisms that can control the allocation of old storage C for new fine root production in perennial species are currently not known and deserve further investigation. If fine roots can be produced by old C reserves, the apparent ^{14}C turnover times of roots in forests or in grasslands containing large amounts of perennial species may yield estimates which are too slow in comparison to grasslands with a higher proportion of annual species, which are mainly built up of contemporary atmospheric ^{14}C (Ahrens et al., 2014). Hence, without more information about the internal redistribution dynamics of C in trees and other perennial plant species, we cannot completely separate the age of root C into a recycling component and a newly grown component.

Although the mean C ages of fine root standing stocks estimated in Chapter 2 represent a mean that can mix faster and slower cycling roots, they enabled a first comparison of the large differences between forests and grasslands. A recently published study aimed at investigating the ^{14}C turnover times of different soil organic matter density fractions in the same study regions showed large differences in $\Delta^{14}C$ values also between the labile light fraction of soil organic matter in grasslands and forests (Fig. 1 in Herold et al., 2014a). The differences in $\Delta^{14}C$ values between grassland and forests were instead not observed for the mineral associated organic matter (Fig. 6.1). Since much of the C contained in the light fraction of organic matter consists of relatively “fresh” plant litter (Gregorich et al., 2006), this suggests that part of the striking difference in radiocarbon between forests and grasslands in the labile light fraction of soil organic matter originates from the older tree roots in forests. A further evidence of large differences in the root C cycling between grasslands and forests is given by the two times lower initial mass loss rates observed for tree fine roots in litterbags compared to herbaceous fine roots, after 12 months of decomposition (Chapter 3).

As discussed in Chapter 2, a good relation exists between the root C mean ages in grasslands and the variation in soil moisture or available soil nutrients. However, these relations are most likely not direct but rather induced by site specific differences in climate, parent material and land management which influence plant diversity and the number of herbaceous perennial species (Hobbie, 1992; Tjoelker et al., 2005; Socher et al., 2012). Chapter 2 shows that, on average, perennial species can yield older fine root mean C ages (up to 5 years) in comparison to annual species. Previous studies have already indicated that an internal redistribution of C occurs in perennial herbaceous species (Milchunas et al., 1985; Veldkamp, 1994). To test whether environmental factors have direct influence on the ^{14}C in roots or if they are rather mediated by their influence on plant species composition and diversity, it would be helpful to separately study the effects of moisture and nitrogen on fine root C ages with a factorial experimental design in annual grasslands.

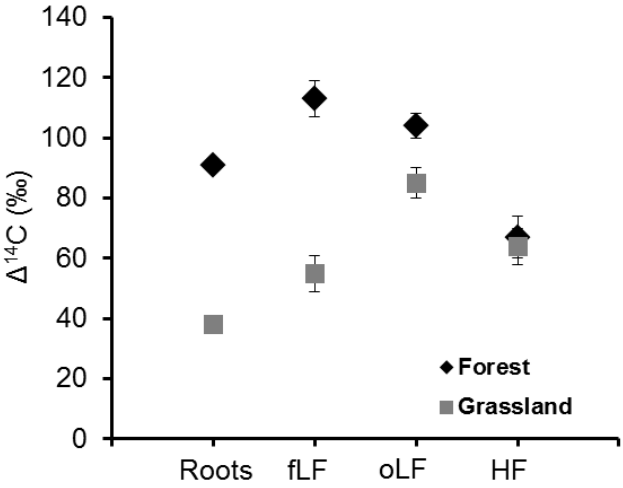

FIGURE 6.1: The mean Δ^{14}C of fine roots in forests and grasslands measured in the Hainich-Dün (HAI) and Schwäbische Alb (ALB) in 2011 (Chapter 2) are superimposed on Fig. 1 in Herold et al. (2014a). Herold et al. (2014a) indicated the mean Δ^{14}C values and standard errors of the particulate organic matter residing outside aggregates (fLF) and inside aggregates (oLF), as well as in the mineral associated fraction (HF) in forest and grassland sites in the Hainich-Dün and Schwäbische Alb which they measured in 2008. The lower values of the roots in comparison to the different soil organic matter fractions are due to the different year of ^{14}C measurements. The average atmospheric Δ^{14}C difference between years 2008 and 2011 is approximately 11‰.

6.2 Decomposition of fine roots

The decomposition of fine roots is an important ecological process which controls the global C budget, not only by affecting the release of C back to the atmosphere but also its transfer from plants to soils. In Chapter 3, soil moisture and soil temperature were found to be the main determinants of the mass loss of fine root litter both among and within study regions. This is supported by the observations of other studies which indicated that the activity of the decomposer community is controlled by soil moisture and soil temperature, which in turn influences the decomposition rates of plant litter (Chen et al., 2000; Dioumaeva et al., 2002). Root litter quality, and in particular the lignin : N ratio, was also observed to be a good predictor of fine root decomposition, explaining 15 % of the variability in temperate grasslands and 10 % of the variability in temperate forests of the Hainich region. This is also in accordance with other studies which showed that the lignin:N ratio is a valuable predictor for plant litter decomposition (Berg, 1984; Bardgett et al., 1998; Scheffer and Aerts, 2000; Janssens et al., 2010). In our study regions, changes in the root lignin:N ratio were related to land management; N addition in grasslands and tree species composition in forests. This indicates that changes in land management can alter fine root decomposition rates through their effects on plant species composition and plant functional types - which determine the chemical quality of the root litter.

Although the variability of fine root decomposition in litterbags was observed to be large across study regions (Chapter 3), similar decomposition rates were observed at different soil depths within a given site (Chapter 5). This result was unexpected, as the increase of organic C age with depth (Paul et al., 1997; Trumbore, 2000) is commonly explained by a reduction in organic matter decomposition along the soil profile. Fine root decomposition is assumed to decrease with depth due to declines in microbial activities and relative variation in soil temperature along the soil profile, more frequent anaerobic conditions, increasing portions of mineral-protected OC, and changes in the quantity and quality of plant litter input in deeper compared to surface soil (Rovira and Ramón Vallejo, 2002; Fierer et al., 2003a; Fontaine et al., 2007; Rumpel and Kögel-Knabner, 2011). The finding of similar decomposition rates at different soil depths overall indicates that a comparable potential to degrade root derived C exists in both topsoil and deeper soil layers. This result is supported by the findings of Sanaullah et al. (2011), who showed that the amount of wheat root derived C and N remaining in the soil was similar in different soil horizons of an arable grassland in southern France

after 3 years of decomposition. Thus suggesting, that the decline of biological activity of the decomposer community along the soil profile is in turn probably limited by reduced resource availability, for instance due to decreases in root biomass, throughfall and organic substrates from leaching, with soil depth (Jobbágy and Jackson, 2000; Kalbitz et al., 2000). Other studies have shown that the radiocarbon age of the more active, physicochemically unprotected C in the free light fraction only slightly increases along the soil profile, while the less active fractions (C occluded in aggregates or in association with minerals) become older with depth (Schöning and Kögel-Knabner, 2006; Schrumpf et al., 2013). Together with our results, this indicates that in both surface and deep soils the free light fraction, which is partly derived from the breakdown of root litter, is preferentially decomposed at all soil depths.

While soil texture was not observed to have a direct influence on the decomposition rates of fine root litter (Chapter 3), it seemed to play an important role in influencing the decomposition rates of fine roots in the local scale mesocosm experiment, aimed at quantifying the conversion efficiency of root litter to soil organic matter in 3 different soil types (Chapter 4). The reason for this discrepancy is probably related to the different sample number between the two experiments or to the fact that the mesocosms were in direct contact with the soil while the fine roots in litterbags were enclosed in a 100 μm polyester mesh screening. Moreover, it is difficult to completely separate soil moisture and soil texture effects on fine root decomposition as soil texture largely controls the amount of pores filled with water (Mitchell and Soga, 1976).

The estimated mass loss of fine root litter in the mesocosm experiment was observed to be approximately 30 $\%$ more in comparison to the mass loss rates of fine roots in litterbags after 18 months of decomposition in the same sites. This may be caused by differences in the root substrates used in the two experiments; for instance, the root litter used in the mesocosom experiment had a lower C:N ratio in comparison to the roots used as standardized root litter in the litterbag experiment. Moreover, although the litterbag method is simple and convenient and therefore widely used in decomposition studies (e.g. Berg, 1986; Hobbie, 1992; Parton et al., 2007; Harmon et al., 2009), this method can bias the mass loss of fine root litter, due to a selection of small mesh sizes which exclude soil macrofauna which contributes to the mechanical breakdown of plant litter. Hence, the differences in mass loss rates presented in Chapter 3 and 4 should not be considered as absolute amounts of total mass losses, but can be used to compare effects of environmental conditions and soil depth on decomposition rates across sites and soil depths. The observed percentages of fine root litter mass losses

studied in litterbags are relatively low, though comparable to the values observed by other studies in forest and grassland ecosystems (McClaugherty et al., 1984; Parton et al., 2007). The estimated initial decomposition rates (*k-values*) are, however, lower than the averaged *k-values* (after 1 year of decomposition) presented in a global meta-analysis by Silver and Miya (2001) which represents data from 32 publications. The relatively cold and dry climatic conditions of temperate ecosystems may be one of the reasons for the slow decomposition rates; for instance Parton et al. (2007) observed higher mass losses of root litter in tropical forests than in boreal forest and tundra.

6.3 Contribution of root C to the mineral associated organic matter

The use of two batches of very differently labelled *Arrhenatherum elatius* root litter added as particulate organic matter to sieved subsoil, enabled us to estimate how much root litter was protected in the soil after 18 months of incubation in mesocosms placed in temperate grasslands (Chapter 5). The density fractionation of soil samples further allowed a quantification of how much root C was efficiently converted to the mineral associated organic matter. Between slightly less than half and one third of the total root litter initially placed in the mesocosms resided in the bulk mineral soil, and of this 16 to 26 % percent was stabilized in the mineral associated organic matter. The variability of these quantifications depends on the different decomposition rates and conversion efficiencies of root C to soil organic matter in diverse soil types.

Both environmental site conditions and differences in root litter chemical quality may influence the rate of decomposition of fine root litter. Hence, it is important to take into account that the portion of root litter residing in the soil and transferred to the mineral associated organic matter may differ for root litter with diverse chemical quality and decomposing in different environmental conditions. Soil texture influenced the persistence of root derived C in soil and its stabilization as mineral associated organic matter. The amount of recovered root C in the bulk mineral soil was observed to be higher in clay and in silty loam soils than in sandy soils, while the largest amount of root C stabilized by mineral association was observed in sandy soils. From this study, it is however difficult to disentangle whether the initial amount of root C transferred to the mineral associated organic matter is lower in soils containing larger amounts of clay, due to slower litter decomposition and less leaching in clay soils (Schimel et al., 1985; Brown et al., 1995; McInerney and Bolger, 2000), or due to the possibility of a higher protection of organic C within aggregates in soils containing larger amounts of

clay (Sørensen, 1981; von Lützow et al., 2006). A more detailed investigation of these samples with secondary ion mass spectrometry at the nanoscale (NanoSIMS), could allow us to explore the exact location of new root derived C and to identify which soil components preferentially protect it (Heister et al., 2012).

In comparison to studies, adopting a similar methodology to aboveground plant litter, this study showed that less root C was lost though microbial respiration or leaching in comparison to leaf litter, and about 10 to 35 % more was observed to reside in the bulk mineral soil (Ngao et al., 2005; Kölbl et al., 2007). Most interestingly, 5 to 15 % more root C than aboveground plant litter C was recovered as mineral associated organic matter after comparable periods of incubation in the soil (Kölbl et al., 2007). The observation of a major contribution of root litter to soil C storage is in line with previous studies which showed that root C is retained more efficiently than are aboveground plant C inputs, such as leafs and needles (Bird and Torn, 2006; Mendez-Millan et al., 2010; Rasse et al., 2005). For instance, Bird and Torn (2006) studied the dynamics of dual-labeled (^{13}C/^{15}N) *Pinus ponderosa* needles and fine roots placed at two depths (O and A horizons) in a temperate conifer forest during two years, and suggested that plant allocation belowground to fine roots results in more C retained and less N mineralized compared with allocation aboveground to needles, primarily due to litter quality differences. Mendez-Millan et al. (2010), who analysed the dynamics of shoot and root-derived biomarkers in soils using a wheat and maize (C3/C4) chronosequence, also showed that during the first six years of maize crop root markers were highly incorporated into soil organic matter possibly due to physical protection. All in all, these results suggest a higher efficiency of conversion of new fine root C into more stabilized pools of soil organic matter in comparison to aboveground litter. A further evidence for new root C transfer into the mineral associated organic matter, is given by recent findings of significant contributions of bomb-produced ^{14}C to the mineral associated organic matter of topsoil layers (Schöning et al., 2013; Herold et al., 2014a). These results also highlight that a portion of organic C is cycling on timescales fast enough to be affected by changes in plant belowground allocation patterns and decomposition rates due to changes in climate and land management.

6.4 Land management and biodiversity

This thesis revealed that long-term land management, independent of study region and soil properties, only had a minor control on fine root decomposition and root mean

C ages, and its effects were mainly indirect via changes in plant species composition and diversity. Changes in plant composition influence ecosystem nutrient cycling in many ways, as was observed in this thesis by changes in litter quality, but also due to variations in biomass production, nitrogen retention and microclimate (Hooper and Vitousek, 1998).

It was also difficult to completely disentangle the effects of land management on root C cycling in soils from the changes driven by local climate conditions and soil properties, such as soil moisture, soil nutrient content, ph and soil biota. A quantification of the consequences related to land management and changes in biodiversity on the global C cycle may be derived from future studies considering different land-use types. A further challenge is also to be able to generalize the the factors and mechanisms that drive the losses of certain types of species across different ecosystems and regions (Handa et al., 2014).

6.5 Implications for future research

A major objective was to determine the environmental factors influencing the initial decomposition rates of fine root litter. Studies have shown that a relatively fast initial phase of litter decomposition seems to be followed by slower decomposition rates at later stages (after 1 or 2 years) with a shift in driving factors (Harmon et al., 2009). Therefore, longer term litter decomposition studies (after 24 months) would be helpful to understand whether the observed differences between ecosystem types and study regions persist over prolonged periods of time. Moreover, it would be interesting to test whether decomposition rates in subsoil may be hampered relative to topsoil at later stages of decomposition, due to a decrease in easily decomposable organic substrates (from the addition of litterbags with new resorces) which may prime microbial activities and initial rates of fine root litter decomposition in deeper soil layers. An interesting task would also be to follow the decomposition of specific components of root litter over time, such as lignin, cellulose and element concentrations. An analysis of this kind could be done on the root samples collected from the litterbags used in this thesis, as they present roots which decomposed in a wide range of different environmental conditions, in different regions of central Europe, partly also with different initial root litter quality. Moreover, the combination of the measured decomposition rates of fine roots in litterbags with analysis of microbial species diversity (i.e., DNA

sequencing and PLFAs) and activity (enzyme analyses) would provide further insights into explaining the variability of fine root decomposition.

In Chapter 5 the total amount of root C persisting in the soil and the portion of root C contributing to the formation of more stable mineral associated organic matter were estimated for different soil types. In order to improve the current belowground nutrient models a future task would be to estimate, not only how much of the root C, but also how much root nitrogen (N), is dissolved in the percolating soil solution during decomposition, as dissolved organic matter is relevant for subsoil organic matter storage (Michalzik et al., 2003). As root labeling experiments associated to soil density fractionations are very laborious, till now most studies have been done in single ecosystem types (Bird and Torn, 2006; Sanaullah et al., 2011), more efforts are needed to explore to what extent root derived C in soils contributes to mineral associated organic matter in different environmental conditions and in different ecosystems.

Estimating fine root productivity in temperate grasslands and forests was beyond the scope of this study and remains a future challenge, as the input of C from fine roots is one of the key factors in the belowground C cycle, as demonstrated in Chapter 5. It is important here to emphasize that no soil organic matter budget study is complete without a quantification of above and belowground biomass inputs to the soil from vegetation.

6.6 Main conclusions

In this thesis research, several field experiments were developed to improve our understanding of the potential factors influencing the formation of soil organic matter from fine roots. These experiments have been located within the Biodiversity Exploratories project. The design of this large-scale and long-term project provided a hierarchical set of standardized experimental field plots in three different regions in Germany encompassing various land management types in temperate forest and grasslands differing in their parent material and climate. Specific attention was given: to understand the effects of land use and management on fine root C mean ages; to determine the driving biotic and abiotic factors influencing initial stages of fine root decomposition at a large spatial scale and at different soil depths; and to quantify the C input from plant roots to soil organic matter. Based on this work the following overarching conclusions can be drawn:

I Radiocarbon measurements of living root tissues in temperate ecosystems show that on average C resides for circa a decade longer in fine roots belonging to trees than in fine roots of herbaceous plant species. This result, together with the finding of twice as fast decomposition rates in grasslands than in forests and the observations by Herold et al. (2014a), of higher radiocarbon contents in the labile light fraction organic matter of forested ecosystems, indicates that root C may cycle faster in topsoils of temperate grasslands than in temperate forests. Moreover, in grasslands the mean age of root C is affected by management induced changes in soil moisture and available nutrients via alterations of plant species diversity and number of perennial species.

II The variability of the initial mass loss rates of fine root litter incubated in litterbags is largely influenced by differences in environmental conditions among and within study regions. Variations in soil moisture and soil temperature largely control fine root decomposition by influencing the activity of the decomposer community. The initial lignin : N ratio of root litter further explains variation for local on-site collected root litter, which in turn is influenced by land use; N addition in grasslands and tree species composition in forests.

III Fine root decomposition rates in litterbags have a larger variability across regions than at different soil depths within a given site. Suggesting that a similar potential to degrade root derived C exists in both surface and deep soils. Moreover, this indicates that climatic or other large-scale differences in environmental conditions are more important for initial stages of litter decomposition than changing conditions with soil depth.

IV Analyses of short term decomposition and C stabilization processes of ^{14}C labeled fine root litter in mesocosms indicate that a significant portion mineral associated organic C is formed from “fresh” fine root organic substrates. Moreover, the amount of root C residing in the soil and transfered to the mineral associated fraction is dependent on the soil type.

This knowledge can be used to assess the relative importance of different mechanisms and environmental factors that determine the formation of new soil organic matter from roots and it can help modelers to test and improve the existing soil organic matter models. The results of this thesis may also be used as a base to develop new experiments and collection of data by other experimental researchers.

7 Summary

Root inputs have increasingly been shown to have a key role in the formation of soil organic matter, the largest active terrestrial reservoir of the global carbon cycle storing about 1500 Pg of organic carbon (C) in the upper meter of the mineral soil (1 Pg=10^{15} g). The amount of organic matter stored in soils is not permanent, but dependent on a number of environmental factors which regulate the balance between the inputs, mainly through root litter, and the outputs through decomposition. Possible predictors of changes in belowground organic C cycling are: climate, differences in soil parent material, variations in land management and biodiversity. But how much C is allocated to fine roots? What are the turnover times of root systems? Do environmental site conditions or differences in root litter quality have a stronger influence on decomposition? How much root litter is stabilized in the soil? Answering these questions is of great importance, given the need to improve our knowledge of belowground C fluxes and develop predictive models to understand how ecosystems will respond to environmental change.

The main aim of this thesis was to study the potential factors that can affect the allocation, storage and loss of fine root ($<$2 mm) derived C in a range of soils in temperate forests and grasslands. Specific attention was given to: i) assess the effects of land use and management on fine root C mean ages estimated from radiocarbon (^{14}C) data; ii) determine the driving biotic and abiotic factors influencing initial stages of fine root decomposition in litterbags at a large spatial scale; iii) study the depth-dependence of fine root decomposition; and iv) quantify the C input from plant roots to the mineral associated organic matter.

To answer these questions, field experiments were conducted and C isotope techniques and soil density fractionations were used. The field experiments were established in a large network of grassland and forest plots, in three different German regions (Schorfheide-Chorin, Hainich-Dün, Schwäbische Alb), belonging to the Biodiversity Exploratories Project. The field plots (50 grassland and 50 forest plots in each

region) encompassed a wide range of climate, parent material, vegetation, and land management.

Chapter 2 presents one of the first attempts to compare fine root C mean ages between 27 grasslands and 27 forests under diverse management. Radiocarbon measurements of fine root biomass were used to determine the mean C age of living fine roots, with a steady state model. These observations demonstrate older ^{14}C in the forest fine roots than in the grassland fine roots by 9 years on average. Further, the mean age of root C in grasslands was shown to be influenced by changes in plant species diversity and number of perennial species which in turn can be affected by changes in soil nutrients and moisture.

Chapter 3 deals with identifying the predictors of fine root litter decomposition in temperate ecosystems, after 12 months of incubation in litterbags. In all 150 forest and 150 grassland plots litterbags (100 μm mesh size) containing a standardized litter consisting of fine roots from European beech (*Fagus sylvatica* L.) in forests, and fine roots from a lowland mesophilous hay meadow in grasslands, were deployed. In the Hainich-Dün study region the decomposition rates of this standardized litter were compared to the decomposition rates of root litter collected on-site, to separate the effect of litter quality from environmental factors. The results of this study indicate that fine root decomposition in temperate grasslands is twice as high as in temperate forests. Moreover, it was observed that at the regional scale fine root decomposition is influenced by environmental variables such as soil moisture, soil temperature and soil nutrient content, which explained the decomposition of both standardized and on-site collected litter. Additional variation for the on-site collected litter was explained by the root lignin:N ratio, which in our study was influenced by land management; for example N addition in grasslands and tree species composition in forests.

Chapter 4 presents a study aimed at understanding whether fine root decomposition in litterbags decreases with increasing soil depth. Although it was hypothesized that fine root decomposition would decline with soil depth, due to previously reported observations of decreasing biological activity along the soil profile, the results of this study indicate that the average amount of root litter remaining after 24 months of field incubation did not vary with soil depth (5, 20, 35 cm). This suggests that a similar potential to degrade root derived C exists in both surface and deep soils. Therefore, biological activity in different soil layers may be limited by the input of new substrates (i.e. root litter). The overall rapid decomposition of root litter along the soil profile is

supported by the consistent young ages of C in labile fractions of soil organic matter observed for different soil layers in other studies.

Chapter 5 assesses how much root litter C is stabilized in the mineral associated organic matter of 3 temperate grasslands with similar land management (mown pastures), but contrasting soil texture (sandy loam, silty loam and clay). The transfer rate of isotopically depleted ^{14}C root *Arrhenatherum elatius* fine root litter (-7 ^{14}C (% Modern)) to the bulk soil and in the mineral associated organic matter was traced in field mesocosms and compared to that of root litter with a natural abundance isotopic ratio (102 ^{14}C (% Modern)). To estimate how much of the root C was transferred to the mineral associated organic matter, soil samples were subjected to soil organic matter density fractionation. On average, about half to 1/3 of the total root C resided in the soil, and of this 16 to 26 percent was stabilized in the mineral organic matter of temperate grasslands after 18 months of incubation in the mesocosms. The variability was related to differences in soil texture.

Overall, older fine root C ages in forests compared to grasslands, and twice as fast decomposition rates in grasslands than in forests indicate that root C may cycle faster in temperate grasslands than in temperate forests. However, more research is required to improve our understanding of possible internal redistribution dynamics of C in roots with different functional roles and of their decomposition rates. Fine root decomposition rates in litterbags are shown to have a larger variability across regions than at different soil depths within a given site, indicating that climatic or other large-scale differences in environmental conditions are more important for initial stages of litter decomposition than changing conditions with soil depth. The quantification of the efficiency of conversion of root litter to soil organic matter in temperate grasslands confirmed that a significant amount of mineral-stabilized C is formed by 'fresh' organic compunds produced from the breakdown of fine root material. A future challenge will be to estimate fine root productivity in temperate grasslands and forests as no soil organic C budget study is complete without a quantification of above and belowground C inputs from vegetation.

8 Zusammenfassung

Der Eintrag von Wurzeln in den Boden spielt eine Schlüsselrolle bei der Entstehung von organischer Bodensubstanz. Organische Bodensubstanz ist der größte aktive terrestrische Speicher für organischen Kohlenstoff im globalen Kohlenstoffkreislauf mit Vorräten von etwa 1500 Pg Kohlenstoff im ersten Meter des Mineralbodens (1 Pg=10^{15} g). Die Vorräte an organischer Substanz im Boden sind nicht gleichbleibend, sondern hängen von einer Anzahl von Umweltfaktoren ab, die die Bilanz zwischen Einträgen – hauptsächlich durch Wurzelstreu – und Austrägen – durch Abbau – regulieren. Mögliche Prädiktoren von Veränderungen im unterirdischen Kreislauf des organischen Kohlenstoffs sind Klima, Unterschiede im Ausgangsgestein des Bodens, Veränderungen in der Landnutzung und Biodiversität. Für das Verständnis des unterirdischen Kohlenstoffkreislaufs und die Entwicklung prädiktiver Modelle, die die Reaktion von Ökosystemen auf Umweltveränderungen vorhersagen, ist die Beantwortung folgender Fragen wichtig: Wieviel Kohlenstoff verteilt sich auf Feinwurzeln ($<$2 mm)? Wie schnell sind die Umsatzzeiten der Wurzeln? Haben Standortfaktoren oder Unterschiede in der Qualität der Wurzelstreu einen stärkeren Einfluss auf den Streuabbau? Welcher Anteil des Wurzelstreueintrags wird im Boden stabilisiert?

Das Hauptziel dieser Arbeit bestand darin, Faktoren, die die Speicherung und den Verlust von Kohlenstoff aus Feinwurzeln beeinflussen, in einer Reihe von Wald- und Grünlandböden der gemäßigten Klimazone zu untersuchen. Besonderer Augenmerk lag dabei auf i) der Bewertung der Effekte von Bewirtschaftung und Landnutzung; ii) der Bestimmung der wesentlichen biotischen und abiotischen Faktoren, die die Initialphase der Abbaus von Feinwurzelstreu beeinflussen; iii) der Untersuchung der Tiefenabhängigkeit des Abbaus von Feinwurzelstreu und iv) der Quantifizierung des Input von Kohlenstoff aus Wurzelstreu in die mineral-assoziierte organische Substanz.

Um diese Fragen zu beantworten, wurden Freilandexperimente durchgeführt und Kohlenstoff-Isotope und Dichtefraktionierungen verwendet. Die Freilandexperimente waren in einem großen Netzwerk von Grünland- und Waldstandorten in drei deutschen Regionen (Schorfheide-Chorin, Hainich-Dün, Schwäbische Alb) angelegt. Diese Stan-

dorte sind Teil der Biodiversitäts – Exploratorien und umfassen ein weites Spektrum von Klimaten, Ausgangsmaterialien und Bewirtschaftungspraktiken.

Kapitel 2 stellt einen der ersten Versuche dar, das mittlere Kohlenstoffalter von Feinwurzeln an 27 Grünlandstandorten und 27 Waldstandorten mit einer Reihe von unterschiedlichen Bewirtschaftungssystemen zu vergleichen. Mit einem steady-state Modell wurde das mittlere Kohlenstoffalter der lebenden Feinwurzeln anhand der Radiokohlenstoff ^{14}C-Gehalte der Feinwurzeln bestimmt. Die Messungen zeigen, dass Feinwurzeln in Wäldern im Durchschnitt ein 9 Jahre längeres ^{14}C/Alter haben als Feinwurzeln im Grünland. Weiterhin hing das mittlere Alter von Kohlenstoff in Wurzeln im Grünland von der Anzahl der mehrjähriger Arten und der pflanzlichen Artenvielfalt ab. Diese Faktoren werden wesentlich von Unterschieden in der Nährstoffversorgung und Bodenfeuchte, die sich u.a. aus unterschiedlichen Bewirtschaftungspraktiken ergeben, beeinflusst.

Kapitel 3 zeigt, welche Variablen die Unterschiede im Abbauverhalten von Feinwurzelstreu in Ökosystemen der gemäßigten Breiten erklären können. Der Streuabbau wurde mit einer Inkubation von Feinwurzeln in Streubeuteln gemessen. An allen 150 Wald- und 150 Grünlandstandorten wurden Streubeutel (100 μm Maschenweite) mit standardisierter Feinwurzelstreu eingebracht. Für die Waldstandorte wurde Feinwurzelstreu von Rotbuchen (*Fagus sylvatica* L.) und für die Grünlandstandorte von einer mageren Arrhenaterion elatoris W. Koch - Mähwiese verwendet. In der Hainich-Dün Region wurde diese standardisierte Feinwurzelstreu mit *in situ* entnommener Wurzelstreu verglichen, um den Einfluss der Streuqualität vom Einfluss der Umweltbedingungen zu separieren. Die Ergebnisse dieser Studie zeigen, dass der Abbau von Feinwurzelstreu in Grünlandböden der gemäßigten Breiten doppelt so schnell ist wie in Waldböden. Auf regionaler Ebene wird der Abbau von Feinwurzelstreu außerdem von Umweltbedingungen wie Bodenfeuchte, Bodentemperatur und Nährstoffversorgung beeinflusst. Die Umweltbedingungen erklären sowohl den Abbau der standardisierten als auch der *in situ* entnommen Wurzelstreu. Für die *in situ* entnommene Wurzelstreu spielt zusätzlich das Lignin/N-Verhältnis der Wurzeln eine Rolle. Das Lignin/N-Verhältnis wurde in unserer Studie von der Bewirtschaftung beeinflusst; zum Beispiel spielten Stickstoffeinträge durch Düngung an den Grünlandstandorten und die Baumartenzusammensetzung an den Waldstandorten eine Rolle.

Das Ziel der Studie in Kapitel 4 war zu untersuchen, ob die Abbaugeschwindigkeit von Feinwurzelstreu mit zunehmender Bodentiefe abnimmt. Obwohl man dies aufgrund von früheren Studien, die eine abnehmende biologische Aktivität entlang des

Bodenprofils zeigten, erwartet, zeigen die Ergebnisse in Kapitel 4, dass die im Durchschnitt verbleibende Streumenge nach einer Freilandinkubation von 24 Monaten nicht von der Bodentiefe (5, 20, 35 cm) abhängt. Dies deutet darauf hin, dass im Ober- und Unterboden ein ähnliches Potential für den Abbau von wurzelbürtigem Kohlenstoff besteht. Daher ist die biologische Aktivität in verschiedenen Bodentiefen im Wesentlichen durch den Input von Wurzelstreu und damit durch den Input von neuem Substrat limitiert. Die Beobachtung, dass Wurzelstreu im gesamten Bodenprofil rasch abgebaut wird, wird durch die durchgängig jungen Radiokohlenstoffalter von labilen Fraktionen der organischen Bodensubstanz aus anderen Studien unterstützt.

Kapitel 5 untersucht, wieviel Kohlenstoff aus der Wurzelstreu in der mineral-assoziierten organischen Substanz von 3 verschiedenen Grünlandböden der gemäßigten Breiten stabilisiert wird. Die 3 Grünlandstandorte werden auf ähnliche Weise bewirtschaftet (als Mähweide), unterscheiden sich aber in der Bodenart (sandiger Lehm, schluffiger Lehm, Ton). Die Transferrate von ^{14}C isotopisch abgereicherter Wurzelstreu (-7 ^{14}C (% Modern)) von *Arrhenatherum elatius* in die organische Bodensubstanz und in die mineral-assoziierte Fraktion wurde im Freiland in Mesokosmen nachverfolgt und mit der Transferrate von Wurzelstreu mit natürlichem Isotopenverhältnis (102 ^{14}C (% Modern)) verglichen. Um zu bestimmen, wieviel wurzelbürtiger Kohlenstoff in die mineral-assoziierte organische Substanz transferriert wird, wurde eine Dichtefraktionierung durchgeführt. Nach einer Inkubation von 18 Monaten in Mesokosmen verblieb im Durchschnitt ungefähr ein Drittel bis die Hälfte des über Wurzelstreu eingebrachten Kohlenstoffs im Boden, wobei davon 16-26 Prozent als mineral-assoziierte organische Substanz stabilisiert wurde.

Insgesamt zeigen die im Vergleich zu Grünlandböden älteren Kohlenstoffalter von Feinwurzeln in Waldböden und die im Vergleich zu Waldböden doppelt so schnellen Abbauraten von Wurzelstreu in Grünlandböden, dass sich Wurzel-Kohlenstoff in Böden unter Grünland der gemäßigten Zone schneller umsetzt als unter Wald der gemäßigten Zone. Weitere Forschungsarbeiten sind nötig, um das Verständnis potentieller interner Umverteilungsdynamiken von Kohlenstoff von Wurzeln mit unterscheidlichen Funktionen zu verbessern. Für Feinwurzel-Abbauraten in Streubeuteln wurde gezeigt, dass die Variabilität zwischen verschiedenen Regionen größer ist als zwischen verschiedenen Bodentiefen an einem Standort. Daher sind klimatische oder andere großräumige Unterschiede in den Umweltbedingungen für die Initialphase des Streuabbaus wichtiger, als sich ändernde Bedingungen entlang des Bodenprofils. Durch die Quantifizierung, wie effizient Wurzelstreu in organische Bodensubstanz in

Grünlandböden umgewandelt werden kann, konnte bestätigt werden, dass der Input von Kohlenstoff über Feinwurzelstreu ein wichtiger Prozess für die Entstehung von organischer Bodensubstanz ist. Eine Herausforderung für die Zukunft ist die Bestimmung der Feinwurzelproduktivität in Grünland- und Waldböden gemäßigter Breiten, da das Budget der organischen Bodensubstanz ohne eine Quantifizierung des ober- und unterirdischen Inputs durch die Vegetation unvollständig ist.

9 Bibliography

Abiven, S., S. Recous, V. Reyes, and R. Oliver. 2005. Mineralisation of c and n from root, stem and leaf residues in soil and role of their biochemical quality. *Biology and Fertility of Soils* **42**, 119–128.

Aerts, R. 1997. Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: A triangular relationship. *Oikos* **79**, 439–449.

Ahrens, B., K. Hansson, E. F. Solly, and M. Schrumpf. 2014. Reconcilable differences: A joint calibration of fine-root turnover times with radiocarbon and minirhizotrons. *New Phytologist* **204**, 932–942.

Alexander, M. 1977. *Introduction to soil microbiology*. John Wiley & Sons.

Anderson, D., and E. Paul. 1984. Organo-mineral complexes and their study by radiocarbon dating. *Soil Science Society of America Journal* **48**, 298–301.

Balesdent, J., and M. Balabane. 1996. Major contribution of roots to soil carbon storage inferred from maize cultivated soils. *Soil Biology and Biochemistry* **28**, 1261 – 1263.

Bardgett, R. D., D. A. Wardle, and G. W. Yeates. 1998. Linking above-ground and below-ground interactions: how plant responses to foliar herbivory influence soil organisms. *Soil Biology and Biochemistry* **30**, 1867–1878.

Berg, B. 1984. Decomposition of root litter and some factors regulating the process: Long-term root litter decomposition in a scots pine forest. *Soil Biology and Biochemistry* **16**, 609–617.

Berg, B. 1986. The influence of experimental acidification on nutrient release and decomposition rates of needle and root litter in the forest floor. *Forest Ecology and Management* **15**, 195–213.

Berner, R. A., A. C. Lasaga, and R. M. Garrels. 1983. The carbonate-silicate geochemical cycle and its effect on atmospheric carbon dioxide over the past 100 million years. *American Journal of Science* **283**, 641–683.

Berthrong, S. T., E. G. Jobbagy, and R. B. Jackson. 2009. A global meta-analysis of soil exchangeable cations, pH, carbon, and nitrogen with afforestation. *Ecological Applications* **19**, 2228–2241.

Bird, J. A., and M. S. Torn. 2006. Fine Roots vs. Needles: A Comparison of ^{13}C and ^{15}N Dynamics in a Ponderosa Pine Forest Soil. *Biogeochemistry* **79**, 361–382.

Bird, J. A., M. Kleber, and M. S. Torn. 2008. ^{13}C and ^{15}N stabilization dynamics in soil organic matter fractions during needle and fine root decomposition. *Organic Geochemistry* **39**, 465–477.

Birkhofer, K., I. Schöning, F. Alt, N. Herold, B. Klarner, M. Maraun, S. Marhan, Y. Oelmann, T. Wubet, A. Yurkov, D. Begerow, D. Berner, F. Buscot, R. Daniel, T. Diekötter, R. B. Ehnes, G. Erdmann, C. Fischer, B. Foesel, J. Groh, J. Gutknecht, E. Kandeler, C. Lang, G. Lohaus, A. Meyer, H. Nacke, A. Näther, J. Overmann, A. Polle, M. M. Pollierer, S. Scheu, M. Schloter, E. D. Schulze, W. Schulze, J. Weinert, W. W. Weisser, V. Wolters, and M. Schrumpf. 2012. General relationships between abiotic soil properties and soil biota across spatial scales and different land-use types. *Plos One*.

Blüthgen, N., C. F. Dormann, D. Prati, V. H. Klaus, T. Kleinebecker, N. Hölzel, F. Alt, S. Boch, S. Gockel, A. Hemp *et al.* 2012. A quantitative index of land-use intensity in grasslands: integrating mowing, grazing and fertilization. *Basic and Applied Ecology* **13**, 207–220.

Boch, S., D. Prati, J. Müller, S. Socher, H. Baumbach, F. Buscot, S. Gockel, A. Hemp, D. Hessenmöller, E. K. V. Kalko, K. E. Linsenmair, S. Pfeiffer, U. Pommer, I. Schöning, E.-D. Schulze, C. Seilwinder, W. W. Weisser, K. Wells, and M. Fischer. 2013. High plant species richness indicates management-related disturbances rather than the conservation status of forests. *Basic and Applied Ecology* **14**, 496–505.

Bocock, K. L., and O. J. W. Gilbert. 1957. The disappearance of leaf litter under different woodland conditions. *Plant and Soil* **9**, 179–185.

Bolinder, M., H. Janzen, E. Gregorich, D. Angers, and A. VandenBygaart. 2007. An approach for estimating net primary productivity and annual carbon inputs to soil for common agricultural crops in canada. *Agriculture, Ecosystems & Environment* **118**, 29 – 42.

Brown, C. D., R. A. Hodgkinson, D. A. Rose, J. K. Syers, and S. J. Wilcockson. 1995. Movement of pesticides to surface waters from a heavy clay soil. *Pesticide Science* **43**, 131–140.

Brunner, I., and D. L. Godbold. 2007. Tree roots in a changing world. *Journal of forest research* **12**, 78–82.

Bryant, D. M., E. A. Holland, T. R. Seastedt, and M. D. Walker. 1998. Analysis of litter decomposition in an alpine tundra. *Canadian Journal of Botany* **76**, 1295–1304.

Butenschön, O., S. Scheu, and N. Eisenhauer. 2011. Interactive effects of warming, soil humidity and plant diversity on litter decomposition and microbial activity. *Soil Biology and Biochemistry* **43**, 1902–1907.

Carreiro, M. M., R. L. Sinsabaugh, D. A. Repert, and D. F. Parkhurst. 2000. Microbial Enzyme Shifts Explain Litter Decay Responses to Simulated Nitrogen Deposition. *Ecology* **81**, 2359–2365.

Castanha, C., S. Trumbore, and R. Amundson. 2008. Methods of separating soil carbon pools affect the chemistry and turnover time of isolated fractions. *Radiocarbon* **50**, 83–97.

Cerli, C., L. Celi, K. Kalbitz, G. Guggenberger, and K. Kaiser. 2012. Separation of light and heavy organic matter fractions in soil – Testing for proper density cut-off and dispersion level. *Geoderma* **170**, 403–416.

Chadwick, O. A., E. F. Kelly, D. M. Merritts, and R. G. Amundson. 1994. Carbon dioxide consumption during soil development. *Biogeochemistry* **24**, 115–127.

Chapin III, F. S., M. C. Chapin, P. Matson, and H. A. Mooney. 2002. *Principles of terrestrial ecosystem ecology*. Springer-Verlag New york Inc., 175 Fifth Avenue, New York, NY.

Chen, H., M. E. Harmon, J. Sexton, and B. Fasth. 2002. Fine-root decomposition and N dynamics in coniferous forests of the Pacific Northwest, USA. *Canadian Journal of Forest Research* **32**, 320–331.

Chen, H., M. E. Harmon, R. P. Griffiths, and W. Hicks. 2000. Effects of temperature and moisture on carbon respired from decomposing woody roots. *Forest Ecology and Management* **138**, 51–64.

Claus, A., and E. George. 2005. 7effect of stand age on fine-root biomass and biomass distribution in three european forest chronosequences. *Canadian Journal of Forest Research* **35**, 1617–1625.

Cortina, J., and V. Vallejo. 1994. Effects of clearfelling on forest floor accumulation and litter decomposition in a radiata pine plantation. *Forest Ecology and Management* **70**, 299–310.

Cox, D. R. 1972. Regression models and life tables. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)* **34**, 187–220.

Cox, P. M., R. A. Betts, C. D. Jones, S. A. Spall, and I. J. Totterdell. 2000. Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. *Nature* **408**, 184–187.

Crawley, M. J. 2007. *Regression*. In: The R Book. Pp. 387–448. John Wiley & Sons.

Cusack, D. F., W. W. Chou, W. H. Yang, M. E. Harmon, W. L. Silver, and Lidet. 2009. Controls on long-term root and leaf litter decomposition in Neotropical forests. *Global Change Biology* **15**, 1339–1355.

Davidson, E. A., K. Savage, P. Bolstad, D. A. Clark, P. S. Curtis, D. S. Ellsworth, P. J. Hanson, B. E. Law, Y. Luo, K. S. Pregitzer, J. C. Randolph, and D. Zak. 2002. Belowground carbon allocation in forests estimated from litterfall and IRGA-based soil respiration measurements. *Agricultural and Forest Meteorology* **113**, 39–51.

Dickinson, N. M., and A. Polwart. 1982. The Effect of Mowing Regime on an Amenity Grassland Ecosystem: Above-and Below-Ground Components. *Journal of Applied Ecology* **19**, 569–577.

Dioumaeva, I., S. Trumbore, E. A. G. Schuur, M. L. Goulden, M. Litvak, and A. I. Hirsch. 2002. Decomposition of peat from upland boreal forest: Temperature dependence and sources of respired carbon. *Journal of Geophysical Research: Atmospheres* **107**, 8222.

Dixon, R. K., A. Solomon, S. Brown, R. Houghton, M. Trexier, and J. Wisniewski. 1994. Carbon pools and flux of global forest ecosystems. *Science* **263**, 185–190.

Dornbush, M. E., T. M. Isenhart, and J. W. Raich. 2002. Quantifying fine-root decomposition: an alternative to buried litterbags. *Ecology* **83**, 2985–2990.

Ellenberg, H., H. Weber, R. Düll, and V. Wirth. 2001. Zeigerwerte von pflanzen in mitteleuropa. *Scripta Geobotanica* **18**, 1–262.

Eusterhues, K., C. Rumpel, M. Kleber, and I. Kögel-Knabner. 2003. Stabilisation of soil organic matter by interactions with minerals as revealed by mineral dissolution and oxidative degradation. *Organic Geochemistry* **34**, 1591–1600.

Fahey, T. J., J. W. Hughes, M. Pu, and M. A. Arthur. 1988. Root decomposition and nutrient flux following whole-tree harvest of northern hardwood forest. *Forest Science* **34**, 744–768.

Falkengren-Grerup, U., D. J. ten Brink, and J. Brunet. 2006. Land use effects on soil N, P, C and pH persist over 40-80 years of forest growth on agricultural soils. *Forest Ecology and Management* **225**, 74–81.

Fan, P., and D. Guo. 2010. Slow decomposition of lower order roots: a key mechanism of root carbon and nutrient retention in the soil. *Oecologia* **163**, 509–515.

Fierer, N., A. S. Allen, J. P. Schimel, and P. A. Holden. 2003a. Controls on microbial CO_2 production: a comparison of surface and subsurface soil horizons. *Global Change Biology* **9**, 1322–1332.

Fierer, N., J. P. Schimel, and P. A. Holden. 2003b. Variations in microbial community composition through two soil depth profiles. *Soil Biology and Biochemistry* **35**, 167–176.

Fischer, M., O. Bossdorf, S. Gockel, F. Hänsel, A. Hemp, D. Hessenmöller, G. Korte, J. Nieschulze, S. Pfeiffer, D. Prati *et al.* 2010. Implementing large-scale and long-term functional biodiversity research: The Biodiversity Exploratories. *Basic and Applied Ecology* **11**, 473–485.

Fog, K. 1988. The effect of added nitrogen on the rate of decomposition of organic matter. *Biological Reviews* **63**, 433–462.

Fontaine, S., S. Barot, P. Barre, N. Bdioui, B. Mary, and C. Rumpel. 2007. Stability of organic carbon in deep soil layers controlled by fresh carbon supply. *Nature* **450**, 277–280.

Friedlingstein, P., P. Cox, R. Betts, L. Bopp, W. Von Bloh, V. Brovkin, P. Cadule, S. Doney, M. Eby, I. Fung, G. Bala, J. John, C. Jones, F. Joos, T. Kato, M. Kawamiya, W. Knorr, K. Lindsay, H. D. Matthews, T. Raddatz, P. Rayner, C. Reick, E. Roeckner, K. G. Schnitzler, R. Schnur, K. Strassmann, A. J. Weaver, C. Yoshikawa, and N. Zeng. 2006. Climate-carbon cycle feedback analysis: Results from the (CMIP)-M-4 model intercomparison. *Journal of Climate* **19**, 3337–3353.

Fröberg, M. 2012. Residence time of fine-root carbon using radiocarbon measurements of samples collected from a soil archive. *Journal of Plant Nutrition and Soil Science* **175**, 46–48.

Gale, W. J., and C. A. Cambardella. 2000. Carbon dynamics of surface residue – and root-derived organic matter under simulated no-till. *Soil Science Society of America Journal* **64**, 190–195.

Gaudinski, J. B., M. Torn, W. Riley, T. Dawson, J. Joslin, and H. Majdi. 2010. Measuring and modeling the spectrum of fine-root turnover times in three forests using isotopes, minirhizotrons, and the radix model. *Global Biogeochemical Cycles*.

Gaudinski, J., S. Trumbore, E. Davidson, A. Cook, D. Markewitz, and D. Richter. 2001. The age of fine-root carbon in three forests of the eastern united states measured by radiocarbon. *Oecologia* **129**, 420–429.

Gill, R. A., and I. C. Burke. 2002. Influence of soil depth on the decomposition of Bouteloua gracilis roots in the shortgrass steppe. *Plant and Soil* **241**, 233–242.

Gleixner, G., N. Poirier, R. Bol, and J. Balesdent. 2002. Molecular dynamics of organic matter in a cultivated soil. *Organic Geochemistry* **33**, 357 – 366.

Goebel, M., S. E. Hobbie, B. Bulaj, M. Zadworny, D. D. Archibald, J. Oleksyn, P. B. Reich, and D. M. Eissenstat. 2011. Decomposition of the finest root branching orders: linking belowground dynamics to fine-root function and structure. *Ecological Monographs* **81**, 89–102.

Golchin, A., J. Oades, J. Skjemstad, and P. Clarke. 1994. Study of free and occluded particulate organic matter in soils by solid state ^{13}C CP/MAS NMR spectroscopy and scanning electron microscopy. *Soil Research* **32**, 285–309.

Gregorich, E., M. Beare, U. McKim, and J. Skjemstad. 2006. Chemical and biological characteristics of physically uncomplexed organic matter. *Soil Science Society of America Journal* **70**, 975–985.

Gregorich, E., P. Rochette, S. McGuire, B. Liang, and R. Lessard. 1998. Soluble organic carbon and carbon dioxide fluxes in maize fields receiving spring-applied manure. *Journal of Environmental Quality* **27**, 209–214.

Grüneberg, E., I. Schöning, E. K. V. Kalko, and W. W. Weisser. 2010. Regional organic carbon stock variability: A comparison between depth increments and soil horizons. *Geoderma* **155**, 426–433.

Grünewald, G., K. Kaiser, R. Jahn, and G. Guggenberger. 2006. Organic matter stabilization in young calcareous soils as revealed by density fractionation and analysis of lignin-derived constituents. *Organic Geochemistry* **37**, 1573–1589.

Guo, D. L., R. J. Mitchell, and J. J. Hendricks. 2004. Fine root branch orders respond differentially to carbon source-sink manipulations in a longleaf pine forest. *Oecologia* **140**, 450–457.

Guo, D., R. J. Mitchell, J. M. Withington, P.-P. Fan, and J. J. Hendricks. 2008. Endogenous and exogenous controls of root life span, mortality and nitrogen flux in a longleaf pine forest: root branch order predominates. *Journal of Ecology* **96**, 737–745.

Handa, I. T., R. Aerts, F. Berendse, M. P. Berg, A. Bruder, O. Butenschoen, E. Chauvet, M. O. Gessner, J. Jabiol, M. Makkonen, B. G. McKie, B. Malmqvist, E. T. H. M. Peeters, S. Scheu, B. Schmid, J. van Ruijven, V. C. A. Vos, and S. Hattenschwiler. 2014. Consequences of biodiversity loss for litter decomposition across biomes. *Nature* **509**, 218–221.

Harmon, M. E., W. L. Silver, B. Fasth, H. U. A. Chen, I. C. Burke, W. J. Parton, S. C. Hart, W. S. Currie, and Lidet. 2009. Long-term patterns of mass loss during the decomposition of leaf and fine root litter: an intersite comparison. *Global Change Biology* **15**, 1320–1338.

Hassink, J. 1997. The capacity of soils to preserve organic c and n by their association with clay and silt particles. *Plant and soil* **191**, 77–87.

Hättenschwiler, S., A. V. Tiunov, and S. Scheu. 2005. Biodiversity and litter decomposition in terrestrial ecosystems. *Annual Review of Ecology, Evolution, and Systematics* Pp. 191–218.

Heim, A., and B. Frey. 2004. Early stage litter decomposition rates for swiss forests. *Biogeochemistry* **70**, 299–313.

Heimann, M., and M. Reichstein. 2008. Terrestrial ecosystem carbon dynamics and climate feedbacks. *Nature* **451**, 289–292.

Heiri, O., A. F. Lotter, and G. Lemcke. 2001. Loss on ignition as a method for estimating organic and carbonate content in sediments: reproducibility and comparability of results. *Journal of paleolimnology* **25**, 101–110.

Heister, K., C. Höschen, G. J. Pronk, C. W. Mueller, and I. Kögel-Knabner. 2012. NanoSIMS as a tool for characterizing soil model compounds and organomineral associations in artificial soils. *Journal of Soils and Sediments* **12**, 35–47.

Herold, N., I. Schöning, B. Michalzik, S. Trumbore, and M. Schrumpf. 2014a. Controls on soil carbon storage and turnover in german landscapes. *Biogeochemistry* **119**, 435–451.

Herold, N., I. Schöning, D. Berner, H. Haslwimmer, E. Kandeler, B. Michalzik, and M. Schrumpf. 2014b. Vertical gradients of potential enzyme activities in soil profiles of european beech, norway spruce and scots pine dominated forest sites. *Pedobiologia* **57**, 181 – 189.

Hishi, T. 2007. Heterogeneity of individual roots within the fine root architecture: causal links between physiological and ecosystem functions. *Journal of Forest Research* **12**, 126–133.

Hobbie, S. E. 1992. Effects of plant species on nutrient cycling. *Trends in Ecology & Evolution* **7**, 336–339.

Hobbie, S. E. 1996. Temperature and plant species control over litter decomposition in alaskan tundra. *Ecological Monographs* **66**, 503–522.

Hobbie, S. E. 2005. Contrasting effects of substrate and fertilizer nitrogen on the early stages of litter decomposition. *Ecosystems* **8**, 644–656.

Hobbie, S. E., and P. M. Vitousek. 2000. Nutrient limitation of decomposition in hawaiian forests. *Ecology* **81**, 1867–1877.

Hobbie, S. E., J. Oleksyn, D. M. Eissenstat, and P. B. Reich. 2010. Fine root decomposition rates do not mirror those of leaf litter among temperate tree species. *Oecologia* **162**, 505–513.

Hooper, D. U., and P. M. Vitousek. 1998. Effects of plant composition and diversity on nutrient cycling. *Ecological Monographs* **68**, pp. 121–149.

Houghton, R. A., J. I. House, J. Pongratz, G. R. van der Werf, R. S. DeFries, M. C. Hansen, C. Le Quéré, and N. Ramankutty. 2012. Carbon emissions from land use and land-cover change. *Biogeosciences* **9**, 5125–5142.

IPCC 2013. *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Jackson, R., H. Mooney, and E.-D. Schulze. 1997. A global budget for fine root biomass, surface area, and nutrient contents. *Proceedings of the National Academy of Sciences* **94**, 7362–7366.

Janssens, I. A., W. Dieleman, S. Luyssaert, J. A. Subke, M. Reichstein, R. Ceulemans, P. Ciais, A. J. Dolman, J. Grace, G. Matteucci, D. Papale, S. L. Piao, E. D. Schulze, J. Tang, and B. E. Law. 2010. Reduction of forest soil respiration in response to nitrogen deposition. *Nature Geoscience* **3**, 315–322.

Jobbágy, E. G., and R. B. Jackson. 2000. The vertical distribution of soil organic carbon and its relation to climate and vegetation. *Ecological Applications* **10**, 423–436.

Joergensen, R. G. 1996. The fumigation-extraction method to estimate soil microbial biomass: Calibration of the kEC value. *Soil Biology and Biochemistry* **28**, 25–31.

Jones, C., and P. Falloon. 2009. *Sources of uncertainty in global modelling of future soil organic carbon storage*. Pp. 283–315. Springer.

Kalbitz, K., and K. Kaiser. 2008. Contribution of dissolved organic matter to carbon storage in forest mineral soils. *Journal of Plant Nutrition and Soil Science* **171**, 52–60.

Kalbitz, K., S. Solinger, J.-H. Park, B. Michalzik, and E. Matzner. 2000. Controls on the dynamics of dissolved organic matter in soils: a review. *Soil science* **165**, 277–304.

Kammer, A., and F. Hagedorn. 2011. Mineralisation, leaching and stabilisation of ^{13}C labelled leaf and twig litter in a beech forest soil. *Biogeosciences* **8**, 2195–2208.

Kindler, R., J. Siemens, K. Kaiser, D. C. Walmsley, C. Bernhofer, N. Buchmann, P. Cellier, W. Eugster, G. Gleixner, T. Grũnwald, A. Heim, A. Ibrom, S. K. Jones, M. Jones, K. Klumpp, W. Kutsch, K. S. Larsen, S. Lehuger, B. Loubet, R. McKenzie, E. Moors, B. Oosborne, K. Pilegaard, C. Rebmann, M. Saunders, M. W. I. Schmidt, M. Schrumpf, J. Seyfferth, U. Skiba, J.-F. Soussana, M. A. Sutton, C. Tefs, B. Vowinckel, M. J. Zeeman, and M. Kaupenjohann. 2011. Dissolved carbon leaching from soil is a crucial component of the net ecosystem carbon balance. *Global Change Biology* **17**, 1167–1185.

Kleber, M., and M. G. Johnson. 2010. Advances in understanding the molecular structure of soil organic matter: implications for interactions in the environment. *Advances in agronomy* **106**, 77–142.

Klotzbücher, T., K. Kaiser, G. Guggenberger, C. Gatzek, and K. Kalbitz. 2011. A new conceptual model for the fate of lignin in decomposing plant litter. *Ecology* **92**, 1052–1062.

Knorr, M., S. D. Frey, and P. S. Curtis. 2005. Nitrogen addition and litter decomposition: a meta-analysis. *Ecology* **86**, 3252–3257.

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.

Kölbl, A., M. von Lützow, C. Rumpel, J. C. Munch, and I. Kögel-Knabner. 2007. Dynamics of ^{13}c - labeled mustard litter (sinapis alba) in particle-size and aggregate fractions in an agricultural cropland with high- and low- yield areas. *Journal of Plant Nutrition and Soil Science* **170**, 123–133.

Kramer, C., S. Trumbore, M. Fröberg, L. M. Cisneros Dozal, D. Zhang, X. Xu, G. M. Santos, and P. J. Hanson. 2010. Recent (< 4 year old) leaf litter is not a major source of microbial carbon in a temperate forest mineral soil. *Soil Biology and Biochemistry* **42**, 1028–1037.

Kurz-Besson, C., M.-M. Coûteaux, J. M. Thiéry, B. Berg, and J. Remacle. 2005. A comparison of litterbag and direct observation methods of Scots pine needle decomposition measurement. *Soil Biology and Biochemistry* **37**, 2315–2318.

Lal, R. 2004. Soil carbon sequestration impacts on global climate change and food security. *Science* **304**, 1623–1627.

Laliberté, E., J. A. Wells, F. DeClerck, D. J. Metcalfe, C. P. Catterall, C. Queiroz, I. Aubin, S. P. Bonser, Y. Ding, J. M. Fraterrigo *et al.* 2010. Land-use intensification reduces functional redundancy and response diversity in plant communities. *Ecology letters* **13**, 76–86.

Langenbruch, C., M. Helfrich, R. G. Joergensen, J. Gordon, and H. Flessa. 2014. Partitioning of carbon and nitrogen during decomposition of ^{13}c and ^{15}n -labeled beech and ash leaf litter. *Journal of Plant Nutrition and Soil Science* **177**, 178–188.

Le Quéré, C., R. J. Andres, T. Boden, T. Conway, R. A. Houghton, J. I. House, G. Marland, G. P. Peters, G. R. van der Werf, A. Ahlström, R. M. Andrew, L. Bopp, J. G. Canadell, P. Ciais, S. C. Doney, C. Enright, P. Friedlingstein, C. Huntingford, A. K. Jain, C. Jourdain, E. Kato, R. F. Keeling, K. Klein Goldewijk, S. Levis, P. Levy, M. Lomas, B. Poulter, M. R. Raupach, J. Schwinger, S. Sitch, B. D. Stocker, N. Viovy, S. Zaehle, and N. Zeng. 2013. The global carbon budget 1959-2011. *Earth System Science Data* **5**, 165–185.

Legendre, P. 2008. Studying beta diversity: ecological variation partitioning by multiple regression and canonical analysis. *Journal of Plant Ecology* **1**, 3–8.

Lehmann, J., D. Solomon, J. Kinyangi, L. Dathe, S. Wirick, and C. Jacobsen. 2008. Spatial complexity of soil organic matter forms at nanometre scales. *Nature Geoscience* **1**, 238–242.

Levin, I., T. Naegler, B. Kromer, M. Diehl, R. J. Francey, A. J. Gomez-Pelaez, L. Steele, D. Wagenbach, R. Weller, and D. E. Worthy. 2010. Observations and

modelling of the global distribution and long-term trend of atmospheric $^{14}co_2$. *Tellus B* **62**, 26–46.

Li, A., T. J. Fahey, T. E. Pawlowska, M. C. Fisk, and J. Burtis. 2015. Fine root decomposition, nutrient mobilization and fungal communities in a pine forest ecosystem. *Soil Biology and Biochemistry* **83**, 76–83.

Liao, C., Y. Luo, C. Fang, and B. Li. 2010. Ecosystem Carbon Stock Influenced by Plantation Practice: Implications for Planting Forests as a Measure of Climate Change Mitigation. *Plos One*.

Lukac, M. 2011. Fine root turnover. Pp. 363–374. In *Measuring Roots: An Updated Approach*. S. Mancuso (ed.). Springer, Heidelberg, Dordrecht, London, New York.

Luyssaert, S., D. Hessenmöller, N. Von Lüpke, S. Kaiser, and E. Schulze. 2011. Quantifying land use and disturbance intensity in forestry, based on the self-thinning relationship. *Ecological Applications* **21**, 3272–3284.

Lynch, D. J., R. Matamala, C. M. Iversen, R. J. Norby, and M. A. Gonzalez-Meler. 2013. Stored carbon partly fuels fine-root respiration but is not used for production of new fine roots. *New Phytologist* **199**, 420–430.

Majdi, H., K. Pregitzer, A.-S. Moren, J.-E. Nylund, and G. I. Ågren. 2005. Measuring fine root turnover in forest ecosystems. *Plant and soil* **276**, 1–8.

Malik, A., and G. Gleixner. 2013. Importance of microbial soil organic matter processing in dissolved organic carbon production. *FEMS Microbiology Ecology* **86**, 139–148.

Matamala, R., M. A. Gonzalez-Meler, J. D. Jastrow, R. J. Norby, and W. H. Schlesinger. 2003. Impacts of fine root turnover on forest NPP and soil C sequestration potential. *Science* **302**, 1385–1387.

McClaugherty, C. A., J. D. Aber, and J. M. Melillo. 1984. Decomposition dynamics of fine roots in forested ecosystems. *Oikos* **42**, pp. 378–386.

Mcdowell, W. H., and T. Wood. 1984. Podzolization: soil processes control dissolved organic carbon concentrations in stream water.. *Soil Science* **137**, 23–32.

McInerney, M., and T. Bolger. 2000. Temperature, wetting cycles and soil texture effects on carbon and nitrogen dynamics in stabilized earthworm casts. *Soil Biology and Biochemistry* **32**, 335–349.

Melillo, J. M., J. D. Aber, and J. F. Muratore. 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. *Ecology* **63**, 621–626.

Mendez-Millan, M., M. F. Dignac, C. Rumpel, D. P. Rasse, and S. Derenne. 2010. Molecular dynamics of shoot vs. root biomarkers in an agricultural soil estimated by natural abundance ^{13}C labelling. *Soil Biology and Biochemistry* **42**, 169–177.

Michalzik, B., E. Tipping, J. Mulder, J. G. Lancho, E. Matzner, C. Bryant, N. Clarke, S. Lofts, and M. V. Esteban. 2003. Modelling the production and transport of dissolved organic carbon in forest soils. *Biogeochemistry* **66**, 241–264.

Michalzik, B., K. Kalbitz, J.-H. Park, S. Solinger, and E. Matzner. 2001. Fluxes and concentrations of dissolved organic carbon and nitrogen – a synthesis for temperate forests. *Biogeochemistry* **52**, 173–205.

Mikan, C. J., J. P. Schimel, and A. P. Doyle. 2002. Temperature controls of microbial respiration in arctic tundra soils above and below freezing. *Soil Biology and Biochemistry* **34**, 1785–1795.

Mikutta, R., M. Kleber, M. S. Torn, and R. Jahn. 2006. Stabilization of soil organic matter: association with minerals or chemical recalcitrance?. *Biogeochemistry* **77**, 25–56.

Milchunas, D. G., W. K. Lauenroth, J. S. Singh, C. V. Cole, and H. W. Hunt. 1985. Root turnover and production by C^{14} dilution - Implications of carbon partitioning in plants. *Plant and Soil* **88**, 353–365.

Mitchell, J. K., and K. Soga. 1976. *Fundamentals of soil behavior*. Wiley New York.

Nadelhoffer, K. J. 2000. The potential effects of nitrogen deposition on fine-root production in forest ecosystems. *New Phytologist* **147**, 131–139.

Naegler, T., and I. Levin. 2006. Closing the global radiocarbon budget 1945–2005. *Journal of Geophysical Research: Atmospheres (1984–2012)*.

Näsholm, T., K. Huss-Danell, and P. Högberg. 2000. Uptake of organic nitrogen in the field by four agriculturally important plant species. *Ecology* **81**, 1155–1161.

Nave, L. E., E. D. Vance, C. W. Swanston, and P. S. Curtis. 2010. Harvest impacts on soil carbon storage in temperate forests. *Forest Ecology and Management* **259**, 857–866.

Neff, J. C., and G. P. Asner. 2001. Dissolved organic carbon in terrestrial ecosystems: synthesis and a model. *Ecosystems* **4**, 29–48.

Ngao, J., D. Epron, C. Brechet, and A. Granier. 2005. Estimating the contribution of leaf litter decomposition to soil CO_2 efflux in a beech forest using ^{13}C depleted litter. *Global Change Biology* **11**, 1768–1776.

NOAA 2014. National oceanic and atmospheric administration. *http://www.esrl.noaa.gov*.

Olson, J. S. 1963. Energy storage and the balance of producers and decomposers in ecological systems. *Ecology* **44**, 322–331.

Ontl, T. A., and L. A. Schulte. 2012. Soil carbon storage. *Nature Education Knowledge* **3**, 35.

Ostertag, R., and S. E. Hobbie. 1999. Early stages of root and leaf decomposition in Hawaiian forests: effects of nutrient availability. *Oecologia* **121**, 564–573.

Ostle, N. J., P. Smith, R. Fisher, F. Ian Woodward, J. B. Fisher, J. U. Smith, D. Galbraith, P. Levy, P. Meir, N. P. McNamara *et al.* 2009. Integrating plant–soil interactions into global carbon cycle models. *Journal of Ecology* **97**, 851–863.

Ostroumov, V. E., and C. Siegert. 1996. Exobiological aspects of mass transfer in microzones of permafrost deposits. *Advances in Space Research* **18**, 79–86.

Parton, W., W. L. Silver, I. C. Burke, L. Grassens, M. E. Harmon, W. S. Currie, J. Y. King, E. C. Adair, L. A. Brandt, S. C. Hart, and B. Fasth. 2007. Global-Scale Similarities in Nitrogen Release Patterns During Long-Term Decomposition. *Science* **315**, 361–364.

Paul, E. A., R. F. Follett, S. W. Leavitt, A. Halvorson, G. A. Peterson, and D. J. Lyon. 1997. Radiocarbon dating for determination of soil organic matter pool sizes and dynamics. *Soil Science Society of America Journal* **61**, 1058–1067.

Pregitzer, K. S., J. L. DeForest, A. J. Burton, M. F. Allen, R. W. Ruess, and R. L. Hendrick. 2002. Fine root architecture of nine North American trees. *Ecological Monographs* **72**, 293–309.

Prescott, C., L. Blevins, and C. Staley. 2000. Effects of clear-cutting on decomposition rates of litter and forest floor in forests of British Columbia. *Canadian Journal of Forest Research* **30**, 1751–1757.

Preston, C., M. Schmidt *et al.* 2006. Black (pyrogenic) carbon: a synthesis of current knowledge and uncertainties with special consideration of boreal regions. *Biogeosciences* **3**, 397–420.

Qualls, R. G., and B. L. Haines. 1992. Biodegradability of dissolved organic matter in forest throughfall, soil solution, and stream water. *Soil Science Society of America Journal* **56**, 578–586.

R Core Team 2012. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing. Vienna, Austria.

Raessler, M., J. Rothe, and I. Hilke. 2005. Accurate determination of Cd, Cr, Cu and Ni in woodlice and their skins–is moulting a means of detoxification?. *Science of The Total Environment* **337**, 83–90.

Randerson, J., I. Enting, E. Schuur, K. Caldeira, and I. Fung. 2002. Seasonal and latitudinal variability of troposphere $^{14}CO_2$: Post bomb contributions from fossil fuels, oceans, the stratosphere, and the terrestrial biosphere. *Global Biogeochemical Cycles* **16**, 1112.

Rasse, D. P., C. Rumpel, and M.-F. Dignac. 2005. Is soil carbon mostly root carbon? mechanisms for a specific stabilisation. *Plant and soil* **269**, 341–356.

Reichstein, M., M. Bahn, P. Ciais, M. D. Mahecha, S. I. Seneviratne, J. Zscheischler, C. Beer, N. Buchmann, D. Frank, D. Papale, A. Rammig, P. Smith, K. Thonicke, M. van der Velde, S. Vicca, A. Walz, and M. Wattenbach. 2013. Climate extremes and the carbon cycle. *Nature* **500**, 287–295.

Riley, W. J., J. B. Gaudinski, M. S. Torn, J. Joslin, and P. J. Hanson. 2009. Fine-root mortality rates in a temperate forest: Estimates using radiocarbon data and numerical modeling. *New Phytologist* **184**, 387–398.

Rovira, P., and V. Ramón Vallejo. 2002. Mineralization of carbon and nitrogen from plant debris, as affected by debris size and depth of burial. *Soil Biology and Biochemistry* **34**, 327–339.

Rumpel, C., A. Chabbi, and B. Marschner. 2012. *Carbon storage and sequestration in subsoil horizons: Knowledge, gaps and potentials*. Pp. 445–464. Springer.

Rumpel, C., and I. Kögel-Knabner. 2011. Deep soil organic matter – a key but poorly understood component of terrestrial C cycle. *Plant and Soil* **338**, 143–158.

Sah, S., C. Bryant, J. Leppälammi-Kujansuu, K. Lõhmus, I. Ostonen, and H.-S. Helmisaari. 2013. Variation of carbon age of fine roots in boreal forests determined from ^{14}c measurements. *Plant and Soil* **363**, 77–86.

Sanaullah, M., A. Chabbi, J. Leifeld, G. Bardoux, D. Billou, and C. Rumpel. 2011. Decomposition and stabilization of root litter in top- and subsoil horizons: what is the difference?. *Plant and Soil* **338**, 127–141.

Sankaran, M., and D. J. Augustine. 2004. Large herbivores suppress decomposer abundance in a semiarid grazing ecosystem. *Ecology* **85**, 1052–1061.

Schaffers, A. P., and K. V. Sỳkora. 2000. Reliability of Ellenberg indicator values for moisture, nitrogen and soil reaction: a comparison with field measurements. *Journal of Vegetation science* **11**, 225–244.

Scharlemann, J. P. W., E. V. J. Tanner, R. Hiederer, and V. Kapos. 2014. Global soil carbon: understanding and managing the largest terrestrial carbon pool. *Carbon Management* **5**, 81–91.

Scheffer, R. A., and R. Aerts. 2000. Root decomposition and soil nutrient and carbon cycling in two temperate fen ecosystems. *Oikos* **91**, 541–549.

Schimel, D., M. A. Stillwell, and R. G. Woodmansee. 1985. Biogeochemistry of C, N, and P in a Soil Catena of the Shortgrass Steppe. *Ecology* **66**, 276–282.

Schimel, D. S., J. I. House, K. A. Hibbard, P. Bousquet, P. Ciais, P. Peylin, B. H. Braswell, M. J. Apps, D. Baker, A. Bondeau, J. Canadell, G. Churkina, W. Cramer, A. S. Denning, C. B. Field, P. Friedlingstein, C. Goodale, M. Heimann, R. A. Houghton, J. M. Melillo, B. Moore, D. Murdiyarso, I. Noble, S. W. Pacala, I. C.

Prentice, M. R. Raupach, P. J. Rayner, R. J. Scholes, W. L. Steffen, and C. Wirth. 2001. Recent patterns and mechanisms of carbon exchange by terrestrial ecosystems. *Nature* **414**, 169–172.

Schlesinger, W. H. 1997. *Biogeochemistry: An Analysis of Global Change*. San Diego, CA: Academic Press.

Schmid, I. 2002. The influence of soil type and interspecific competition on the fine root system of Norway spruce and European beech. *Basic and Applied Ecology* **3**, 339–346.

Schmidt, M., C. Rumpel, and I. Kögel-Knabner. 1999. Particle size fractionation of soil containing coal and combusted particles. *European Journal of Soil Science* **50**, 515–522.

Schmidt, M. W., M. S. Torn, S. Abiven, T. Dittmar, G. Guggenberger, I. A. Janssens, M. Kleber, I. Kögel-Knabner, J. Lehmann, D. A. Manning *et al.* 2011. Persistence of soil organic matter as an ecosystem property. *Nature* **478**, 49–56.

Schöning, I., and I. Kögel-Knabner. 2006. Chemical composition of young and old carbon pools throughout Cambisol and Luvisol profiles under forests. *Soil Biology and Biochemistry* **38**, 2411–2424.

Schöning, I., E. Grüneberg, C. A. Sierra, D. Hessenmüller, M. Schrumpf, W. W. Weisser, and E.-D. Schulze. 2013. Causes of variation in mineral soil C content and turnover in differently managed beech dominated forests. *Plant and Soil* **370**, 625–639.

Schrumpf, M., E. D. Schulze, K. Kaiser, and J. Schumacher. 2011. How accurately can soil organic carbon stocks and stock changes be quantified by soil inventories?. *Biogeosciences* **8**, 1193–1212.

Schrumpf, M., K. Kaiser, G. Guggenberger, T. Persson, I. Kögel-Knabner, and E. D. Schulze. 2013. Storage and stability of organic carbon in soils as related to depth, occlusion within aggregates, and attachment to minerals. *Biogeosciences* **10**, 1675–1691.

Schwarz, M. T., S. Bischoff, S. Blaser, S. Boch, B. Schmitt, L. Thieme, M. Fischer, B. Michalzik, E.-D. Schulze, J. Siemens, and W. Wilcke. 2014. More efficient

aboveground nitrogen use in more diverse central european forest canopies. *Forest Ecology and Management* **313**, 274–282.

Sedell, J., and C. Dahm. 1990. Spatial and temporal scales of dissolved organic carbon in streams and rivers. *Organic acids in aquatic ecosystems* Pp. 261–279.

Semmartin, M., L. Garibaldi, and E. Chaneton. 2008. Grazing history effects on above- and below-ground litter decomposition and nutrient cycling in two co-occurring grasses. *Plant and Soil* **303**, 177–189.

Shannon, C. E. 1948. A mathematical theory of communication. *Bell System Technical Journal* **27**, 379–423.

Silver, W. L., and R. K. Miya. 2001. Global patterns in root decomposition: comparisons of climate and litter quality effects. *Oecologia* **129**, 407–419.

Six, J., R. Conant, E. Paul, and K. Paustian. 2002. Stabilization mechanisms of soil organic matter: implications for c-saturation of soils. *Plant and soil* **241**, 155–176.

Socher, S. A., D. Prati, S. Boch, J. Müller, H. Baumbach, S. Gockel, A. Hemp, I. Schöning, K. Wells, F. Buscot, E. K. V. Kalko, K. E. Linsenmair, E.-D. Schulze, W. W. Weisser, and M. Fischer. 2013. Interacting effects of fertilization, mowing and grazing on plant species diversity of 1500 grasslands in germany differ between regions. *Basic and Applied Ecology* **14**, 126–136.

Socher, S. A., D. Prati, S. Boch, J. Müller, V. H. Klaus, N. Hölzel, and M. Fischer. 2012. Direct and productivity-mediated indirect effects of fertilization, mowing and grazing on grassland species richness. *Journal of Ecology* **100**, 1391–1399.

Sohi, S. P., N. Mahieu, J. R. Arah, D. S. Powlson, B. Madari, and J. L. Gaunt. 2001. A procedure for isolating soil organic matter fractions suitable for modeling. *Soil Science Society of America Journal* **65**, 1121–1128.

Sollins, P., C. Swanston, M. Kleber, T. Filley, M. Kramer, S. Crow, B. A. Caldwell, K. Lajtha, and R. Bowden. 2006. Organic C and N stabilization in a forest soil: evidence from sequential density fractionation. *Soil Biology and Biochemistry* **38**, 3313–3324.

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

Sørensen, L. H. 1972. Stabilization of newly formed amino acid metabolites in soil by clay minerals. *Soil Science* **114**, 5–11.

Sørensen, L. H. 1981. Carbon-nitrogen relationships during the humification of cellulose in soils containing different amounts of clay. *Soil Biology and Biochemistry* **13**, 313–321.

Steinhof, A., G. Adamiec, G. Gleixner, T. Wagner, and G. van Klinken. 2004. The new ^{14}C analysis laboratory in Jena, Germany. *Radiocarbon* **46**, 51–58.

Stewart, G. B., and A. S. Pullin. 2008. The relative importance of grazing stock type and grazing intensity for conservation of mesotrophic 'old meadow' pasture. *Journal for Nature Conservation* **16**, 175–185.

Strand, A. E., S. G. Pritchard, M. L. McCormack, M. A. Davis, and R. Oren. 2008. Irreconcilable differences: fine-root life spans and soil carbon persistence. *Science* **319**, 456–458.

Stuiver, M., and H. A. Polach. 1977. Discussion; reporting of ^{14}c data. *Radiocarbon* **19**, 355–363.

Sun, T., Z. Mao, L. Dong, L. Hou, Y. Song, and X. Wang. 2013. Further evidence for slow decomposition of very fine roots using two methods: litterbags and intact cores. *Plant and Soil* **366**, 633–646.

Taboada, M. A., and R. S. Lavado. 1988. Grazing effects of the bulk density in a natraquoll of the flooding pampa of argentina. *Journal of Range Management* **41**, 500–503.

Thoms, C., A. Gattinger, M. Jacob, F. M. Thomas, and G. Gleixner. 2010. Direct and indirect effects of tree diversity drive soil microbial diversity in temperate deciduous forest. *Soil Biology and Biochemistry* **42**, 1558–1565.

Tierney, G. L., and T. J. Fahey. 2001. Evaluating minirhizotron estimates of fine root longevity and production in the forest floor of a temperate broadleaf forest. *Plant and Soil* **229**, 167–176.

Tierney, G. L., and T. J. Fahey. 2002. Fine root turnover in a northern hardwood forest: a direct comparison of the radiocarbon and minirhizotron methods. *Canadian Journal of Forest Research* **32**, 1692–1697.

Tilman, D., D. Wedin, and J. Knops. 1996. Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature* **379**, 718–720.

Tjoelker, M. G., J. M. Craine, D. Wedin, P. B. Reich, and D. Tilman. 2005. Linking leaf and root trait syndromes among 39 grassland and savannah species. *New Phytologist* **167**, 493–508.

Torn, M., C. Swanston, C. Castanha, and S. Trumbore. 2009. Storage and turnover of organic matter in soil. *Biophysico-chemical processes involving natural nonliving organic matter in environmental systems. Wiley, Hoboken* Pp. 219–272.

Trumbore, S. 2000. Age of soil organic matter and soil respiration: radiocarbon constraints on belowground C dynamics. *Ecological Applications* **10**, 399–411.

Trumbore, S. 2009. Radiocarbon and soil carbon dynamics. *Annual Review of Earth and Planetary Sciences* **37**, 47–66.

Trumbore, S. E. 1997. Potential responses of soil organic carbon to global environmental change. *Proceedings of the National Academy of Sciences* **94**, 8284–8291.

Trumbore, S. E., and C. I. Czimczik. 2008. Geology - An uncertain future for soil carbon. *Science* **321**, 1455–1456.

Trumbore, S. E., and J. B. Gaudinski. 2003. The secret lives of roots. *Science* **302**, 1344–1345.

Trumbore, S. E., J. Vogel, and J. Southon. 1989. Ams ^{14}c measurements of fractionated soil organic matter; an approach to deciphering the soil carbon cycle. *Radiocarbon* **31**, 644–654.

Valenzuela-Estrada, L. R., V. Vera-Caraballo, L. E. Ruth, and D. M. Eissenstat. 2008. Root anatomy, morphology, and longevity among root orders in Vaccinium corymbosum (Ericaceae). *American Journal of Botany* **95**, 1506–1514.

van Huysen, T. L., M. E. Harmon, S. S. Perakis, and H. Chen. 2013. Decomposition and nitrogen dynamics of ^{15}n - labeled leaf, root, and twig litter in temperate coniferous forests. *Oecologia* **173**, 1563–1573.

Vance, E. D., P. C. Brookes, and D. S. Jenkinson. 1987. An extraction method for measuring soil microbial biomass C. *Soil Biology and Biochemistry* **19**, 703–707.

Vargas, R., N. Hasselquist, E. Allen, and M. Allen. 2010. Effects of a hurricane disturbance on aboveground forest structure, arbuscular mycorrhizae and belowground carbon in a restored tropical forest. *Ecosystems* **13**, 118–128.

Vargas, R., S. E. Trumbore, and M. F. Allen. 2009. Evidence of old carbon used to grow new fine roots in a tropical forest. *New Phytologist* **182**, 710–718.

Veldkamp, E. 1994. Organic-carbon turnover in 3 tropical soils under pasture after deforestation. *Soil Science Society of America Journal* **58**, 175–180.

Vivanco, L., and A. T. Austin. 2006. Intrinsic effects of species on leaf litter and root decomposition: a comparison of temperate grasses from north and south america. *Oecologia* **150**, 97–107.

von Lützow, M. v., I. Kögel-Knabner, K. Ekschmitt, E. Matzner, G. Guggenberger, B. Marschner, and H. Flessa. 2006. Stabilization of organic matter in temperate soils: mechanisms and their relevance under different soil conditions – a review. *European Journal of Soil Science* **57**, 426–445.

Waisel, Y., A. Eshel, and U. Kafkafi. 2002. *Plant roots - the hidden half. 3rd edn*. Vol. 90. Marcel Decker, New York.

Wattel-Koekkoek, E. J. W., P. P. L. van Genuchten, P. Buurman, and B. van Lagen. 2001. Amount and composition of clay-associated soil organic matter in a range of kaolinitic and smectitic soils. *Geoderma* **99**, 27–49.

Weaver, J. E. 1947. Rate of decomposition of roots and rhizomes of certain range grasses in undisturbed prairie soil. *Ecology* **28**, 221–240.

Xia, M., D. Guo, and K. S. Pregitzer. 2010. Ephemeral root modules in fraxinus mandshurica. *New Phytologist*.

Yang, H., R. Yan, H. Chen, C. Zheng, D. H. Lee, and D. T. Liang. 2005. In-depth investigation of biomass pyrolysis based on three major components: Hemicellulose, cellulose and lignin. *Energy & Fuels* **20**, 388–393.

Zechmeister, H. G., I. Schmitzberger, B. Steurer, J. Peterseil, and T. Wrbka. 2003. The influence of land-use practices and economics on plant species richness in meadows. *Biological Conservation* **114**, 165–177.

10 Curriculum Vitae

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Education

05/2011–07/2014	International Max Planck Research School for Global Biogeochemical Cycles, Jena, Germany
05/2011–07/2014	PhD student: Department for Biogeochemical Processes, Max Planck Institute for Biogeochemistry, Jena, Germany; Department of Geography, Friedrich-Schiller-Universität Jena, Germany
06/2013–09/2013	Visiting Researcher, Department for Global Ecology, Carnegie Institution for Science, Field Lab, Stanford, CA, USA
10/2008–10/2010	MSc in Environmental Science and Management, University of Torino. Awarded cum laude (110/110 con lode e dignità di stampa). Thesis: Monitoring phenology in a subalpine *Nardus stricta* grassland: applying a multi-source data integrated approach. Supervisor: Prof. Dr. Consolata Siniscalco
10/2005–10/2008	BSc in Natural Sciences, University of Torino. Awarded with honours (108/110). Main subjects: biology, botany, ecology. Thesis: Cellular and molecular analysis of the first phases of interaction between *Medicago truncatula* and a symbiotic fungus. Supervisor: Prof. Dr. Paola Bonfante
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Publications

Solly, E., I. Schöning, S. Boch, J. Müller, S. A. Socher, S. E. Trumbore, and M. Schrumpf. 2013. Mean age of carbon in fine roots from temperate forests and grasslands with different management. *Biogeosciences* **10**, 4833–4843.

Solly, E. F., I. Schöning, S. Boch, E. Kandeler, S. Marhan, B. Michalzik, J. Müller, J. Zscheischler, S. E. Trumbore, and M. Schrumpf. 2014. Factors controlling decomposition rates of fine root litter in temperate forests and grasslands. *Plant and Soil* **382**, 203–218.

Ahrens, B., K. Hansson, E. F. Solly, M. Schrumpf. 2014. Reconcilable Differences: A Joint Calibration of Fine-Root Turnover Times with Radiocarbon and Minirhizotrons. *New Phytologist*. **204**, 932–942.

Solly, E. F., I. Schöning, N. Herold, S. E. Trumbore, and M. Schrumpf. 2015 No depth-dependence of fine root litter decomposition in temperate beech forest soils. *Plant and Soil*. doi: 10.1007/s11104-015-2492-7.

Allan, E., P. Manning, F. Alt, J. Binkenstein, S. Blaser, N. Blüthgen, S. Böhm, F. Grassein, N. Hölzel, V. Klaus, T. Kleinebecker, E.K. Morris, Y. Oelmann, D. Prati, S.C. Renner, M.C. Rillig, M. Schäfer, M. Schloter, B. Schmitt, I. Schöning, M. Schrumpf, E. F. Solly, E. Sorkau, J. Steckel, I. Steffen-Dewenter, B. Stempfhuber, M. Tschapka, C.N. Weiner, W.W. Weisser, M. Werner, C. Westphal, W. Wilcke, M. Fischer. In revision. Effects of land-use intensification on ecosystem multifunctionality are driven by biodiversity loss and functional composition shifts. *Ecology letters*.

Selbständigkeitserklärung

Ich erkläre, dass ich die vorliegende Arbeit selbständig und unter Verwendung der angegebenen Hilfsmittel, persönlichen Mitteilungen und Quellen angefertigt habe.

Jena,

11 Author Contributions

Manuscript 1: Solly, E., I. Schöning, S. Boch, J. Müller, S. A. Socher, S. E. Trumbore, and M. Schrumpf. 2013. Mean age of carbon in fine roots from temperate forests and grasslands with different management. *Biogeosciences* **10**, 4833–4843.

- E. Solly is the first author and responsible for writing this paper. She carried out the sampling campaign, obtained the data in the laboratory, analyzed and discussed the data.
- I. Schöning, S. E. Trumbore and M. Schrumpf were responsible for the overall experimental design, reviewed and edited drafts of the manuscript. Ingo Schöning was further involved in the sampling campaign and in its organization.
- S. Boch, J. Müller and S. A. Socher recorded the vegetation data, provided the Ellenberg indicator value for soil moisture and nutrient availability. They also reviewed and edited drafts of the manuscript.

Manuscript 2: Solly, E. F., I. Schöning, S. Boch, E. Kandeler, S. Marhan, B. Michalzik, J. Müller, J. Zscheischler, S. E.Trumbore, and M. Schrumpf. 2014. Factors controlling decomposition rates of fine root litter in temperate forests and grasslands. *Plant and Soil* **382**, 203–218. doi: 10.1007/s11104-014-2151-4.

- E. F. Solly is the first author and responsible for writing this paper. She designed and carried out the sampling campaign and field experiment, obtained the data in the laboratory, analyzed and discussed the data.
- I. Schöning, S. E. Trumbore, B. Michalzik and M. Schrumpf were responsible for the overall experimental design, reviewed and edited drafts of the manuscript. Ingo Schöning was further involved in the sampling campaign and in its organization.
- S. Boch and J. Müller recorded the vegetation data. They also reviewed and edited drafts of the manuscript.

- E. Kandeler and S. Marhan obtained the data on the carbon content in the microbial biomass. They also reviewed and edited drafts of the manuscript.

- J. Zscheischler helped with the data analysis and edited drafts of the manuscript.

Manuscript 3: Solly, E. F., I. Schöning, N. Herold, S. E. Trumbore, and M. Schrumpf. 2015. No depth-dependence of fine root litter decomposition in temperate beech forest soils. *Plant and Soil*. doi: 10.1007/s11104-015-2492-7.

- E. F. Solly is the first author and responsible for writing this paper. She designed and carried out the experiment and the sampling campaign, obtained the data in the laboratory, analyzed and discussed the data.

- I. Schöning, S. E. Trumbore, and M. Schrumpf designed the experiment, reviewed and edited drafts of the manuscript. Ingo Schöning collected the soil samples and recorded their C and N concentrations and stocks.

- N. Herold reviewed and edited drafts of the manuscript. She also recorded soil pH, soil texture and enzyme activities in different soil horizons.

Manuscript 4: Solly, E. F., I. Schöning, S. E. Trumbore, B. Michalzik, and M. Schrumpf. In preparation. Formation of new mineral associated organic matter from roots in temperate grasslands.

- E.F. Solly is the first author and responsible for writing this paper. She designed and carried out the experiment and the sampling campaign, obtained the data in the laboratory, analyzed and discussed the data.

- I. Schöning, S.E. Trumbore, B. Michalzik and M. Schrumpf designed the experiment, reviewed and edited drafts of the manuscript.