

Fine root productivity and C dynamics in temperate grasslands and forests with different land uses

Bachelorarbeit

Zur Erlangung des Grades „Bachelor of Science“
im Studiengang Biogeowissenschaften
an der Chemisch- Geowissenschaftlichen Fakultät
der Friedrich- Schiller- Universität Jena



seit 1558

Vorgelegt von:
Katharina Stolze

Matrikelnummer: 120797

Jena, 2013

Erstgutachter: Dr. Marion Schrumpf (Max- Planck- Institut für Biogeochemie, Jena)
Zweitgutachter: Prof. Dr. Georg Büchel (Institut für Geowissenschaften, FSU Jena)

Jena, 22.07.2012

Contents

List of abbreviations	4
List of figures	5
List of tables.....	7
Statement of authorship	8
Abstract.....	9
1 Introduction.....	10
1.1 The global carbon cycle	10
1.2 The role of fine roots in the global C cycle	12
1.3 Fine root productivity and turnover.....	12
1.4 Objectives and aims	13
2 Materials and methods	14
2.1 Study regions	14
2.2 Ingrowth core preparation and distribution in the field.....	16
2.3 Ingrowth core collection.....	17
2.4 Fine root productivity	18
2.5 C/N analysis	19
2.5.1 Sample preparation	19
2.5.2 Measuring principle.....	20
2.5.3 Process.....	20
2.5.4 Detection.....	21
2.6 Radiocarbon measurement.....	21
2.6.1 Sample preparation	22
2.6.2 Measuring principle.....	22
2.6.3 Detection.....	23
2.7 Plant diversity and soil properties.....	23
2.8 Statistics	24
3 Results	24
3.1 Root Productivity	24
3.2 C/N analysis	29
3.3 ¹⁴ C measurements.....	30
4 Discussion	33
5 Conclusions.....	36
6 Acknowledgements.....	37
7 References	38
8 Appendix.....	42

List of abbreviations

C	–	Carbon
ppmv	–	parts per million by volume
NPP	–	Net primary production
HAI	–	Hainich- Dün
SCH	–	Schorfheide- Chorin
e.g.	–	exempli gratia
i.e.	–	id est

List of figures

Figure 1. The plot shows the CO₂ concentration at Mauna Loa. In the past 50 years the concentration has increased from 315.98 ppmv (1959) to 377.38 ppmv (2004).

Figure 2. Examples of two “very intensive plots. In grasslands and forests. In the plot charts, the subplots associated with various projects are shown in different colours (Fischer et al., 2010)

Figure 3. Example of an ingrowth core.

Figure 4. It is important to collect the ingrowth cores with some centimetres of surrounding soil (left), so that each root grown in the ingrowth core can be collected (right).

Figure 5. Roots, present in the soil and the plastic mesh were carefully collected for further analysis.

Figure 6. A homogenous sample is established by a flint mill (left image). Therefore, the samples are filled in the grinding beakers.

Figure 7. Tin boats, in which the samples are filled, have a size of 6 x 6 x 12 mm.

Figure 8. Model of target press (AMS facility Jena)

Figure 9. Comparison of the fine root productivity between the forest and grassland plots across the two study regions ($p=1.05$). A significant effect of land- use types (i.e. grasslands and forests) was observed across the study regions as well as a significant difference of land-use type within the study regions (Tab. 5).

Figure 10. Fine root productivity of both grassland sites SCH and HAI correlated with the plant diversity. It is noticeable that the root productivity increases with rising plant diversity ($p=0.1097$, $R^2=0.152$).

Figure 11. Plant diversity increases in grassland plots in HAI (left) in a lower degree ($p=0.3111$, $R^2=0.1455$) than in SCH (right) ($p=0.1418$, $R^2= 0.2814$)

Figure 12. Fine root productivity showed no correlation with the plant diversity in the forest plots in the HAI ($p=0.7098$, $R^2= 0.009501$), whereas the correlation was significant ($p= 0.01664$, $R^2= 0.3088$) in SCH.

Figure 13. Differences between conifers and broadleaved trees are less marked in HAI (left) than in SCH (right). Although both are statistically not significant.

Figure 14. Soil organic C in the two study areas ($p=0.006787$).

Figure 15. Soil organic C correlated with fine root productivity in the grassland plots of HAI ($p=0.05545$, $R^2=0.4292$) (left) and SCH ($p=0.4494$, $R^2=0.08398$) (right).

Figure 16. Soil organic C correlated with fine root productivity in the forest plots of HAI ($p=0.5807$, $R^2=0.054$) (left) and SCH ($p=0.46$, $R^2=0.081$) (right).

Figure 17. Distribution of soil moisture in the two study regions ($p=0.05788$).

Figure 18. The difference of fine root productivity between the study areas was significant ($p=0.0206$), whereas there was no effect of fertilization across the study areas and no significant differences between fertilized and unfertilized plots within the study regions (Tab. 3).

Figure 19. C_{org} content of fine roots grown in the ingrowth cores, differentiated between the two study areas ($p=0.00349$).

Figure 20. Total N content of fine roots grown in the ingrowth core ($p=0.3537$).

Figure 21. C/N ratio of the fine roots in both study areas ($p=0.04812$).

Figure 22. Mean $\Delta^{14}C$ measured in the fine roots. There was no significant difference between the two study sites ($p=0.7581$).

Figure 23. Mean fine root ages in the two study sites. The difference between them was not statistically significant ($p=0.1192$).

Figure 24. Fine root C ages were positively correlated with plant diversity ($p=0.04153$, $R^2=0.2488$) in both study areas.

Figure 25. Plant diversity effects on the fine root C age were not significant in the HAI (left) ($p=0.1198$, $R^2=0.3539$) but showed a positive correlation in the SCH (right) ($p=0.00822$, $R^2=0.6551$).

Figure 26. The fine root mean age showed tendencies of a negative correlation with the total root N content. However, this regression is not statistically significant ($p=0.1762$, $R^2=0.1184$).

List of tables

Table 1. Main geographic and environmental characteristics of the study regions (Solly et al., 2013)

Table 2. Detailed description of the research plots in the Hainich- Dün and Schorfheide- Chorin.

Table 3. Measured $\Delta^{14}\text{C}$ - values and the resultant fine root ages.

Table 4. Mean soil conditions and Shannon diversity of both grassland and forest plots as well as C and N contents of the fine roots sampled in the grassland plots.

Table 5. ANOVA results of fine root productivity, fine root C and N concentrations and fine root C/N ratio. Variance between study regions and differences between grassland and forest plots (i.e. land- use) and fertilization were compared.

Statement of authorship

Ich erkläre hiermit, dass die vorliegende Arbeit selbstständig und nur unter Verwendung der aufgeführten Literatur angefertigt wurde.

Katharina Stolze

Jena, 22.07.2013

Abstract

Feinwurzeln (hier definiert <1 mm) sind essentielle Komponenten des Kohlenstoffkreislaufs in Wald- und Grünlandökosystemen, da sie als eine der Hauptquellen der organischen Substanz im Boden dienen. Die Produktivität von Feinwurzeln und die daraus folgende Verteilung von Kohlenstoff werden von verschiedenen Faktoren beeinflusst. Beispielsweise die jährliche, mittlere Temperatur, Pflanzendiversität, Bodentyp und damit verbundene Bodeneigenschaften sowie verschiedene Landnutzungstypen.

In dieser Bachelorarbeit wurde die Produktivität von Feinwurzeln während des Winters untersucht. Hierzu wurde die „Ingrowth core“ Methode in zwei deutschen Gebieten verwendet. Diese Studie wurde in 18 Grünland- und 18 Waldplots mit unterschiedlicher Landnutzung und Bodentypen durchgeführt. Des Weiteren wurde der Radiocarbongehalt (^{14}C) analysiert. Hierbei soll festgestellt werden, ob Pflanzen den, während der Photosynthese assimilierten Kohlenstoff direkt in das Wurzelwachstum investieren oder ob in der Pflanze gespeicherter Kohlenstoff hierfür remobilisiert wird.

Die Produktivität von Feinwurzeln war durchschnittlich höher in den Grünlandplots (58.86 ± 39.71 g/m²) als in den Waldplots (18.12 ± 12.52 g/m²). Während eine Zunahme der Pflanzendiversität einen positiven Effekt auf die Produktivität hatte, hatte eine Düngung der Graslandplots keinen signifikanten Einfluss auf die Produktivität zwischen gedüngten und nicht gedüngten Plots. Zudem zeigte das durchschnittliche Kohlenstoffalter in den Wurzeln der Grünländer der Untersuchungsgebiete (0.66 ± 0.24 yrs), das jährliche und mehrjährige Pflanzen hauptsächlich Kohlenstoff aus der Atmosphäre nutzen um neue Wurzeln zu bilden.

1 Introduction

1.1 The global carbon cycle

Carbon (C) plays a very important role for life on Earth, since living organisms need this element in large quantities to build and maintain tissues (Adams, 2010). The major reservoirs of carbon are contained in three pools: the atmosphere, the ocean and the terrestrial biosphere (organic material found on the land surface). Carbon is exchanged naturally in these pools on decadal to centennial time scales, whereas human activities like the burning of fossil fuel carbon and land use and management have a strong impact on the concentrations of carbon (Christopher, 2005) by adding C to the atmosphere and directly modifying the carbon cycle and its components.

In the atmosphere, carbon is predominant in the form of carbon dioxide (CO_2). It is characterized as a trace gas with a contemporary concentration of circa 380 parts per million by volume (ppmv)(Christopher, 2005). Despite these low concentrations CO_2 has a great impact on the global climate since it is a greenhouse gas which absorbs long wavelength radiations in the atmosphere. CO_2 concentrations have been rising during the last decades (Fig. 1).

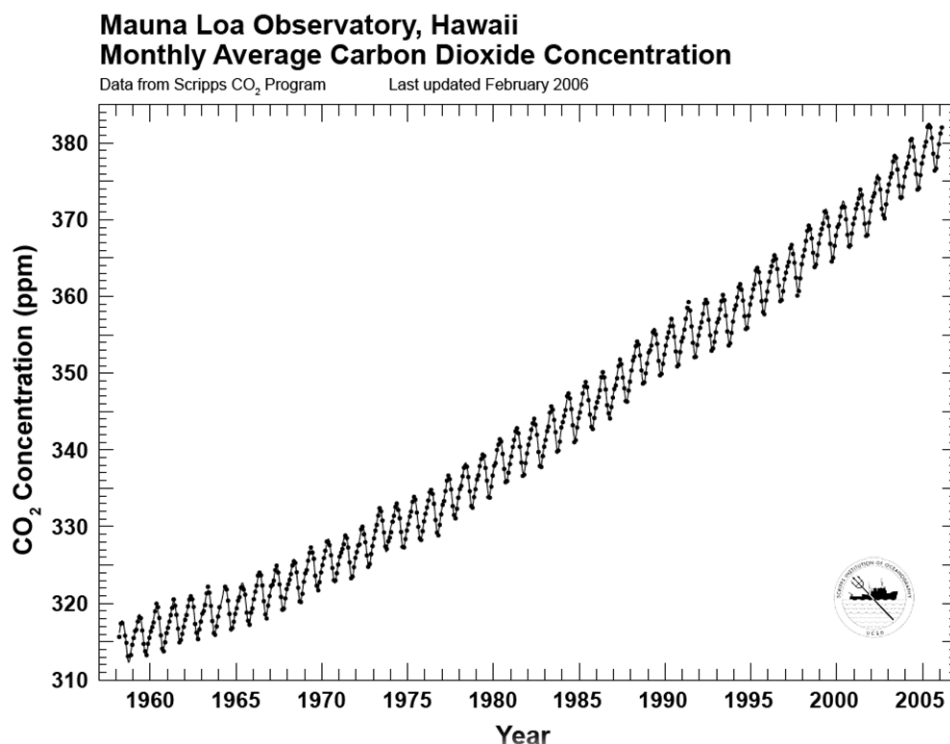


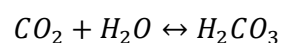
Figure 1. The plot shows the CO_2 concentration at Mauna Loa. In the past 50 years the concentration has increased from 315.98 ppmv (1959) to 377.38 ppmv (2004).

[http://www.esrl.noaa.gov/gmd/obop/mlo/programs/coop/scripps/img/img_scripps_co2_record.gif]

The CO_2 from the atmosphere has a direct exchange with the terrestrial biosphere pool. Plants are able to take up carbon through photosynthesis and use it to form organic plant materials.

Thus, plenty of carbon is stored in plants, especially in trees (Adams, 2010). Carbon is then returned to the atmosphere through various forms of respiration. The uptake and release of carbon by plants is nearly in balance on an annual basis (Christopher, 2005). The difference between photosynthesis and respiration is defined as net primary production (NPP). At a global scale it is about 57 petagrams of carbon per year ($1 \text{ Pg} = 10^{15} \text{ g} = 1 \text{ billion metric tonnes}$) for land plants (Christopher, 2005). Through soil respiration, which includes respiration by microorganisms, saprophytes and plant roots the CO_2 that was taken up during photosynthesis is released to the atmosphere (Schlesinger, 2000). But plant derived organic matter, which is formed by breakdown of uneaten plant material like fallen leaves, wood and roots, also represents a large store of carbon in soils (Adams, 2010) (see paragraph 1.2). The amount of C contained in soil organic matter is not permanent but dependent on a number of abiotic and biotic factors regulating organic C input (mainly from the vegetation) and decomposition (mainly by soil microorganisms). For instance, if the mean annual temperature is low, like in boreal regions, decomposition is slowed down (due to less microbial activity) and the amount of carbon stored as soil organic matter rises. In contrast in tropical regions, which are characterised by high temperatures, the activity of decomposers and related decomposition rates are higher (Schlesinger, 2000). Soil organic matter is further affected by cultivation practices. For example by management practices such as ploughing, aeration of soil and soil moisture can be altered. This may lead to improved conditions for microorganisms and saprophytes and increase decomposition (Schlesinger, 2000).

In addition to the C uptake of plants from the atmosphere, there is a second way how carbon is uptaken from atmosphere, the weathering. Here, carbonic acid reacts with the silicate minerals of igneous rocks. Carbonic acid (H_2CO_3) is formed by CO_2 and H_2O (rainwater) like in the following reaction:



The products of the carbonic acid weathering are considerably components of soils: clays, quartz sand grains, iron oxide and salts (Adams, 2010). Because of the bonding of CO_2 out of the atmosphere, this form of weathering counts as carbon sink (Archer, 2010).

Ions, including bicarbonates, which are dissolved from igneous rocks can end up through rivers in the third reservoir of carbon – the ocean. It contains 50 times more CO_2 than the atmosphere and 10 times more than the terrestrial biosphere. The Ocean exchanges CO_2 with the atmosphere through the difference in the partial pressure of CO_2 in the ocean relative to the atmosphere (Christopher, 2005). The uptake of CO_2 from the atmosphere also occurs by phytoplankton through photosynthesis.

Changing land use managements in the past centuries has had a large impact on the CO_2 concentration in the atmosphere and thus also on the global carbon cycle. Sources of CO_2 emissions are mostly deforestation (20% decrease of the global forest area) and conversion

of natural vegetation into agriculture. This may lead not only to biomass loss, but to increased decomposition of soil organic matter caused by disturbance and energy costs of various agricultural practices. The terrestrial pool functions as a sink for atmospheric CO₂, since all plants from cold climates and most agricultural crops may respond to increasing atmospheric CO₂ levels by enhancing their photosynthetic uptake of carbon.

1.2 The role of fine roots in the global C cycle

Fine roots (here defined as <1 mm in diameter) play an important role in the global carbon cycle in forest and grassland ecosystems, since they contribute largely to below-ground C fluxes (Finer, 2010). Although fine roots represent only a minor part of the total plant biomass, especially in trees, they can consume up to 30- 50 % of the annual primary production (Vogt et al., 1996; Ruess and others 1996; Xiao et al, 2003) accounting for 33 % of the global annual NPP (Gill and Jackson, 2000). Fine roots, further constitute an interface between plants and soil and are responsible for the uptake of water and nutrients (Lukac, 2012). Assuming the amount of C allocated to fine roots and the associated fine root productivity and turnover time of root systems still remains unclear, since a direct observation and quantification of roots in situ is limited (Majdi et al., 2005; Trumbore and Gaudinski, 2003, Solly et al., 2013).

1.3 Fine root productivity and turnover

Previous studies have shown that fine root productivity is affected by the availability of nutrients and water in the soil, with lower productivity at sites characterized by a higher amount of available nutrient (Vogt, 1996) and less water availability (Leuschner et al., 2004). Furthermore, root longevity is influenced by soil conditions like soil moisture and soil temperature, vegetation types, and the presence or absence of mycorrhizae (Sah et al., 2012).

Gill and Jackson (2000) estimated a fine root turnover time ranging from 5 months to 2 years. Whereas recent estimates that are based on ¹⁴C- measurements assume that the carbon mean age of living roots is about 3 to 18 years in forests (Gaudinski et al., 2001) and 0 to 4 years in grasslands (Solly et al., 2013). Accordingly, ¹⁴C investigations can be used to estimate average fine root C ages rather than the direct turnover time of root systems.

However this data represents the turnover of a population of roots grown in different years, rather than a homogenous sample of fine roots grown during a season.

The radiocarbon method is based on the ¹⁴C (half-life of 5730 years) content in the atmosphere. Naturally, ¹⁴C is formed by a nuclear reaction caused by cosmic radiation (Pandow et al., 1960). In the atmosphere the formed isotope reacts immediately with oxygen to ¹⁴CO₂ and is assimilated by oceans and terrestrial organisms (Levin and Kromer, 2004). Thermonuclear weapons explosions lead to an increase of atmospheric ¹⁴C during the 1950s and early 1960s (Trumbore, 2009). The so called “bomb peak”, resulting from the explosions can be used to

consider the time elapsed since C was fixed in plants by photosynthesis (Gaudinski et al., 2001).

Similar to the root production, land use can influence the ^{14}C age in roots. Previous studies have shown that more fertile forest soils with a higher amount of nutrients contain roots with younger ^{14}C compared to fine roots found in less fertile soils, due to a minimization of carbon costs (Helmisaari et al., 2007). Also, the ^{14}C age in fine roots was found to be older in mineral soils than in organic layers, due to less competition in mineral soils (Sah et al., 2012).

1.4 Objectives and aims

In this thesis I aimed in investigating whether fine root production during the winter season differs between grasslands and forests and whether various soil properties as well as different land use have an impact on fine root productivity. For the determination of fine root productivity we used the ingrowth core method in 18 grasslands and 18 forest plots with different management in two regions in Germany. We were also interested in using the radiocarbon technique in order to analyse whether the carbon assimilated by plants during photosynthesis is directly used for fine root growth or if older carbon – stored in the plant – is subsequently recycled to produce fine roots. For this we will compare the mean C ages of fine roots grown inside the ingrowth cores with the mean C ages of the standing biomass of fine roots on the same plots. The mean C ages of the standing biomass of fine roots were previously estimated by Solly et al. (2013).

2 Materials and methods

2.1 Study regions

This study was conducted in 36 plots distributed in two German study regions, of the Biodiversity Exploratories project (Fischer et al., 2010). The Hainich- Dün (HAI), which is located in Central Germany and the Schorfheide- Chorin (SCH) in North- Eastern Germany.

The parent material in the HAI consists mainly of Triassic limestone, overlain by Loess. Soils developed from this substrate are usually classified as Luvisols in forests and Cambisols and Stagnosols in grasslands (Fischer et al., 2010). The geomorphology of the SCH was influenced by the last glacial period. The predominant geological substrate found in this study region is glacial till, which is frequently covered by glacio- fluvial or aeolian sand. As a consequence the soils are, mainly Dystric Cambisols in forests and Histosols and Gleysols in the grasslands. They have a texture from loamy sand to pure sand (Fischer et al., 2010). More characteristics of these study regions are listed in table 1.

Table 1. Main geographic and environmental characteristics of the study regions (Solly et al., 2013)

	Hainich- Dün (HAI)	Schorfheide- Chorin (SCH)
Location	Central Germany	NE Germany
Size	~ 1300 km ²	~ 1300 km ²
Geology	Calcareous bedrock and loess cover	Young glacial landscape
Coordinates	N 51° 9' E 10° 28'	N 53° 0' E 13° 46'
Altitude a.s.l.	285 – 550 m	3 – 140 m
Annual mean temperature	6,5 – 8°C	8 – 8,5 °C
Annual mean precipitation	500 – 800 mm	500 – 600 mm

In each plot a meteorological station was set up to measure air temperature and moisture at 2 m and 10- 20 cm above ground, and soil temperature and moisture at 10, 20 and 50 cm belowground. These sites were selected according to three different management types with different land use intensity. In the grasslands we selected three pastures, three meadows and three mown pastures, the mown pastures were fertilized in the HAI and not fertilized in the SCH. In the forests we selected three unmanaged beech (*Fagus sylvatica* L.) forests, three beech forests under age class management and three conifer plantations (Norway spruce *Picea abies* (L.) H. Karst) in the HAI and Scots pine (*Pinus sylvestris* L.) in the SCH). A detailed description of the investigated plots is given in table 2.

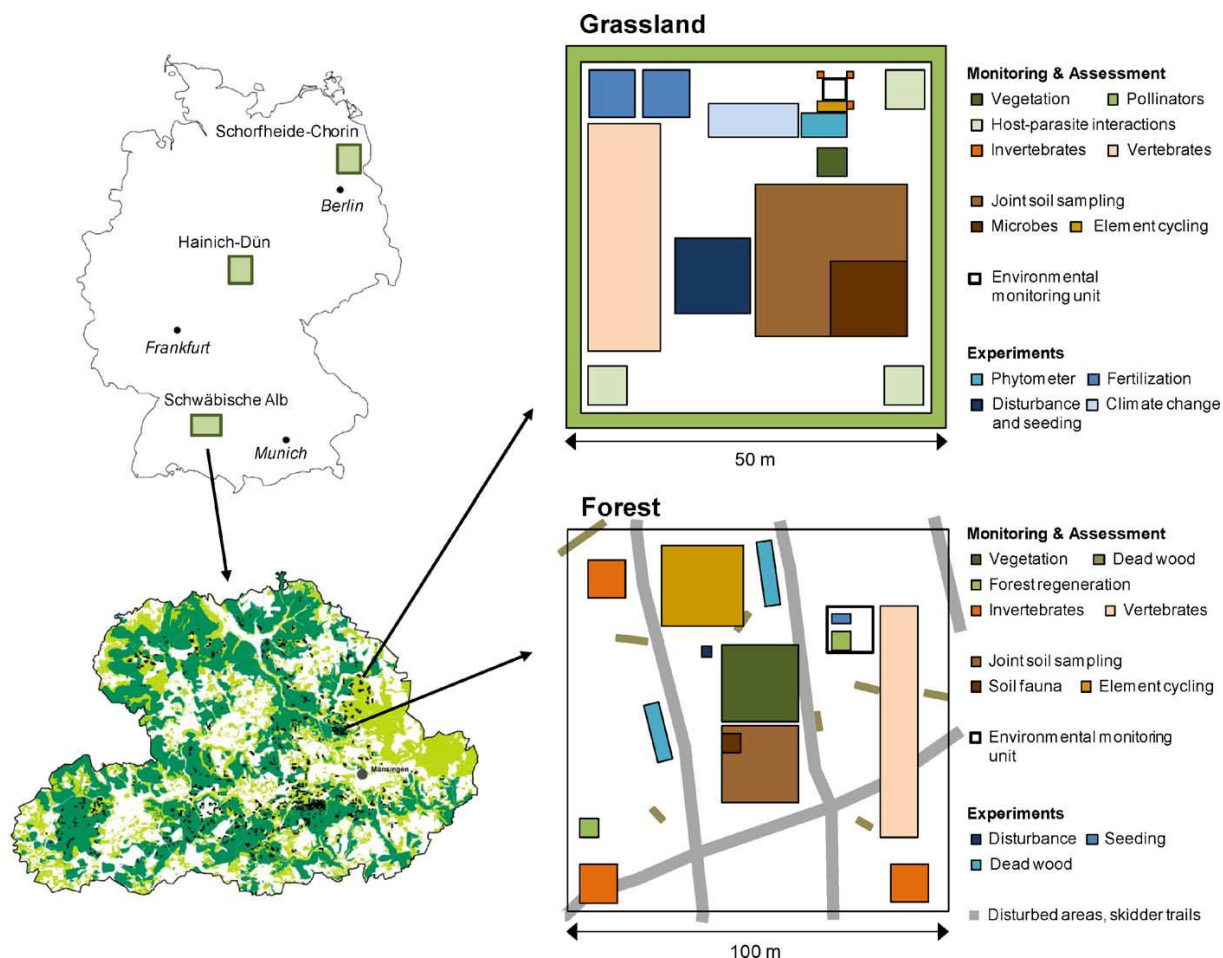


Figure 2. Examples of two plots in grasslands and forests. In the plot charts, the subplots associated with various projects are shown in different colors (Fischer et al., 2010)

Table 2. Detailed description of the research plots in the Hainich- Dün and Schorfheide- Chorin

Plot	Soil type	Land use	Vegetation type	Animals	Cuttings	Fertilization
HEG1	Cambisol	meadow		-	2	yes
HEG2	Vertisol	meadow		-	3	yes
HEG3	Vertisol	meadow		-	3	yes
HEG4	Stagnosol	mown pasture		cattle	1	yes
HEG6	Stagnosol	mown pasture		cattle	1	yes
HEG7	Stagnosol	pasture		cattle	-	-
HEG8	Stagnosol	pasture		cattle	-	-
HEG33	Cambisol	pasture		cattle	-	yes
HEG34	Cambisol	mown pasture		cattle	1	yes
HEW1	Stagnosol	managed forest	Conifer	-	-	-
HEW2	Stagnosol	managed forest	Conifer	-	-	-
HEW3	Luvisol	managed forest	Conifer	-	-	-
HEW5	Luvisol	managed forest	Broadleaved	-	-	-
HEW6	Luvisol	managed forest	Broadleaved	-	-	-

HEW10	Stagnosol	natural forest	Broadleaved	-	-	-
HEW11	Luvisol	natural forest	Broadleaved	-	-	-
HEW12	Luvisol	natural forest	Broadleaved	-	-	-
HEW13	Luvisol	managed forest	Conifer	-	-	-
HEW21	Luvisol	managed forest	Broadleaved	-	-	-
SEG1	Histosol	meadow		-	3	yes
SEG2	Histosol	meadow		-	2	yes
SEG3	Histosol	meadow		-	2	yes
SEG4	Histosol	mown pasture		cattle	1	-
SEG5	Gleysol	mown pasture		cattle	1	-
SEG6	Histosol	mown pasture		cattle	1	-
SEG8	Gleysol	pasture		cattle	-	-
SEG9	Histosol	pasture		cattle	-	-
SEG39	Cambisol	pasture		cattle	-	-
SEW1	Cambisol	managed forest	Conifer	-	-	-
SEW2	Cambisol	managed forest	Conifer	-	-	-
SEW3	Cambisol	managed forest	Conifer	-	-	-
SEW4	Cambisol	managed forest	Conifer	-	-	-
SEW5	Cambisol	managed forest	Broadleaved	-	-	-
SEW6	Cambisol	managed forest	Broadleaved	-	-	-
SEW7	Cambisol	natural forest	Broadleaved	-	-	-
SEW8	Albeluvisol	natural forest	Broadleaved	-	-	-
SEW9	Cambisol	natural forest	Broadleaved	-	-	-

2.2 Ingrowth core preparation and distribution in the field

To measure fine root production ingrowth cores are very suitable, especially for systems with fast root growth. They are defined as a 3- dimensional root- free zone within the soil profile, inside which root growth is observed for a defined period of time (Lukac, 2012). Advantages of this method are its simplicity and low costs. The greatest drawback is likely caused by the disturbance of the soil profile while inserting the ingrowth cores. In the ingrowth cores the nutrient availability and soil structure are severely altered compared to the soil profile (Majdi et al., 2005). Initially, fine roots are growing in an absence of competition from other roots in the ingrowth cores, what may lead to an overestimation of fine root productivity (Lukac, 2012).

We used the ingrowth core method to study fine root productivity in the HAI and SCH study areas. We inserted the ingrowth cores in holes which we created with a soil split- tube corer with a diameter of 5 cm. The ingrowth cores were surrounded by a plastic- mesh (mesh size: 4 mm x 11 mm) in order to separate the soil of the cores from the soil profile (Lukac, 2012). Subsequently we filled the ingrowth cores with soil. In this study we used root free sieved soil

up to a size of 2 mm from a Cambisol in Sulza where the upper 5 cm of an agricultural crop land was sampled. The cores have a diameter of 4.5 cm and are 13 cm long (Fig. 3).



Figure 3. Example of an ingrowth core.

We installed the ingrowth cores in the 18 forest and 18 grassland plots in October 2012. In each plot, we placed six ingrowth cores an equal distance of 50 cm along a transect. We disposed the transect approximately 4 m away from the meteorological station in the grasslands and 1 m away from the meteorological station in the forests. In the forests we comprised an area between two trees and at least 3 m away from the tree trunks, in order to allow a comparison between forest plots.

2.3 Ingrowth core collection

After a period of about 7 months the ingrowth cores were collected in April 2013. The positions of the aluminium cores in the grasslands were determined with a metal detector, while in the forests individual labels were used to mark the ingrowth cores. Afterwards, three out of six cores were cut out from the soil profile together with some cm of the surrounding soil, so that each root grown in the core or mesh was collected (Fig. 4).



Figure 4. It is important to collect the ingrowth cores with some cm of surrounding soil (left), so that each root grown in the ingrowth core can be collected (right).

2.4 Fine root productivity

In the lab we picked out all roots which were present in the ingrowth core and on the plastic mesh with tweezers (Fig. 5). The roots and the soil were then packed in a bag and weighed. Afterwards, the roots were carefully cleaned from the attached soil particles with distilled water. We used a sieve with a mesh size of 500 μm for the roots of the grasslands and forest plots respectively. The more strongly attached particles of soil on the roots were removed manually in a tray filled with distilled water. We measured the root diameter with a binocular microscope. The roots were placed on a glass slide and were capped with another glass slide, which contained different indicator scales from 0.01 mm to 70 mm. All roots had a diameter smaller than 2 mm and ranged between 0.08 mm and 1 mm and were classified as living roots according to the colour and breakability characteristics.

Then, the roots were weighed again and dried at 40°C to constant weight. The dried roots were used for the C/N analysis, the radiocarbon measurements and their weight was used to determine the fine root productivity during the winter season.



Figure 5. Roots, present in the soil and the plastic mesh were carefully collected for further analysis.

2.5 C/N analysis

2.5.1 Sample preparation

To analyse the total C and N concentrations in the fine root samples we used an element analyzer “Vario EL” (Elementar Analysensysteme GmbH, Hanau, Germany). Before analysis, we prepared a composite sample with the fine root material from the three ingrowth cores collected in each plot and then grounded the fine root material with a mill (RETSCH MM200, Fig. 5). To facilitate the grinding, the roots were cut in smaller pieces using scissors. The roots were then filled in the grinding beakers (Fig. 6) and ground for 5 minutes to obtain a particle size of $< 2 \mu\text{m}$.



Figure 6. A homogenous sample was prepared by a mill (left image). Therefore, the samples were filled in the grinding beakers.

Subsequently, we filled the fine-grained powder in glass cups and dried the samples again at 70°C to constant weight. In a second step, we weighed 20 to 25 mg of each grounded sample and filled them in small tin boats (Fig. 6). Those tin boats were then folded and pressed, to make sure that no air was left in them because this would affect the analysis of nitrogen. After checking that the packages were well closed and lost no material they were positioned in a sample- tray.



Figure 7. Tin boats, in which the samples are filled, have a size of 6 x 6 x 12 mm.

2.5.2 Measuring principle

The vario EL is a fully automatic machine for quantitative CHNOS- analysis. The measuring principle is characterized by catalytic combustion under oxygenation and high temperatures. During the process the flue gases are cleaned from foreign gases like volatile halogens. The elements are separated from each other by specific adsorption columns. In order to determine each gas, they are desorbed consecutively from the columns and measured with a thermal conductivity detector (TCD). Here, the difference of the thermal conductivity between the gas to be examined and helium, which is used as flushing and carrier gas, is detected and thus provides information about the content of the elements. (Instruction sheet vario EL, Elementar Analysensysteme GmbH)

2.5.3 Process

The tin packages, which include the samples, were inserted in a sample disposer – a bulging disk. As a first step of the process the automatic zero balance of the measured signal was conducted by the detector so that the balk valve opened in a 180° rotation. The bulging disk moved a step further whereby a sample fell into the blind hole of the balk valve. Subsequently, the balk valve rotated 90° so that the aperture was closed. Through these movements atmospheric nitrogen got into the construction and was flushed out by the carrier gas helium. Another rotation of 90° caused that the sample fell in the ash crucible of the combustion tube, where

the tin packages burned explosively due to a highly oxygenated atmosphere. The temperature in the combustion tube is around 1150°C and can heat up to 1500°C since the tin packages react exothermally in the combustion. In this reaction elements like C, H, N and S react to CO₂, H₂O, NO_x, SO₂ and SO₃, while copper oxide (Cu₂O) is used as catalyzer to accelerate the reaction (Instruction sheet vario EL, Elementar Analysensysteme GmbH).

For this study, the operating mode CHN/CN/N was used to measure the total C and N content in the roots. Unsolicited compounds like volatile fluoride were chemically bounded on cerium oxide and a filling of lead chromate absorbed the generated sulphur compounds (SO₂, SO₃). In the reduction tube, the nitrogen oxides (NO_x) were reduced quantitative to elemental nitrogen (N₂) through the contact with copper. In addition volatile halogen compounds were removed at the exit of the reduction tube by silver wool (Instruction sheet vario EL, Elementar Analysensysteme GmbH).

The TCD cannot distinguish between the different elements so that the gases had to be measured separately and consecutively. The separation was carried out by specific adsorption on heated columns. The nitrogen was not influenced by the adsorption and was measured first. After this measurement the next element is desorbed and measured. The adsorption/desorption- principle is also called “purge and trap”. For the C/N analysis, the H₂O was removed by a desiccant before the adsorption columns and only the adsorption column was required, which adsorbs CO₂ (Instruction sheet vario EL, Elementar Analysensysteme GmbH).

2.5.4 Detection

The TCD consists of two measuring cells. During the measurement, the reference cell is rinsed by the carrier gas helium whereas the other cell is flowed through by reaction gas (He/N₂ or He/CO₂).

The electrical detuning, which arises from the two measurement cells, constitutes a direct degree of the elemental ratio in the reaction gas. As a function of time the output voltage is logged, digitalised, integrated and described as an integral number. This number can be allocated via a calibration, to an absolute content of elements. The percental elemental content is then calculated with the absolute content and the weighted sample (Instruction sheet vario EL, Elementar Analysensysteme GmbH). As reference material spruce needles (CRM T101) and beech leaves (CRM T100) was used (Hilke et al., 2012).

2.6 Radiocarbon measurement

We measured the ¹⁴C content of the fine root samples at the acceleration mass spectrometry (AMS) facility in Jena, Germany. The AMS technique is an often used method for estimating

C dynamics in soil and root systems. An advantage of this method is that the carbon isotopes of samples of mg size or less can be detected (Steinhof et al., 2004).

2.6.1 Sample preparation

After combusting the fine root samples like in the C/N analysis the CO₂ gas is reduced in a catalytic reaction with H to graphite at 625°C (Solly et al., 2013). Iron powder is used as catalyst. The reduction facility is arranged in a line so that 10 samples can be reduced simultaneously. The produced H₂O is frozen out at – 25°C.

The graphite is then pressed with special pins in targets. The construction for this procedure is shown in figure 7. The pin that has contact with the graphite, may not contain carbon and is therefore made of aluminium (4). This pin is extended by two other pins which are for pressing. To build up a sufficiently high pressure (35 t/cm²), a hydraulic pump is used (AMS facility Jena). The targets are then positioned in a sample wheel, which is assembled in the ion source of the AMS (AMS C14- Labor, Erlangen).

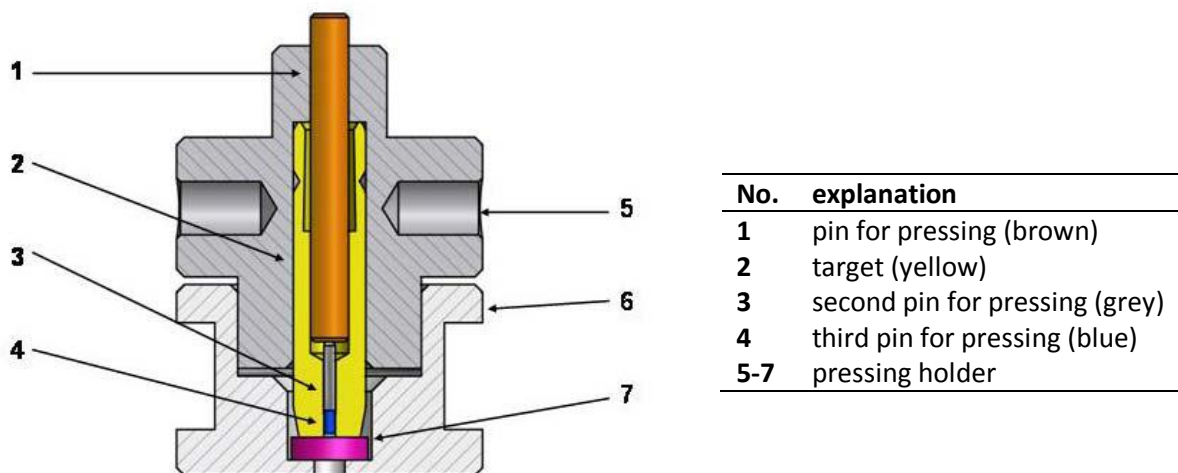


Figure 8. Model of target press (AMS facility Jena)

2.6.2 Measuring principle

The AMS is a physical technique used to detect rare isotopes and measure the ratio of the carbon isotopes ¹²C, ¹³C and ¹⁴C directly. The AMS consists of a mass spectrometry construction and an accelerator to remove distracting molecules or atoms, e.g. ¹³CH and ¹⁴N.

Initially, Cs- ions are radiated on the samples in a Sputter- ion source. Though, negative ions arise they are accelerated away from the source through a negative potential of – 52,5 kV. Subsequently, an energy selection is performed in a selection field, where all ions which were not produced in the ion source are removed. In order to measure carbon isotopes (¹²C, ¹³C and ¹⁴C) they are separated by their mass and electric charge in a 90°- analysing magnet.

Therefore, high- voltage is applied in the insulated vacuum chamber of the magnet. Through this temporary energy change it is possible to differentiate between the three carbon isotopes. The negatively charged ions are then located in the tandem accelerator, where they are accelerated to the tandem middle by a positive potential of 6 MV. Here, the ions are chemically reloaded to positive charged carbon ions and molecules are broken up and removed. The carbon ions are accelerated away from the tandem middle and exit the accelerator. Subsequently, the ions are arranged by their charges in an electrical field and are separated in the 55°- magnet by their masses (12, 13 or 14) (AMS C14- Labor, Erlangen).

2.6.3 Detection

To detect the isotope ^{14}C a gas ionisation detector is used. Here, the ions lose their kinetic energy through the ionisation of the carrier gas (Ar). To distinguish the ^{14}C isotope from background particles the total energy loss and the differential energy loss is measured. The stable isotopes (^{12}C & ^{13}C) can be analysed by measuring the current intensity of the ion beam in Faraday cups. The number of ^{14}C ions measured in the detector are set in a relationship with the isotopes ^{13}C and ^{12}C in the Faraday cups. After correction calculations of the ^{14}C content can be determined (AMS C14- Labor, Erlangen). The radiocarbon content is described as $\Delta^{14}\text{C}$ which is defined as the difference in parts per thousand (‰) between the $^{14}\text{C}/^{12}\text{C}$ ratio in the samples. It is corrected for mass dependent isotope fractionation to a common $\delta^{13}\text{C}$ value of - 25 ‰ in comparison to an oxalic acid universal standard. This standard is corrected for decay between 1950 and the year of measurement y (Trumbore, 2009).

$$\Delta^{14}\text{C} = \left[\frac{\left[\frac{^{14}\text{C}}{^{12}\text{C}} \right]_{\text{sample}-25}}{\left[0,95 \frac{^{14}\text{C}}{^{12}\text{C}} \right]_{\text{Ox1,-19}} \exp\left(\frac{(y-1950)}{8267}\right)} - 1 \right] \times 1000$$

2.7 Plant diversity and soil properties

In addition, we used soil organic carbon contents, soil moisture and plant diversity (Shannon diversity) values determined in previous studies taken out in the same plots estimating their possible influences on fine root productivity. The vegetation assessment was conducted in 2008: In forests both in spring and summer and in grasslands only in summer. Plant species diversity was calculated with the “Shannon Index”. Soil organic C was measured in the top mineral soils up to a depth of 10 cm. Soil moisture was measured continuously every 30 minutes with soil humidity probes (DeltaT ML2X) installed at a soil depth of 10 cm. We present the 6 monthly average.

2.8 Statistics

All analyses were conducted with the R version 3.0.1 (The R Project for Statistical Computing). To examine statistical differences of root productivity, C and N concentrations in soil and roots, fertilization and fine root C age between the study sites and between grassland and forest plots we used the t-test as well as analysis of variance (ANOVA). Furthermore, we used linear regression to constitute the effect of plant diversity and soil organic C on fine root productivity and fine root C age. To achieve the requirements for the ANOVA the values of the fine root productivity were transformed on a square rooted scale.

3 Results

3.1 Root Productivity

Fine root productivity showed considerable differences between grassland and forest plots in the same regions, but also between the two study regions (Fig. 9). In the HAI grassland sites root productivity was very variable and ranged from 9.65 g/m² to 90.95 g/m². The average root productivity was 37.74 ± 25.15 (mean ± sd). From the ANOVA resulted that there was a difference in fine root productivity between the two study regions but it was not significant (Tab. 5). By contrast the different land use types (i.e. grasslands and forests) had a highly significant effect across the study regions ($p < 0.001$). The mean grassland root productivity in the SCH was significantly higher ($p = 0.03$) than in the HAI with an average root productivity of 79.99 ± 41.39 g/m² (Range: 22.22 g/m² to 131.83 g/m²).

Moreover, there was no significant difference in fine root productivity in the forest plots of SCH and HAI. Fine root productivity in the SCH forest plots had a mean value of 16.18 ± 10.67 g/m² (Range: 2.72 g/m² to 36.26 g/m²), whereas in the HAI forest sites we observed a root productivity of 20.30 ± 14.75 g/m² (Range: 5.87 g/m² to 45.48 g/m²). One plot could not be considered in the analysis, because the ingrowth cores which should be collected at this site were dug by wild boars. Thus, the comparability with other plots was not given.

Also within the research sites differences occurred, since the effect of different land use types was significantly different across the study regions ($p = 0.024$). The trend was observed in both study regions, SCH and HAI, but it increased in different intensities: Generally, the productivity was higher in grassland plots compared to the forest plots, whereas the production of new roots in the grasslands of HAI was not as high as in the SCH (Tab. 4).

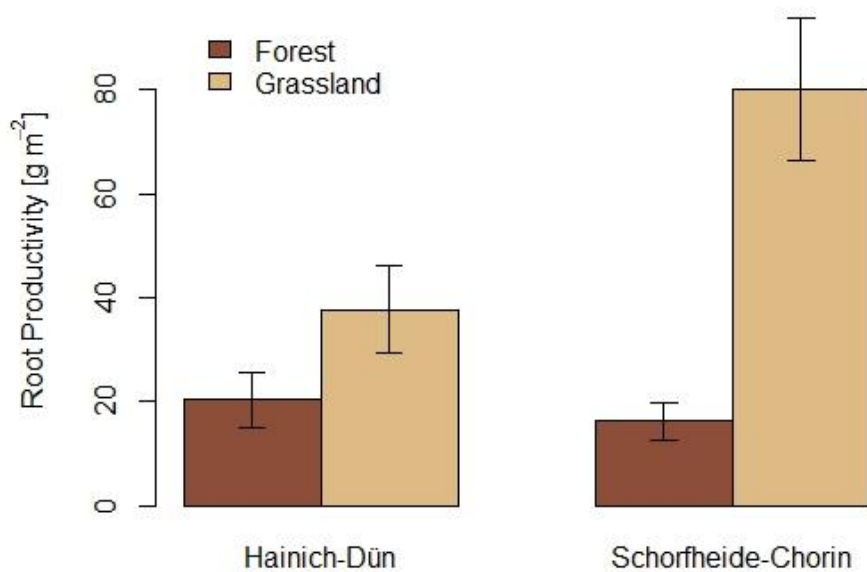


Figure 9. Comparison of the fine root productivity between the forest and grassland plots across the two study regions ($p=1.05$). A significant effect of land- use types (i.e. grasslands and forests) was observed across the study regions as well as a significant difference of land- use type within the study regions (Tab. 5).

Effect of plant diversity on fine root productivity

The plant diversity (Shannon diversity) shows that there are great differences between grassland and forest sites: the grasslands are more diverse. The differences between the two study areas are small (Tab. 4). While the plant diversity of the forest plots in HAI is significantly higher than in SCH ($p=0.01007$), a difference in the plant diversity of the grassland plots of both study regions was not observed. We observed that the fine root productivity seems to increase with increasing plant diversity on the grassland plots and forest plots of both regions (Fig. 10-12). The slope of the linear regressions were not significant for grassland plots and for the forest plots of HAI, whereas the correlation was significant in the SCH ($p=0.01664$).

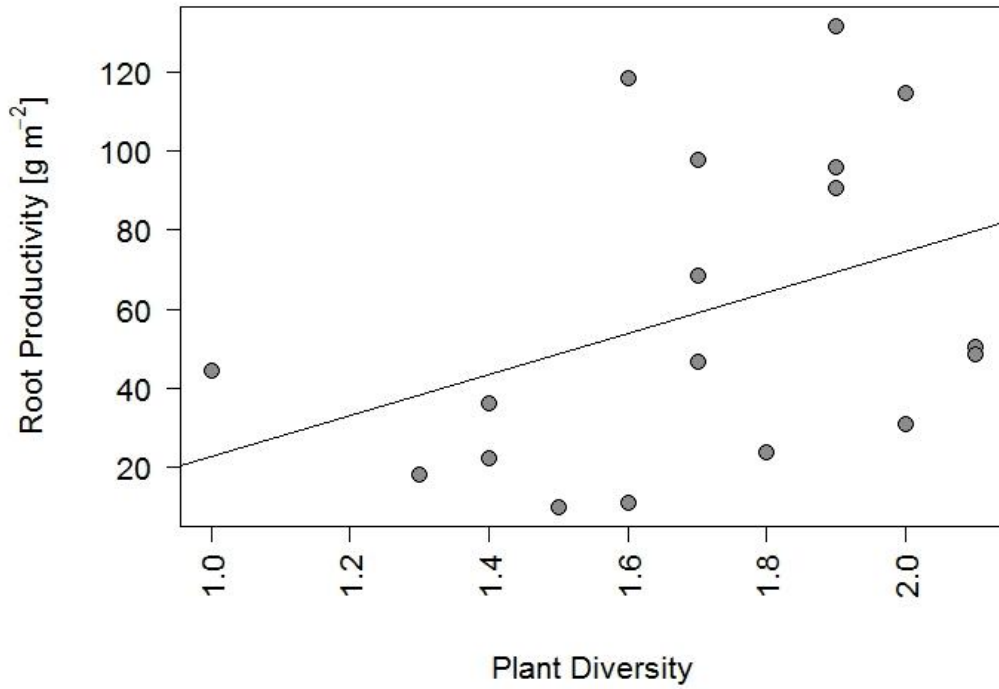


Figure 10. Fine root productivity of both grassland sites SCH and HAI correlated with the plant diversity. It is noticeable that the root productivity increases with rising plant diversity ($p=0.1097$, $R^2=0.152$).

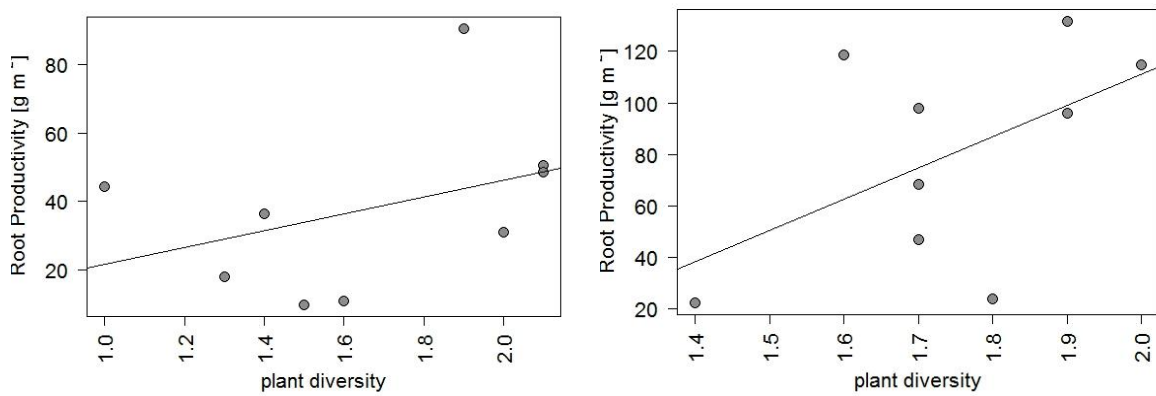


Figure 11. Plant diversity increases in grassland plots in HAI (left) in a lower degree ($p=0.3111$, $R^2=0.1455$) than in SCH (right) ($p=0.1418$, $R^2=0.2814$)

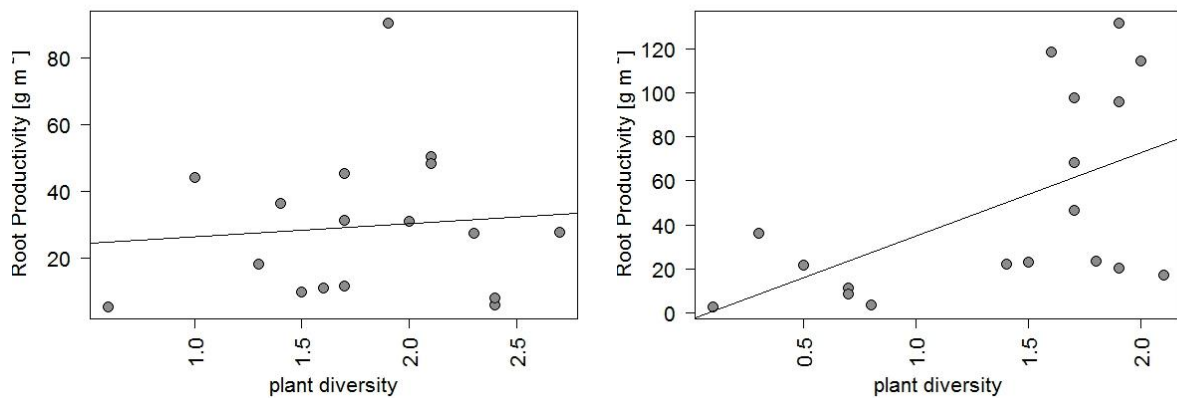


Figure 12. Fine root productivity showed no correlation with the plant diversity in the forest plots in the HAI ($p=0.7098$, $R^2= 0.009501$), whereas the correlation was significant ($p= 0.01664$, $R^2= 0.3088$) in SCH.

Effects on the fine root productivity through differences in the forests, like broadleaved trees or conifers are shown in figure 13. The fine root productivity seemed higher in conifer stands than in broadleaved stands in SCH, while this effect was not as high in the HAI. However, this relationship was not significant.

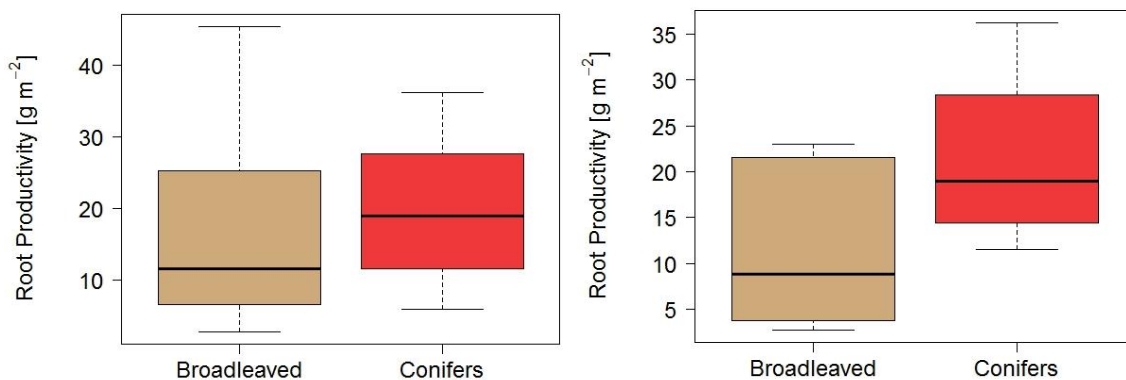


Figure 13. Differences between conifers and broadleaved trees are less marked in HAI (left) than in SCH (right). Although both are statistically not significant

Effect of soil organic C and soil moisture on fine root productivity

We could show that in grasslands the soil organic C content is much higher in SCH than in HAI (Fig. 14). Figure 15 shows that fine root productivity increases marginally significantly ($p = 0.055$) for increasing soil organic C content in the HAI, whereas a similar trend could not be found in the SCH. Here fine root productivity seems to decrease with rising organic carbon content. However, the slope of the linear regression was not significant ($p = 0.44$). In the forest sites of both study regions no relation between fine root productivity and organic C content was detected (Fig. 16, see appendix).

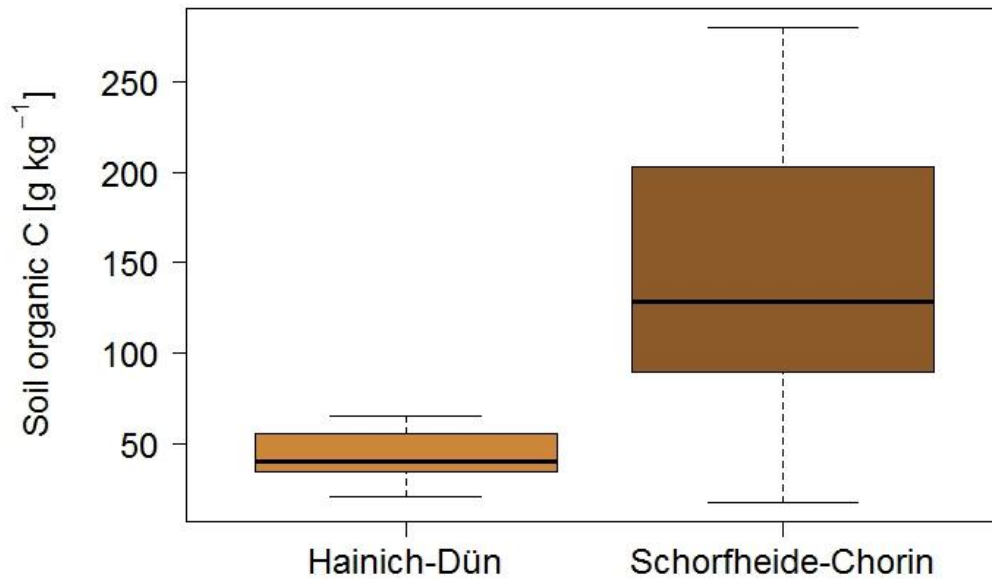


Figure 14. Soil organic C in the two study areas ($p=0.006787$).

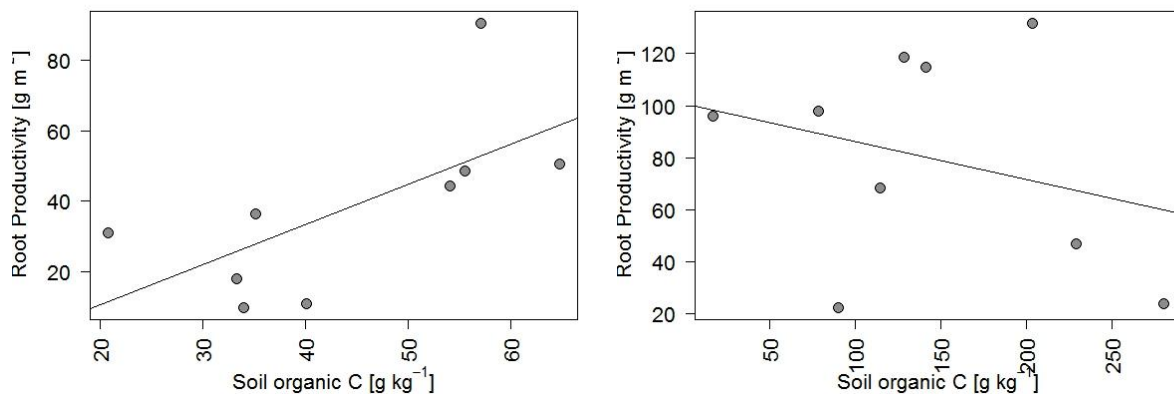


Figure 15. Soil organic C correlated with fine root productivity in the grassland plots of HAI ($p=0.05545$, $R^2=0.4292$) (left) and SCH ($p=0.4494$, $R^2=0.08398$) (right).

The soil moisture was significantly higher in the SCH than in HAI ($p=0.05788$) (Fig. 17). But we did not observe a direct effect of soil moisture on fine root productivity.

Management effect on fine root productivity in grasslands

Resulting from the ANOVA, there was a significant difference in fine root productivity across the study regions ($p=0.0206$). But the effect of fertilization across the study areas and the differences of fertilized and unfertilized plots in the different study plots was not significant (Tab. 5). Considering the study areas separately, in the grassland plots of HAI the fine root productivity is higher on unfertilized plots than on fertilized with a marginal significance ($p = 0.11$). By

contrast, the SCH indicates a higher production of fine roots on fertile plots compared to unfertilized plots. However, this effect is far from being significant (Fig. 18). Other management practices like mowing and grazing had no significant influences on the fine root productivity.

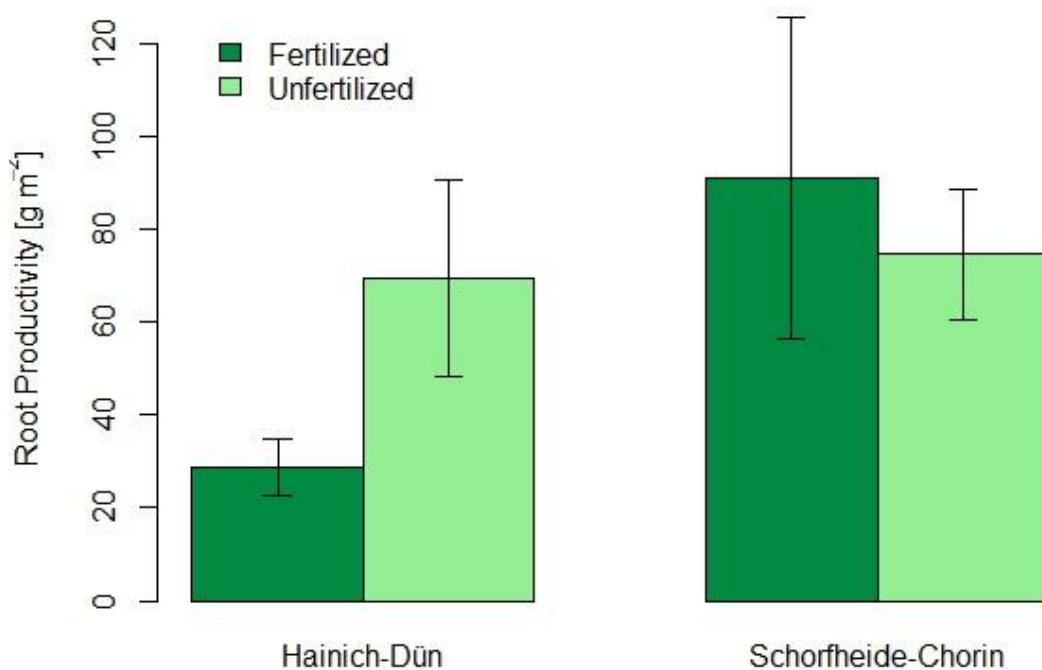


Figure 18. The difference of fine root productivity between the study areas was significant ($p=0.0206$), whereas there was no effect of fertilization across the study areas and no significant differences between fertilized and unfertilized plots within the study regions (Tab. 3).

3.2 C/N analysis

The analysis of the C and N content was only conducted in the grassland plots of the SCH and HAI, since the biomass in the forest plots was too little for analysis. There were great differences of the C content between the two study regions but smaller differences of N content (Fig 19-21).

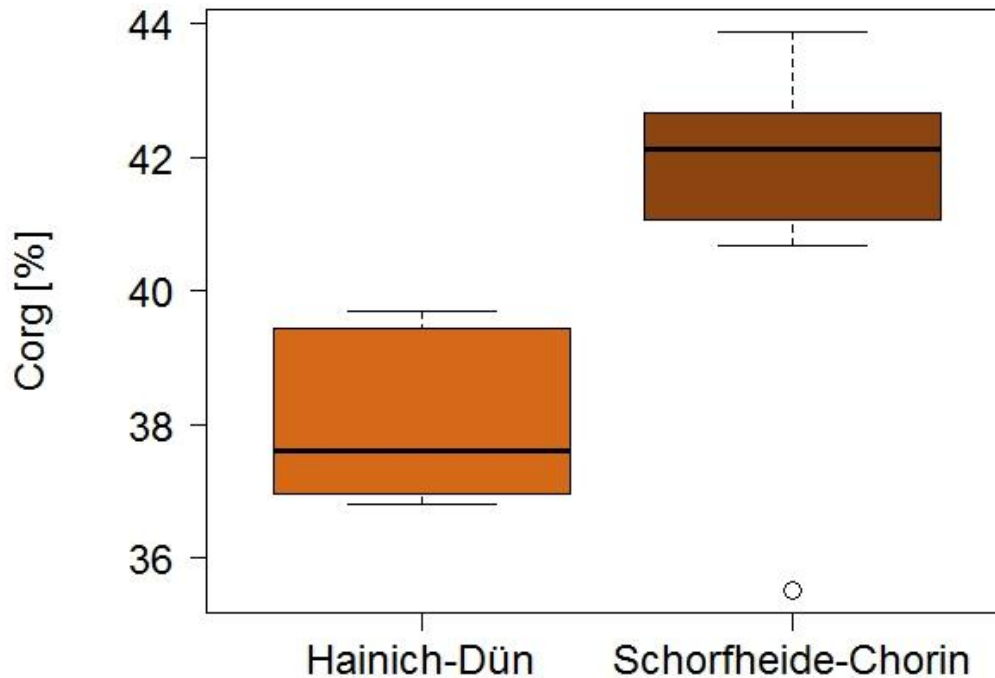


Figure 19. C_{org} content of fine roots grown in the ingrowth cores, differentiated between the two study areas ($p=0.00349$).

The fine roots of the SCH contained significantly more C (41.39 ± 2.44 %) than those of the HAI (38.07 ± 1.25 %), whereas the N contents differed not significantly between the study regions (SCH (1.44 ± 0.38 %) and HAI (1.58 ± 0.23 %)).

The C/N ratio in the fine roots was significantly higher in the SCH (30.36 ± 7.05) than in HAI (24.50 ± 3.59).

3.3 ^{14}C measurements

All ^{14}C values were less than the atmospheric mean in 2012 measured at Schauinsland (32.5‰ in September 2012, Levin, Kromer & Hammer, 2013). This implies that the sampled roots do not contain stored carbon or that they used extremely old carbon for root growth (e.g. fossil fuels, soil respiration). The $\Delta^{14}C$ values ranged in HAI from $12.3 \pm 2.7\text{‰}$ to $21.9 \pm 2.6\text{‰}$, whereas they differed in the SCH from $1.5 \pm 3.9\text{‰}$ to $25.0 \pm 2.8\text{‰}$ (Fig. 22). There were no great differences of fine root ages in the HAI and SCH. Except of two plots in the SCH (SEG1, SEG4) which reached an age over 1 year, all roots had an age of about a half year. The mean age of fine roots (Fig. 23) did not differ significantly between the two study sites ($p=0.1192$). All $\Delta^{14}C$ values and fine root ages are shown in table 4.

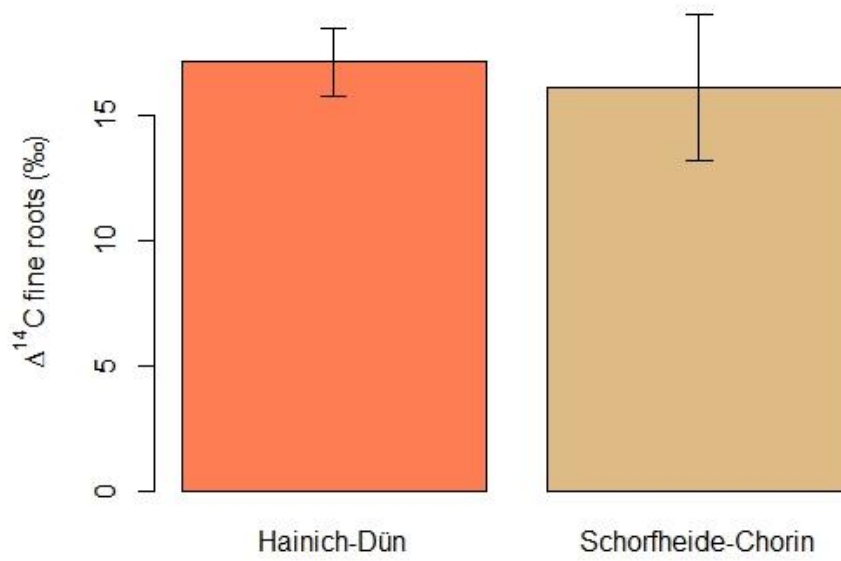


Figure 22. Mean $\Delta^{14}\text{C}$ measured in the fine roots. There was no significant difference between the two study sites ($p=0.7581$).

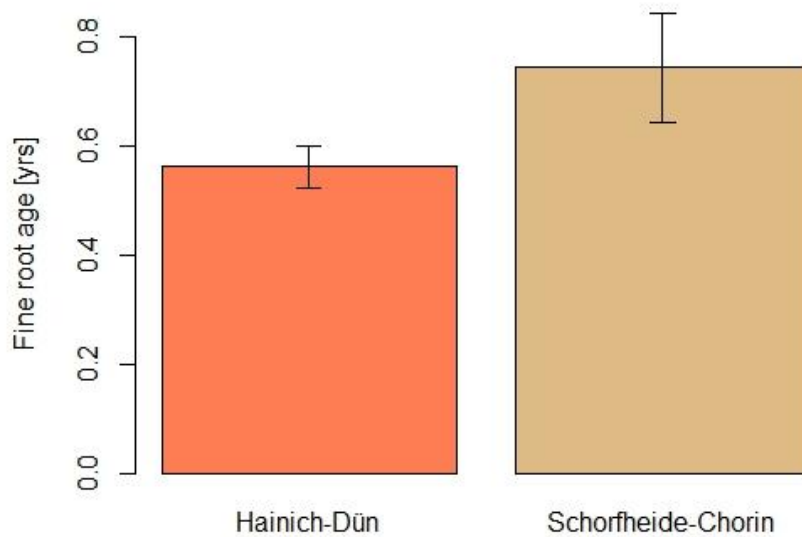


Figure 23. Mean fine root ages in the two study sites. The difference between them was not statistically significant ($p=0.1192$).

Figure 24 shows that the fine root C age increased significantly with the plant diversity for both study regions ($p=0.04153$), but considered separately the correlation was only significant in the SCH (Fig. 25). A negative correlation appeared regarding the relationship between fine root C age and the total N content in the roots (Fig. 26). Since this correlation was not significant ($p=0.1762$) it could be more considered as a tendency.

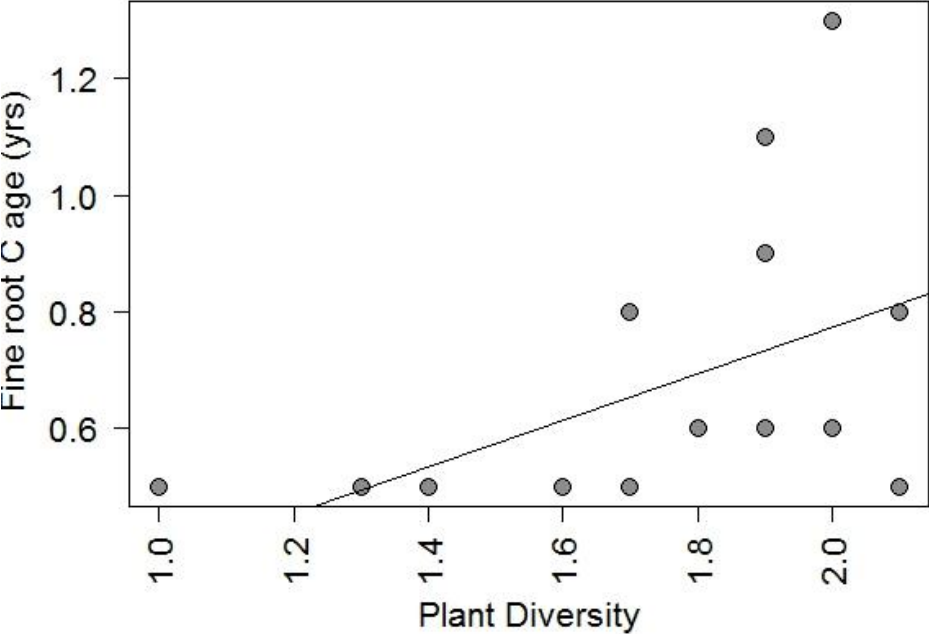


Figure 24. Plant diversity effects on the fine root C age were not significant in the HAI (left) ($p=0.1198$, $R^2=0.3539$) but showed a positive correlation in the SCH (right) ($p=0.00822$, $R^2=0.6551$)

4 Discussion

Our findings of significant higher fine root winter productivity in grasslands ($58.86 \pm 39.71 \text{ g/m}^2$) than in forests ($18.12 \pm 12.52 \text{ g/m}^2$). Together with previous results suggesting the standing root biomass is made of older C on average in forests compared to grasslands, confirm that grasslands are cycling C faster belowground than forests in temperate regions. We can however only refer to the upper 15 cm of the mineral soil, and it is possible that in forests litter input to subsoils are larger than in grasslands. Most previous ingrowth core studies are conducted for one year, so the fine root biomass exceeds the biomass we measured (Brunner et al., 2012; Lukac & Godbold, 2010; Persson & Stadenberg, 2009). Since we conducted our investigation beyond the growing season which ranges from April to October in temperate regions it is likely that the production of fine roots rises within the summer months.

While we did not observe significant differences in the productivity of fine roots in the forests of the two study regions, fine root productivity was significantly higher in the grasslands of the SCH (79.99 ± 41.39) compared to the grasslands of the HAI (37.74 ± 25.15).

We relate differences among study regions in grasslands to variations in climate and soil properties like moisture and nutrient content, which may lead to variations in plant resource acquisition strategies and in their need to produce fine roots.

Greater N contents and soil moisture contents (i.e. SCH) could for example favor plants with rapid acquisition of resources rather than conservation of resources (Tjoelker et al., 2005), which may be characterized by a larger productivity of fine roots especially at the beginning of the growing season. Furthermore, the soil organic C content in the SCH is significantly higher than in the HAI due to the organic soils and humic layers (Histosols and Gleysols) in the grasslands which enhance the water-holding capacity and fertility. Although, a correlation between fine root productivity and organic C content yielded in the grassland plots of SCH in no coherence, the high amount of organic C seems to increase the fine root productivity, since the productivity of fine roots was here significantly higher than in the HAI. Additionally, through decomposition of organic carbon (i.e. carbon mineralization) a higher amount of nutrients is released. Less productivity in nutrient poor sites may be explained by the necessity of plants to optimize the uptake of nutrients by reducing carbon and nutrient expenses in fine root productivity. Furthermore soils which are rich in silt and clay and that are often waterlogged like the Stagnosols in HAI, may favor plants with resource conservation strategies which produce less fine roots during the growing in order to prevent for oxygen deficiency conditions.

The temperature in the study regions could also reflect differences in fine root productivity. Since the mean temperatures are higher in SCH than in HAI, plants in SCH could have grown in a larger amount of newly grown roots than plants in HAI. And we collected samples in spring, what might have resulted in a relatively larger contribution of new fine roots in SCH (Solly et al., 2013). Also, Gill and Jackson (2000) reported that fine root production is increased with

soil warming in the spring. An anomaly this year was the long and cold winter, which could have inhibited the growth.

Although fertilization addition can alter the concentration of nutrients in the soil, we did not observe a significant effect of fertilization on fine root productivity. This might be due to small a number of samples. However, since root systems can alter their morphological, physiological plasticity and spatial proliferation depending on nutrient availability (Yuan and Chen, 2012) fine roots might spread more in unfertilized plots than fertilized. Also, Majdi and Andersson (2005) reported that spruce roots were generally longer, and thus were more productive in unfertilized sites. Additionally, the manner of how roots respond to N fertilization might be dependent on other soil characteristics and on the land use history (Wang et al., 2012).

Considering the soil total N concentrations of the soils in the grassland plots of HAI and SCH, the N content in SCH is much higher than in HAI. Since production of fine roots is limited by nutrients like N it is a logical conclusion that it rises with increasing availability of N. But if the amount of N is as high as in the SCH it could be possible that plants are not as dependent on nutrient supply as in HAI (Socher et al., 2012). Other nutrients like phosphorus could be more limited and therefore driving the root growth. So the response of fertilization seems to be stronger in HAI than in SCH. Furthermore, the type of fertilization could be different, since organic fertilizers are more unspecific than mineral fertilizers.

Since fine roots take up nutrients, it is possible that higher amounts of available N leads to a greater concentration in fine roots (Majdi and Andersson, 2005; Yuan and Chen, 2012). In the HAI 7 out of 9 investigated plots in the grasslands were fertilized whereas in the SCH only 3 out of 9. Since the total fine root N concentration is higher in HAI than in SCH, it may indicate that the roots of HAI take up more N than those in the SCH, which could be related to the fertilization. Moreover, it could be possible that the amount of N₂-fixing legumes is higher in HAI than in SCH. This might be due to a combination of mowing and the high soil moisture in the SCH, since these properties are favored by shallow rooted grass species and not by deeper rooting herb and legume species (Socher et al., 2012).

Furthermore, Wang et al. (2012) as well as Yuan and Chen (2012) suggested that allocated C to roots decreases with increasing soil N availability. This probably leads to the loss of biomass, since the enhanced uptake of nutrients may lead to a faster metabolism in fine roots so that more nutrients are transported to aboveground tissues. In addition the turnover rate seems to increase with rising N availability as well as in nutrient rich soils (Yuan and Chen, 2012). This might result in a rapid underground carbon cycling, what implies that nutrient and carbon cycles are related (Wang et al., 2012). Considering the C/N ratios of the roots in the two study regions it is conspicuous that the C/N ratio in the HAI is significantly lower than in the SCH. In comparison with a global value of 42 (Jackson et al., 1997) those from the study areas were less. As mentioned, the allocation of C to fine roots decreases with available N, which should be visible

in the C/N ratio of the roots. The lower ratio in the HAI (24.50 ± 3.59) results from higher N concentrations and lower C concentrations than in the SCH (C/N ratio = 30.36 ± 7.05) what indicates that less C could be allocated to the roots in the grassland plots of HAI.

Previous studies reported that plant diversity is affecting the fine root productivity, too (Meinen et al., 2009; Brassard et al., 2010; Brassard et al., 2013, Lei et al., 2012). Thus, the annual fine root productivity is as well as the fine root biomass significantly higher in mixed than single-species stands in both forests and grasslands (Meinen et al., 2009; Brassard et al., 2010; Lei et al., 2012). Positive effects of plant diversity are explained by an increase of total resource use through niche differentiation or facilitation (Hooper et al., 2005). This means, that different species use light, water and nutrients in different ways on a spatial and temporal scale due to distinctions in crown structure, rooting length or nutrient preference (Lei et al., 2012; Tilman et al., 1996; Spehn et al., 2005). In this study the fine root productivity showed tendencies to increase with rising plant diversity, whereas only the correlation in the forest plots in the SCH was significant. In general the plant diversity did not show differences in the grasslands between HAI and SCH but the forest plots of HAI were more diverse than SCH.

Furthermore, fine root biomass occupies more soil space in mixed stands than in single-species stands what is described as soil space filling which is due to niche differentiated rooting (Brassard et al., 2010; Brassard et al., 2013).

By contrast, different land use managements can affect the plant diversity in a negative way. Socher et al. (2012) presented the influences of fertilization, mowing and grazing in grasslands of the same study regions. Hence, fertilization caused a decrease in species richness whereas the effect was greater in HAI than in SCH which may be due to the organic soils.

Caused by the higher plant diversity in the forest plots of HAI, the higher fine root productivity could be explained. Furthermore, there might be tendencies that the fine root productivity is higher in coniferous sites than in broadleaved sites which was also reported by Yuan and Chen (2012), while a study of Ruess et al. (1996) reported the opposite.

The measurements of the ^{14}C content in the fine roots indicated that the C used to grow new roots was fixed within the past half year. The determined age of C in fine roots was older in SCH (0.74 ± 0.3 yrs) than in HAI (0.56 ± 0.11 yrs). The C ages of fine roots grown in the ingrowth cores during the winter season, differed from the root C ages of standing fine root biomass observed by Solly et al. (2013) where the root C age was older in HAI than in SCH. Whereas the fine root mean age in SCH was nearly equal (0.7 ± 0.1 yrs) the ages of the roots were 69% less in the HAI (1.8 ± 0.3). Nevertheless, the fine root C age was almost equivalent to the standing biomass fine root age which implies that annual and perennial plants using mainly atmospheric-derived C and possibly stored C in higher order roots from perennial species. Previous studies reported similar assumptions (Guo et al., 2004; Gaudinski et al., 2001) that perennial species are able to store C in higher order roots in form of cellulose (Guo et al.,

2004). Furthermore, Keel et al. (2012) found that more C is available for root growth in the late summer and that here C is stored for the following season. Also a study by Gaudinski et al. (2008) referred that photosynthates are fixed in the plant and are used to build roots in the following season. By contrast annual species are using atmospheric- derived C and the C contained in their seed (Solly et al., 2013).

We observed a positive correlation between fine root C age and plant diversity, implying that the fine root C age increases with higher plant diversity. This confirms the findings of Solly et al. (2013). Moreover, there is a tendency of a negative correlation between the fine root C age and the total root N content that suggests a rapid turnover time of roots with a high N content. Since we detected a higher N content in the roots in HAI, the fine root C age could possibly be due to the concentration and the following rapid turnover in lower order roots. Guo et al. (2004) reported a life- span of first order roots of 3- 4 months. Furthermore, the fertilization has a negative effect on the number of perennial species and the species richness (Solly et al., 2013) but there were no marked differences of numbers of perennial species between the HAI and SCH.

The measured $\Delta^{14}\text{C}$ values in both HAI and SCH seemed to be all lower than the contemporary atmospheric ^{14}C concentration. Solly et al. (2013) assumed that the lower ^{14}C values might define the local atmospheric ^{14}C , but the differences to the measured values in the HAI ($17.14 \pm 3.80\text{‰}$) and the SCH ($16.12 \pm 8.77\text{‰}$) are great so that other reasons could also influence the ^{14}C concentration. On the one hand this effect could be caused by air pollution through fossil fuels because these have a very low ^{14}C signature. On the other hand plants could take up CO_2 released from the soil through respiration. The organic matter in the Histosols of the SCH could contain old ^{14}C . Moreover, some plants might be able to take up extremely old carbon in form of amino acids, which could also influence the signature in the roots (Nashölm et al., 2000). Because of this possibilities and the great difference to the contemporary atmospheric concentration the calculated ages might be questionable.

5 Conclusions

Our findings of the fine root productivity in two different regions in Germany suggests that the fine root productivity was higher in grassland than forest plots. Fine root productivity may had positive correlations with soil properties (e.g. organic C content, soil moisture and N content), plant diversity and climatic conditions. Furthermore, mean root C age of the grassland plots indicated that herbaceous grassland species mainly use atmospheric- derived C. The decreasing fine root C age with rising root N content implies that the fine root turnover is faster in nutrient rich soils. Studies with a higher sample number might reinforce these assumptions. Additionally, it would be interesting to analyse the mean C age in fine roots of the forest plots, if trees use older C than plants in the grassland plots to grow new roots.

6 Acknowledgements

I would like to thank Marion Schrumpf for the opportunity to write my bachelor thesis in her working group and that she has taken on the task of the first reviewer. Furthermore, my thanks go to Prof. Dr. Georg Büchel who agreed to be the second supervisor for my thesis.

I thank Ines Hilke and Birgit Fröhlich for the CN analysis and Axel Steinhof for the radiocarbon analysis.

My special thanks go to my supervising tutor Emily Solly. Her ideas, comments and corrections were very inspiring and helpful. For proofreading and helpful hints I also want to thank Ingo Schöning.

7 References

- Adams, J.: Vegetation- climate interaction: how plants make the global environment, Springer Verlag Berlin Heidelberg New York, second edition, 266, 2010
- AMS C14- Labor, Erlangen (<http://www.14c.uni-erlangen.de/> [17.05.2013])
- AMS facility Jena ("Targetpresse"- pdf- document)
- Archer, D.: The global carbon cycle, Princeton University Press, 205, 2010
- Brassard, B.W., Chen, H.Y.H., Bergeron, Y., and Paré, D.: Differences in fine root productivity between mixed- and single- species stands, *Functional Ecology*, 25, 238-246, 2011
- Brassard, B.W., Chen, H.Y.H., Cavard, X., Laganière, J., Reich, P.B., Bergeron, Y., Paré, D., and Yuan, Z.: Tree species diversity increases fine root productivity through increased soil volume filling, *Journal of Ecology*, 101, 210- 219, 2013
- Brunner, I., Bakker, M.R., Björk, R.G., Hirano, Y., Lukac, M., Aranda, X., Borja, I., Eldhuset, T.D., Helmissaari, H.S., Jourdan, C., Konopka, B., López, B.C., Miguel Pérez, C., Persson, H., and Ostonen, I.: Fine- root turnover rates of European forests revisited: an analysis of data from sequential coring and ingrowth cores, *Plant Soil*, 362, 357- 372, 2013
- Christopher, S.L.: Global Carbon Cycle, *Encyclopedia of life sciences*, 2005
- Elementar Analysensysteme GmbH: Bedienungsanleitung vario EL, Funktion des vario EI, 4/1 – 4/6.
- Finér, L., Ohashi, M., Noguchi, K., and Hirano, Y.: Factors causing variation in fine root bio mass in forest ecosystems, *Forest Ecology and Management*, 261, 265-277, 2011
- Fischer, M., Bossdorf, O., Gockel, S., Hansel, F., Hemp, A., Hessenmoller, D., Korte, G., Nieschulze, J., Pfeiffer, S., Prati, D., Renner, S., Schoning, I., Schumacher, U., Wells, K., Buscot, F., Kalko, E.K.V., Linsenmair, K.E., Schulze, E.D., and Weisser, W.W: Implementing large- scale and long- term functional biodiversity research: The Biodiversity Exploratories, *Basic and Applied Ecology*, 11, 473- 485, 2010.
- Gaudinski, J. B., Trumbore, S. E., Davidson, E. A., Cook, A. C., Markewitz, D., and Richter, D. D.: The age of fine-root carbon in three forests of the eastern United States measured by radiocarbon, *Oecologia*, 129, 420-429, 2001.
- Gaudinski, J.B., Torn, M.S., Riley, W.J., Swanston, C., Trumbore, S.E., Joslin, J.D., Majdi, H., Dawson, T.E., and Hanson, P.J.: Use of stored carbon reserves in growth of temperate tree roots and leaf buds: analyses using radiocarbon measurements and modeling, *Global Change Biology*, 15, 992- 1014, 2009
- Guo, D.L., Mitchel, R.J., and Hendricks, J.J.: Fine root branch orders respond differentially to carbon source- sink manipulations in a longleaf pine forest, *Oecologia*, 140, 450-457, 2004

- Gill, R.A., and Jackson, R.B.: Global patterns of root turnover for terrestrial ecosystems, *New Phytologist*, 147, 13- 31, 2000.
- Helmisaari, H.S., Derome, J., Nöjd, P., and Kukkola, M.: Fine root biomass in relation to site and stand characteristics in Norway spruce and Scots pine stands, *Tree Physiol*, 27, 1493- 1504, 2007
- Hilke, I., Fröhlich, B., Rosenlöcher, S., Gruner, K., Ziermann, M., Ludwig, N.: „Elemental analysis of solids“ - Improving the precision and accuracy of project- specific samples, 2012.
- Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A.J., Vandermeer, J., and Wardle, D.A.: Effects of biodiversity on ecosystem functioning: a consensus of current knowledge, *Ecological Monographs*, 75, 3-35
- Keel, G.S., Campbell, D.C., Högberg, M.N., Richter, A., Wild, B., Zhou, X., Hurry, V., Linder, S., Näsholm, T., and Högberg, P.: Allocation of carbon to fine root compounds and their residence times in a boreal forest depend on root size class and season
- Jackson, R.B., Mooney, H.A., and Schulze, E.D.: A global budget for fine root biomass, surface area, and nutrient contents, *Ecology*, 94, 7362- 7366, 1997
- Lei, P., Scherer- Lorenzen, M., and Bauhus, J.: The effect of tree species diversity on fine- root production in a young temperate forest, *Oecologia*, 169, 1105- 1115, 2012
- Levin, I., Kromer, B., and Hammer, S.: Atmospheric ¹⁴CO₂ trend in Western European background air from 2000 to 2012, *Chemical and physical meteorology, series B*, 1-7, 2013
- Leuschner, C., Hertel, D., Schmid, I., Koch, O., Muhs, A., and Hölscher, D.: Stand fine root biomass and fine root morphology in old-growth beech forests as a function of precipitation and soil fertility, *Plant and Soil*, 258, 43-56, 2004
- Lukac, M.: Fine Root Turnover, *Measuring Roots: An Updated Approach*, edited by: Mancuso, S. Springer- Verlag Berlin Heidelberg, 363-373, 2012.
- Lukac, M., and Godbold, D.L.: Fine root biomass and turnover in southern taiga estimated by root inclusion nets, *Plant Soil*, 331, 505- 513, 2010
- Majdi, H., Pregitzer, K., Moren, A.S., Nylund, J.E., and Agren, G.I.: Measuring fine root turnover in forest ecosystems, *Plant and Soil*, 276, 1-8, 2005.
- Majdi, H., and Andersson, P.: Fine root Production and Turnover in a Norway Spruce Stand in Northern Sweden: Effects of Nitrogen and Water Manipulation, *Ecosystems*, 8, 191- 199, 2005
- Matamala, R., González- Meler, M.A., Jastrow, J.D., Norby, R.J., and Schlesinger, W.H.: Impacts of Fine Root Turnover on Forest NPP and Soil C Sequestration Potential, *Science*, 302, 1385- 1387, 2003
- Meinen, C., Hertel, D., and Leuschner, C: Root Growth and Recovery in Temperate Broad-

- Leaved Forest Stands Differing in Tree Species Diversity, *Ecosystems*, 12, 1103-1116, 2009.
- Nadelhoffer, K.J., and Raich, J.W.: Fine Root Production Estimates and Belowground Carbon Allocation in Forest Ecosystems, *Ecology*, 73, 1139- 1147, 1992
- Nashölm, T., Huss- Danell, K., and Hogberg, P.: Uptake of organic nitrogen in the field by four agricultural important plant species, *Ecology*, 81, 1155-1161, 2000
- Pandow, M., MacKay, C., and Wolfgang, R.: The reaction of atomic carbon with oxygen: significance for the natural radio-carbon cycle, *J. Inorg. Nucl. Chem.*, 14, 153-158, 1960
- Persson, H.A., and Stadenberg, I.: Fine root dynamics in a Norway spruce forest (*Picea abies* (L.) Karst) in eastern Sweden, *Plant Soil*, 330, 329-244, 2010
- Ruess, R.W., VanCleve, K., Yarie, J., and Viereck, L.A.: Contributions of fine root production and turnover to the carbon and nitrogen cycling in taiga forests of the Alaskan interior, *Canadian Journal of Forest Research-Revues Canadienne De Recherche Forestiere*, 26, 1326- 1336, 1996.
- Sah, S.P., Jungner, H., Oinonen, M., Kukkola, M., and Helmisaari, H.S.: Does the age of fine root carbon indicate the age of fine roots in boreal forests?, *Biogeochemistry*, 104, 91-102, 2011
- Schlesinger, W., and Andrews, J.A.: Soil respiration and the global carbon cycle, *Biogeochemistry*, 48, 7-20, 2000
- Socher S.A., Prati, D., Boch, S., Müller, J., Valentin, H.K., Hölzel, N., and Fischer, M.: Direct and productivity- mediated indirect effects of fertilization, mowing and grazing on grassland species richness, *Journal of Ecology*, 100, 1391- 1399, 2012
- Solly, E., Schöning, I., Boch, S., Müller, J., Socher, S.A., Trumbore, S.E., and Schrumppf, M.: Mean age of carbon in fine roots from temperate forests and grasslands with different management, *Biogeosciences discussion*, 1- 31, 2013.
- Spehn, E.M., Hector, A., Joshi, J., Scherer- Lorenzen, M., Schmid, B., Bazeley- White, E., Beierkuhnlein, C., Caldeira, M.C., Diemer, M., Dimitrakopoulos, P.G., Finn, J.A., Freitas, H., Giller, P.S., Good, J., Harris, R., Högberg, P., Huss- Danell, K., Jumpponen, A., Koricheva, J., Leadley, P.W., Loreau, M., Minns, A., Mulder, C.P.H., O'Donovan, G., Otway, S.J., Palmborg, C., Pereira, J.S., Pfisterer, A.B., Prinz, A., Read, D.J., Schulze, E.D., Siamantziouras, A.S.D., Terry, A.C., Troumbis, A.Y., Woodward, F.I., Yachi, S., and Lawton, J.H.: Ecosystem effects of biodiversity manipulations in European grasslands, *Ecological Monographs*, 75, 37-63, 2005
- Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M., and Siemann, E.: The influence of functional diversity and composition on ecosystem processes, *Science*, 277, 1300-1302

- Tjoelker, M.G., Craine, J.M., Wedin, D., Reich, P.B., and Tilman, D.: Linking leaf and root trait syndromes among 39 grassland and savannah species, *New Phytologist*, 167, 493-508, 2005
- Trumbore, S: Radiocarbon and Soil Carbon Dynamics, *Annu. Rev. Earth Planet. Sci.*, 37, 47-66, 2009.
- Trumbore, S.E., and Gaudinski, J.B.: The secret lives of roots, *Science*, 302, 1344-1345, 2003
- Vogt, K.A., Vogt, D.J., Palmiotto, P.A., Boon, P., Ohara, J., and Asbjornson, H.: Review of root dynamics in forest ecosystems grouped by climate, climatic forest type and species, *Plant and Soil*, 187, 159-219, 1996.
- Wang, C., Han, S., Zhou, Y., Yan, C., Cheng, X., Zheng, X., and Li, M.: Responses of Fine Roots and Soil N Availability to Short- Term Nitrogen Fertilization in a Broad- Leaved Korean Pine Mixed Forest in Northeastern China, *Plos One*, 7, 1-7, 2012
- Xiao, C.W., Yuste, J.C., Janssens, I.A., Roskams, P., Nachtergale, L., Carrara, A., Sanchez, B.Y., and Ceulemans, R.: Above- and belowground biomass and net primary production in a 73-year-old Scots pine forest, *Tree Physiology*, 23, 505- 516, 2003.
- Yuan, Z.Y., and Chen, Y.H.: A global analysis of fine root production as affected by soil nitrogen and phosphorus, *Proceedings of the Royal Society*, 279, 3796- 3802, 2012

8 Appendix

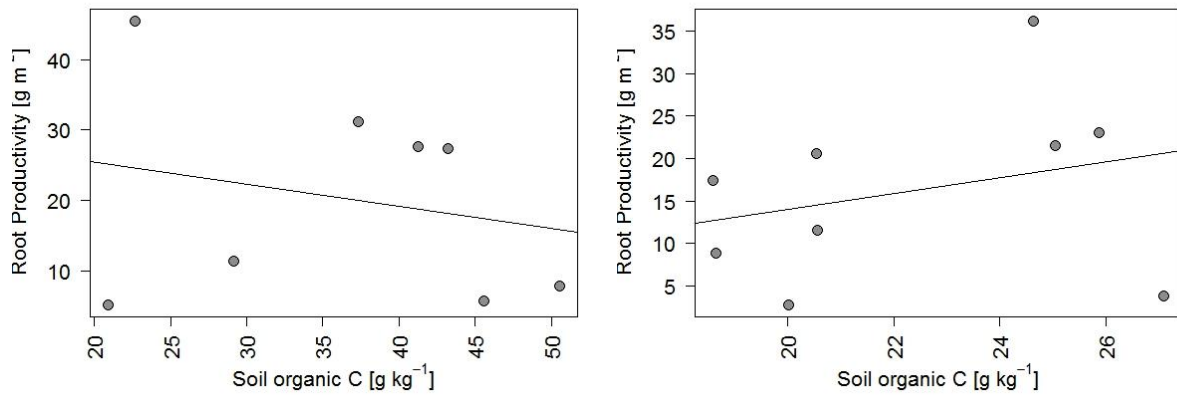


Figure 16. Soil organic C correlated with fine root productivity in the forest plots of HAI ($p=0.5807$, $R^2=0.054$) (left) and SCH ($p=0.46$, $R^2=0.081$) (right).

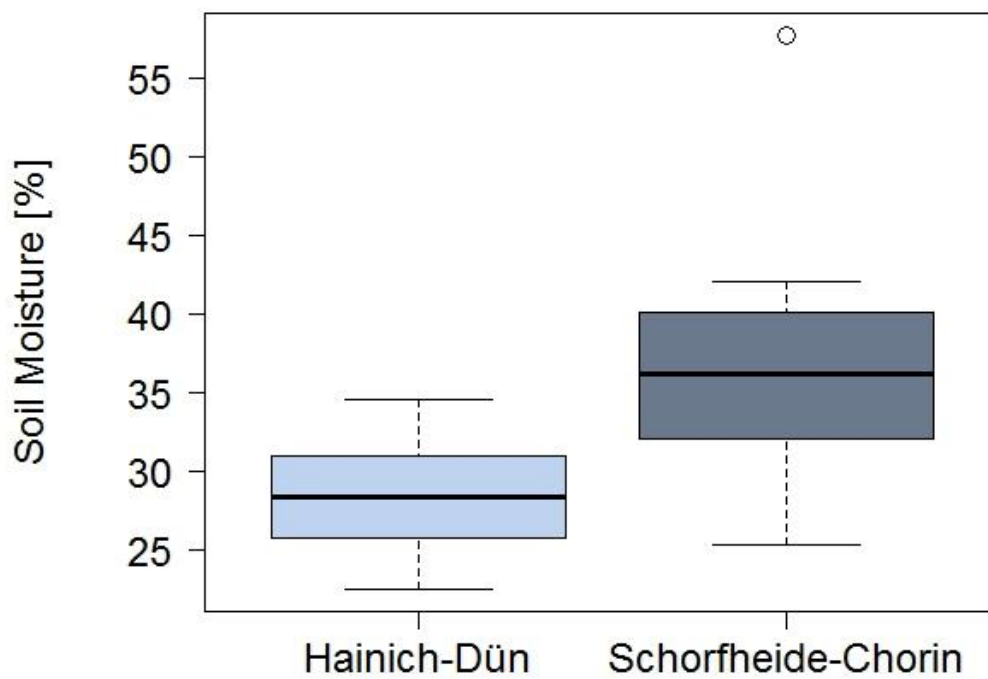


Figure 17. Distribution of soil moisture in the two study regions ($p=0.05788$).

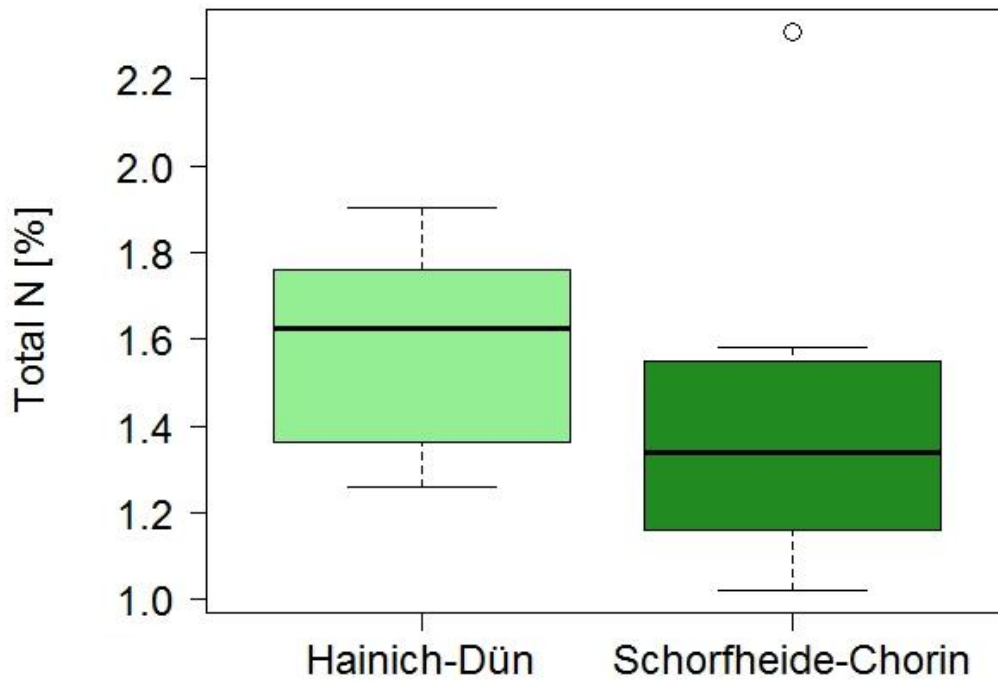


Figure 20. Total N content of fine roots grown in the ingrowth core ($p=0.3537$).

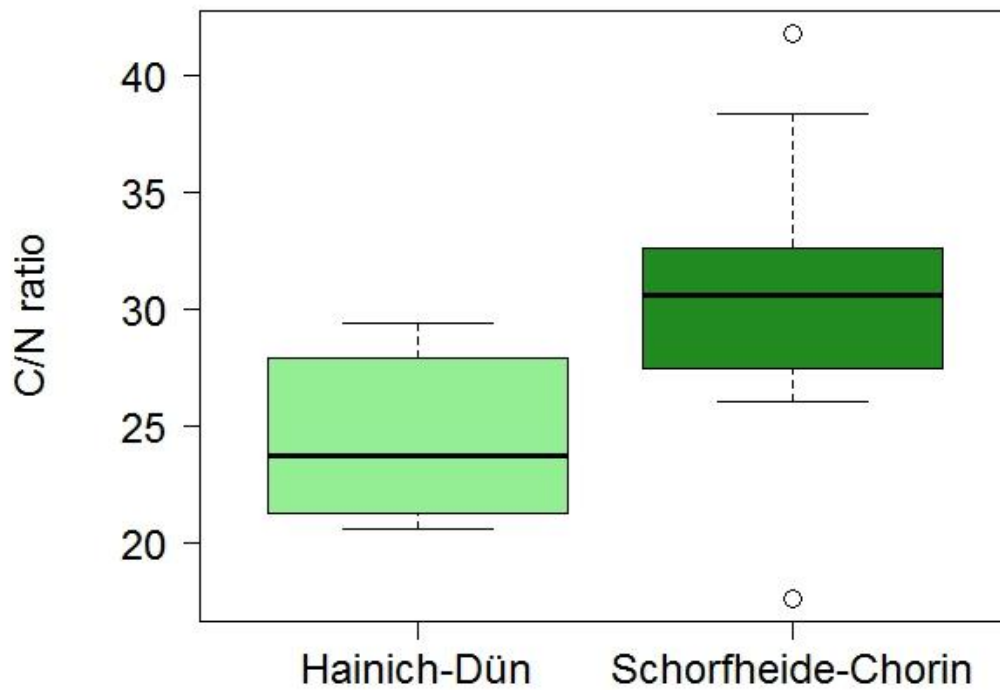


Figure 21. C/N ratio of the fine roots in both study areas ($p=0.04812$).

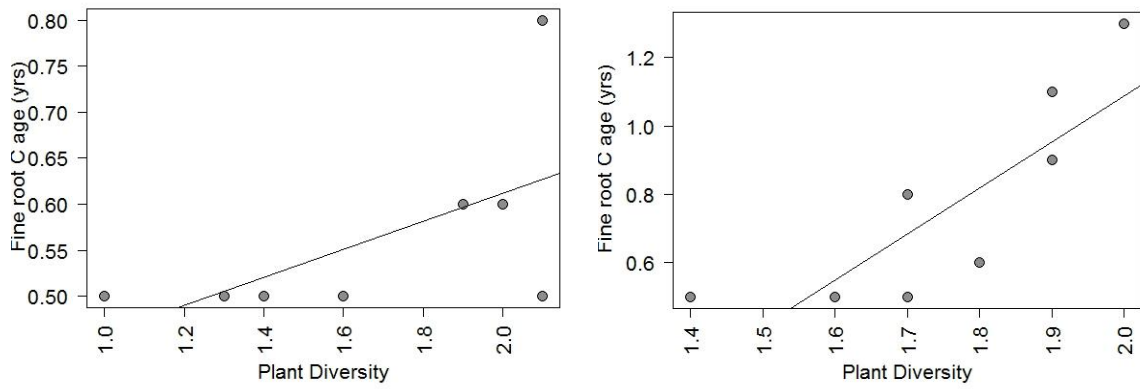


Figure 25. Plant diversity effects on the fine root C age in the HAI (left) were not significantly correlated ($p=0.1198$, $R^2=0.3539$) but in the SCH (right) ($p=0.00822$, $R^2=0.6551$)

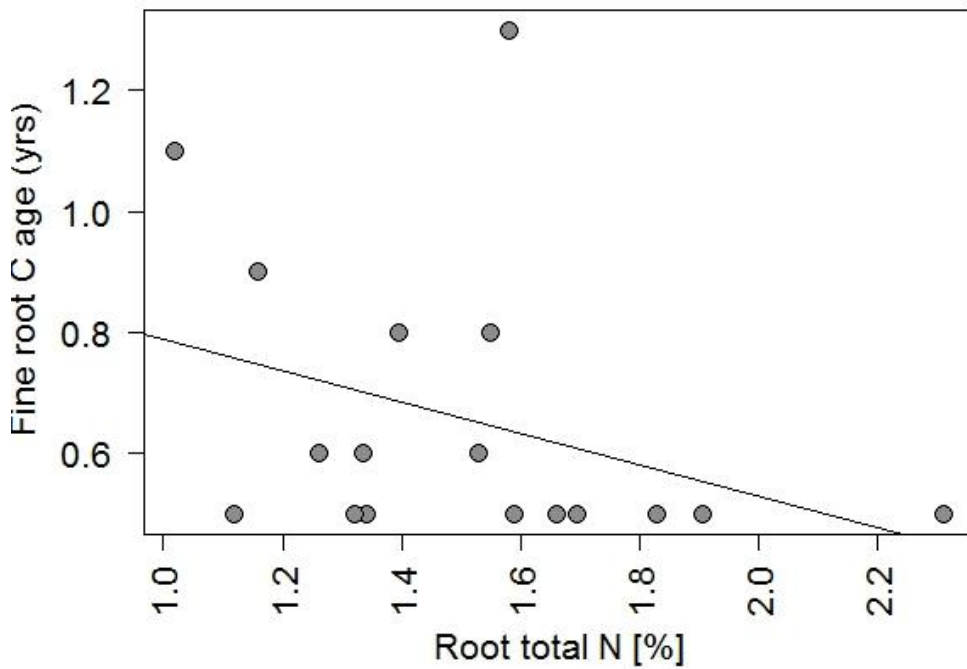


Figure 26. The fine root mean age showed tendencies of a negative correlation with the total root N content. However, this regression is not statistically significant ($p=0.1762$, $R^2=0.1184$).

Table 3. Measured $\Delta^{14}\text{C}$ - values and the resultant fine root ages.

Plot	$\Delta^{14}\text{C}$ (‰)	Fine root age (yrs)
HEG1	18.2 ± 2.8	0.5
HEG2	12.5 ± 2.8	0.5
HEG3	14.1 ± 2.6	0.5
HEG4	21.9 ± 2.6	0.8
HEG6	19.9 ± 2.9	0.6
HEG7	17.1 ± 3.0	0.5
HEG8	21.1 ± 2.7	0.6
HEG33	12.3 ± 2.7	0.5
	Average: 17.14 ± 3.80	Average: 0.56 ± 0.11
SEG1	23.8 ± 3.2	1.1
SEG2	14.6 ± 3.3	0.5
SEG3	1.5 ± 3.9	0.5
SEG4	25.0 ± 2.8	1.3
SEG5	5.8 ± 3.6	0.5
SEG6	20.9 ± 3.5	0.6
SEG8	8.8 ± 2.7	0.5
SEG9	21.8 ± 2.9	0.8
SEG39	22.9 ± 2.9	0.9
	Average: 16.12 ± 8.77	Average: 0.74 ± 0.3

Table 4. Mean soil conditions and Shannon diversity of both grassland and forest plots as well as C and N contents of the fine roots sampled in the grassland plots.

	Hainich-Dün		Schorfheide- Chorin	
	Grassland	Forest	Grassland	Forest
Productivity [g/m²]	37.74 ± 25.15	20.30 ± 14.75	79.99 ± 41.39	16.18 ± 10.67
pH	6.66 ± 0.74	5.14 ± 0.99	7.21 ± 2.42	3.35 ± 0.11
Soil moisture	28.36 ± 10.15	28.67 ± 4.93	37.63 ± 18.85	15.06 ± 3.19
Soil temperature [°C]	10.53 ± 5.66	9.47 ± 3.95	14.15 ± 6.24	6.91 ± 3.68
Total N (soil) [g/kg]	4.37 ± 1.45	3.01 ± 1.01	12.86 ± 6.48	1.20 ± 0.25
Organic C (soil) [g/kg]	43.83 ± 14.50	39.99 ± 14.99	142.57 ± 82.12	22.33 ± 3.30
C/N ratio (soil)	10.04 ± 0.28	13.19 ± 1.17	10.79 ± 1.02	18.85 ± 2.27
Clay	466.33 ± 99.54	332 ± 128.13	177.67 ± 54.32	27.89 ± 15.51
Silt	480.67 ± 105.30	600.11 ± 111.53	470.11 ± 203.93	84.11 ± 52.52
Sand	53.00 ± 17.99	67.89 ± 24.50	352.22 ± 176.34	888 ± 61.37
Plant Diversity (Shannon Diversity)	14.67 ± 3.97	1.99 ± 0.64	15.67 ± 2.87	0.96 ± 0.71
Total C (roots) [%]	38.07 ± 1.25		41.39 ± 2.44	
Total N (roots) [%]	1.58 ± 0.23		1.44 ± 0.38	
C/N ratio (roots)	24.50 ± 3.59		30.36 ± 7.05	

Table 5. ANOVA results of fine root productivity, fine root C and N concentrations and fine root C/N ratio. Variance between study regions and differences between grassland and forest plots (i.e. land-use) and fertilization were compared.

Dependent variables	Study region			Land- use			Study region x Land use		
	Df	F	P	df	F	P	df	F	P
Fine root productivity	1	2.789	0.105	1	23.376	<0.001	1	5.633	0.024
Fine root C concentration	1	11.98	0.00349						
Fine root N concentration	1	0.871	0.365						
C/N ratio	1	4.484	0.0513						

	Study region		Fertilization		Study region x Fertilization				
Dependent variable	df	F	P	df	F	P			
Fine root productivity	1	6.806	0.0206	1	0.695	0.4185	1	2.392	0.1443