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SECTION: BIODIVERSITY, ECOLOGY AND NATURE CONSERVATION

EFFECTS OF EARTHWORMS AND TREE SPECIES (*FAGUS SYLVATICA* L., *FRAXINUS EXCELSIOR* L.) ON GREENHOUSE TRACE GAS FLUXES IN MIXED DECIDUOUS BROAD-LEAVED FORESTS

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Die Endlosigkeit des wissenschaftlichen Ringens sorgt unablässig dafür, daß dem forschenden Menschengeist seine beiden edelsten Antriebe erhalten bleiben und immer wieder von neuem angefacht werden:
Die Begeisterung und die Ehrfurcht.
-Max Planck-

For my Family

SUMMARY

Despite the large number of studies and the associated knowledge gain uncertainties on the determinants of greenhouse gas fluxes from terrestrial ecosystems still exist. It is important to bridge these gaps as land use and particularly land use change as the important driver of the feedback loops between the atmosphere and the land surface. One major process is the direct emission of greenhouse gases as land use and land use change is ranking second behind burning of fossil fuels. During the past decades, global land-use and land-cover changed dramatically and thus, the biogeochemical interactions were altered at similar dimensions between terrestrial biosphere, pedosphere, and atmosphere. To minimize or mitigate these feedbacks the underlying processes must be understood. One major gap of knowledge is the effect of biodiversity and species-specific effects on greenhouse gas fluxes from terrestrial ecosystems. In the present study, the main objective was to identify effects of earthworms (*Lumbricus terrestris* and *Aporrectodea caliginosa*) and European beech and European ash (*Fagus sylvatica* and *Fraxinus excelsior*) on the greenhouse gas fluxes of N_2O, CH_4 and CO_2 between soil and atmosphere. A stepwise experimental approach was used to extent the knowledge of terrestrial forest ecosystems in their regulating function as net sink or source for greenhouse-gas fluxes. The first step was a laboratory experiment with soil incubation with earthworms and common ash to investigate the influences on the N_2O, CH_4 and CO_2 fluxes (Chapter 2). The next step was a laboratory experiment with incubated forest soil to investigate the influence of photosynthesis and root-growth of growing saplings of ash and beech on the N_2O fluxes from soil (Chapter 3). A combination of the two soil column experiments was the third step, a rhizotron experiment. This experiment investigates the influence of earthworms and photosynthetic active ash and beech saplings with ash and beech litter, on the N_2O, CH_4 and CO_2 fluxes from soil (Chapter 4). Finally a field study investigated the impacts of ash and beech on CO_2, N_2O, and CH_4 fluxes from soil before and during frondescence (Chapter 5).

The investigation of Chapter 2 exposed, over an incubation period of about 90 days, an increased, but not significantly higher N_2O emission influenced by earthworm. Over the time span of about 90 days a significant difference of the N_2O fluxes was found between the treatment ash compared to the treatment earthworm. However, a 30 day split (0-30 d / 30 – 60 d and 60 – 90 d) over the experimental time, made it possible to detect the “hot moments” of N_2O emission during incubation time and found other significant differences between the treatments. In reference to the CH_4 uptake from the atmosphere into the soil a difference was

found between the treatments with earthworms and the treatment without earthworms. The soil without earthworms increase the CH_4 uptake into the soil and the earthworm treated soil reduce this uptake. In relation to the CO_2 emission, soil columns planted with ash showed higher emissions than the unplanted earthworm treated soil columns or the pure soil of the treatment control. In addition, between the unplanted treatments a significant difference was found of the treatment earthworm compared to the treatment control. The experiment (90 days) showed that earthworms caused a reduction of atmospheric CH_4 uptake of about 40 – 60 % while provoking higher N_2O emissions of about 12 – 40 % and 7 – 18 % higher CO_2 fluxes. As shown before soil under ash showed markedly decreased N_2O emission.

The study on the species-specific influence of Chapter 3 indicated that, under climate chamber conditions, beech and ash influence GHG effluxes from soil species specifically. The potential of ash saplings to reduce N_2O emissions was even higher then the beech treated soil columns. Moreover, this study showed that a photosynthesis effect and reduced cumulative N_2O fluxes of ash planted soils of around 50 % exist. These results showed that global warming can decline by changing tree species during afforestation and that, based on the confirmed photosynthesis effect on N_2O fluxes, calculations of N_2O ecosystem fluxes for deciduous forests and their potential impact on global warming should be rethought by scientists.

The investigation of Chapter 4 showed the influence of earthworms on the dynamics of greenhouse gas fluxes (N_2O, CH_4 and CO_2) in a rhizotron experiment. The soil incubated nearly undisturbed in layer and was planted with ash and beech. This experiment was conducted over a time span of about 416 days and combined the treatments of the soil column experiments. It had the potential to supply sophisticated outcomes to support the results from the soil column experiments. This design showed effects of leaf litter mineralisation by the earthworms and effects on the trace gas fluxes. Rhizotrons applied with earthworms and ash-litter as forage increased the cumulative N_2O emission (169 mg N-N_2O m^{-2}) from soil and supported the CH_4 uptake (219 mg C-CH_4 m^{-2}). We conclude that earthworms have a significant influence on the forest soil as a source for greenhouse gases.

In Chapter 5 the field study "**SP**ecies **L**itter **I**dentity and **D**iversity effect on the **RH**izosphere of trees **EX**periment" (SPLIDRHEX) was investigated. The main objective of this chapter is to identify the species-specific influence before and during frondescence of beech and ash saplings on GHG fluxes from soil under natural conditions in a field experiment. The hypothesis was that a species-specific root activity before frondescence exists and species-specifically influences the GHG fluxes. The emissions showed a consistent low fluxes for

both tree species within the photosynthetic inactive phase. Before frondescence, the emissions of soil planted with beech increased slower than for soils planted with ash. Therefore, emission for ash was higher than for beech planted soils. During frondescence, emissions continued to increase and no constant emissions were observed. The strongest reduction of N_2O emission was observed for soils planted with ash. The gas measurements during the inactive phase of trees showed that the CH_4 uptake remained constant over time. Uptake was higher for soil planted with ash than for beech planted soil. Fluxes of CO_2 from plots with beech were higher than plots with ash but not significantly.

A combination of the results of the laboratory experiment and the field study showed decreased N_2O fluxes from soil and an increased CH_4 uptake into the soil of the treatments planted with ash.

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LIST OF ABREVIATONS

$CaCl_2$	-	Calcium chloride
C	-	Carbon
CO_2	-	Carbon dioxide
CO_2e	-	CO_2 – equivalents
CH_4	-	Methane
H_2O	-	Water
KCl	-	Potassium chlorid
KNO_3	-	Potassium nitrate
K_2SO_4	-	Potassium sulfate
Mg	-	Magnesium
N	-	Nitrogen
N_2	-	Molecular Nitrogen
N_2H_4	-	Hydrazine
NH_3	-	Ammonia
NH_4^+	-	Ammonium
NH_2OH	-	Hydroxylamine
NO	-	Nitric oxide
NO_3^-	-	Nitrate
NO_2^-	-	Nitrite
N_2O	-	Nitrous oxide
R-NH_2	-	Amine dihydridonitrogen
O_2	-	molecular Oxygen
^{15}N	-	stable nitrogen isotope
^{63}Ni	-	stable Nickel isotope
MMO	-	Methane monooxygenase
pMMO	-	Particulate MMO
sMMO	-	Soluble MMO
DNRA	-	Dissimilatory nitrate reduction to ammonium
Anammox	-	Anaerobic ammonia oxidation

SI-UNITS

atm	-	standard atmosphere
g	-	gram
h	-	hour
K	-	Kelvin
L	-	Liter
M	-	1000 mol L^{-1}
m	-	Meter
ppm	-	parts per million
ppb	-	parts per billion
yr	-	year

ABBREVIATIONS OF WORDS

a.s.l	-	About sea level
dw	-	Dry weight
EC	-	Electric Conductivity
fw		Fresh weight
GC	-	Gas chromatography
GHG	-	Greenhouse gas
GEE	-	Gross ecosystem exchange
GPP	-	Gross primary production
NEE	-	Ecosystem respiration
NBP	-	Net biome production
NEP	-	Net ecosystem production
SOM	-	Soil organic matter
SOC	-	Soil organic carbon
SPLIDRHEX	-	Species Litter Identity and Diversity effects on the RHizosphere of trees EXperiment

CHAPTER 1

GENERAL INTRODUCTION

1.1 GREENHOUSE GASES AND THE INFLUENCE ON CLIMATE CHANGE

The discussion about the influence of climate change on flora and fauna is an ongoing debate. These days the major task for science is to find the answer for how to deal with the changes and to draw up scenarios which could occur. The concentration of the main greenhouse gases (GHGs), water vapour (H_2O), carbon dioxide (CO_2), nitrous oxide (N_2O), and methane (CH_4) has been increasing since the beginning of the industrial revolution 250 years ago (IPCC, 2013). Those GHGs are the main drivers of the climate change and have been enriched in the atmosphere due to anthropogenic activities caused by consuming fossil fuels and land-use changes (FORSTER et al., 2007). According to the IPCC (2013) these activities are responsible for the increasing GHG concentration in the atmosphere, which led to an enhanced greenhouse effect (REAY et al., 2007). On average the surface temperature of the earth increased by approximately 0.74°C in the last 100 years (IPCC, 2013). The increase of GHGs in the atmosphere and the consequences on the radiative forcing are the central discussion of modern climate science. An essential task is to determine the potential of terrestrial ecosystems as sinks or sources for GHGs.

Not only how these systems react to climate change but how do they interact – it is known that the ecosystems take up more CO_2 since there is more available – otherwise concentrations would have increased even more – what about the other gases are ecosystems becoming greater sinks too or greater sources.

The main focus of this PhD thesis lays on forest ecosystems and their soils, because forests are main contributors to the carbon and nitrogen cycle and recently received great attention. In addition to the importance of forest ecosystems referring to CO_2, temperate forest soils are the most relevant terrestrial sinks for CH_4 from the atmosphere caused by methane oxidizing micro-organisms in soils. Furthermore, terrestrial ecosystems and especially forest soils are major sources of N_2O – besides agricultural soils (JUNGKUNST et al., 2006; KESIK et al., 2005), but their contribution to the global emissions is still unknown (PIHLATIE et al., 2005).

Abiotic factors like soil temperature, bulk density, pH-value, and soil moisture as well as their influence on GHG-emissions are well studied (CIARLO et al., 2008; LE MER & ROGER, 2001).

Different abiotic and biotic impacts are simulated with a focus on the role of earthworms in soils. Earthworms are considered as “ecosystems engineers” (EISENHAUER, 2010) and have profound influence on the quality and the distribution of organic matter in soils (DON et al., 2008). Furthermore, earthworms support the soil's “coarse” structure with a magnitude of

effects on organic matter turnover and nutrient release, which have to be considered as positive in an agricultural sense (CASTELLANOS-NAVARRETE et al., 2012). As a consequence, earthworms are suspected to increase greenhouse gas emissions from soils and there is certain evidence for that (LUBBERS et al., 2013).

The scientific task of this study is to determine biotic factors like species-specific effects and their interactions with roots in soil microbial communities influencing GHG emissions from soil. This PhD thesis aims to identify influences of European beech (*Fagus sylvatica* L.), European ash (*Fraxinus excelsior* L.), saplings and earthworms (*Lumbricus terrestris* and *Aporrectodea caliginosa*) on GHG fluxes under controlled conditions in a climate chamber. Field experiments were carried out to compare the results of a soil column experiment to field conditions.

The chosen tree species are the most common ones in Central European forests. They are gaining more importance for the economic forestry (ELLENBERG & LEUSCHNER, 2010). They were preferred because of their differences in root-growth, root-morphology, mycorrhiza constitution (MEINEN et al., 2009) and shoot morphology as well as growth.

Furthermore, the influences of the bioturbation of earthworms are also investigated. The formations of horizontal and vertical tubes are studied, which seem to be important for gas fluxes and the homogenization of soils. This fact builds up our interest on their potential influence on N_2O, CO_2 and CH_4 fluxes in forest soils incubated in a soil column and a rhizotron experiment.

1.1.1 N_2O

Nitrous oxide (N_2O) is one of the most important GHGs. Since the onset of the industrial revolution the atmospheric concentration has increased from 270 ppb to 319 ppb in 2005. A single gram of N_2O has the same effect on global warming as 298 grams of CO_2 for the time span of 100 years (GWP_{100}) (FORSTER et al., 2007). N_2O has a radiative forcing potential of about 0.16 $W \cdot m^{-2}$ and is one of the main GHGs (FORSTER et al., 2007). Due to human activities N_2O emission increased through fossil fuel burning, intensive agricultural land use and general land use changes (IPCC, 2013; REAY et al., 2007). The main reason for increased levels of N_2O from ecosystems is nitrogen (N) overloading in course of direct fertilization and atmospheric depositions. Industrial processes resulted in global source strength of 4.1–8.1 $Tg \cdot yr^{-1}$ (DENMAN et al., 2007).

1.1.1.1 NITROGEN CYCLE AND N_2O EFFLUXES

The main source of nitrogen is the atmosphere where it is found as N_2. However, it is not accessible for most organisms including plants. Nitrogen deposes into soils by microbial fixation, whereby molecular nitrogen (N_2) is transformed to organic N-containing compounds (BLUME et al., 2010; ROBERTSON & GROFFMAN, 2007). To access the biological cycle, N_2 must be assimilated or oxidized by electrical discharge or combustion (SCHULZE, 2000). Nitrogen occurs in reduced or oxidized inorganic or organic forms, which are associated with amino- and nucleic acid (SCHULZE, 2000). SCHULZE (2000) explained that plants assimilate inorganic N and release organic N into the environment as litter. In soil nine different forms of nitrogen can occur, corresponding to different oxidative states (ROBERTSON & GROFFMAN, 2007, Tab. 1.1):

Tab. 1.1**:** Main forms of nitrogen in soil and their oxidation states (ROBERTSON & GROFFMAN, 2007).

Name	Chemical formula	Oxidation state
Nitrate	NO_3-	+5
Nitrogen dioxide (g)	NO_2	+4
Nitrite	NO_2-	+3
Nitric oxide (g)	NO	+2
Nitrous oxide (g)	N_2O	+1
Nitrogen (g)	N_2	0
Ammonia (g)	NH_3	-3
Ammonium	NH_4+	-3
Organic N	R_{NH3}	-3

(g) = Gases occur both free in the soil atmosphere and dissolved in soil water

An important biological process is the N_2 fixation where nitrogen enters the biological pool of soils (ROBERTSON & GROFFMAN, 2007). Hence, the essential transformations are presented in Fig. 1.1.

The N mineralization (ammonification) is the conversion of organic N to its inorganic form ammonium (NH_4^+), which is accessible for plants. The N immobilization is the uptake or assimilation of inorganic N by heterotrophic soil microorganisms. The aerobic conversion of ammonium (NH_4^+) to nitrite (NO_2^-) and finally to nitrate (NO_3^-) is called nitrification. Denitrification is the anaerobic conversion of NO_3^- to N_2O and finally to N_2. Nitrogen mineralization and immobilization is the conversion of organic forms of nutrients into mineral soluble forms (detritus), whereby it can be taken up by plants and microbes (ROBERTSON & GROFFMAN, 2007).

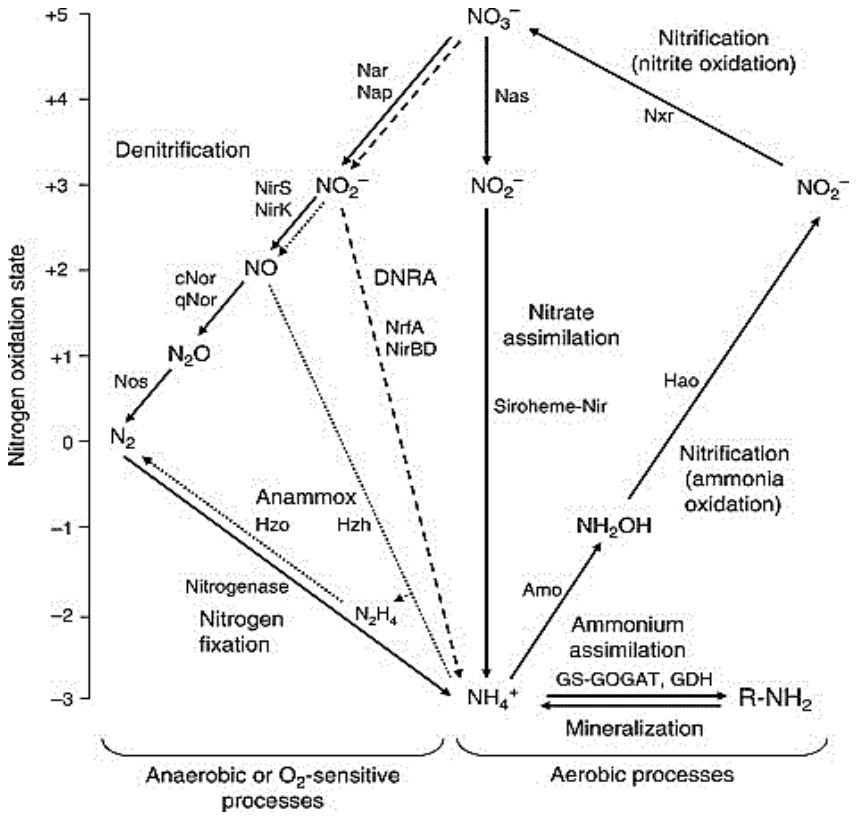

Fig. 1.1: The biological nitrogen cycle. The different nitrogen compounds are arranged according to their oxidation states. The main oxidative or reductive pathways. Anaerobic ammonia oxidation (anammox). Dissimilatory nitrate reduction to ammonia (DNRA) (CABELLO et al., 2009).

The conversion takes place during the consumption of detritus by prokaryotes (OTTOW, 2011). During the ammonification, organic N compounds (mainly the amino group) are transformed to R-NH_2, NH_3, and NH_4^+ by degrading proteins into amino acids (OTTOW, 2011; BLUME et al., 2010; ROBERTSON & GROFFMAN, 2007). The process of deamination with release of NH_4^+ follows the process of ammonification. A surplus of released NH_4^+, which is unused by microorganisms, can leach out or will be oxidized by nitrification. Finally, if the concentration of N in the converted organic matter is too low, NH_4^+ will be assimilated and fixed by microorganisms (OTTOW, 2011; BLUME et al., 2010; ROBERTSON & GROFFMAN, 2007).

Generally, the N_2O release from soils is driven by two microbial processes. Primarily, nitrification implies a microbial anaerobic oxidation of reduced forms of nitrogen to its oxidized forms (generally NH_4^+ to NO_2^- and NO_3^-). Subsequent anaerobic denitrification proceeds the NO_3^- reduction to the gases NO, N_2O and N_2 (BLUME et al., 2010; ROBERTSON & GROFFMAN, 2007; SMITH et al., 2003).

Autotrophic bacteria support the classical process of the N_2O production in soils (ROBERTSON & GROFFMAN, 2007; WRAGE et al., 2001). Nitrifer denitrification is a process of nitrification in which NH_3 is oxidized to nitrite followed by the reduction to nitric oxide (NO), nitrous oxide (N_2O) and molecular nitrogen (N_2) (WRAGE et al., 2001). During the nitrification, autotrophic bacteria gain 440 $kJ \cdot mol^{-1}$ of energy while producing NO_3^- (ROBERTSON & GROFFMAN, 2007). Also, the autotrophic nitrification proceeds with two steps carried out by two different kinds of bacteria: the first step by the ammonia (NH_3) and the second step by nitrite (NO_2^-) oxidizers (Fig. 1.2, WRAGE et al., 2001).

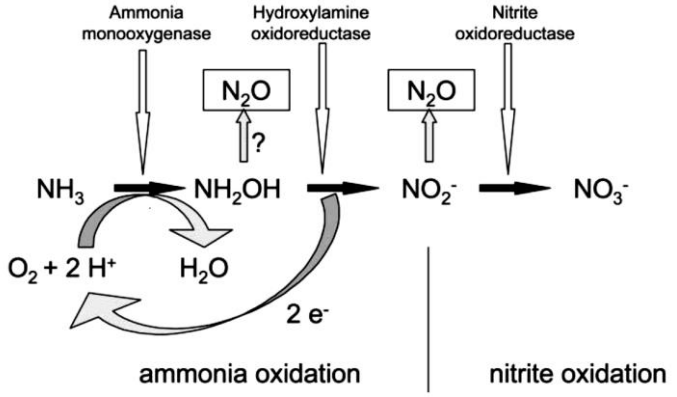

Fig. 1.2: Nitrification: outline of the pathway and enzymes involved (WRAGE et al., 2001).

The two groups are defined as *Nitrobacteriaceae,* whereof *Nitrosomonas* are the most studied autotrophic NH_3-oxidizers. *Nitrobacter* are common NO_2^--oxidizers. The first step, which includes the oxidation of NH_3 to hydroxylamine (NH_2OH), is catalyzed by the enzyme ammonia mono-oxygenase (CABELLO et al., 2009; ROBERTSON & GROFFMAN, 2007; WRAGE et al., 2001). Moreover, two electrons are necessary for the reduction of molecular oxygen (O_2) to water (H_2O). Those electrons are derived from the oxidation of NH_2OH to NO_2^-. This step is catalyzed by the enzyme hydroxylamine oxidoreductase (CABELLO et al., 2009; ROBERTSON & GROFFMAN, 2007; WRAGE et al., 2001). Finally, the one-step oxidation from NO_2^- to NO_3^- is catalyzed by the enzyme nitrite oxidoreductase. During the oxidation of NH_3 through chemical decomposition of intermediates between NH_3 and NO_2^- such as NH_2OH to NO_2^-, a pathway exists where N_2O can be released (Fig. 1.4).

The anaerobic reduction of NO_3^- to the gases NO, N_2O and N_2 is named denitrification (Fig. 1.3). On occasion, heterotrophic bacteria can denitrify, whereby they use NO_3^- rather than oxygen as electron acceptor during their respiration. Furthermore, they use soluble carbon as an energy source or as electron donator (CABELLO et al., 2009; ROBERTSON & GROFFMAN, 2007; WRAGE et al., 2001).

The involved microbial groups in this process are *Archaea* and *Proteobacteria* (generally) *Pseudomonas, Alcaligenes* and to a lesser extent *Bacillus, Agribacterium,* and *Flavibacterium* and even certain fungi (CABELLO et al., 2009; ROBERTSON & GROFFMAN, 2007; WRAGE et al., 2001).

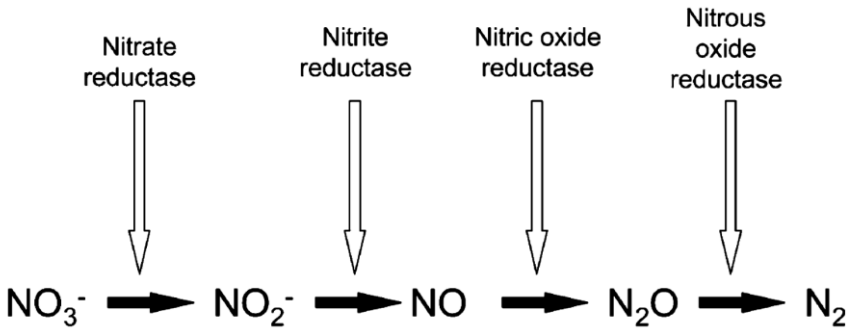

Fig. 1.3: Denitrification: outline of the pathway and enzymes involved. Arrows with cropped tails are gaseous releases. (WRAGE et al., 2001).

After KOOL et al. (2011) and WRAGE et al. (2005 and 2001) nitrifier denitrification is a path of nitrification in which the oxidation of NH_3 to NO_2^- is followed by the denitrification of NO_2^- to N_2 with the intermediate N_2O (Fig. 1.4). The highest amount of N_2O production occurs in this path (WRAGE et al., 2001). The microorganisms which are involved in both processes are probably only autotrophic NH_3-oxidizers, which are produced under wet soil conditions, low organic carbon and acidic pH contents (KOOL et al., 2011; WRAGE et al., 2005; WRAGE et al., 2001).

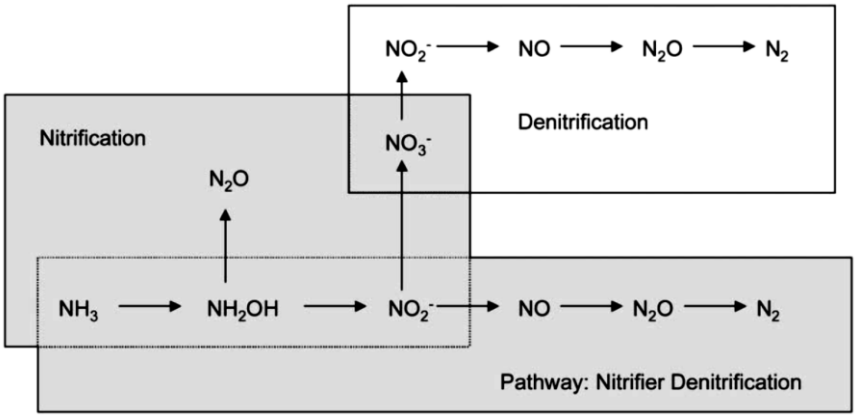

Fig. 1.4: Transformations of mineral nitrogen in soil (WRAGE et al., 2001).

Dissimilatory nitrate reduction to ammonium (DNRA) is another anaerobic nitrogen transformation of nitrate to nitrite and finally to ammonium (Cabello et al., 2009; ROBERTSON & GROFFMAN, 2007). This anaerobic process allows respiration in absence of O_2. There is a large uncertainty about the role of DNRA in the production of N_2O; however, the DNRA seems to be a common and essential process in some tropical forest soils, where the flow of inorganic N in DNRA is more important than denitrification and nitrification (ROBERTSON & GROFFMAN, 2007).

The anaerobic ammonium oxidation (anammox) is a process in which ammonium and nitrate are converted to N_2 under strict anaerobic conditions (BORAN et al., 2011). For a long time, anammox was unidentified, but in BORAN et al. (2011) found out that the anammox-bacteria (*Kuenenia stuttgartiensis)* use an organelle (anamoxosom) to reduce NO_2^- via NO to hydrazine (N_2H_4) and finally to N_2. BORAN et al. (2011) assumed that 50% of the atmospheric N is formed by this reaction, but a large uncertainty still exists.

Furthermore, the non-enzymatic process of nitrite decomposition is chemo-denitrification. Under aerobic conditions NO_2^- reacts within soil to form N_2 or nitric oxide (NO_x) (ROBERTSON & GROFFMAN, 2007; KAPPELMEYER et al., 2003).

N_2O, NO and N_2 effluxes from soil are influenced by environmental conditions. The transformation cycles of N to gaseous N_2O, NO, and N_2 and possible ways out are described above. The 'hole-in-a-pipe' model, developed by FIRESTONE & DAVIDSON (1989), shows the transformation processes of the N_2O fluxes and their affecting factors (Fig. 1.5).

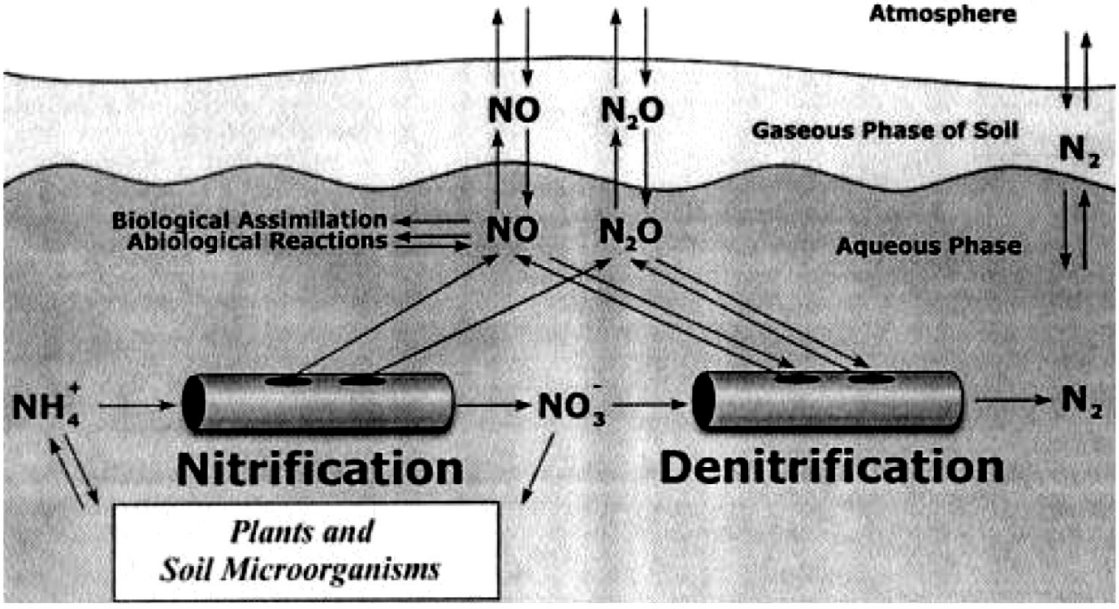

Fig. 1.5: The conceptual "hole-in-the-pipe model" (DAVIDSON, 2000).

The microbial and ecological factors, which influence the emission of N_2, NO and N_2O from soil into atmosphere are explained by this illustration. The production and consumption of nitrogen by the microorganism is depicted as a fluid flowing through the pipes analog to the rates of nitrification and denitrification (DAVIDSON, 2000; FIRESTONE & DAVIDSON, 1989). Moreover, the size of pipes is variable due to the availability of C and N (JUNGKUNST et al., 2006; DAVIDSON, 2000; FIRESTONE & DAVIDSON, 1989). The ratio of N_2O:NO emissions is symbolized by fluxes through the "holes" in the pipe. The influence of the holes depends primarily on water-filled pore space (WFPS) and less on other soil conditions such as pH-

value (JUNGKUNST et al., 2006). Oxygen transport into soil and the transport of NO, N_2O, and N_2 out of soil is controlled by the WFPS (DAVIDSON, 2000). According to DAVIDSON (2000) emissions of those gases from soil depend on the balance of production, consumption, and diffusive transport. This oxidative process of nitrification is dominant in dry and well-vented soil and the more oxidized NO gas flows out from soil before it is consumed (Fig. 1.6).

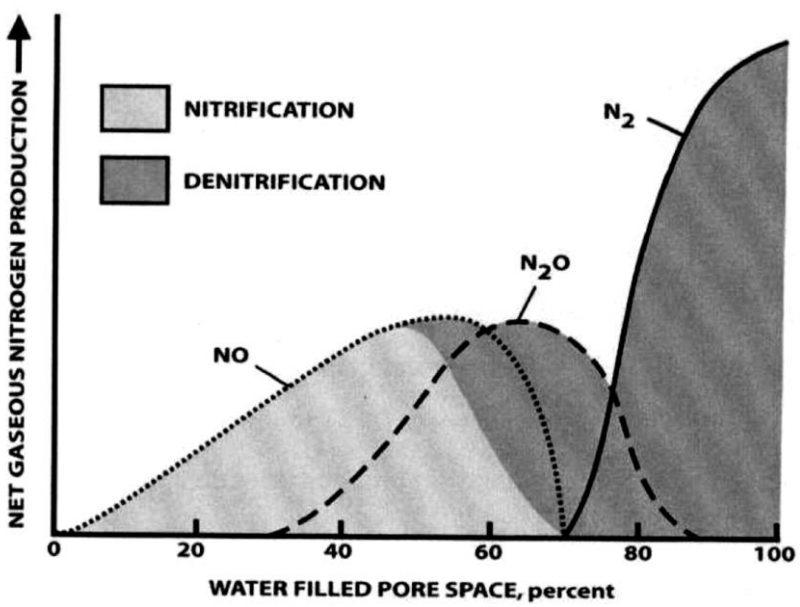

Fig. 1.6: The relative relationship of water-filled pore space and nitrification & denitrification and the contributions to NO, N_2O, and N_2 emissions. (DAVIDSON, 2000 and extended with ROBERTSON & GROFFMAN, 2007).

DAVIDSON (2000) continues that for wet soils, in which diffusivity is lower and aeration is reduced. Much of the NO is reduced before it flows out from soil, and the reduced N_2O is the dominant end product, which finally flows out. The denitrification typically occurs at a WFPS of 60% or higher (ROBERTSON & GROFFMAN, 2007; BATEMAN & BAGGS, 2005). In addition, VAN DER WEERDEN et al. (2012) presented that the main N_2O emissions are between a WFPS of 60% and 95% with a peak between 70% and 85%.

1.1.2 CO_2

The most important human-induced GHG of the global C cycle is CO_2. Since industrial revolution (1750) the CO_2 concentration increased from 278 to 379 ppm in 2005 (FORSTER et al., 2007). Mainly, the CO_2 concentration in the atmosphere increased in the past three decades due to anthropogenic activities like burning fossil fuels and land use change (FORSTER et al., 2007). CO_2 has a relative radiative forcing value of about 1.66 $W \cdot m^{-2}$ (IPCC, 2013). About 8 $Gt \cdot C \cdot yr^{-1}$ of anthropogenic CO_2 emissions were compensated by natural CO_2

sinks like forests, which incorporate about 3 $Gt \cdot C \cdot yr^{-1}$ (FORSTER et al., 2007). The aboveground biomasses of forests are storage pools for carbon from CO_2 and they sequester it below ground in the pedosphere as well as in the rhizosphere. Mainly, forest soils of the Northern hemisphere play an important role in the greenhouse gas balance for terrestrial ecosystems (IPCC, 2013; JANSSENS et al., 2003; UNFCCC, 1997).

The assimilation of carbon (C) is driven by photosynthesis of marine and terrestrial ecosystems like phytoplankton and plants, which are the dominant processes of atmospheric CO_2 consumption.

1.1.2.1 CARBON CYCLE AND CO_2 EFFLUXES

The carbon cycle is mainly determined by relative flux rates of decomposition by plant necromass, root-respiration and photosynthesis (MORRIS & BLACKWOOD, 2007). These processes are influenced by plants, soil-fauna, fungi, microbes and their interactions. Soil organic matter (SOM) is incorporated in different carbon fractions such as flora and fauna and deposits at various stages of decomposition (dead SOM). Edaphon is the living SOM as well as other biogenic substances produced by microorganisms.

According to HORWATH (2007), the major GHG fluxes produced by the C-cycle are CO_2 and CH_4. Photosynthesis is the well-known process turning inorganic C (CO_2) into usable organic C. This process mainly contributes to the gross primary production (GPP, Fig. 1.7).

Through plant and root respiration (autotrophic respiration), the inorganic gaseous carbon dioxide (CO_2) is released to the atmosphere (KUZYAKOV & LARIONOVA, 2005). Residual carbon is converted in plant biomass (net primary production – NPP). Microbial and faunal autothrophic organisms also contribute to GPP and NPP (HORWATH, 2007). The net secondary production (NSP) is the consumption of NPP by fauna and microorganisms. The GPP without the autotrophic respiration (photosynthesizers such as plants and algae) and heterotrophs (microbial decomposers like bacteria, fungi, actinomycetes, protozoans, and soil macrofauna) are the net ecosystem production (NEP). The decomposition of dead plant biomass by decomposers results in C assimilated accumulation in soils. Secondly, CO_2 effluxes from soils are the largest carbon fluxes in most ecosystems and are responsible for 60-90% of the total ecosystem respiration (LONGDOZ et al., 2000).

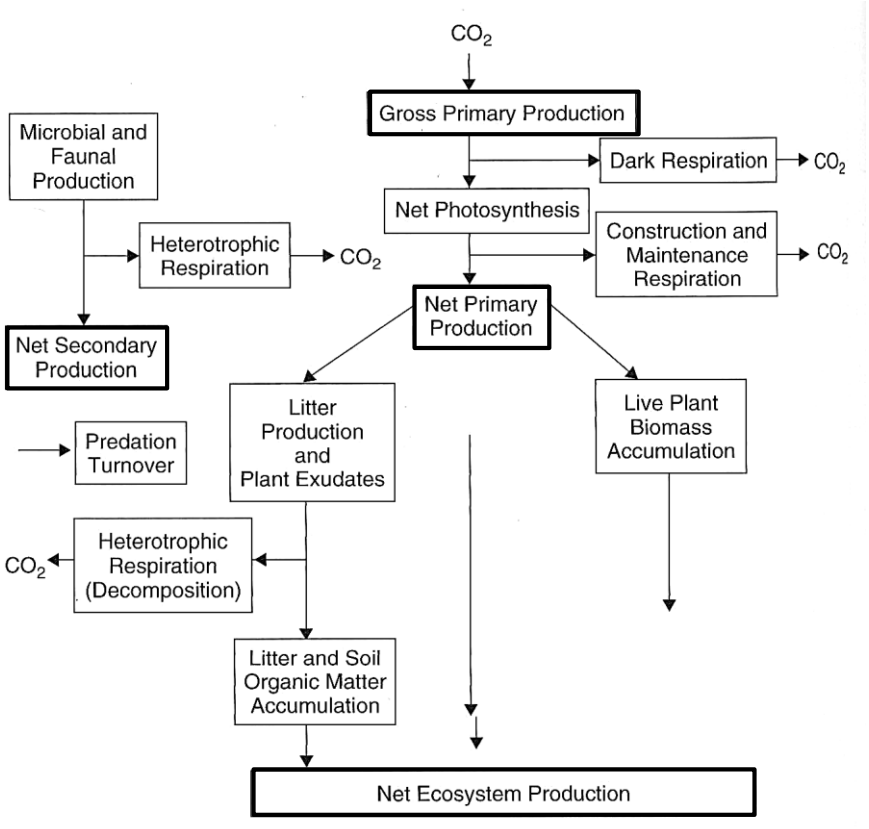

Fig.1.7: Various components of gross primary production and net ecosystem production (PAUL, 2007).

KUZYAKOV & GAVRICHKOVA (2010) and KUZYAKOV (2006) differentiate CO_2 emissions from soil into five general sources (Fig. 1.8): Roots supply plants with water and nutrients. Thereby, roots absorb oxygen from soil to get energy for the metabolism to consume and apply photosynthetic products. In the next step roots release CO_2 into the soil. The rhizomicrobial respiration means microbial decomposition of rhizodeposits (organic excretions) from living roots. The microbial respiration is the respiration during decomposition of dead plant residues. Living plants change the environmental conditions in the rhizosphere and affect the rate of SOM decomposition. Short-term changes of the SOM decomposition are a result of priming effect as it may increase the decomposition 3- to 5-fold or decrease it by 10% to 30%. Some mechanisms, which are discussed by KUZYAKOV (2002), cause the priming effect.

The basal respiration by microbial decomposition of SOM occurs in root free soils without undecomposed plant residues. A smaller extent of CO_2 could leave an ecosystem by the leach of C containing compounds such as dissolved organic- (DOC) or dissolved inorganic- (DIC) carbon, through rivers or by single events (e.g. fire, harvest or strong precipitation).

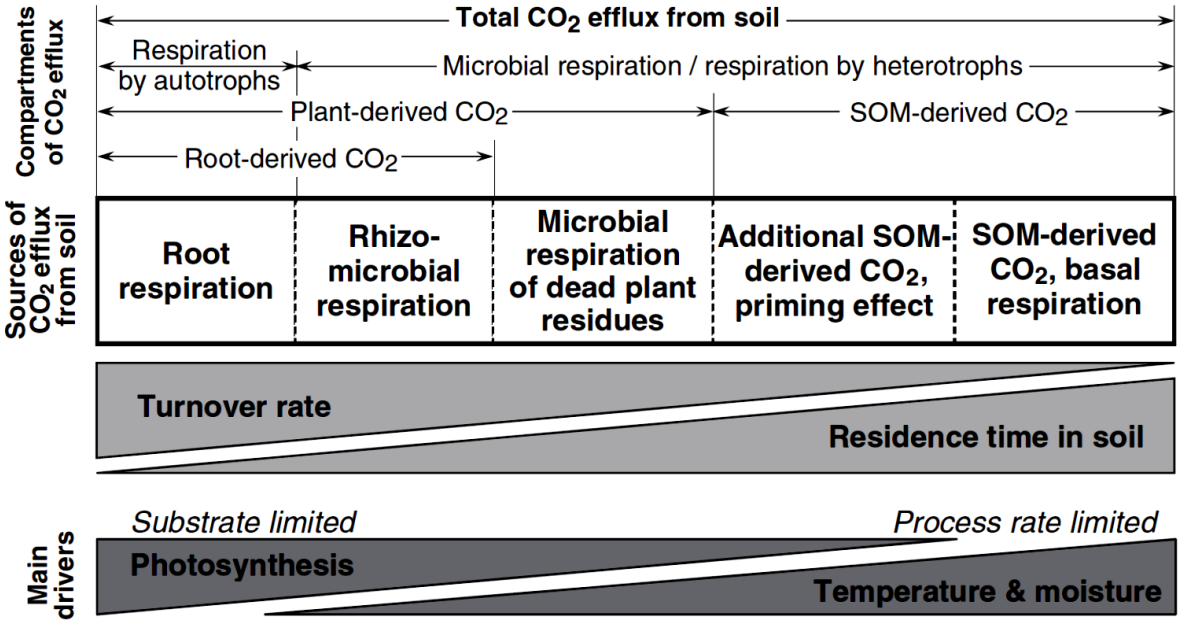

Fig. 1.8: Five main biogenic sources of CO_2 efflux from soil, ordered according to the turnover rates and mean residence times of carbon (C) in soil. The sources and compartments of the CO_2 consider C pools with different turnover rates and mean residence time (MRT), the localization of C pools and the agents of CO_2 production. The limiting factors and the dependence of individual CO_2 sources on photosynthesis and soil temperature are presented at the bottom. (KUZYAKOV & GAVRICHKOVA, 2010).

In addition to chemical soil properties soil respiration is also influenced by physical soil properties like soil moisture and soil temperature (OTTOW, 2011). The correlation between the rate of mineralization and temperature can be described by the Q_{10}-factor. Q_{10} implies that the decomposition rate of organic matter in the soil exponentially increases by a temperature increase of 10 Kelvin (KIRSCHBAUM, 1995).

1.1.2 CH_4

The methane concentration increased from a pre-industrial value of ca. 715 ppb to 1774 ppb in 2005 (IPCC, 2007). The global carbon budget contains less than 1% CH_4 (HORWATH, 2007). Despite the short residence time of approximately 12 years methane has a GWP_{100} of about 25 (FORSTER et. al., 2007). CH_4 is found as natural gas in catharses compounds in ice (e.g. permafrost), hydrates in the ocean bed, in fossil fuels or in the atmosphere. The radiative forcing of CH_4 increased up to around 0.48 (± 0.05) $W \cdot m^{-2}$ (IPCC, 2007). The natural sources of methane are estimated of about 200 $Tg \cdot yr^{-1}$ and the part of human activities caused an emission of about 350 Tg yr^{-1} (DENMAN et al., 2007). Natural sources of methane emission are wetlands and the main anthropogenic sources are the energy production. Waste disposal, cattle breeding, rice agriculture and biomass burning are further sources (Denman et al., 2007).

1.1.3.1 CARBON CYCLE AND CH_4 EFFLUXES

A strong sink of CH_4 is the chemical oxidation by methanotrophs in aerobic soils with a deposit rate of about 511 $Tg \cdot yr^{-1}$ (DENMAN et al., 2007; LE MER & ROGER, 2001; SMITH et al., 2000). The effect of biological oxidation in aerobic soils and through loss to the stratosphere is small. Nevertheless, they are sinks for atmospheric CH_4 (LE MER & ROGER, 2001; SMITH et al. 2000). The microbial production of CH_4 in anaerobic soils results from the decomposition of organic matter without oxygen by methanogens. CO_2 is used as an electron acceptor and the reduced organic part is used as the donor (HORWATH, 2007). HORWATH (2007) proposed that CO_2 flux is decrease in soils under reducing conditions such as wet environments or where oxygen diffusion is limited (e.g. soil aggregates). Under aerobic conditions the methanotrophs oxidize CH_4 and use it as their own energy and carbon source for growing (DEDYSH & DUNFIELD, 2011; SEMRAU et al., 2011). Those organisms have the ability to use methane monooxygenase enzymes (particulate MMOs (pMMO) & soluble MMOs (sMMO)) to catalyze the oxidation of methane to methanol (DEDYSH & DUNFIELD, 2011). After the oxidation to methanol a further oxidation to formaldehyde, formate and endue with CO_2 (WHALEN, 2005) follows.

Studies have shown that with the attendance of ammonium (NH_4^+) the oxidation of CH_4 is inhibited by the oxidized phase of nitrogen (N) nitrogen nitrate ($N\text{-}NO_3^-$) (REAY & NEDWELL, 2004; WANG & INESON, 2003). HÜTSCH et al. (1994) and BÉDARD & KNOWLES (1989) explained the competition between NH_4 and CH_4 during the first step of the methane oxidation on the binding sites of the catalyzing enzyme MMO which results in an enhanced NH_4^+ oxidation instead of CH_4 oxidation (BÉDARD & KNOWLES, 1989). KING & SCHNELL (1994) quantify that during the oxidation of NH_4^+ toxic nitrite (NO_2^-) is produced. FENDER et al. (2012[a]) observed that labile carbon (glucose) supports the oxidation of CH_4. Stimulated by these heterotrophic microbial processes an impulse activates the methylotrophic bacteria to change from CH_4 as a preferred substrate to other multicarbons or side-products of glucose-utilizing bacteria. This process is suspected to have an important effect on the CH_4 oxidation in forests' soils or soils under anthropogenic N inputs via fertilization or atmospheric deposition (SUWANWAREE & ROBERTSON, 2005; SMITH, 2000). Under natural conditions, the oxidation of CH_4 and NH_4^+ occurs in the same soil-horizon between 4-10 cm soil depths (JÄCKEL, 2001; CONRAD, 1996). Hence, the additional nitrogen input decreases the CH_4 oxidation in soils (VITOUSEK et al., 1997).

1.2 THE ROLE OF EARTHWORMS ON GREENHOUSE GASES

Earthworms are considered as "ecosystems engineers" (EISENHAUER, 2010) and have a profound influence on the quality and the distribution of organic matter in soils (DON et al., 2008). Furthermore, earthworms support soil "coarse" structure with a magnitude of effects on organic matter turnover and nutrient release which have to be considered positive in a farming sense (SHIPITALO et al., 2004; SANDER & GERKE, 2008; CASTELLANOS-NAVARRETE et al., 2012). A very striking and illustrative example for the effect of earthworms on soils is shown in North America (BURTELOW et al., 1998; HENDRIX & BOHLEN, 2002; HALE et al., 2005) where earthworms are an invasive species. Big layers of organic matter on soils have been considerably diminished within only decades. Clearly, earthworms enhance the incorporation of organic matter into the mineral soil and to some extend the turnover rates. As a consequence, earthworms are suspected to increase greenhouse gas emissions from soils and there is evidence to support these "ideas" (LUBBERS et al., 2013). Based on this knowledge, it can be roughly calculated how much additional greenhouse gases were emitted by these invasive earthworms in North America. As heterotrophic organisms they are not adding to the overall carbon and nitrogen supply and therefore higher emission values could very well be peak events. That is common particularly for N_2O showing frost-thaw and dry-wet peaks (MUHR et al., 2008; JUNGKUNST, 2010; DIJKSTRA et al., 2012). Therefore, the differences between earthworm treated and untreated plant-soil systems may level off at longer termed perspectives.

The displacement of organic substances to lower soil depths by earthworms is essential for soils' fertility and structure. Varying earthworm species accomplish this differently: *Lumbricus terrestris* is an anecic species that subsists on plant detritus and incorporates it down to a soil depth of maximal 200 cm in permanent and semi-permanent worm tubes. *Aporrectodea caliginosa* is an endogeic species and has its habitat in mineral soils and consumes humificated organic soil substrate (EDWARDS & BOHLEN, 1996). Both types are usually coexisting in forest soils. However, a study of the earthworm species *Megascolediae* and *Lumbricidae* in New Zealand showed that the N_2O production is not influenced by taxonomy and geographical region (WÜST et al., 2009). Some studies described the influence of earthworms on GHG-fluxes from soils of about 1.5 nmol $N_2O \cdot h^{-1}g^{-1}h^{-1}\cdot$/ g earthworm (fresh weight) as direct emitter of N_2O (DRAKE & HORN, 2007). Such emissions of N_2O are influenced by the activity of denitrifying bacteria in earthworm guts (Fig. 1.9) (IHSSEN et al., 2003; DRAKE & HORN, 2007).

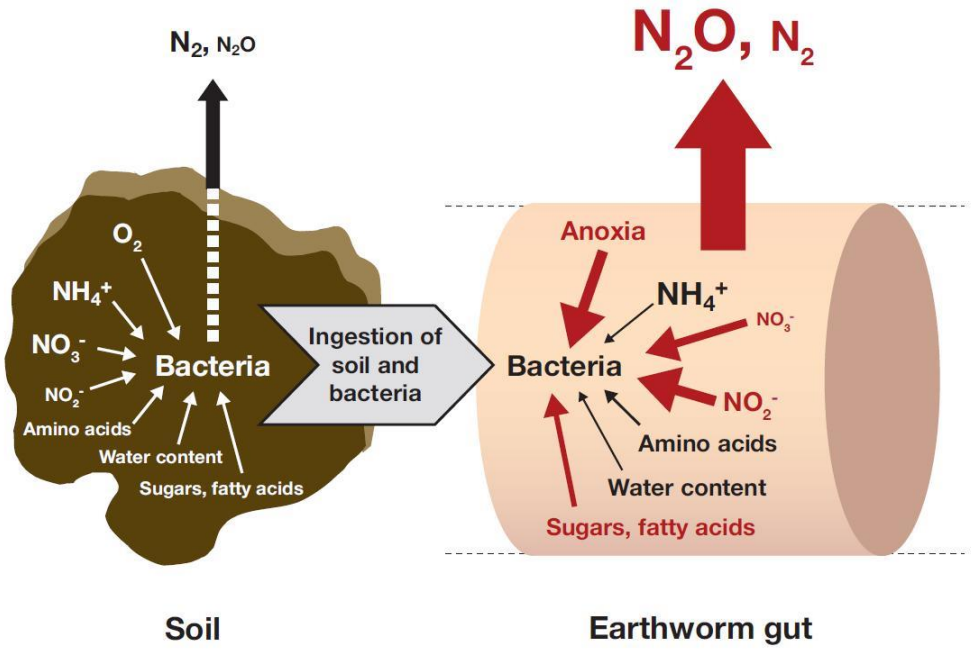

Fig. 1.9: Hypothetic model of stimulating factors for the N_2O and N_2-production caused by bacteria inside the earthworm gut. The relative concentration of the compounds is symbolized by thickness of the litter. The influence of the compounds for the N_2O and N_2 production are symbolized by the thickness of the arrows. The main factors are written in red (DRAKE & HORN, 2007).

High moisture and comprised anoxia as well as resources of nitrate and nitrite support denitrification in the earthworm gut (DRAKE & HORN, 2007). IHSSEN et al. (2003) measured that the number of denitrifiers in earthworm guts is about $6\times10^{6}\cdot g^{-1}$ (dry mass). This is two dimensions higher than the amount in soil. Besides being direct emitters, earthworms may also enhance the microbial activity in the soil itself. Earthworms support the microbial activity with excreta next to the worm tubes (drilosphere). In this zone higher microbial activity and increasing N_2O and CO_2 emissions were observed (EDWARDS & BOHLEN, 1996). The litter and excreta input through *Lumbricus terrestris* into the mineral soil produce a higher concentration of carbon and nitrogen directly into the soil and the turnover through the bacteria causes higher GHG emission. Excreta of the Earthworms contain ammonia and urea nitrogen (EDWARDS & BOHLEN, 1996). Direct and indirect emissions of earthworms by supporting the turnover of organic matter in the soil cannot be separated by net GHG measurements from soils. Furthermore, it is unclear if these GHGs will eventually reach the atmosphere since N_2O and CH_4 can easily be consumed within soils (CLOUGH et al., 2005; CONEN & NEFTEL, 2007; PEARSON et al., 2012). However, a significant increase of N_2O fluxes of about 57% as well as a reduction of methane oxidation was measured in presence of *Lumbricus terrestris* in an incubation experiment with calcareous soil (BORKEN et al., 2000). Other studies also confirmed these findings (EDWARDS, 2004; BOSSUYT et al., 2005; DRAKE & HORN, 2006; FRELICH et al., 2006; TIMMERMAN et al., 2006; MARHAN et al., 2007;

EISENHAUER & SCHEU, 2008; SPERATTI & WHALEN, 2008; BUTENSCHOEN et al., 2009; CONTRERAS-RAMOS et al., 2009; CHAPUIS-LARDY, 2010; GIANNOPOULOS et al., 2010; MARHAN et al., 2010; LAOSSI et al., 2011; LUBBERS et al., 2011; NEBERT et al., 2011; BRADLEY et al., 2012).

SIMEK and PIZL (2010) measured a positive influence of *Aporrectodea caliginosa* on soil-derived CO_2 fluxes and an increase of the microbial activity, which leads to elevated microbial biomass, higher glucose induced respiration, and significantly higher enzyme activity.

SVENSSON et al. (1986) measured a significantly higher denitrification rate of *Lumbricus terrestris* excreta elevated N_2O fluxes as well as increasing CO_2 fluxes resulting from a higher microbial activity.

This work basically aimed at testing these outcomes on net GHG fluxes from a temperate forest soil with and without tree (ash) saplings. The investigation of the influence of earthworms on CH_4 and N_2O fluxes from soil will also be an essential part of this project. The rhizotron experiment of FENDER et al. (2012[b]) has shown that soil planted with ash had lower N_2O emissions, higher CO_2 emissions and higher CH_4 uptake than the soils planted with beech. This experiment tested if the activity of earthworms in soils increases the uptake effect of CH_4.

1.3 THE ROLE OF PHOTOSYNTHESIS ON GREENHOUSE GASES

Photosynthesis is a very important factor for generating herbal life in the earth's ecosystem. Plants use the photosynthesis process to convert CO_2 into carbon compounds for produce biomass. The important energy source for phototrophis under natural conditions is sunlight. During this process they need sun energy to divide CO_2 into C and O_2 and H_2O is used as electron donor. A secondary process is the transpiration of O_2 used by autotrophic organisms for respiration. Non-converted CO_2 is passed through the plant and is respirated by roots or leaves during the photosynthetic inactive phase.

Photosynthesis is mostly coupled with the release of resolvable sugars, like root exudates, into the rhizosphere (KUZYAKOV & GAVRICHKOVA, 2010). Mycorrhiza and microorganisms convert these exudates rapidly and contribute to the CO_2 release from roots (Fig. 1.10). Another CO_2 source, which is coupled with photosynthesis, is root respiration. According to SUBKE et al. (2009) and XU et al. (2008) increasing evidence suggests that assimilates from photosynthetically active plants affect root respiration and contribute to CO_2 fluxes from soil. Therefore, the microbial activity in soil would be supported by these release processes

of the rhizosphere, which are a consequence of photosynthetic production and allocation of organic carbon compounds (KORANDA et al., 2011).

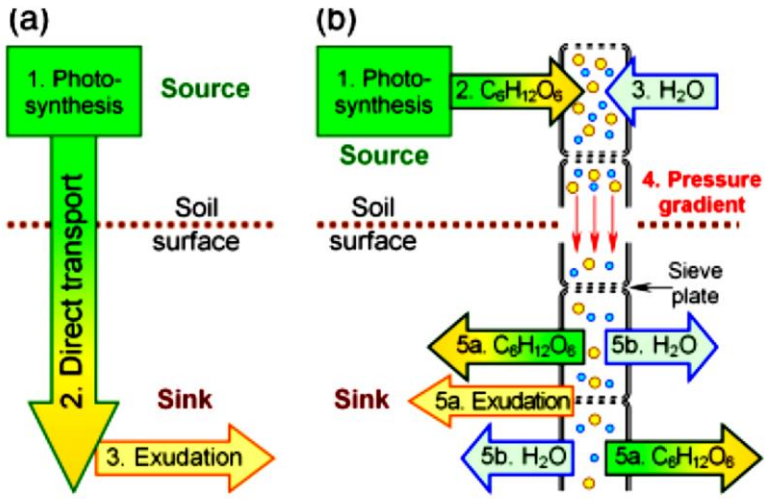

Fig. 1.10: Increased photosynthesis leads to two response mechanisms to release soluble organic substances and transport assimilates from leaves through stem and roots to the rhizophere: (a) direct transport of molecules and (b) indirect response of the release of soluble organics from roots by phloem loading and pressure-concentration waves (KUZYAKOV & GAVRICHKOVA, 2010).

The mineralization and conversion of nitrogen in soils is described in part 1.1. For plants nitrogen is essential as a nutrient to produce biomass. Without photosynthesis plants do not reduce nitrogen and that causes a greater amount of reactive nitrogen for oxidation in the soil pores for the production of N_2O (SCHULZE et al., 2002).

Suggesting that nitrogen compounds such as ammonium influence the oxidation of CH_4 (FENDER et al., 2012[a]), a reducing process through the plant caused by photosynthesis activity might be possible.

1.4 THE ROLE OF EUROPEAN FOREST SOILS AS A SINK AND SOURCE FOR GREENHOUSE GASES

European forests have a substantial influence on the greenhouse gas balance on earth. The European forests have a total tree carbon stock of 8000 Tg·C with a sink of 101.3 $Tg \cdot C \cdot yr^{-1}$ (GOODALE et al., 2002; NABUURS et al., 1997). The European (EU-25) forests with a size of about 1.32 to 1.55 × 10^6 km² have in relation to carbon, a net primary productivity (NPP) of 520 ± 75 $g \cdot C \cdot m^{-2} \cdot yr^{-1}$ where long-term carbon sinks of the net biome production (NBP) is quantified to 75 ± 20·$g \cdot C \cdot m^{-2} \cdot yr^{-1}$ (LUYSSAERT et al., 2010). LUYSSAERT et al. (2010) indicated that the storage into forest soils reaches ca 30 % ± 15 % of the NBP (22 $g \cdot C \cdot m^{-2} \cdot yr^{-}$

[1]), which means that the soil carbon stocks in European forests range from 5.000 to 14.000 Tg (NABUURS et al., 2003; GOODALE et al., 2002; LISKI et al., 2002) and store ca. 1.5 times more carbon than trees (BARITZ et al., 2010). According to VALENTINI et al. (2000) this total net sink for carbon interacts with the CO_2 emissions from forest soils; which represent the respiration of forest ecosystems. LUYSSAERT et al. (2010) distinguished the respiration into heterotrophic respiration, which emits an average rate of 368 ± 107 $g \cdot C \cdot m^{-2} \cdot yr^{-1}$ and autotrophic respiration, which emits 507 ± 152 $g \cdot C \cdot m^{-2} \cdot yr^{-1}$. PARÉ et al. (2011) and BERGER et al. (2005) showed that the emissions of CO_2 of broad-leaved forests are higher than needle-leaved forests. Putting the focus on broad-leaved forests VESTERDAL et al. (2012) measured varying emissions of CO_2 from soil under different tree species. These authors measured higher respiration under *Fraxinus excelsior* L. than under *Fagus sylvatica* L..

Another reason for the importance of soils is the function of anerobic soils as a sink for atmospheric CH_4 (SUWANWAREE & ROBERTSON, 2005; KRAVCHENKO et al., 2002; CASTRO et al., 1995). WATSON et al. (1992) estimated that the global CH_4 sink has a total amount of 15-45 $Tg \cdot yr^{-1}$ and this is about 3-10 % of the global emissions. For example, temperate and tropical oxic soils are CH_4 sinks (LE MER & ROGER, 2001). According to LE MER & ROGER (2001) temperate and tropical oxic soils are CH_4 sinks and usually exhibit low level oxidation of atmospheric CH_4, but by covering large areas, they absorb ca. 10 % of atmospheric CH_4. The oxidation of CH_4 in temperate forest soils is estimated at 22.4 $Tg \cdot CH_4 \cdot yr^{-1}$: Nevertheless; they are not specified in broad-leaved or needle-leaved forests (GRUNWALD et al., 2012; DUTAUR & VERCHOT, 2007).

For N_2O forest soils emit about 18 Tg $N\text{-}N_2O \cdot yr^{-1}$ of the global N_2O whereof about 10 Tg $N\text{-}N_2O \cdot yr^{-1}$ arise from natural sources (REAY et al., 2007)

In Europe, besides agricultural soils, the major natural sources of N_2O are forest soils (JUNGKUNST et al., 2006; KESIK et al., 2005). REAY et al. (2008) published that in the future the greatest natural source of N_2O derives from forest soils. Otherwise, the last decades of research activities focussed on fertilized agricultural systems and thus abiotic factors like soil moisture, soil pH and C/N ratio, as well as soil organic carbon (SOC). These parameters influence GHG fluxes from soil, which are well studied (WESLIEN et al., 2009; PILEGAARD et al., 2006).

REAY et al. (2007) also assumed that temperate forest soils emissions are estimated at ca. 2 Tg $N\text{-}N_2O \cdot yr^{-1}$ whereof forest soils emits 50% and temperate grassland soils the other 50%. The results of SCHULZE et al. (2009) described that the N_2O fluxes from land-derived biological GHG fluxes increase for the EU-25. But this research is only based on the N_2O

fluxes for agroecosystems (70 ± 35 $Tg \cdot yr^{-1}$). AMBUS et al. (2006) and BUTTERBACH-BAHL & KIESE (2005) showed that in most events the emissions of N_2O are higher from broad-leaved forest soils than from needle-leaved forest soils.

1.5 SPECIES-SPECIFIC INFLUENCE OF ASH & BEECH ON C & N CYCLING

The influence of tree species on nutrient and water input, output and cycling are manifold (LANGENBRUCH et al., 2012). Conifers and their abiotic effects on the soil's biochemical properties are well studied, but the influence of biotic factors of broadleaved species has research potential (LANGENBRUCH et al., 2012; MARESCHAL et al., 2010; VARGAS & ALLEN, 2008). Most studies analyzed chemical and physical soil properties under broad-leaved tree species. The pH-value as well as the base saturation are lower in the topsoil under mullmoder-forming species (beech) compared to mull-forming species such as ash (MARESCHAL et al., 2010). The concentrations and stocks of organic and total nitrogen in the forest floor are presented by VESTERDAL et al. (2008). The study showed that the concentrations are higher under beech than under ash. This showed the influence of tree species on soil's chemical properties as well as CH_4 uptake or N_2O release through differences in the input of leaf litter and its specific chemistry (LANGENBRUCH et al., 2012; VESTERDAL et al., 2012; VESTERDAL et al., 2008). According to LANGENBRUCH et al. (2012) and HOLZWARTH et al. (2011) beech is commonly known to have the lowest calcium (Ca) and magnesium (Mg) contents (beech: 1.5 mg $Mg \cdot g^{-1}$; ash: 2.7 mg $Mg \cdot g^{-1}$) in their leaf litter. Furthermore, beech litter showed the lowest N concentrations and the highest C:N ratio (beech: 50; ash: 32). In addition, the influence on GHG fluxes between soil and atmosphere can be owed to throughfall (GUCKLAND et al., 2010; GUCKLAND et al., 2009), and root activity such as exudates (LANGENBRUCH et al., 2012).

1.6 THE INFLUENCE OF ROOTS ON C & N CYCLING

The influence of fine roots on the C and N cycling is manifold and research has a high potential to contribute to the understanding of this complex process. The partial pressure of oxygen can be altered in the rhizosphere, because of root-respiration, root-associated microorganisms, consumption of water by roots, and penetration of roots into the soil, which creates capillaries or small dikes for gas transfer (PHILIPPOT et al., 2009; CHENG & GERSHENSON, 2007). The rhizodeposition and plants also release available organic compounds into the soil whereby the root exudates take the largest part (NGUYEN, 2003).

This exudate influences as the main driver microbial processes in the rhizosphere (PHILIPPOT et al., 2009; NANNIPIERI et al., 2007). The research of PHILIPPOT et al. (2009) continues that fluctuations in the rhizosphere due to root uptake influences the concentrations of nitrate and ammonium and the rhizosphere of plants affects the nitrification with several factors.

Some field experiments showed that increased organic matter input in combination with increased aeration by plants stimulate nitrification (PHILIPPOT et al., 2009; ENWALL et al., 2007). Rhizospheres negative effect on nitrification is shown by many studies (PHILIPPOT et al., 2009). This negative effect along the roots is presented by the study of HERMAN et al. (2006). Close to older root sections the nitrification was lower than near the root tips due to faster NH_4^+ uptake by the older parts of the roots, which can decrease the rates of nitrification.

In general, the denitrification is influenced by nitrate concentration and the water-filled pore space of soil. A positive correlation showed the denitrification rate with total carbon or soluble organic carbon content in the soil, which the microbes use as energy source. The carbon release into the soil is a primary driver of rhizo-microbial communitys' activity. PHILIPPOT et al. (2009) showed the quantity of N_2O that is produced in dependency on the distance of roots (Fig. 1.11).

RUST & SAVILL (2000) described the species-specific differences in root growth between ash and beech. Moreover, ash root systems have a superficial and far-reaching growth behavior with tough horizontal roots, which branch lateral roots vertically downwards under natural conditions. The main growth direction of beech roots is downwards and early dividing into increasing fine rootlets to fine tips at the end (RUST & SAVILL, 2000). The concentrations of the fine roots are in clumps and between this clumps are root-free zones.

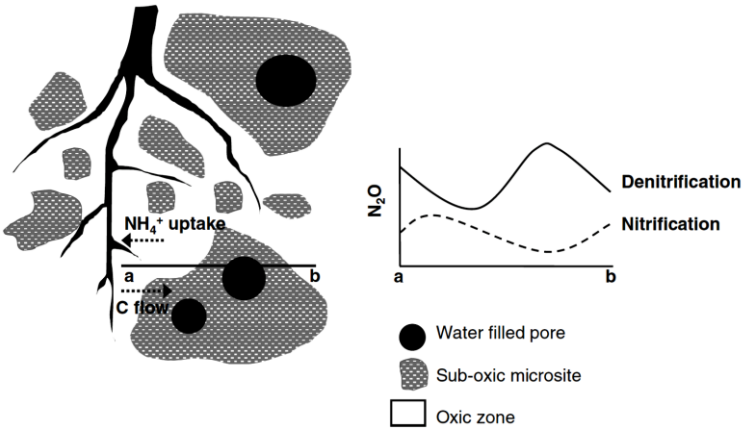

Fig. 1.11: Conceptual representation of the spatial arrangement of microsites in the rhizospere and hypothesized N_2O production by nitrification and denitrification with the distance from a plant root influenced by carbon, oxygen and NH_4^+ gradients (PHILIPPOT et al., 2009).

1.7 STUDY OBJECTIVES AND HYPOTHESIS

The present PhD study was conducted as a part of an interdisciplinary project: "Biodiversity Manipulation in Rhizosphere and Soil - MicroRhizo" of the Functional Biodiversity Research Cluster of Excellence at the Georg-August-University of Göttingen. The rhizosphere of beech and ash was investigated in a laboratory experiment under controlled abiotic conditions using homogenized soil for the soil columns experiments and soil horizon layer for the novel double-split-root rhizotron experiment. The soil was taken from Hainich Nation Park, Thuringia, Germany. The results from the laboratory experiments get a step closer to compare these results with a field experiment. The field study was the "**S**pecies **L**itter **I**dentity and **D**iversity effect on the **RH**izosphere of trees **EX**periment" (SPLIDRHEX). The experimental approach aimed at separating the influences of diverse soil biota in the rhizosphere of *Fagus sylvatica* L. (European beech), *Fraxinus excelsior* L. (European ash) and the earthworm species *Lumbricus terrestris* and *Aporrectodea caliginosa*. The main objective was to identify the species-specific effects on the carbon and nitrogen fluxes in forest soil and the greenhouse gas fluxes (N_2O, CO_2 and CH_4) between soil and atmosphere.

This Study focused on

I. the influence of ash saplings and earthworms on the N_2O, CO_2 and CH_4 fluxes in soil columns (Chapter 2).
II. the specific species' effects of beech and ash on the N_2O fluxes in soil columns (Chapter 3).
III. the multiple path on influence of beech and ash saplings in combination with earthworms and ash or beech litter, with focus on the resulting greenhouse gas fluxes in double-split-root rhizotron (Chapter 4).
IV. the testing of the results from the soil columns study with the field study under natural conditions (Chapter 5).

Within the Chapters 2 – 5 of this thesis, the following hypotheses were tested:
Chapter 2: (1) earthworms support the release of CO_2 and N_2O and the uptake of CH_4 in the soil and consequently elevate the net-total GHG (CO_2-aquivalent) fluxes, (2) these altered fluxes due to the activity of the earthworms are enduring effects (at least for 90 days), (3) earthworm effects are independent of ash treatments.

Chapter 3: (1) there is an effect of photosynthesis on N_2O emissions from soils (2), there are differences between ashes and beeches in this photosynthesis effect, and finally (3) diurnal trends exist which affect N_2O fluxes during the course of the day in the climate chamber.

Chapter 4: (1) earthworms support the release of N_2O and CO_2 and the uptake of CH_4 in the soil and lead to an increase of the net-(CO_2-aquivalent) emission from soil, (2) the described earthworm effect is an enduring effect (for a longer period about 416 days).

Chapter 5: (1) CO_2 fluxes increase before frondescence and the CO_2 fluxes are generally higher for *F. excelsior* than for *F. sylvatica* and during frondescence, (2) the CH_4 uptake is consistent in the inactive phase and higher for soils planted with *F. excelsior* and CH_4 uptake increases before frondescence. The CH_4 uptake is generally higher for *F. excelsior* than for *F. sylvatica* planted soils. The CH_4 uptake is generally higher in soil-plant systems with *F. excelsior* than for systems with *F. sylvatica.* (3) the N_2O emissions are consistent in the inactive phase. Before frondescence, emissions of *F. excelsior* planted soils are lower than soils planted with *F. sylvatica* and both are lower than control.

1.8 STUDY MATERIALS AND EXPERIMENTAL DESIGN

For the soil columns and the split-root-rhizotron experiment we used soil and plant material from the Hainich National Park, Thuringia, Germany (51°04'N 10°30'E, about 350 m a.s.l.). The Hainich National Park is a temperate mixed broad-leaved forest of up to 14 co-occurring tree species per hectare. The climate conditions are sub-atlantic with a precipitation of 590 mm p.a. and a mean annual temperature of 7.5 °C (DEUTSCHER WETTERDIENST, 2005). The dominating tree species at the sampling site are *Acer pseudoplatanus* L., *Acer platanoides* L., *Carpinus betulus* L., *Fagus sylvatica* L., *Fraxinus excelsior* L., *Tilia cordata* Mill., and *Tilia platyphyllos* Scop. (FENDER et al., 2012[b]).

The morphology, physiologies and phylogenies of the chosen tree species are very different and are co-occurring in several broad-leaved forest communities of Central Europe and are very interesting for economic forestry (ELLENBERG & LEUSCHNER, 2010). The chosen species have a differentiation of root morphology, type of mycorrhizae, root tip abundances and specific root surface area (Tab. 1.2).

Tab. 1.2: Root morphology of beech and ash; after HÖLSCHER et.al. (2002) and MEINEN et al. (2009). Shown are mean ± 1 SE.

	Mycorrhization	**Branching Intensity**	**Specific root tip Abundance [number mg^{-1} dw]**	**Specific fine root area [$cm^{-2}g^{-1}$]**	**Average root diameter [mm]**
***Fagus sylvatica* L.**	Ectomycorrhized	High	40.2 ± 3.5	394 ± 25	0.38 ± 0.01
***Fraxinus excelsior* L**	Arbuscular mycorrhized	Low	3.0 ± 0.05	289 ± 10	0.60 0.02

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CHAPTER 2

ON THE INFLUENCE OF EARTHWORMS (*LUMBRICUS TERRESTRIS*, *APORRECTODEA CALIGINOSA*) ON THE TEMPORAL DYNAMICS OF GREENHOUSE GAS FLUXES (N_2O, CH_4 AND CO_2) FROM SOIL PLANTED WITH ASH (*FRAXINUS EXCELSIOR* L.)

2.1 ABSTRACT

Results on the temporal dynamics of greenhouse gas fluxes between soil and atmosphere as influenced by earthworms are presented. Recent research revealed that earthworms can enhance N_2O emission from soils. Evidence is missing though, that a better soil structure, due the presence of earthworms, may support the uptake of CH_4. Earthworm activities may also enhance microbial activities and therefore CO_2 emission. For extrapolating the effect it is important to know if identified impacts of earthworms on GHG dynamics from soils are solely inducing "hot moments" (event driven) and overall fluxes stay alike or if the effects are of prolonging nature. To investigate these trace gas fluxes a laboratory experiment was designed with soil and ash saplings (*Fraxinus excelsior* L.) from a temperate mixed broad-leaved forest to study the effects of earthworms (*Lumbricus terrestris* and *Aporrectodea caliginosa*) on the temporal pattern of greenhouse gas fluxes. The experiment (90 days) showed that earthworms caused a reduction of atmospheric CH_4 uptake of 40 – 60 % while provoking higher N_2O emissions of 12 – 40 % and 7 -18 % higher CO_2 fluxes. As shown before soil under ash showed decreased N_2O emission ($P = 0.02$)

Our study shows that earthworms can have a substantial influence on the temporal pattern of greenhouse gas fluxes but apparently some of these "hot moments" are equalized at a longer term perspective within experiment significant differences for the cumulative values of 90 days.

Keywords: *Lumbricus terrestris, Aporrectodea caliginosa, Fraxinus excelsior* L., greenhouse gases

2.2 INTRODUCTION

Nitrous oxide (N_2O), methane (CH_4) and carbon dioxide (CO_2) are the three major natural greenhouse trace gases (GHG). The mean residence time of N_2O in the atmosphere is about 120 years, which is a major reason for its high global warming potential for the time span of 100 years (GWP_{100}), 1kg of N_2O = 298 kg CO_2 (FORSTER et al., 2007). Despite the short residence time of approximately 12 years, methane still has a GWP_{100} of about 25 (FORSTER et. al., 2007). For the shorter time perspective its GWP_{20} is 72. Soils are prominent sources for these three greenhouse gases mainly originating from microbial-driven turnover of organic matter (CONRAD, 1996). The turnover of organic matter in soils is highly influenced by temperature, oxygen and water supply as well as the composition of the organic matter and physical protection by association with mineral soil material (VON LÜTZOW & KÖGEL-KNABNER, 2009; HELFRICH et al., 2010). It has been shown that earthworms have profound influence on the quality and the distribution of organic matter in soils (Don et al., 2008). Furthermore earthworms support soil structure with a magnitude of effects on organic matter turnover and nutrient release, which have to be considered as positive in terms of agriculture (SHIPITALO et al., 2004; SANDER & GERKE, 2008; CASTELLANOS-NAVARRETE et al., 2012). A very striking and illustrative example for the effect of earthworms on soils was shown for North America (BURTELOW et al., 1998; HENDRIX & BOHLEN, 2002; HALE et al., 2005) where earthworms are invasive species. Big layers of organic matter on soils considerably diminished only within decades. As a consequence earthworms are suspected of increasing greenhouse gas emissions from soils and there is evidence to support these hypotheses (LUBBERS et al., 2013). On base of that knowledge a rough calculation on the additional greenhouse gas emissions by these invasive earthworms in northern America could be made. However, these higher emissions values could very well be peak events (MCCLAIN et al., 2003) just like those particularly found for N_2O during frost-thaw and dry-wet events (MUHR et al., 2008; JUNGKUNST, 2010; DIJKSTRA et al., 2012). Consequently these high rates described for short termed experiments should not be taken for such an upscale. Being heterotrophic organisms, earthworms are not adding to the overall carbon (C) and nitrogen (N) supply and therefore the differences between earthworm treated and untreated plant-soil systems may level off at longer termed perspectives.

Ihssen et al. (2003) measured that the number of denitrifiers in earthworm gut of 6×10^6 g^{-1} (dry mass) is two orders of magnitudes higher than in soil. Some studies described the influence of earthworms on the GHG-fluxes from soils of about 1.5 nmol N_2O h^{-1} g^{-1} per h and gram earthworm (fresh weight) as direct emitter of N_2O (Drake & Horn, 2007). Such

emissions of N_2O are influenced by the activity of denitrifying bacteria in the earthworm gut (IHSSEN et al., 2003; DRAKE & HORN, 2007). High moisture and comprised anoxia as well as resources of nitrate and nitrite supports the denitrification in the earthworm gut (DRAKE & HORN, 2007). Besides being direct emitters earthworms may also enhance the microbial activity in the soil itself. Earthworms support the microbial activity with excreta next to the worm tubes (drilosphere). In this zone a higher microbial activity and increasing N_2O and CO_2 emissions were observed (Edwards & Bohlen, 1996). The litter and excreta input through *Lumbricus terrestris* into the mineral soil produce higher concentration of carbon and nitrogen directly into the soil and the turnover through the bacteria causes higher GHG emission. Excreta of the Earthworms contain ammonia and urea nitrogen (Edwards & Bohlen, 1996). The displacement of organic substance to lower soil depths by earthworms is essential for soil fertility and soil structure. Different earthworm species do this differently: *Lumbricus terrestris* is an anecic species (vertical driller) that feeds on plant detritus and incorporates it down to maximal 200 cm depth in permanent and semi-permanent worm tubes. *Aporrectodea caliginosa* is an endogeic species (horizontal driller) and lives in mineral soil to a depth of also 200 cm and consumes humificated organic soil substrate (EDWARDS & BOHLEN, 1996). Both types usually coexist in forest soils. An earthworm study of *Megascolediae* and *Lumbricidae* in New Zealand showed that the N_2O production is not influenced by taxonomy and geographical region (WÜST et al., 2009). Direct and indirect emissions of earthworms by supporting the turnover of organic matter in the soil cannot be separated by net GHG measurements from soils. Furthermore, it is uncertain to which parts do these GHG eventually reach the atmosphere since N_2O and CH_4 can easily be consumed within soils (CLOUGH et al., 2005; CONEN & NEFTEL, 2007; PEARSON et al., 2012). These production and consumption processes will vary across different soil conditions.

Nevertheless, significant increases of N_2O fluxes of about 57% in presence of *Lumbricus terrestris* were measured in calcareous soil columns as well as a reduction of methane oxidation (BORKEN et al., 2000), which was supported by other studies (EDWARDS, 2004; BOSSUYT et al., 2005; DRAKE & HORN, 2006; FRELICH et al., 2006; TIMMERMAN et al., 2006; MARHAN et al., 2007; EISENHAUER & SCHEU, 2008; SPERATTI & WHALEN, 2008; BUTENSCHOEN et al., 2009; CONTRERAS-RAMOS et al., 2009; CHAPUIS-LARDY, 2010; GIANNOPOULOS et al., 2010; MARHAN et al., 2010; LAOSSI et al., 2011; LUBBERS et al., 2011; NEBERT et al., 2011; BRADLEY et al., 2012). SIMEK & PIZL (2010) measured a positive influence of *Aporrectodea caliginosa* on soil-derived CO_2 fluxes and an increase of the

microbial activity, which leads to elevated microbial biomass, higher glucose induced respiration and significant higher enzyme activity. SVENSSON et al. (1986) measured a significant higher denitrification rate of *Lumbricus terrestris* excreta, elevated N_2O fluxes as well as increasing CO_2 fluxes resulting from a higher microbial activity.

It remains an open question, if the found effects indicate generally enhanced GHG fluxes from soils at the longer term or do they create single "hot moments" (McClain et al., 2003) which level off and longer termed fluxes are less affected. Hence, the effects of earthworm species (*Lumbricus terrestris*, *Aporrectodea caliginosa*) on the net N_2O, CH_4 and CO_2 fluxes of incubated temperate broad-leaved forest soils were examined for 90 days with and without *Fraxinus excelsior* (European Ash).

Ash was selected not only because it is common throughout Europe, but because it has been shown to have significant effects on CH_4 and N_2O emission. The research question, if these differences prevail by introducing these ecosystem engineers, was to be answered. FENDER et al. (2012) showed that soil under ash had lower N_2O emission rates, higher CO_2 emission rates and higher CH_4 uptake than soil under beech. With this experiment it was tested if earthworms influence these tree species effects. Following hypotheses were put forward:

(1) earthworms support the release of CO_2 and N_2O and the uptake of CH_4 in the soil and consequently elevate the net-total GHG (CO_2-aquivalent) fluxes.
(2) these altered fluxes due to the activity of the earthworms are enduring effects (at least for 90 days).
(3) earthworm effects are independent of ash treatments.

2.3 MATERIAL AND METHODS

2.3.1 SOIL, PLANT AND EARTHWORMS

Saplings of *Fraxinus excelsior* and soil were collected from a mixed deciduous broad-leaved forest of the Hainich National Park, Thuringia, Germany (51°04' N 10°30 'E). The soil type was a stagnic Luvisol with a silty texture of 2.9% sand, 56.5% silt and 40.6% clay. The pH-value measured in KCl was 5.3. The ash saplings were collected in spring 2011, near the place where the soil material was retrieved, and were planted in soil columns with minimal disturbance of the root system. Five randomly chosen ash saplings of which all had approximately the same age and biomass, were fractionated to determine biometric parameters (stem-length, dry-weight of leaves, stem and fine- and coarse-roots > 2mm),

before the start of the experiment. The used saplings were three to five years old and had an initial shoot height of 15.21 ± 0.69 cm, respectively.

After the ash saplings were planted and established, two individuals of *Lumbricus terrestris* and four individuals of *Aporrectodea caliginosa* were placed into the randomly chosen columns. The mean weight for *Lumbricus terrestris* was 1.3 ± 0.5 g per individual and for *Aporrectodea caliginosa* 0.5 ± 0.2 g per individual.

2.3.2 EXPERIMENTAL SETUP

The investigation was set up in a greenhouse with stable conditions of 20°C air temperature and 80% air moisture, using sixteen soil columns in a fully randomized design. The soil was homogenized by passing it through a 2 mm-sieve. Sixteen Plexiglas cylinders (50 cm in height, 17 cm in diameter) were each filled with 4.5 kg of the freshly sieved soil. For soil setting the columns were left untreated for 19 days (pre-experimental phase). Then the treatments were established and maintained for 90 days (May 19, 2011 to August15, 2011). Soil water content was adjusted at a water-filled pore space (WFPS) level of about ~75%. The pore volume and the water-filled pore space were calculated by a particle density of 2.65 g cm^{-3} (SCHLICHTING et al., 1995) by referring to the measured soil bulk density at the beginning of the experiment.

Four control columns (C) were covered solely by 5 g ash litter. The experiment comprised three different treatments consisting of four columns each treated like the control but with:

Treatment E: addition of 6 earthworms two individuals of *Lumbricus terrestris* and four individuals of *Aporrectodea caliginosa*.

Treatment A: Planted with one ash and no earthworms

Treatment A/E: Combination of one ash sapling and six earthworms.

The surface of the soil columns were exposed for 12 consecutive hours of low top-light (100 µmol m^{-2} s^{-1} PPFD; EYE Clean-Ace, Metal Halide Lamp, 400 W, Tokyo, Japan).

2.3.3 TRACE GAS MEASUREMENT

Before start sampling all soil columns were covered with a black hood, to interrupt photosynthetic activities. To retrieve a gas sample, the columns were closed gas-tight with a lid. A catheter needle in the lid was connected to a 60 mL syringe to take a gas sample of the column's headspace 0.3 – 0.32 m above the soil surface. The columns were closed for

45 minutes. The first gas sample (T_0) was taken immediately, after 15 min (T_1), 30 min (T_2) and 45 min (T_3), further gas samples were taken.

The gas concentrations were analyzed with an auto-sample, computer-controlled (PROBE 64+1, V1.31, LOFTFIELD, 1997) gas chromatograph (Shimadzu GC-14B, Tokyo, Japan). CO_2 and N_2O were detected by a ^{63}Ni electron capture detector and the CH_4 with a flame ionization detector. On the assumption of constant gas fluxes, a linear regression was used to calculate the increase or decrease of gas concentrations between the T_0, T_1, T_2 and T_3 measurements of N_2O, CH_4, and CO_2. The gas flux rates from the soil into the air were calculated by using a formula introduced by LESSARD et al. (1997) that considers the slope and time intervals of the measurements.

On base of 24 measurements during the experimental period of 90 days, the measurements were interpolated and the cumulative gas fluxes calculated. The cumulative gas fluxes were calculated for each soil column by creating the mean between two measurement days. The cumulative gas flux was calculating by summing up all measurements for each column a day before and the mean of a measurement day.

2.3.4 STATISTICS

Statistical analyses were performed with IBM SPSS software (2011, 20.0, IBM corporation, Armonk, USA) and with Microsoft Excel software (2010, 14.0, Microsoft corporation, Redmond, USA). Cumulative gas fluxes were calculated by summing up all measurements for each rhizotron, considering the number of measurements taken and the length of the entire measuring period (90 d). The gas fluxes varied considerably between the different measurement days as it is common for GHG fluxes from soil, so that we refrained from showing the time course. Frequency distributions were tested for normality with the Kolmogorov-Smirnov test. The one-factor variance analyses (ANOVA) was used to identify significant differences among the treatment means, which showing normal distribution. With a significance level of P =0.05.

2.4. RESULTS

2.4.1 N_2O EMISSION

The treatment ash had the lowest cumulative emission (64 ± 17 mg N-N_2O m^{-2}) while the other treatments had nearly the same level of emissions ranging from 151 ± 52 to 172 ± 115 mg N-N_2O m^{-2} (Fig. 2.5). However the emission peaks (hot moments) occurred at different times. The treatments with earthworms showed peak emissions before their counterparts.

The ash/earthworms had after 80 days the first peak emission 262 ± 102 µg $N\text{-}N_2O$ m^{-2} h^{-1} and the ash treated treatment nine days later (122 ± 87 µg $N\text{-}N_2O$ m^{-2} h^{-1}). The earthworm treatment reacted peak emissions of 254 ± 134 µg $N\text{-}N_2O$ m^{-2} h^{-1}, synchronously to the ash treatment at day 89, but eight days before the control (258 ± 52 µg $N\text{-}N_2O$ m^{-2} h^{-1}) which is its counterpart. The N_2O emissions (Fig. 2.1) revealed 3 periods of the N_2O emission which was the reason why the total 90 days were additionally calculated as three 30 days periods. The first period had relative low N_2O emissions (5 ± 5 to 124 ± 80 µg $N\text{-}N_2O$ m^{-2} h^{-1}). The second period could be defined as a "hot moment" showing rapid increase of the N_2O emissions for nearly all treatments. Solely the control reacted delayed and its peak emissions (258 ± 52 µg $N\text{-}N_2O$ m^{-2} h^{-1}) were found within the third period while all other treatments returned to low emissions (34 ± 37– 3 ± 4 µg $N\text{-}N_2O$ m^{-2} h^{-1}).

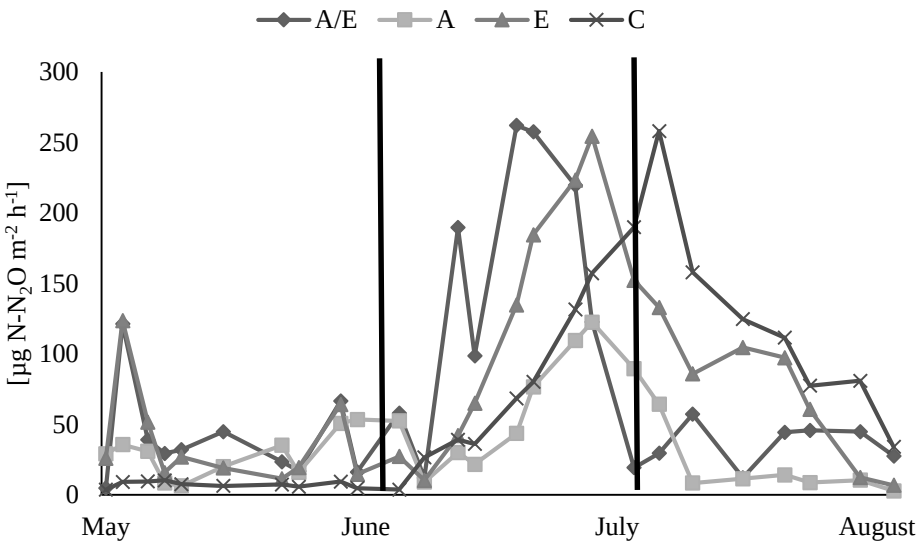

Fig. 2.1: Average fluxes of N_2O (µg $N\text{-}N_2O$ m^{-2} h^{-1}) from the soil columns of the treatments ash/earthworms (A/E), ash (A), earthworms (E) and control (C) on base of 24 measurements over 90 days.

During the first period (0-30 days) all treatments showed similar low emission rates. The treatment ash and earthworm A/E had the highest cumulative fluxes of approximately 29 ± 7 mg $N\text{-}N_2O$ m^{-2}. The treatment ash A and E had nearly the same emission of 22 ± 30 – 23 ± 15 mg $N\text{-}N_2O$ m^{-2}. The control C had the lowest cumulative emission of 5 ±1 mg $N\text{-}N_2O$ m^{-2} (Fig. 2.2). An ANOVA revealed that difference between the treatments are not significant not even between E and C ($P = 0.07$).

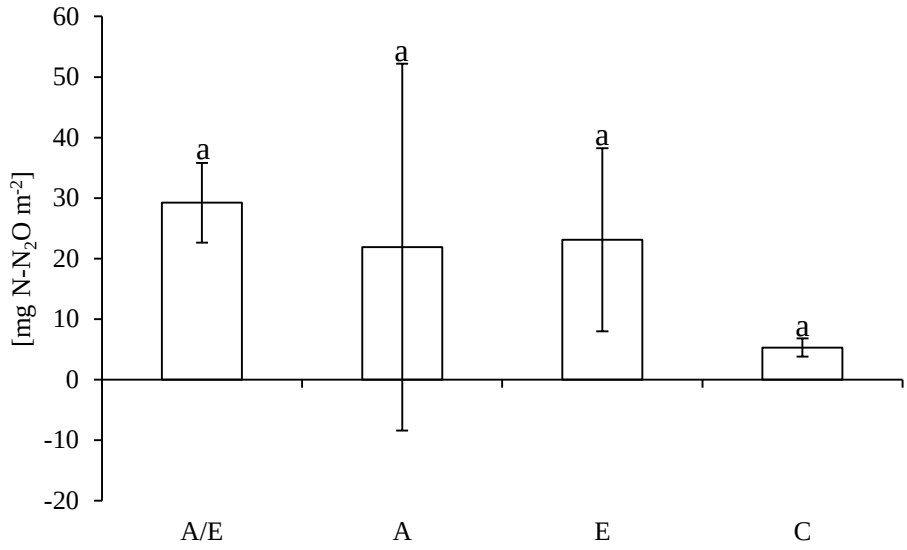

Fig. 2.2: Cumulative gas fluxes of N_2O (mg N-N_2O m^{-2}) and SD during the first period (0-30 days). Bars with the same letter are not significantly different.

During the second period, treatment A/E emitted cumulatively 104 ± 42 mg N-N_2O m^{-2} followed by treatment E with a cumulative flux of 85 ± 24 mg N-N_2O m^{-2}. The Non-earthworm treatments A and C revealed lower emission levels of 42 ± 26 - 49 ± 16 mg N-N_2O m^{-2} (Fig. 2.3). An ANOVA revealed significance difference between the treatments A/E and A (P = 0.01) and between A/E and C (P = 0.02).

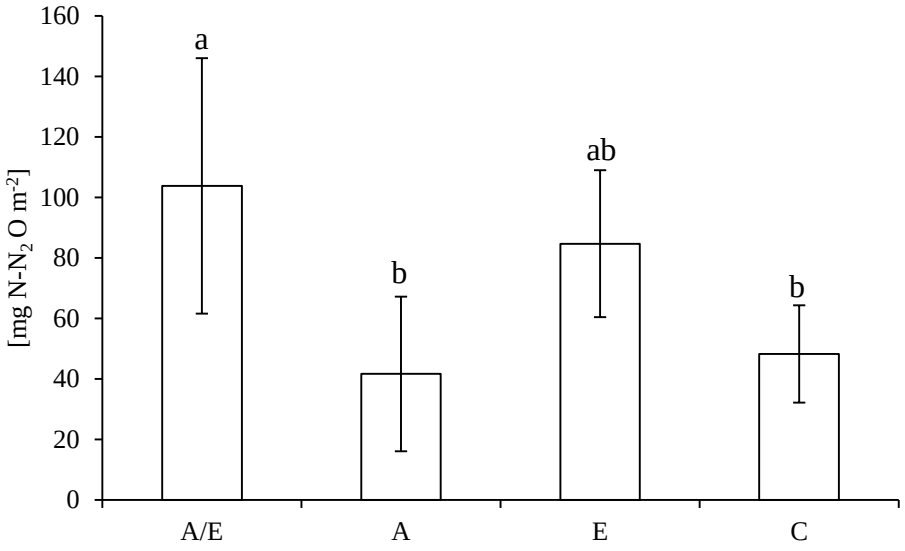

Fig. 2.3: Cumulative gas fluxes of N_2O (mg N-N_2O m^{-2}) and SD during the second period (30-60 days). Bars with same letters are not significant different.

During the third experimental period the soil columns of treatment C showed its highest emission and the highest of this period with a cumulative emission rate of approximately 98 ± 51 mg N-N_2O m^{-2}. The treatments with earthworms emitted from 28 ± 16 to 65 ± 88 mg N-N_2O m^{-2}. Extremely low cumulative fluxes were found for the pure ash treatment (A)

revealing a cumulative emission rate of solely 0.7 ± 0.3 mg N-N_2O m^{-2} (Fig. 2.4). After testing with ANOVA the treatments showed significance differences. The difference between ash and control prevailed (P = 0.02) but not between earthworm and control.

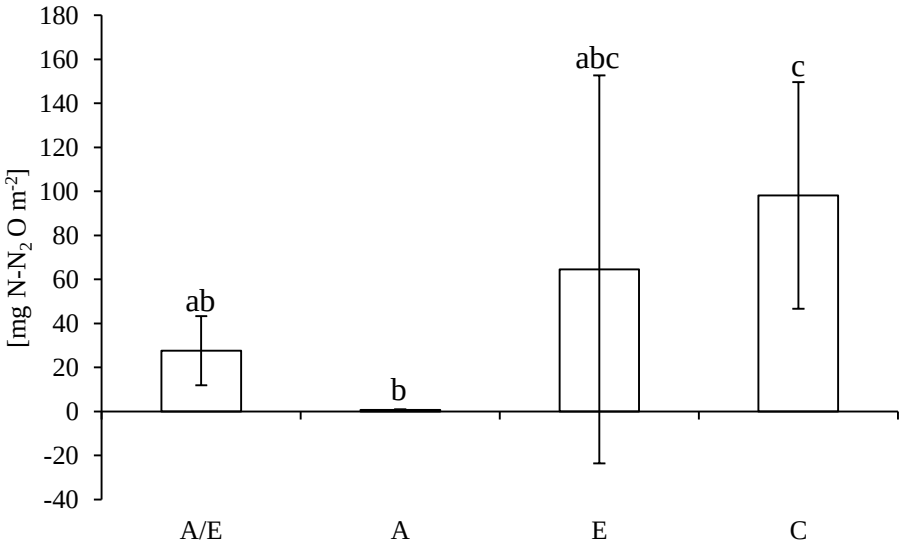

Fig. 2.4: Cumulative gas fluxes of N_2O (mg N-N_2O m^{-2}) and SD during the third period (60-90 days). Bars with the same letter are not significantly different.

Figure 2.5 shows the cumulative gas fluxes of N_2O during the whole experimental time of 90 days. The N_2O fluxes of the treatments with earthworms (A/E and E) showed the highest N_2O emission. The treatment earthworms had the highest N_2O emissions with cumulative mean of 172 ± 115 mg N-N_2O m^{-2}, followed by the treatment ash/earthworms with a mean emission rate of 161 ± 40 mg N-N_2O m^{-2}. The control revealed emissions of 152 ± 52 mg N-N_2O m^{-2}. The lowest emissions were found for ash treatment with cumulative emissions of 64 ± 17 mg N-N_2O m^{-2} which were significantly different (P = 0.04) than of the treatment earthworm while the emissions of the earthworm treatment were not significantly higher than those of the control. The difference between the treatments A/E and A are not even significant (P = 0.07).

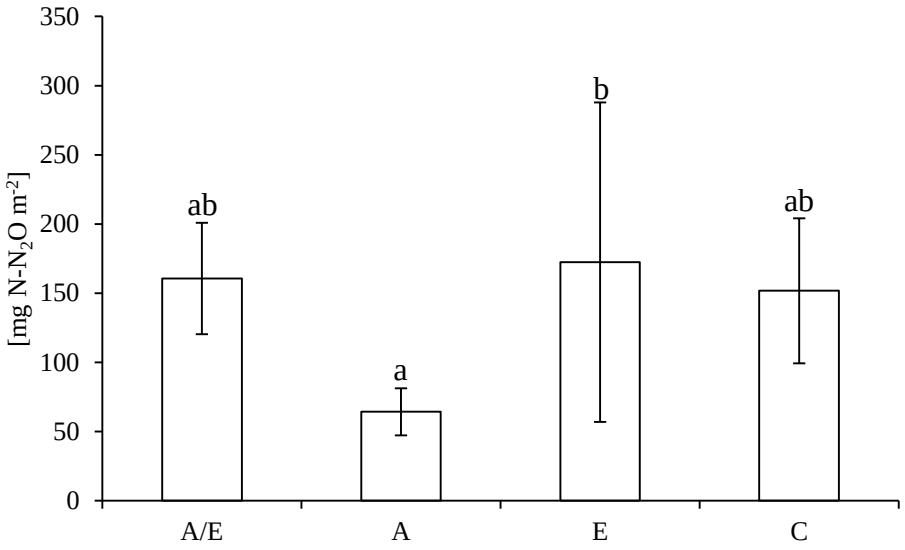

Fig. 2.5: Cumulative gas fluxes of N_2O (mg $N\text{-}N_2O$ m^{-2}) and SD during experimental time (90 days). Bars with the same letter are not significantly different.

2.4.2 CH_4 EMISSION

An increasing CH_4 uptake over the time of the experiment was observed. While the CH_4 uptake of the treatments ash and control increased continuously, the treatments with earthworms showed at the beginning of the study period a decreasing uptake (Fig. 2.6).

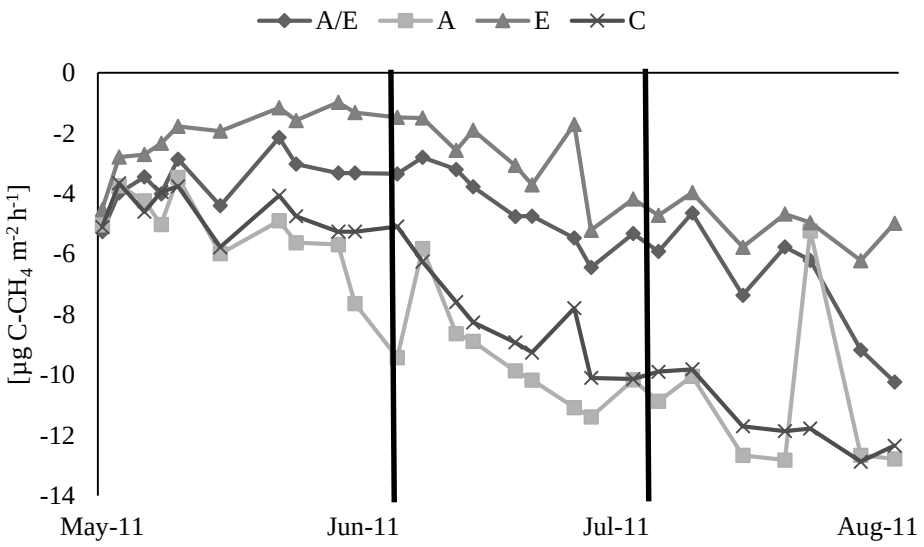

Fig. 2.6: Average fluxes of CH_4 (µg $C\text{-}CH_4$ $m^{-2}h^{-1}$) from the soil columns of the treatments ash/earthworms (A/E), ash (A), earthworms (E) and control (C) on base of 24 measurements over 90 days.

During the whole experimental time the treatments with earthworms (A/E and E) had a smaller CH_4 uptake rate and the treatment with earthworms alone had the smallest uptake rate. The temporal development of the CH_4-emission of the treatments showed several times increases and decreases.

Showing an average CH_4 uptake of -5 ± 2 µg C-CH_4 m^{-2} h^{-1} by earthworms and -5 ± 2 µg C-CH_4 m^{-2} h^{-1} of ash/earthworms respectively, the mean uptake of CH_4 in absence of earthworms was higher. The treatment ash showed an uptake of -8. ± 3 µg C-CH_4 m^{-2} h^{-1} and the control had also an uptake of -8 ± 3 µg C-CH_4 m^{-2} h^{-1}.

During the first period (0-30 days) the treatment ash and earthworm A/E had a cumulative uptake of approximately -2 ± 1 mg C-CH_4 m^{-2}. The treatment ash (A) the highest uptake -4 ± 2 mg C-CH_4 m^{-2} and treatment E had a low uptake of -1 ± 0.7 mg C-CH_4 m^{-2}. The control (C) had a cumulative uptake of -3 ± 0.4 mg C-CH_4 m^{-2} (Fig. 2.7). An ANOVA revealed significance difference (P = 0.02) between the cumulative CH_4-uptake the treatments ash and earthworm and a significant difference between control and earthworm (P = 0.04).

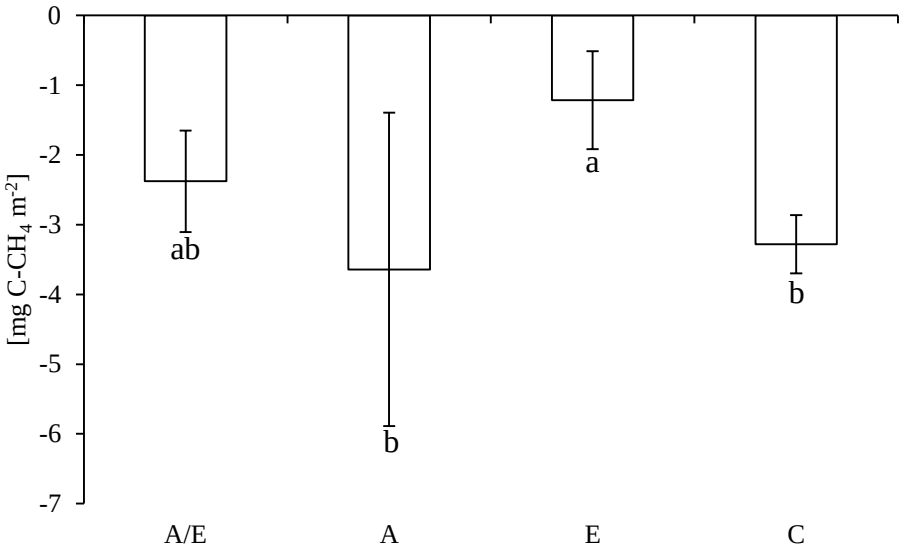

Fig. 2.7: Cumulative gas fluxes of CH_4 (mg C-CH_4 m^{-2}) and SD during the first period (0-30 days). Bars with the same letter are significantly different ($P \leq 0.1$).

During the second period, the treatment A/E had a cumulative uptake of -3 ± 0.4 mg C-CH_4 m^{-2}. The treatment E had a low cumulative uptake of -2 ± 0.7 mg C-CH_4 m^{-2}. The Non-earthworm treatments A and C revealed higher uptake levels of -7 ± 3 and -6 ± 0.3 mg C-CH_4 m^{-2} (Fig. 2.8). The treatments A/E and A were significantly different at P = 0.007 and the treatments A and E are significant different (P = 0.001). The treatment C is significant to E (P = 0.004) and A/E (P = 0.03).

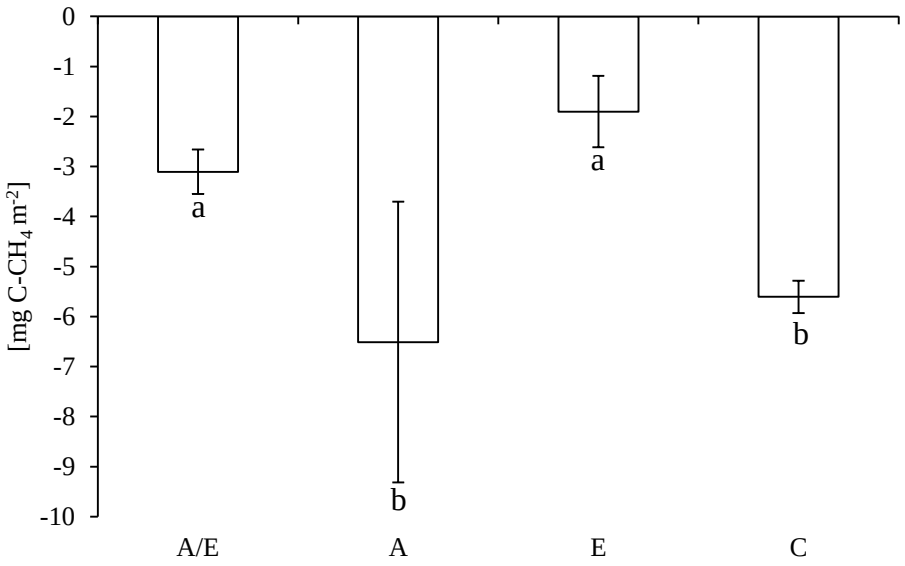

Fig. 2.8: Cumulative gas fluxes of CH_4 (mg C-CH_4 m^{-2}) and SD during the second period (30-60 days). Bars with the letter are not significantly different.

During the third experimental period the soil columns of treatment C showed its highest uptake and the highest of this period with a cumulative uptake rate of approximately -8 ± 0.3 mg C-CH_4 m^{-2}. Treatments with earthworms took up from -5 ± 1 to -4 ± 1 mg C-CH_4 m^{-2}. Also a high cumulative CH_4 uptake rate was found for the pure ash treatment (A) revealing a cumulative uptake rate of -7 ± 2 mg C-CH_4 m^{-2} (Fig. 2.9). After testing with ANOVA the treatments showed significance differences between A/E and A (P = 0.02) and A/E to C (P = 0.006). The treatment A is significant different to E (P = 0.003) and E to C (P = 0.001).

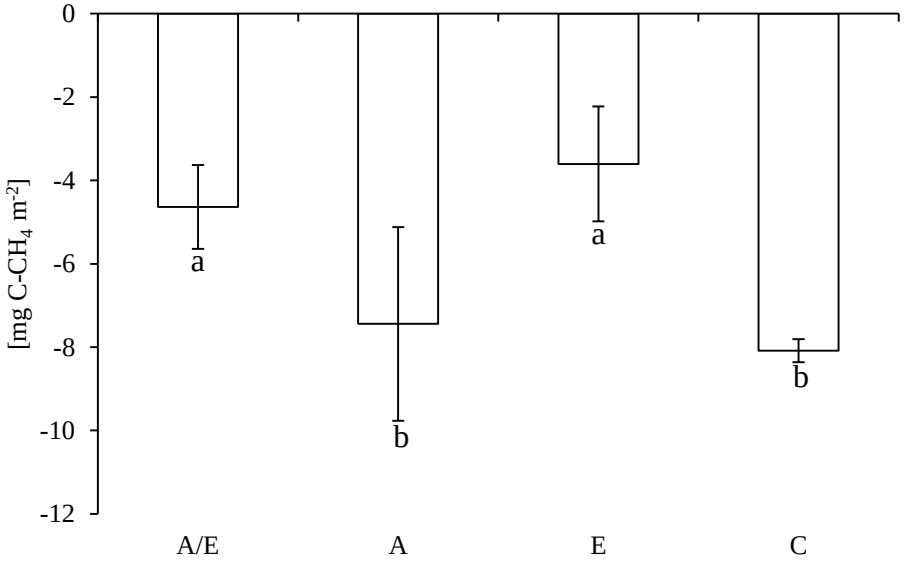

Fig. 2.9: Cumulative gas fluxes of CH_4 (mg C-CH_4 m^{-2}) and SD during the third period (60-90 days). Bars with the same letter are not significantly different.

Figure 2.10 shows the cumulative CH_4 gas fluxes (µg C-CH_4 m^{-2}). After testing the results with a one-factor variance analysis (ANOVA) a significant difference was found between A/E and A (P = 0.02) and A/E to C (P = 0.03), A and E (P = 0.002) and between the treatments E and C (P = 0.003). Mean cumulative results for the CH_4 uptake of the treatments ash/earthworm (A/E) (-10 ± 2 µg C-CH_4 m^{-2}, ash (A) (-18 ± 7 µg C-CH_4 m^{-2}), earthworms (E) (7 ± 2 µg C-CH_4 m^{-2}), control (C) (-17 ± 0.5 µg C-CH_4 m^{-2}).

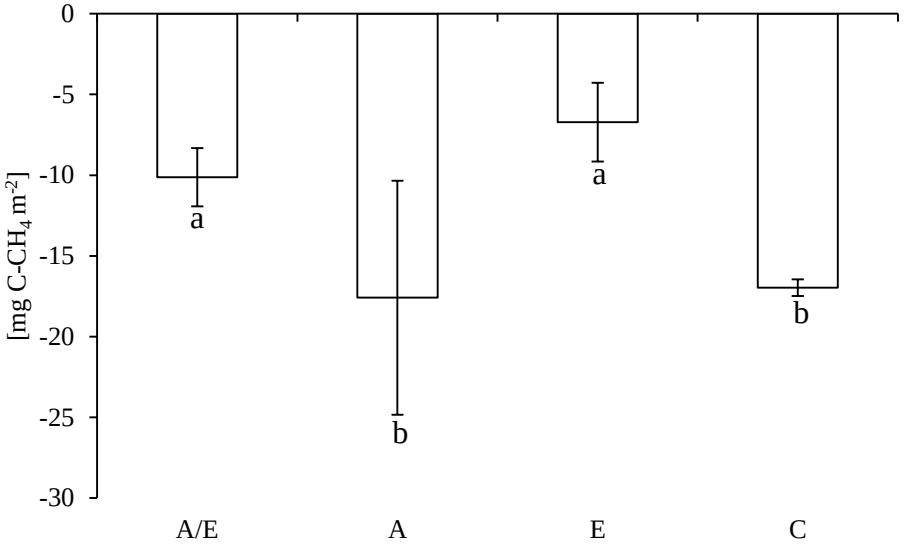

Fig. 2.10: Cumulative gas fluxes of CH_4 (µg C-CH_4 m^{-2}) while experimental time (90 days). Bars with the same letter are not significantly different.

2.4.3 CO_2 EMISSION

The CO_2 fluxes are in comparison to the other two gases relatively constant throughout the 90 days (Fig. 2.11). The treatments with ash and earthworm showed the highest mean value of 51 ± 8 mg C-CO_2 m^{-2} h^{-1} followed by the treatment ash (47 ± 7mg C-CO_2 m^{-2} h^{-1}). The CO_2-emission of the earthworm treatment was in-between the ash treatments and the pure soil control with a mean emission of 33 ± 5 mg C-CO_2 m^{-2} h^{-1}. The control (C) had the lowest CO_2 fluxes with a mean of 27 ± 4 mg C-CO_2 m^{-2} h^{-1}.

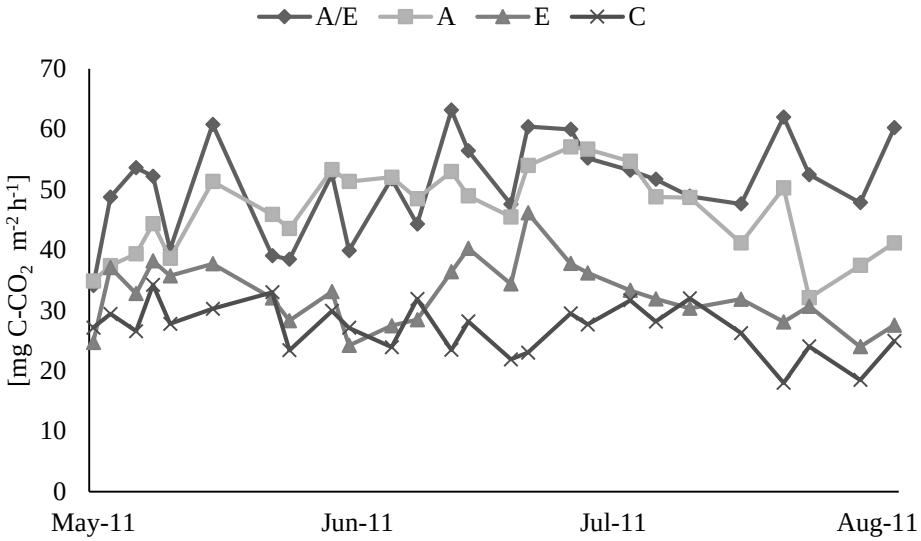

Fig. 2.11: Average fluxes of CO_2 (µg C-CO_2 m^{-2} h^{-1}) from the soil columns of the treatments ash/earthworms (A/E), ash (A), earthworms (E) and control (C) on base of 24 measurements over 90 days.

Figure 2.12 shows the cumulative gas fluxes of CO_2 (mg C-CO_2 m^{-2}) during the 90 days of the experimental time span. The treatments showed following flux rates: Ash/earthworms (A/E) (62 ± 7 g C-CO_2 m^{-2}), ash (A) (58 ± 15 g C-CO_2 m^{-2}), earthworms (E) (40 ± 2 g C-CO_2 m^{-2}) and the treatment control (C) (33 ± 3 g C-CO_2 m^{-2}).

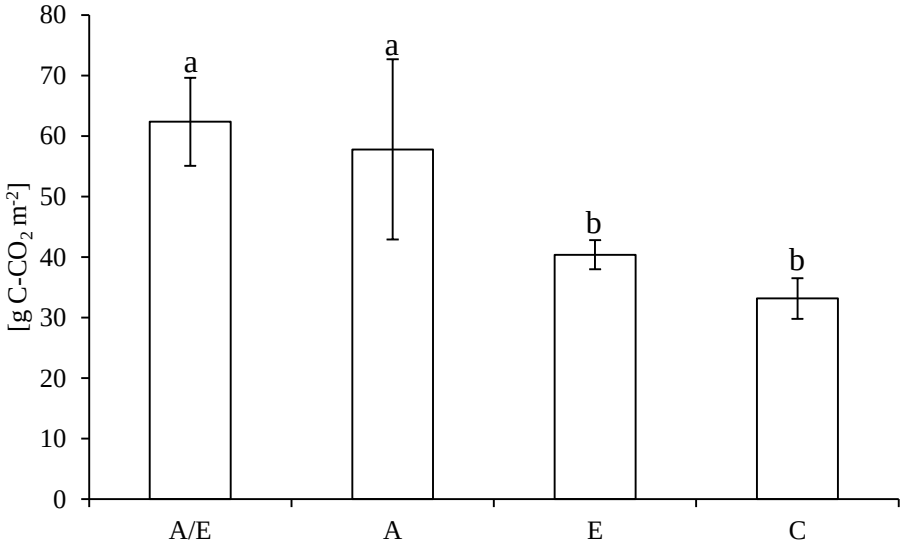

Fig. 2.12: Cumulative CO_2 fluxes in (g C-CO_2 m^{-2}) and SD during the experimental time (90 days). Bars with the same letter are not significantly different.

The statistical differences between the cumulative values of the total 90 day period were displayed in figure 2.12. The difference between the treatment A/E and E was significant

different (P = 0.003) and between A/E and C (P = <0.001). The difference between A and E was (P = 0.01) and A to C (P = 0.002).

2.4.4 COMBINATION OF THE GAS FLUXES OF EXPERIMENTAL TIME

To combine the results of the treatments in terms of the Global Warming Potential (GWP) of N_2O, CH_4 and CO_2 released from soil, the CO_2-equivalent (CO_2e) is used. The results are shown in Tab. 2.1. All treatments were net-sources for greenhouse gases. The treatment ash/earthworms had the highest net-emission (303 g CO_2e m^{-2}), followed by the treatments ash (241 g CO_2e m^{-2}) and earthworm (228 g CO_2e m^{-2}). The treatment control showed the lowest net-emission during the experimental time (192 g CO_2e m^{-2}).

Tab. 2.1: Relative parts of carbon and nitrogen of the net emission (CO_2e) during the experimental time.

Treatment	Balance (CO_2e)	C-(CO_2e)		N-(CO_2e)	
	g/m^{-2}	g/m^{-2}	%	g/m^{-2}	%
Ash/Earthworm	303	228	75	75	25
Ash	241	211	88	30	12
Earthworm	228	148	65	80	35
Control	192	71	63	71	37

CO_2 dominated the net-emission from the treatments (Tab. 2.1). In particular, the treatments ash 88%, ash/earthworm 75% and earthworm 65 % had a high percentage of CO_2 on the net-emission. The treatments planted with ash had a lower percentage of N_2O than the unplanted treatments. CH_4 was irrelevant in terms of CO_2 equivalents.

2.5. DISCUSSION

2.5.1 N_2O

The measured N-N_2O fluxes are comparable to the results of BORKEN et al., (2000). The results of them also showed peaks of the pure soil treatments with earthworm after nearly two month of incubation. The control had a small peak after 3.5 month. The main question to be answered by this experiment was, if the influence of earthworms on GHG fluxes prevails for planted soil representing a more complete ecosystem model experiment. It has been recognized that N_2O emissions of these experiments were at relative low levels (9-42 µg N-N_2O m^{-2} h^{-1}) during the first 37 days. In the following 29 days, N_2O emission of nearly all treatments showed a strong increase, but with different timing. The treatments ash/earthworm reacted 9 days prior as the earthworm treatment and their non-earthworm counterparts, whereas the treatments with ash reacted faster (8 days) than those without ash.

For the complete measurement duration of 90 days solely the pure ash treatment revealed to be different to the others. Hence, an enduring earthworm effect was solely found for the plant-soil system but not for the pure soil systems. During the "hot moment" phase of days 30 to 60 the elevated differences between earthworm treatments and non-earthworm treatments were significant. A temporal differentiation of the impact of earthworm on greenhouse gases from soil seems, therefore to be appropriate.

Consequently, with respect to hypothesis 1, that earthworms support the release of N_2O, our results solely fully support this assumption for planted soils. The differences between the treatments with ash/earthworms and the treatment ash had a significant difference of $P = 0.07$ an influence of the earthworms on N_2O emission can be derived from the results.

The very high N_2O emission of the treatments ash/earthworm and earthworms are probably due to changes to the soil structure caused by the placement of the earthworms and the creation of burrows (tunnel effect) (BORKEN et al., 2000). Studies on the influence of earthworms on microbial activity in soils provide evidence for our assumption (SVENSSON et al., 1986; EDWARDS & BOHLEN, 1996; PARKIN & BERRY, 1999; TIUNOV & SCHEU, 1999; BERTORA et al., 2007; RIZHIYA et al., 2007; SIMEK & PIZL, 2010;). According to these studies, a higher microbial activity and thus higher greenhouse gas emissions due to earthworm activity via incorporation of litter were to be expected. This proved to be very true for the high emission phase but not so clear for the longer termed cumulative N_2O emissions.

A reason for the enhance turnover of the nitrogen reserve in soil with earthworms could be a surface increase of the soil through mechanical bioturbation. Additionally exudation of rich C- and N-bindings what support the microbial activity. Apparently the influence is not immediately but delayed by some 30 days which is reasonable as bioturbation and turnover of leaf litter driven by earthworms may need some time to initiate changed biogeochemical cycling. Far more interesting is the fact of different delay times between soil-plant and pure soil systems and why these elevated emissions rates ebb off after 17 days. The latter mostly likely is due to limited C and N sources in such an experiment. Therefore this outcome needs to be verified in a longer termed experiment with C and N sources coming from plants or other autotrophic organisms receiving external N sources as well. This would preferable happen in a field study. Indication that plants matter here is given by this experiment, as significantly differences between earthworm treatment and non-earthworm treatment prevail over 90 days in the presence of ash saplings.

To appear the relative parts of N_2O to the net emission (CO_2e) of the treatments ash and ash/earthworms, that *in vivo* emissions took place like in the study from DRAKE & HORN (2007). When relative part of the net N_2O emission from the treatment ash gets only 12% and the relative part of the treatment ash/earthworms had with about 25% a higher relative part of the net emission of N_2O then an influence of the earthworms was possible. The relative parts of the unplanted group are higher 35 – 37 %.

Hypothesis 3, that earthworm effects are independent of ash and control treatment could only be proofed in the "hot moment" since the influence was statistical significant for A/E and A ($P = 0.01$) and A/E and C ($P = 0.02$). Nevertheless for the entire experiment only a difference was found between the treatment A and E ($P = 0.04$). Hypothesis 3 has, therefore, to be rejected and it is stated that earthworm effect depend on ash treatment.

2.5.2 CH_4

It was shown that earthworms apparently reduce the uptake rates of this soil. Cumulative CH_4 gas fluxes of the treatment earthworms (-7 ± 2.4 mg C-CH_4 m^{-2}) in comparison to the control (-17 ± 0.5 mg C-CH_4 m^{-2}) were significantly lower ($P = <0.001$) of about 60%. For the planted treatments this difference was 42% ($P = 0.02$) cumulative C-CH_4 uptake rates -18 ± 7 mg C-CH_m^{-2} for ash and -10 ± 2 mg C-CH_4 m^{-2} for ash/earthworm.

Hypothesis 1, that earthworms had a higher CH_4 uptake into the soil has to be rejected and the opposite appears true that earthworm reduce CH_4 uptake. The treatments ash/earthworm and ash ($P = 0.02$) are significantly different. There are no studies describing earthworms as direct CH_4 emitters due metabolic processes (DRAKE & HORN, 2007; IHSSEN et al., 2003; KARSTEN & DRAKE, 1997), consequently it is assumed that the reduced CH_4 uptake either refers to a decreased activity of methanotrophic bacteria in the soil columns or a reduced diffusion. The latter appears unlikely as earthworms create large holes and should therefore increase the bulk density of the soil. During experimental time a progressive soil settlement was observed, due earthworm activity and thus reduced pore volume. The major prerequisite for CH_4 uptake in the soil is that the methanotrophic bacteria decrease the CH_4 concentration and thus enhance the diffusive gradient between soil and atmosphere (BLUME et al., 2010). Sufficient oxygen availability is necessary for CH_4 uptake and is determined by soil structure and ventilation (FIEDLER, 2001). Regarding the observed soil settlement, we suppose that oxygen diffusion from the atmosphere into the soil was limited, and thus lead to a relative inhibition of the methanotrophic bacteria in the soil columns.

Setting of the soil is obviously due to the bioturbation of the earthworms (in mean (A/E) -2 ± 0.3 cm 90 d^{-1} and (E) -2 ± 0.3 cm 90 d^{-1}) in relation to the treatments without earthworms (in mean (A) -0.8 ± 0.3 cm 90 d^{-1} and (C) -0.4 ± 0.3 cm 90 d^{-1}). The soil material consumed by the earthworms for the metabolism and changes it in smaller homogenized parts. The soil columns with earthworms showed a lot of "bio pores", but the high WFPS reduced the gas diffusion since *Aporrectodea caliginosa* is a horizontal driller (EDWARDS & BOHLEN, 1996) its tubes do not support vertical aeration of the soil.

Another possibility could be the stimulation of microbial activity in the worm scat and drilosphere to such an extent that microbial oxygen consumption is higher than the oxygen supply by diffusive transport from the atmosphere. As a consequence a reduced activity of methanotrophic bacteria and even methanogenesis could be possible. Accounting for the low influence of earthworms on CO_2 fluxes during the experimental time, the processes mentioned above seem negligible. In particular the CO_2 emission from aerobe soils is equimolar to the consumption of oxygen (BLUME et al., 2010).

A desorption of NH_4^+ from cation exchange sites by high activities of H^+, Na^+ and K^+ cations is one possible mechanism reducing CH_4 oxidation (FENDER et al., 2012) and the excreta of the earthworms contain ammonia and urea nitrogen (EDWARDS & BOHLEN, 1996), which reduces the CH_4 uptake.

Hypothesis 2 that the described earthworm effect is an enduring effect could be supported for the experimental time, but a steady-state effect after a longer time is possible. This solely applies to CH_4 but not for N_2O that has to be rejected there.

2.5.3 CO_2

The cumulative CO_2-emissions of the treatment earthworm compared to the control were statistically different (P = 0.02). Differences in cumulative CO_2-emission between earthworms (40±2 g C-CO_2 m^{-2}) and control (33 ± 3 g C-CO_2 m^{-2}) add up to 7 g C-CO_2 m^{-2} which is 18% higher. Regarding the treatments ash/earthworms (62 ± 7 g C-CO_2 m^{-2}) and ash (58 ± 15 g C-CO_2 m^{-2}), the average difference of 5 g C-CO_2 m^{-2} was similar but just not statistically significant (P =0.5). Thus, earthworms enhanced the CO_2 release from the soil columns.

In this regard, our hypothesis that earthworms stimulate CO_2 release from soils could basically be supported, but the results were only for the unplanted soil columns statistically significant. The field study of BORKEN et al. (2000) showed similar results. The authors found no significant differences of soil gas fluxes of CO_2 influenced by earthworms.

However they measured a significantly higher CO_2 emission in the first 4-5 weeks, which is explained by the construction of wormholes and the incorporation of detritus in the mineral soil. The question arises, if this study underestimates the temporal dimension of the mineralization process. The contribution of earthworms to soil respiration is small (EDWARDS & BOHLEN, 1996). So it is conceivable that the mineralization of ash litter needs a longer time to significantly influence the CO_2 emission. But ash litter would anyhow influence the soil respiration regardless if earthworms are present or not.

2.5.4 COMBINATION OF THE GAS FLUXES OF EXPERIMENTAL TIME

After calculating the gas fluxes of N_2O, CH_4 and CO_2, net emission of soil greenhouse gases in terms of CO_2-equivalent (CO_2e) of the treatment earthworms (228 g C-CO_2e m^{-2}) was higher than the control (192 g C-CO_2e m^{-2}), however the results were statistically not significant (P =0.067).

The hypothesis 1, that earthworms support the net emission (CO_2e) from the soil columns could be supported but was statistically not significant for planted treatment.

The hypothesis 2, that the described earthworm effect is an enduring effect (for a longer period) could not be supported.

CO_2 dominated the net-emission from the treatments (Tab. 2.1). In particular, the treatments ash 88%, ash/earthworm 75% and earthworm 65 % had a high percentage of CO_2 on the net-emission. The treatment ash and ash/earthworm had a lower percentage of N_2O 12% - 25% than the other treatments. The decreased cumulative N_2O emission from the treatment ash was caused of rhizosphere effects (FENDER et al., 2012). That shows the results of the calculated net emission (g CO_2e m^{-2}).

The relative influence from the plant-soil system on N_2O fluxes to the total GHG forcing was relevant and approximately double than compared to the treatment without earthworms and planted with ash (25% versus 12 %), whereas for the pure soil comparison the relative contribution of N_2O is about the same (37 vs 35%) but higher with earthworms.

The root respiration caused the higher percentage on the CO_2 emission (HANSON et al., 2000). The measurements take place without photosynthetic activity, so the CO_2 uptake over photosynthesis was shut down and the root respiration took place.

2.6 CONCLUSIONS

Based on this study, earthworms apparently do have an impact on the net fluxes of GHG from soils. Therefore other studies are mainly confirmed and additionally it was shown that

it matters if the effect is tested for pure soils or for plant-soil systems. This proofed to be true not only for the rather trivial case of CO_2 (as plants assimilate and respire CO_2) but for other two gases as well. For N_2O it was shown that earthworms increase the emission and for CH_4 it was measured that earthworms decrease the uptake. The difference between plants treated earthworm treatments and soil earthworm treatments were tested. Not only plants matter on the impact of earthworm but its temporal aspect. Here it was shown for N_2O that the elevated emissions may be of short term character and the overall fluxes may be leveled to non-significant differences, but for the plant-soil comparison this was not true. The methane uptake decreased by earthworm and the differences of the CO_2 emission are clearly influenced by the metabolisms of plants. Hence for future studies care has to be taken that plants are included and we need longer termed experiments to see if accelerated GHG fluxes by earthworms is an enduring effect or not.

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CHAPTER 3

ON THE SPECIES-SPECIFIC INFLUENCE OF PHOTOSYNTHESIS AND ROOT ACTIVITY OF BEECH AND ASH SAPLINGS ON N_2O FLUXES FROM SOIL

3.1 ABSTRACT

Knowledge about the influence of terrestrial ecosystems and their regulating function as net sink or source for greenhouse-gas fluxes is limited. During the past decades, land-use and land-cover changed and thus the interactions between the terrestrial biosphere, pedosphere, and atmosphere were altered. Modern research confirmed the importance of these ecosystem compartments to counteract human enforced climate change since industrial revolution 200 years ago. In this context, data on species-specific soil-plant interactions on carbon and nitrogen-cycles is helpful but rare. A laboratory experiment with incubated forest soil was conducted to investigate deciduous tree impacts on N_2O fluxes from soil. In a pre-experiment we detected reduced N_2O emission rates of ash – soil systems during photosynthetic activity. This study tested three hypothesis related to the influence of photosynthesis from saplings of ash (*Fraxinus excelsior* L.) and beech (*Fagus sylvatica* L.). The hypotheses were (1) there is an effect of photosynthesis on N_2O emissions from soils (2) There are differences between ashes and beeches with respect to their photosynthesis effect, and finally (3) diurnal trends exist which affect N_2O fluxes during the course of the day under climate chamber conditions. The N_2O emissions from soil were reduced during photosynthetic activity of both species. A diurnal trend in the reduction of N_2O emissions from the atmosphere by ash saplings was not observed. The potential of ash saplings to reduce N_2O emissions was even higher than of beech saplings. With photosynthesis, soils with ash had the lowest cumulative $N\text{-}N_2O$ emissions (1.1 mg $N\text{-}N_2O$ m^{-2}). In relation to the controls (8.5 mg $N\text{-}N_2O$ m^{-2}), emissions of ash-treatments were reduced by 88 %. The cumulative emissions of beech-treatments (3.9 mg $N\text{-}N_2O$ m^{-2}) were 55% lower than emissions from the control.

To conclude, tree species may relevantly affect the source/sink potential of terrestrial forest soils for N_2O emissions species specifically. In this experiment, during active photosynthesis, ash showed similar reduction effects on N_2O emissions than beech.

Keywords: Nitrogen emission, *Fraxinus excelsior* L., *Fagus sylvatica* L., photosynthesis, greenhouse gas

3.2 INTRODUCTION

Nitrous oxide (N_2O) is a major greenhouse gas (GHG) which is involved in global warming. Atmospheric concentrations are increasing since the onset of the industrial revolution as is true for the other GHGs. This is due to human activities, which mainly are burning of fossil fuel and land use and land use change (IPCC, 2007). A single gram of N_2O has the same global warming effect as 298 grams of CO_2 for the time span of 100 years (GWP_{100}), (FORSTER et al., 2007). The main reason for increased N_2O from ecosystems is nitrogen overloading in the course of direct fertilization and atmospheric depositions. Therefore, it is an essential task to identify potential processes reducing GHG losses to the atmosphere. Forest soils of the northern hemisphere play an important role in the C and N cycling and therefore in the GHG exchange with the atmosphere (IPCC, 2007; JANSSENS et al., 2003; UNFCCC, 1997). It is well established that the origin of GHG emissions from soils are mainly produced by microorganisms and are influenced by abiotic factors like soil temperature, bulk density, pH-value and soil moisture (CIARLO et al., 2008; LE MER & ROGER, 2001). Less knowledge about biotic influences like species identity, root activities or photosynthetic activity exists which all have an influence on rhizosphere biogeochemistry. Therefore, soil microbial activity may also be driven by species specific above ground litter and root quality (PFEIFFER et al., 2013) which has influence on the net GHG emissions from soils (FENDER et al., 2012[b]). Moreover, Fender et al. (2012[b]) showed that GHG emissions differed markedly between ash and beech.

These tree species are most common in central European forests and are important for modern economic forestry (ELLENBERG & LEUSCHNER, 2010). For this study they were chosen because of their differences in root-growth, -morphology and mycorrhizae constitution (MEINEN et al., 2009) and because of their different shoot morphology and growth. During the studies of Fender et al. (2012[b]) there were indications that photosynthetic activity may have influence on the measured N_2O fluxes. The present study is designed to investigate this indication in more detail in a long-term greenhouse study.

The hypotheses were:

(1) there is an effect of photosynthesis on N_2O emissions from soils

(2) there are differences between ashes and beeches in this photosynthesis effect, and finally

(3) diurnal trends exist which affect N_2O fluxes during the course of the day

Further material about interaction of organisms on N_2O in soils is presented in Chapter 1.

3.3 MATERIAL & METHODS

3.3.1 PLANT AND SOIL MATERIAL

The soil used for the soil column experiment in this study was retrieved from a mixed deciduous broad-leaved forest in the Hainich National Park, Thuringia, Germany (51°04'N 10°30'E). The dominant tree species at the sampling site were *Acer pseudoplatanus* L., *Acer platanoides* L., *Carpinus betulus* L., *Fagus sylvatica* L., *Fraxinus excelsior* L., *Tilia cordata* Mill. and *Tilia platyphyllos* Scop. (FENDER et al., 2012[b]). The soil was a stagnic Luvisol with a texture of silty clay (2.9% sand, 56.5% silt and 40.6% clay) and a pH_{KCl} of 5.3. The soil was sampled from the upper 10 cm (A_h-horizon) and homogenized by passing through a 2 mm mesh sieve. It was assumed that the microbial community had sufficiently adapted to the experimental conditions in the columns under greenhouse conditions (PFEIFFER et al., 2013). Soil fertilization with 25 kg KNO_3 ha^{-1} was carried out to simulate atmospheric N deposition and because the fluxes were low due to N uptake by plants (FENDER et al., 2012[a]). To enrich the soil with labile carbon, fertilization with 100 mL soluble C (5g L^{-1} powdered ash litter) was applied which was done to simulate natural condition (leave fall). The detection of the differences between the treatments are of a higher quality if fluxes are higher and not limited by carbon or nitrogen simulating near nature conditions (FENDER et al., 2012[a]). The C/N-ratio at the start of the measurement was 11.8 with 1.82 % organic carbon (C_{org}). The nitrate and ammonia concentrations are shown in Tab. 3.1 and already varied due to tree specific effects.

Tab. 3.1: Nitrate and ammonia concentrations (Means ± SE [$mg\,l^{-1}$]) at three dates of the experiment. Soil samples were taken at the beginning of the experiment (11/22/2011), before first fertilization (01/22/2012) and at the end (05/01/2012).

Date	***F. excelsior***		***F. sylvatica***		**Ctrl**	
	NO_3^-	**NH_4^+**	**NO_3^-**	**NH_4^+**	**NO_3^-**	**NH_4^+**
11/22/2011 (start of measurements)	4.2 ± 2.1	0.3 ± 0.0	10.7 ± 2.4	0.3 ± 0.1	4.7 ± 2.7	0.3 ± 0.0
01/22/2012	6.0 ± 1.4	0.1 ± 0.0	6.3 ± 2.1	0.1 ± 0.0	11.3 ± 2.9	0.2 ± 0.0
05/01/2012	6.2 ± 2.2	0.2 ± 0.0	9.4 ± 1.9	0.1 ± 0.0	11.2 ± 2.0	0.3 ± 0.1

3.3.2 EXPERIMENTAL SETUP

15 acrylic glass cylinders (height: 50 cm, diameter: 17 cm) were filled with 5 kg of freshly sieved (2 mm) soil. The cylinders were planted with 3-6-year-old saplings of approximately identical biomasses (15-20 cm height) resulting in the following treatments:

- 5 columns planted with two ash saplings (*Fraxinus excelsior* L., Treatment A)
- 5 columns planted with two beech saplings (*Fagus sylvatica* L., Treatment B)
- 5 columns without plants (controls, Ctrl.).

The soil columns were placed in a climate chamber with a mean air temperature of 20°C, and a mean relative air humidity of 80%. Illumination of the trees was maintained by lamps 203 ± 10 µmol m^{-2} s^{-1} PPFD; (Eye Lighting, Clean Ace, Mentor, OH, USA). The water-filled pore space was calculated for each soil column and was adjusted to 75-80 %. Soil moisture was controlled once a week.

3.3.3 TRACE GAS MEASUREMENTS

The long-term experiment began in November 2011 and ended in May, 2012. Over a time period of 143 days the gas fluxes were measured bi-weekly (14 times). During each measurement the light permeable acrylic glass columns were closed gas-tight with a lid, but leaving the cylindrical wall uncovered for maintaining the photosynthesis activity of the tree saplings (modus 'PS = 1'). To determine the potential effect of photosynthesis on trace gas fluxes, these measurements were repeated 10 minutes after darkening the entire columns with a black scrim (modus 'PS = 0', Fig. 3.1). Between both modi, the columns were opened for equilibration of air inside and outside of the columns.

Per column, both measuring modi alternated, starting with 'PS = 1' or with 'PS = 0'. During the setting with photosynthesis, NEE (net ecosystem exchange) was measured. R_{ECO} (ecosystem respiration) was measured without photosynthesis, whereby gross ecosystem exchange could be calculated with GEE = NEE - R_{ECO}.

A catheter needle installed in the lid provided a gas-tight connection with a 60 mL syringe for gas sampling in the headspace of each soil column, about 0.3 – 0.32 m above the soil surface. The columns were closed for 20 minutes. Samples were taken at time 0, 10, and 20 min after closing the columns.

Fig. 3.1: Illustration of the soil columns planted with tree saplings of either species. The measuring modus under maintenance of photosynthesis (PS = 1) is shown to the left, and under complete dark conditions to the right (PS = 0).

3.3.4 24-HOUR MEASUREMENT

It was assumed that it will have an effect at which time of the day the photosynthesis effect on N_2O fluxes from the soil will be measured. The effect should be greater in the morning when plants just started with photosynthesis than in the evening when plant have been photosynthetically active for a maximum time. It was assumed that the possible effect of photosynthesis is related to root derived metabolic organic substances (C and N sources). The concentrations of these metabolites should be maximum (filled up reservoirs) in the evening and minimum in the morning (after longer time of no production but steady consumption). In consequence turning off the light in the morning should lead to a fast depletions of these reservoir and therefore and effect on the N_2O fluxes, whereas in the evening these reservoirs will be used up at a much longer time.

The method of taking gas samples was the same as in the long-term experiment. However, gas samples were taken only for the soil columns planted with ash because they showed the greatest effect of photosynthesis on trace gas fluxes. The samples were taken on 1st and 2nd of May, 2012 in 3-hour intervals starting at 5 a.m. and ended at 2 a.m., respectively. The gas fluxes were first measured under exclusion of photosynthesis and afterwards during photosynthesis activity, because it was shown that it did not matter if fluxes were first

measured with or without photosynthetic activity. The day before the onset of gas flux measurements (April, 30th) the water-filled pore space was adjusted to 75-80 %. After the experiment, all columns were weighed again. The calculation of WFPS for every sampling time based on the assumption that WFPS decreases linearly during 24 hours by evaporation and water consumption of the trees (Tab. 3.2).

Tab. 3.2: Decreasing WFPS during the 24h experiment.

Time of day	**Hours after watering**	**WFPS [%]**				
		Column 11	**Column 12**	**Column 14**	**Column 16**	**Column 17**
	0	75	75	75	75	75
5:00 AM	14	73.77	75.00	71.70	73.70	71.40
8:00 AM	17	73.60	74.80	71.50	73.50	70.70
11:00 AM	20	73.40	74.60	71.30	73.30	70.10
2:00 PM	23	73.20	74.35	71.10	73.10	69.40
5:00 PM	26	72.90	74.12	70.90	72.90	68.75
8:00 PM	29	72.80	73.90	70.70	72.70	68.10
11:00 PM	32	72.80	73.60	70.50	72.50	67.50
2:00 AM	35	72.30	73.40	70.30	72.20	66.60

3.3.5 ANALYSIS OF TRACE GAS SAMPLES

The gas concentrations were analysed with an auto-sample, computer-controlled (Probe 64+1, V1.31, LOFTFIELD, 1997) gas chromatograph (Shimadzu GC-14B, Tokyo, Japan). CO_2 and N_2O were detected by a ^{63}Ni electron capture detector and the CH_4 with a flame ionization detector. A linear regression was used to calculate the increase or decrease of gas concentrations between N_2O measurements at T_0, T_1, and T_2. The gas flux rates from the soil to the atmosphere were calculated by the ideal gas law using a formula given by LESSARD et al. (1997), which considers the slope and time intervals of the measurements.

3.3.6 ANALYSIS OF SOIL PROPERTIES

To analyze the concentrations of nitrate (NO_3^-) and ammonium (NH_4^+), soil samples were taken from all soil columns at the end of the pre-study (05/11/12), before fertilizing the soils (02/28/12), and at the end of this experiment (05/02/12). An continuous flow injection

colometry (SAN+ Continuous Flow Analyzer, Skalar Instruments) were used. NO_3^- was determined with the copper-cadmium-reduction method (ISO 13395), and NH_4^+ was determined with the Berthelot-reaction method (ISO 11732). The soil samples for measurement of the pH-value were taken on 11 May 2011, and on 02 May 2012.

3.3.7 STATISTICAL ANALYSIS

Statistical analyses were performed using R 2.15.0 (03/30/2012) for Microsoft Windows (The R Foundation for Statistical Computing) with the "agricolae", "coin" and "exactRankTests" packages. All data were tested for normal distribution with the Shapiro-Wilk test. If any factor like tree species or photosynthesis influenced gas fluxes was tested by using the F-test.

All gas fluxes showed non-normal distribution. In order to identify significant differences among the gas fluxes and the tree treatment, means for the cumulative gas fluxes and the gas fluxes for each measurement day, the Least Significant Difference (LSD) – test from the "agricolae"-package including the multiple comparisons through the method of the minimum significant difference was used. For the single measurement days, a level of significance of $P = 0.1$ and for the cumulative gas fluxes of $P = 0.05$ was used.

To test the influence of the photosynthesis, absolute differences between a gas flux measured without and with photosynthesis (named Δ (delta)) setting were calculated and tested by the t-test if the means of Δ are significant different to 0 with an $P = 0.05$. If delta provides a negative value, emissions were reduced by photosynthesis activity.

A correlation analysis was conducted to relate the fluxes and environmental parameters (temperature, WFPS, content of NO_3^- or NH_4^+). For non-normal distributed data the correlation was tested after Spearman and for normal-distributed data the test after Pearson. The difference from PS=0 and PS=1 tested with the t-Test. A photosynthesis effect between the measurement with and without photosynthesis on the N_2O fluxes was defined as Δ-delta. If Δ-delta showed a negative value then the N_2O fluxes decreased, if Δ-delta is positive the N_2O fluxes increased.

3.4 RESULTS

3.4.1 LONG-TERM SOIL COLUMN EXPERIMENT

Soils planted with trees reduced N_2O emissions from soils for 8 out of 14 (PS=0) and 10 out of 14 (PS=1) measurements dates. Emissions from soils planted with ash were significantly lower than from the soils planted with beech. With respect to the planted soil columns, the

influence of photosynthesis on N_2O reduction during daytime was highly significant ([PS=0 - PS=1] is significantly different to zero) for most of the measurement dates. Significant differences between the controls and planted soil columns are shown in Figure 3.2.

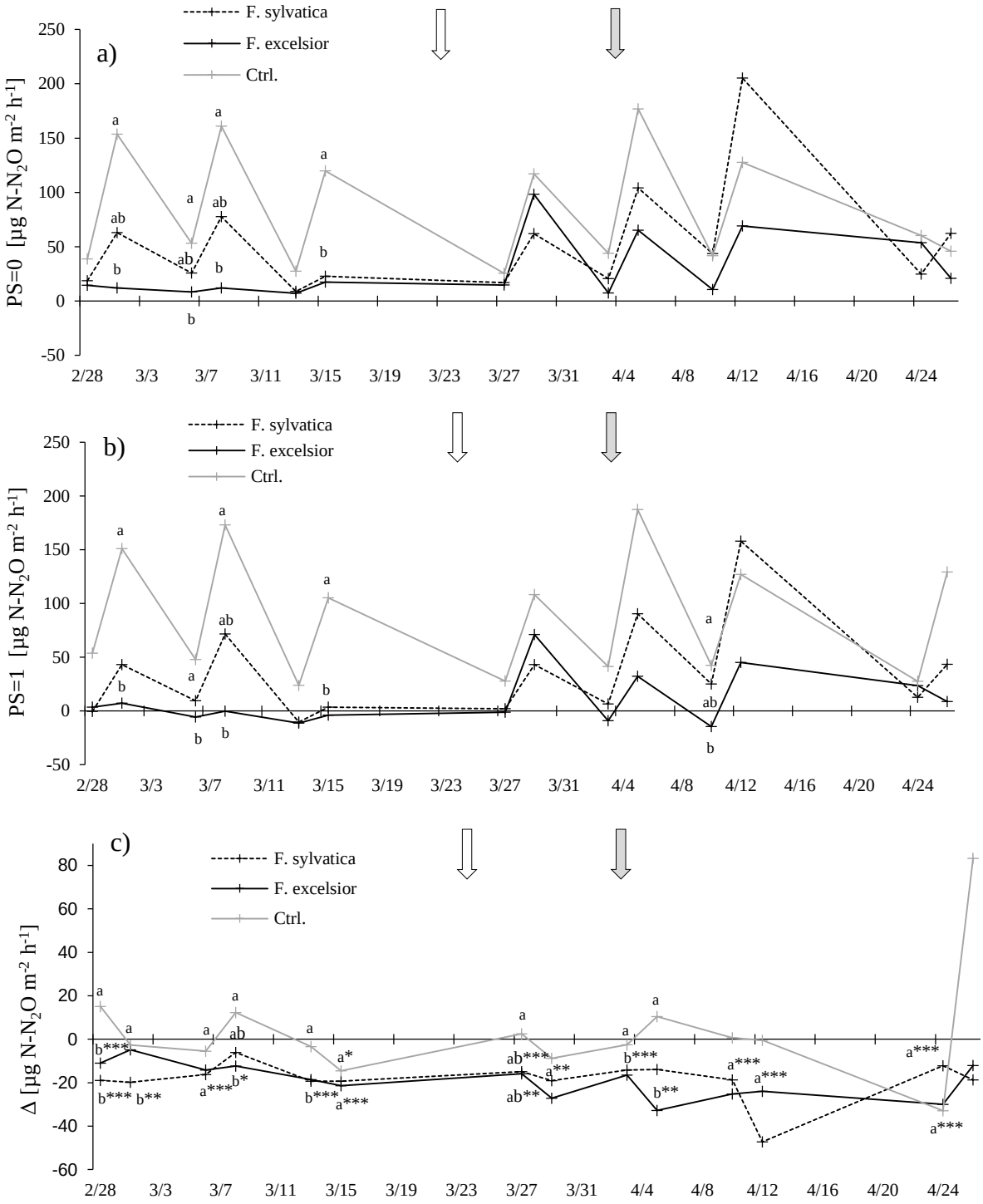

Fig. 3.2: Mean net N-N_2O flux (a) without (PS=0) and (b) with (PS=1) photosynthesis and (c) absolute difference between PS=0 and PS=1 (Δ-delta) for incubated soils. Significant differences between the gas fluxes are indicated by different letters ($P < 0.1$) using LSD-based pairwise comparisons. White arrow = date of NO_3^-fertilization with 100 mL solution corresponding to 100 kg KNO_3 ha^{-1}; Grey arrow = Date of fertilization with 100 mL soluble C (5g L^{-1} powdered ash litter). Fluxes significantly different from zero symbolized with: $P < 0.1$ (*), 0.05 (**), and 0.01 (***).

3.4.2 CUMULATIVE N_2O EXCHANGE

Without consideration of photosynthesis, the cumulative N_2O-flux from soil planted with ash was 60 % (2 g N-N_2O m^{-2}) lower than the control (5.1 g N-N_2O m^{-2}). Emissions from soils planted with beech (3.4 g N-N_2O m^{-2}) were 33% lower than those of control soils (Fig. 3.3).

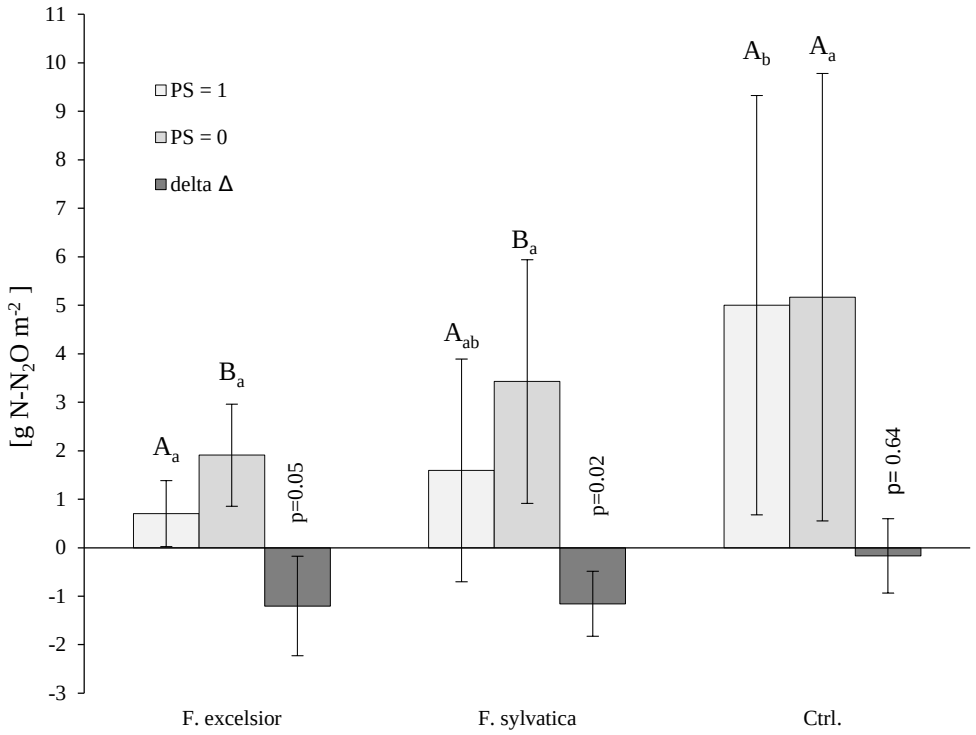

Fig. 3.3: Mean net cumulative N-N_2O fluxes without (PS=0) and with (PS=1) photosynthesis and absolute difference between PS=1 and PS=0 (Δ-delta) at the end of whole measuring period. The cumulative gas fluxes with same capital letters are not significantly different ($P > 0.05$; differences between PS=0 and PS=1) and the treatments with same indexed letters are not significantly different ($P > 0.05$; differences between ash, beech, and control) using the LSD-based pairwise comparisons test. The delta of all tree species were tested with the one sample t-test if delta's means are significantly different to 0 (when the *P* -Value is lower than 0.05); for ash and beech n=5, means ± SD.

With photosynthesis, soils with ash had the lowest cumulative N-N_2O emissions (0.7 g N-N_2O m^{-2}). In relation to the controls (5 g N-N_2O m^{-2}), emissions of ash-treatments were reduced by 86 %. The cumulative emissions of beech-treatments (1.6 g N-N_2O m^{-2}) were 68% lower than emissions from control.

Summarizing, the influence of photosynthesis reduced the N-N_2O emissions of ash from 2 to 0.7 g N-N_2O m^{-2}. This is a reduction by 65% compared to the PS=0 emissions. For soils with beech, emissions were reduced from 3.4 to 1.6 g N-N_2O m^{-2}. This is a reduction of fluxes by 53 % of the PS=0 emissions from soils planted with beech.

For each planted treatment, PS=0 and PS=1 are significantly different ($P \leq = 0.05$, shown as capitalized letters). Soils with ash tended to be different from soils with beech but were solely significantly different from the control (shown as small indexed letters). The influence of photosynthesis is shown by Δ and must be significant to zero (tested with the t-test) to be approved. The *P*-values showed that the photosynthesis had a significant influence on N-N_2O effluxes for planted soil column (*P*-values are all ≤ 0.05).

3.4.3 N_2O FLUXES OF THE 24H MEASUREMENT CAMPAIGN

The following figures 3.7 a-c show gas fluxes during the 24h measuring period from May, 1st to 2nd 2012. Every single tree is displayed in the figures in addition to their overall mean.

The mean of all emissions increased from 25 up to 50 µg N-N_2O m^{-2} h^{-1} during the 24 h measurement time, whereas individual fluxes varied considerably. For instance, column 11 and 17 persisted on a consistent level, but column 16 and 14 increased notably. Soil column 12 increased slightly. The variation ranged from ±17 µg N-N_2O m^{-2} h^{-1} on 5:00 AM up to ± 60 µg N-N_2O m^{-2} h^{-1} at the end of the experiment.

The extent of effluxes for PS=1 largely decreased but they mainly gained during the time (Fig. 3.7 b). For most of the time, fluxes of each soil column were in a more homogeneous range around the mean for PS=0 (Fig. 3.7 a). The mean rates ranged from ±17 µg N-N_2O m^{-2} h^{-1} at 5:00 AM and ±45 µg N-N_2O m^{-2} h^{-1} at 2:00 AM.

The absolute difference between both photosynthesis settings was as variable as the fluxes. Figure 3.4 c shows the difference between PS=1 and PS=0.

All individual fluxes measured with light were lower than if fluxes were measured in the dark. Absolute values increased under light conditions from 5 am to 2 pm, whereas a similar effect for the dark measurements was not found showing even more steady fluxes.

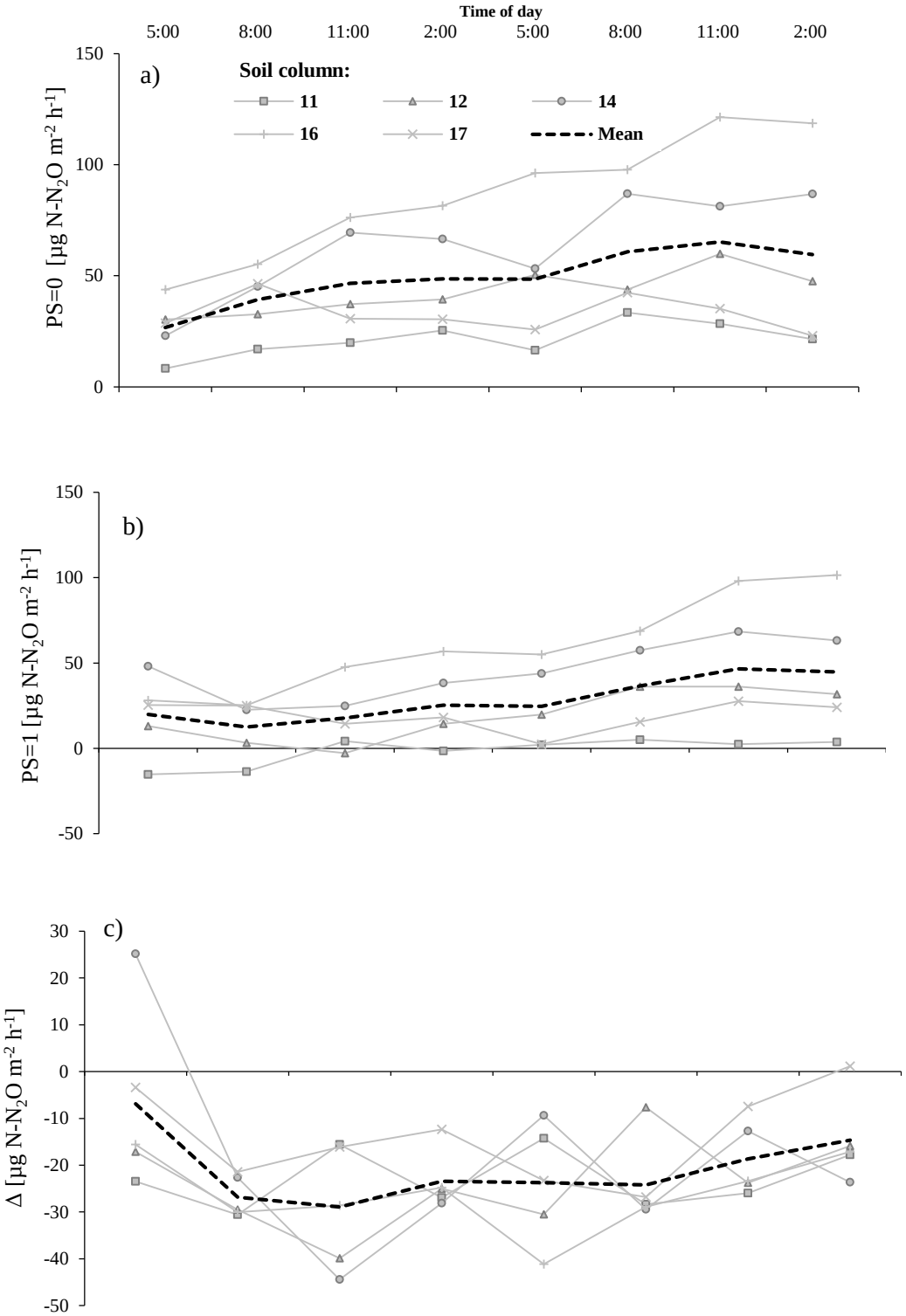

Fig. 3.4: N-N_2O fluxes for the 24h experiment (a) without (PS=0) and (b) with (PS=1) photosynthesis and (c) absolute difference between them (Δ). Grey lines with different symbols are the ash planted soil columns; dashed line is the mean of them

With photosynthesis, all N_2O fluxes were reduced by 50-75 %. Additionally, mean changes increased from -52 % at 5:00 AM to -85 % at 8:00 AM and afterwards decreased to the end of experiment at 2:00 AM. The N-N_2O fluxes decreased around 50 % between 8:00 AM and 2:00 AM at the end of the experiment (Fig. 3.5).

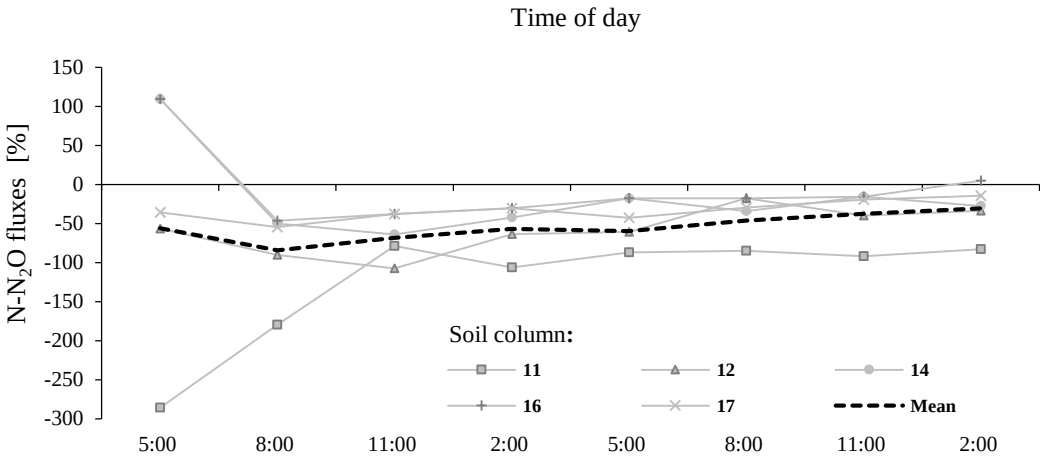

Fig. 3.5: Relative N-N_2O exchange between PS=0 and PS=1. Grey lines with different symbols are the ash planted soil columns; dashed line is the mean of them.

3.5 DISCUSSION

3.5.1 IMPACT OF SPECIES SPECIFIC PHOTOSYNTHESIS EFFECTS ON N_2O FLUXES

The influence of photosynthesis reduced the cumulative N-N_2O emissions of ash from 2350 to 1060 µg N-N_2O m^{-2}. This is a reduction of roughly 55%. For beech, emissions were reduced from 5100 to 3860 µg N-N_2O m^{-2}. This is a reduction of approximately 24%. Generally the results are comparable with those of FENDER et al., (2012[b]) stating that cumulative N_2O emissions from soils planted with ash were 50-60 % lower than from identical soils planted with beech.

This study shows for the first time that photosynthesis has an instantaneous reduction effect of N_2O emissions from soils. These reductions were substantially larger for ash than for beech and the whole plant-soil system occasionally even switched from net emissions to net uptake. It was confirmed that N_2O emissions from ash soil systems were lower than from beech – soil systems. The new aspect is that beech-soil systems shows the same reduction behavior during photosynthesis as ash soil system. The uptake rates of ash-soil-systems have to be interpreted very carefully as these flux rates are very close to the detection limits. These negative fluxes, however, appear reasonable as fluxes are already highly reduced by ash as compared to beech. The reasons for all these reduction from soils unfortunately have to remain speculative. It is somehow puzzling that fluxes from soils mainly mediated from soil bacteria react so instantaneously to illumination of the plants. Here future research has to be done. It appears unlikely that the plant uptake of reactive N from soils has such an immediate impact. In a first small pre-experiment, FENDER et al. (2012[b]) bagged treetops (to separate it from soil fluxes), and it was indicated that the ash itself lowers atmospheric N_2O

concentrations. All uncertainties of these pre-experiment have to be minimized and replicated, but it appears possible that the photosynthetical effect on N_2O fluxes are not restricted to soil processes. A correlation between net CO_2 uptake (NEE) and N_2O fluxes during photosynthesis, as found for the ash (Fig. 3.6), indicates a similar pathway into the plant.

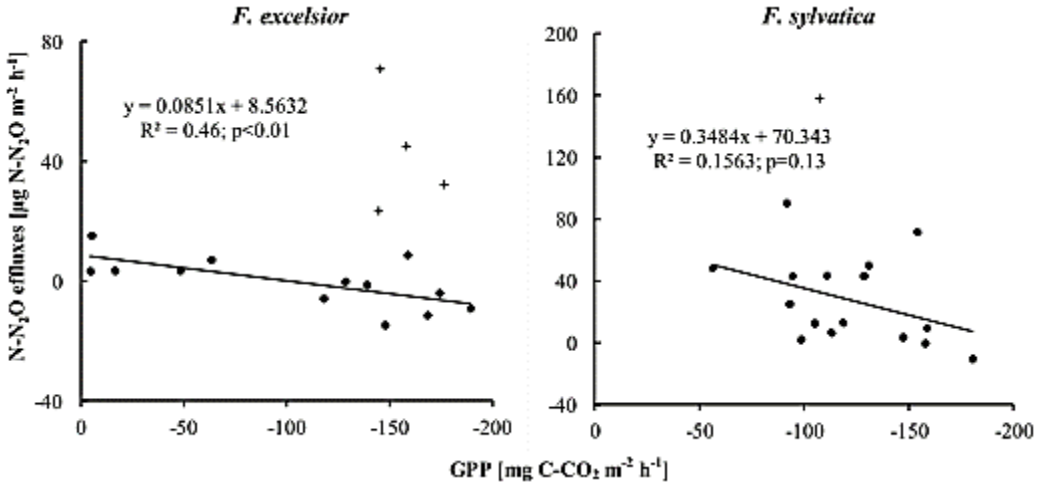

Fig. 3.6: Dependence of N_2O emissions on NPP for both treatments. Correlation was created without extreme values (+).

3.5.2 CHANGES OF PHOTOSYNTHESIS EFFECTS DURING THE COURSE OF THE DAY

Originated from the assumption that the reductions of N_2O emissions are a diurnal trend, the 24 hour experiment was conducted. Since the reduction of N_2O emissions was significantly larger for ash in the long-term experiment, the experiment was carried out only with this species. The general increasing trend of N_2O emissions during the 24h experiment was affected by declining WFPS as correlations between both indicated (Fig. 3.7). No correlation was found for column 17 (for both settings $R^2<0.06$; $P>0.5$).

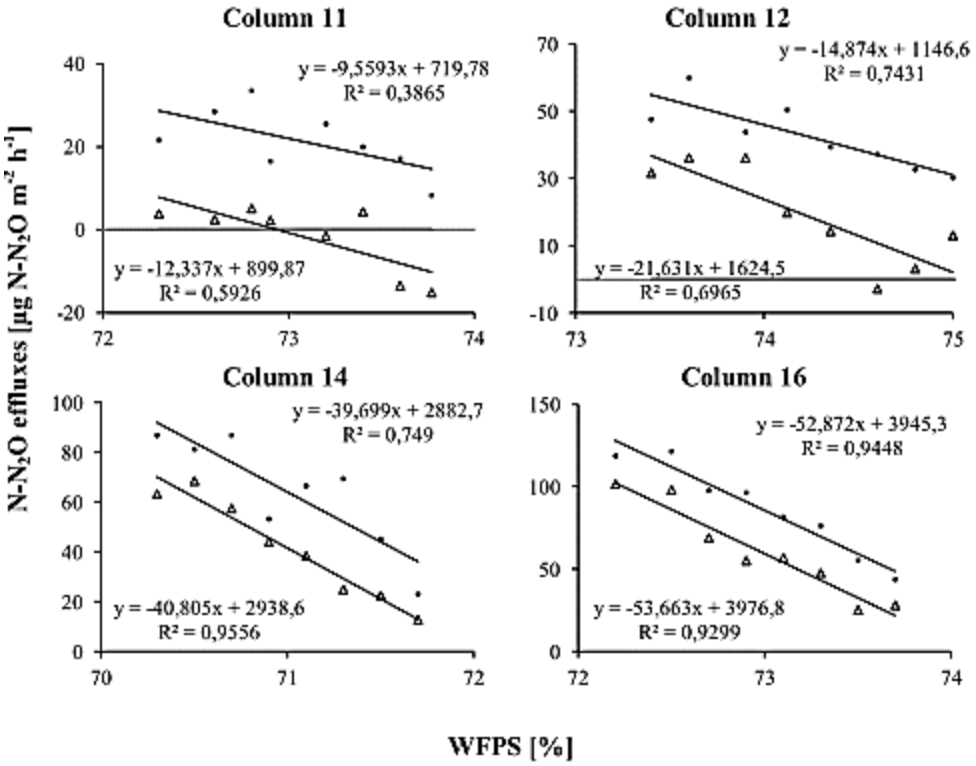

Fig. 3.7: Dependence of N_2O fluxes on WFPS. Δ = with photosynthesis; • = without photosynthesis.

Contrary to the hypothesis that there would be a diurnal trend of the absolute- and relative reduction of N_2O in the course of photosynthesis there solely seems to be a minimum in the very early morning (5:00-8:00 AM, Fig. 3.4 c).

Thereafter, reduction decreased during noon and afternoon. This observation supports the assumption about the photosynthesis effects of ash and confirmed hypothesis 3. According to KUZYAKOV (2006), a higher photosynthesis rate results in higher releases of root exudates. The transport of assimilates through the phloem occurs with an average flow rate between 0.5 to 1 m h^{-1}. These exudates act as an energy source for nitrifying and denitrifying microorganisms (YANG & CAI, 2006). Therefore, the photosynthesis activity rate may affect N_2O production and consumption in planted soils in three possible ways: (a) release of root-exudates as energy source for nitrification and denitrification; (b) withdrawal of reactive N compounds by roots during photosynthetically active plants and (c) direct N_2O reduction by ash itself.

3.6 CONCLUSIONS

Hypothesis 1 and 2: There is an effect of photosynthesis on N_2O emissions from soils and there are differences between ashes and beeches in case of this photosynthesis effect.

These hypotheses were supported. Impact of photosynthetic activity was shown for beech as well as for ash planted soil, but the reduction of emissions was higher for soil planted with ash, confirming hypothesis 1. As a consequence, photosynthesis activity of both species reduced the N_2O emissions with the same absolute rate which was significantly different to zero. Therefore, it is apparently important for ecosystems GHG flux measurements to consider if plants receive light or not.

Whole measuring duration:
Cumulative N_2O emissions were reduced by about 55 % for soils planted with ash and 24 % for soils planted with beech from PS=0 to PS=1.

Hypothesis 3: There is a diurnal trend of photosynthesis activity
During the course of the day, the reduction of N_2O emissions showed an increase, possibly stimulated by additional photosynthesis activity. Consequently, all absolute differences are significantly different at the 5 AM (Fig. 3.4 c) measurement. But for further measurements, the absolute differences showed the same slight decreasing trend during the day. This supported hypothesis 3.
A general increasing trend of N_2O emissions was observed and correlates with decreased WFPS during the day. Furthermore, a prominent negative-peak of the N_2O emissions was observed in the morning.

To sum up, this study indicated undercontrolled climate conditions, that beech and ash species-specifically influence N_2O effluxes from soil. The potential of ash saplings to reduce N_2O emissions was even higher. While beech planted soils released 4.2 ± 0.4 cumulative CO_2-eq m^{-2}, soils planted with ash showed 2.6 times lower release of 1.5 ± 0.2 cumulative CO_2-eq m^{-2}. Moreover, this study showed that a photosynthesis effect exists and reduced cumulative N_2O fluxes of ash planted soils around 50 % from 1.1 ± 0.3 to 0.5 ± 0.1 CO_2-eq m^{-2}. For soils planted with beech, the potential was larger. Reduction of N_2O emissions in beech planted soils changed about 75% from 2.4 ± 0.4 to 1.8 ± 0.4 CO_2-eq m^{-2}. These results showed that (a) global warming can decline by changing tree species during afforestation and (b) based on the confirmed photosynthesis effect on N_2O fluxes, calculations of N_2O ecosystem fluxes for deciduous forest and its potential impact on global warming should be rethought by scientists.

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CHAPTER 4

ON THE INFLUENCE OF EARTHWORMS (*LUMBRICUS TERRESTRIS*, *APORRECTODEA CALIGINOSA*) ON THE DYNAMICS OF GREENHOUSE GAS FLUXES (N_2O, CH_4 AND CO_2) IN A RHIZOTRON EXPERIMENT WITH LAYERED SOIL PLANTED WITH ASH (*FRAXINUS EXCELSIOR* L.) AND BEECH (*FAGUS SYLVATICA* L.)

4.1 ABSTRACT

Physical- and chemical-influence of earthworms, plants and leaf litter, can cause an enormous effect on chemical and physical soil properties. However, there is hardly knowledge of species-specific effects of earthworms and roots on greenhouse gas fluxes between forest soils and the atmosphere. Therefore we planted saplings of beech (*Fagus sylvatica* L.) and ash (*Fraxinus excelsior* L.) in rhizotrons and added two earthworm species, four individuals each of *Lumbricus terrestris* and *Aporrectodea caliginosa* and used beech- and ash-litter as forage. Under defined climatic and soil conditions (layered soil horizons) in the rhizotrons, we tested hypotheses related to potential earthworm and tree induced species effects on the emission of N_2O, and CO_2 and the uptake of CH_4 from the soil. The gas fluxes were measured weekly using the closed chamber technique; the N_2O, CO_2 and CH_4 fluxes derived from earthworms, soil and roots were estimated over a time span of 416 days. This design showed effects of leaf litter mineralisation by the earthworms and effects on the trace gas fluxes. Rhizotrons applied with earthworms and ash-litter as forage increased the cumulative N_2O emission (169 mg N-N_2O m^{-2}) from soil and supported CH_4 uptake (-219 mg C-CH_4 m^{-2}). However, rhizotrons planted with beech and ash added by beech-litter without earthworms had an increased cumulative N_2O (112 mg N-N_2O m^{-2}) and CO_2 emission (368 g C-CO_2 m^{-2}) (presumably root respiration) and a high CH_4 uptake (-178 mg C-CH_4 m^{-2}). We conclude that earthworms have a significant influence on the forest soil as a source or sink for greenhouse gases.

Keywords: Rhizotron, *Lumbricus terrestris*, *Aporrectodea caliginosa*, *Fagus sylvatica* L., *Fraxinus excelsior* L., greenhouse gas exchange, root respiration

4.2 INTRODUCTION

To combine the experimental setup of the soil column experiment 1 (ash/earthworm in Chapter 2) and the soil column experiment 2 (ash/beech in Chapter 3), a double-split-root rhizotron experiment was installed.

The combination of the soil column treatments into the rhizotron experiment included the treatments ash/beech, with and without earthworms and ash- or beech-litter as forage. The double-split-root system showed results (Chapter 2) in the interaction between ash and earthworm with ash-litter. Chapter 3 described the interaction between ash and beech. Furthermore the double-split-root rhizotron experiment supported the root detection through the acrylic windows. To make a separation or interaction of the ash- and beech roots possible, a barrier was installed (Fig. 4.1a). In the soil columns experiment (Chapter 2) we tested the hypothesis if treatments with earthworms have increased N_2O and CO_2 fluxes and if earthworms in soil supports the methane uptake from the atmosphere to the soil. But the earthworm/ash soil column experiment did not support this hypothesis. Nevertheless, plants take up nitrogen compounds in soil and this results in a reduction of N_2O emission from soil and earthworms' gut produce N_2O (DRAKE & HORN, 2007, BORKEN et al., 2000). The earthworms transport litter into deeper soil compartments and improve the oxygen and carbon/nitrogen transport in the soil due the "worm tubes". That could support the carbon oxidation (CO_2). However, earthworm initiated a soil compaction by construction of "worm tubes", which reduces methane uptake from the atmosphere into the soil. In deeper soil horizons the effects of earthworms may be reduced, because *Lumbricus terrestris* and *Aporrectodea caliginosa* may live in the deeper soil regions (200 cm) and only reach the soils' surface for their ingestion (especially *Lumbricus terrestris*). *Aporrectodea caliginosa* lives in minerals soil and find their organic resources in this depth for their metabolism. The different litter variants of ash and beech treatments might show the feeding behaviour of the earthworms and which of type of litter was preferred.

Most of the trials with earthworms were carried out over relatively short times (10 to 120 day; RIZHIYA, 2007, BORKEN et al., 2000; BURTELOW et al., 1998). The double-split-root rhizotron experiment was carried out over 416 days with regular gas measurements.

In the rhizotron experiment basically aimed at testing these outcomes on net GHG fluxes from a temperate forest soil with beech and ash saplings. Beech and ash were selected because both are common tree species throughout Europe and support to investigate if earthworms are important as ecosystem engineers. Our experiment tested if earthworms under nearly natural soil conditions increase the CH_4 uptake effect from the atmosphere into

the soil. If so, are these earthworms really inducing relevant fluxes on ecosystem scales and over a longer time scale/perspective?

Therefore following hypotheses were tested if:
(1) earthworms support the release of N_2O and CO_2 and the uptake of CH_4 in the soil and lead to an increasing of the net-(CO_2-aquivalent) emission from soil.
(2) the described earthworm effect is an enduring effect (for a longer period about 416 days).

In the main introduction (Chapter 1) are described more information about the GHG fluxes and the influences by plants and earthworms.

4.3 METHODS

4.3.1 EXPERIMENTAL SETUP

The double-split-root rhizotrons are made of anodised aluminium plates with a transparent 10 mm acrylic glass front to observe root growth and earthworm activity. The volume of a rhizotron is in total 15.2 L (600 mm * 900 mm * 30 mm, w * h * d, Fig. 4.1), which is split by two vertical bars in three compartments with a volume ratio of 1:2:1. The rhizotrons were thermally regulated by a cooling pipe system of circulating water, which was installed in the back plate and driven by a water pump (Master DW 5500e, Sicce S.p.A., Pozzoleone, Italy). This system guaranteed a thermal homogeneity in the 15 split-root rhizotrons (used in this experiment and simulated the lower soil temperature in deeper soil horizons).
In the front plate of each rhizotron are 24 acrylic windows installed with a reduced thickness (1 mm), which made the soil, root and earthworm observation possible. To induce the root growth and earthworm activity along the transparent front plate, the rhizotrons were tilted by 35° in forward direction. During the experiment, the front plates were kept covered with black draperies to exclude light infiltration (reduce algae activity) to the soil which influence root growth and soil fauna activity.
A two-factorial fully randomised experiment with 15 double-split-root rhizotrons was set up, the first factor being litter type (beech or ash) and the second factor being earthworm presence or absence. Therefore, experiment consisted of four treatments, three treatments replicated for four times and one treatment for three times. Each rhizotron was planted with one ash and one beech sapling. Four rhizotrons applied with ash litter and earthworms (E/A), four with beech litter and earthworms (E/B), four with ash litter without earthworms (A) and three with beech litter without earthworms (B). All rhizotrons were filled with layered

($O/A_h/A_l/B_t$) soil material (from the Hainich National Park). The soil material was frozen for 14 days (-18°C), to inhibit soil fauna activity especially the earthworms.

On 15/April/2011 the construction of the rhizotron experiment started. After four days, four *Lumbricus terrestris* and four *Aporrectodea caliginosa* were added and the surfaces of every rhizotron were supplied with 2 g dw^{-1} of ash or beech litter as forage for the earthworms. The litter layer was covered with a small net to prevent the earthworm escape and to fix the litter on the soil surface of the rhizotron. Beech and ash saplings were planted above one separating aluminium bar in the boxes for 14 days after the earthworm application. The three created soil compartments (α, β, γ compartment) gave the roots of the two saplings a free choice of growing into the three soil compartments (Fig. 4.1).

Tab. 4.1: Fine, coarse and total root biomass at the beginning and root biomass + depth at the end of the experiment (day 552). Below the table earthworm biomass at the beginning and the end of the experiment is represented (d 566). All rhizotrons planted either with one beech and one ash. Rhizotrons with earthworms (E/A and E/B) were applied with four individuals each of *Lumbricus terrestris* and *Aporrectodea caliginosa*. Means ± 1 SE (n = 4 / B n = 3).

Start of the experiment				**End of the experiment**							
	Beech	**Ash**		**E/A ash**	**E/A beech**	**E/B ash**	**E/B beech**	**A ash**	**A beech**	**B ash**	**B beech**
Root $mass_{fine}$	0.33 ±0.10	0.81 ±0.16	**0-20 cm**	0.94 ±0.64	1.13 ±0.95	1.48 ±1.49	1.06 ±0.57	1.16 ±1.57	1.71 ±1.15	1.93 ±1.43	1.17 ±0.86
Root $mass_{coarse}$	1.28 ±0.33	1.12 ±0.12	**20-40 cm**	0.54 ±0.31	1.38 ±1.00	0.70 ±0.64	0.96 ±0.57	0.38 ±0.55	0.91 ±0.56	0.88 ±0.69	0.96 ±1.11
Root $mass_{total}$	1.61 ±0.42	1.94 ±0.16	**40+ cm**	1.93 ±3.56	1.16 ±0.81	1.29 ±1.35	0.94 ±0.65	0.68 ±1.18	0.65 ±0.58	0.68 ±0.64	1.36 ±1.89
			Root $mass_{total}$	1.48 ±4,51	3.67 ±2.76	3.47 ±3.48	2,96 ±1.79	2.22 ± 3.3	3.27 ±2.29	3.49 ±2.76	3.49 ±3.86
	E/A	**E/B**		**E/A mean**	**E/A Δ R**	**E/B mean**	**E/B Δ R**				
Lumbricus terrestris	1.31 ±0.46	1.93 ±0.79		1.1 ±0,52	-0.69 ±0.84	0.45 ±0.17	-1.81 ±0.88				
Apporectodea calinginosa	0.41 ±0.15	0.48 ±0.19		0.37 ±0.28	-0.18 ±0.31	0.45 ±0.37	-0.25 ±0.35				

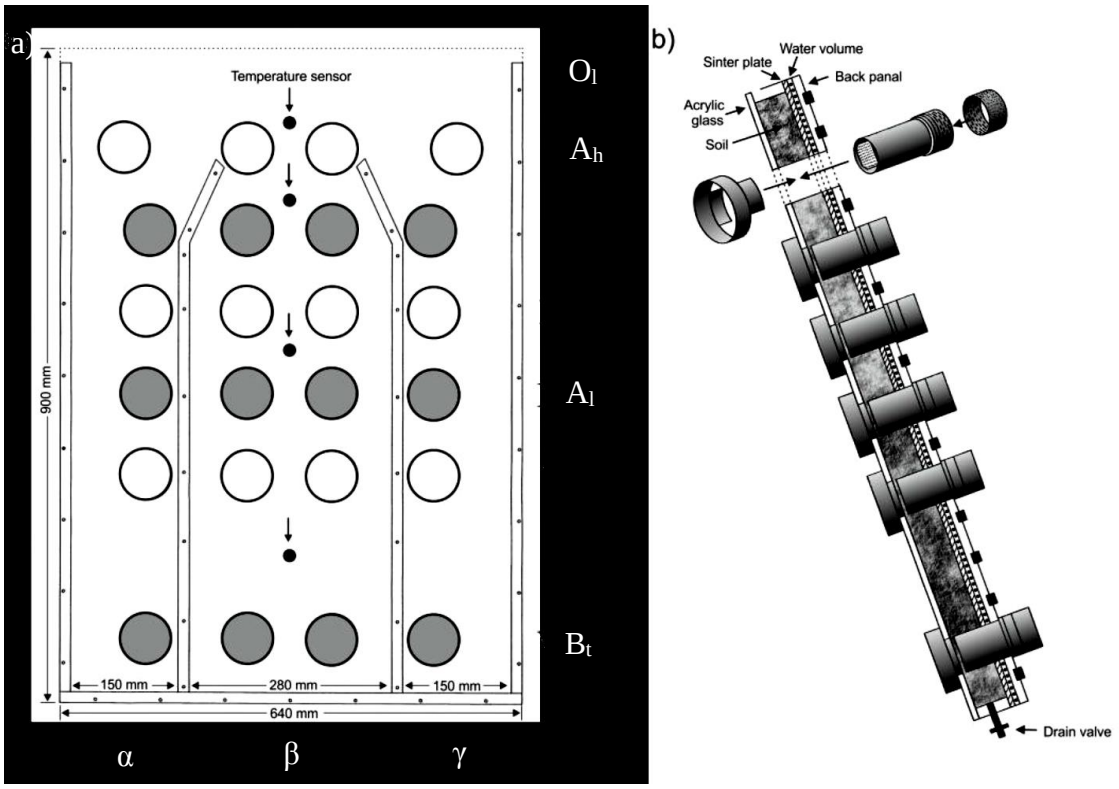

Fig. 4.1: a) Front view of a double-split-root rhizotron. The two metal barriers separated the soil volume into three compartments (α, β, γ) in a ratio of 1:2:1. Roman numerals mark the six soil layers in the rhizotron that were accessible by each four cylindrical openings. Black dots mark the position of temperature sensors. The circles mark the position of the observation windows b) longitudinal view of a rhizotron. The soil layer in the rhizotron had a width of 30 mm. For the uppermost soil layer, the design of a raster access port (upper side) and the front ring of 1 mm thick acrylic glass of the observation window (lower side) are shown in detail. The black squares symbolise the position of the water circulation system for thermal regulation of the soil (FENDER et al., 2012).

The used saplings were three to five year old beeches (*Fagus sylvatica* L.) and ashes (*Fraxinus excelsior* L.) which were collected close to the soil sampling site in spring 2011. The saplings had an initial shoot height of 19.42 ± 1.33 cm (mean ± 1 SE) and 18.31 ± 0.79 cm, respectively. At the beginning of the experiment, the ash saplings had 4-13 leaves and beech saplings 3-9 leaves. The initial root characteristics were measured at 5 randomised chosen ash and beech saplings.

The experiment was conducted in two climate chamber under constant climate conditions (20 °C air temperature, ~80% relative air humidity) and 10 (autumn-winter) to 14 h (spring-summer) daylight with 203 ± 10 µmol m^{-2} s^{-1} PPFD (EYE Lighting, Clean Ace, Mentor, OH, USA) from April/15/2011 until October/5/2012 (540 d). Soil temperature was measured with four NTC thermistors per rhizotron (Epcos, Munich, Germany), positioned vertically in the centre of the rhizotron (compartment β) at soil depths of 80, 200, 425, and 705 mm with 20 mm distance to the acrylic glass front plate. Data were recorded in 15 min-intervals with a CR1000 data logger (combined with two AM416 Relay Multiplexers, Campbell Scientific Inc., Utah, USA).

4.3.2 MEASUREMENT AND ANALYSIS OF GAS FLUXES

The rhizotrons were established 108 days before starting the gas flux measurements in order to adapt the soil to the experimental conditions and to balance out the gas exchange after the disturbing the natural soil structure. Gas fluxes were measured weekly on the soil surface for a period of 416 days until harvest, by applying the closed-chamber technique. A chamber was positioned between the two saplings of each rhizotron (soil surface of compartment β). To create a sufficiently large headspace volume of 1.75 L we used brass chambers with dimensions of 350 mm * 170 mm * 29.5 mm (h * w * d). During the gas flux measurements, the chambers were closed for 45 min. After 0, 15, 30 and 45 min, gas samples were taken from the chambers headspace by flushing gas-tight 60 mL-sample syringes with headspace air, using a cannula and two two-way valves. The gas concentrations were analysed by a gas chromatographic (GC) system. A detailed description of the GC configuration is presented in LOFTFIELD et al. (1997). The fluxes were calculated from the linear concentration change during the time of chamber closure. Based on 45 measurements during the experimental period of 416 days, the data was interpolated and the cumulative gas fluxes calculated. Interpolation was done by calculating the average of the preceding and following measurement.

4.3.3 PLANT HARVESTING AND SOIL ANALYSIS

At the first day of harvest (552 d after planting), the shoot length and root diameter of each sapling were measured. Therefore the roots were carefully excavated from the soil, washed and cleaned from adherent soil particles. All biomass samples were oven-dried (70 °C, 48 h) and weighed for dry weight determination.

During the harvest, soil samples from the upper 20 cm-layer, located below the gas flux sampling area, were extracted for chemical analysis. To exclude an effect of soil depth on soil properties additional samples were taken from each soil horizon. The soil pH was analysed in a suspension of 5 mL soil and 25 mL buffer solution (H_2O / 1 M KCl / 0.01 M $CaCl_2$) using a pH meter inoLab pH Level 2 (WTW GmbH, Weilheim, Germany). The nitrate (mg N-NO_3^- kg^{-1} dw) and ammonium (mg N-NH_4^+ kg^{-1} dw) concentrations were estimated by extracting soil samples in 0.5 M K_2SO_4 solution (1:3 wet soil mass to solution ratio) directly after collection. The samples were shaken for 1 h and passed through folded filters (150 mm in diameter, 65 g m^{-2}, Sartorius Stedim, Aubagne, France). The NO_3^- and NH_4^+ concentrations of the filtered extracts were analysed using continuous flow injection colorimetry (SAN^{++} Continuous Flow Analyzer, Skalar Instruments, Breda, The

Netherlands). NO_3^- was determined by the copper cadmium reduction method (ISO method 13395) and NH_4^+ by the Berthelot reaction method (ISO method 11732). The bulk density of soil was determined in 5 cm soil depth under the gas flux sampling area using plastic cores with a defined volume of 10.8 cm^{-3} after SCHLICHTING et al. (1995). The gravimetric soil water content was determined by weighing the soil samples before and after drying at 105 °C for 24 h.

4.3.4 DATA ANALYSIS

Statistical analyses were performed with IBM SPSS software (2011, 20.0, IBM corporation, Armonk, USA) and with Microsoft Excel software (2010, 14.0, Microsoft corporation, Redmond, USA). Cumulative gas fluxes were calculated by summing up all measurements for each rhizotron, considering the number of measurements taken and the length of the entire measuring period (416 d). The gas fluxes varied considerably between the different measurement days as it is common for GHG fluxes from soil, so that we refrained from showing the time course. All data were tested for normal distribution using the Kolmogorov-Smirnov test and for homogeneity of variances (F-test). To investigate the effects of earthworms and litter on various parameters, a two-way ANOVA with Fisher's least significant difference (LSD) as post-hoc test was used. In all analyses, significance was determined at the value of $P < 0.05$.

4.4 RESULTS

4.4.1 N_2O EMISSION

The N_2O fluxes of the treatment beech-litter (B) showed the highest mean N_2O emission of the experiment 12 ± 9 µg $N\text{-}N_2O$ m^{-2} h^{-1}. A mean emission of about 10 ± 9 µg $N\text{-}N_2O$ m^{-2} h^{-1} was observed in the treatment E/A, followed from the treatment E/B with an emission of about 7 ± 5 µg $N\text{-}N_2O$ m^{-2} h^{-1}. The treatment A showed with 5 ± 5 µg $N\text{-}N_2O$ m^{-2} h^{-1} the lowest N_2O emissions.

The timescale indicates 2 phases of the N_2O emissions (Fig. 4.2). In the beginning during the first four weeks of the experiment the N_2O emissions were considerably higher. In this period, the mean emission of all treatments increased up to 82 ± 66 µg $N\text{-}N_2O$ m^{-2} h^{-1}. In the second period the emissions were 6 ± 3 µg $N\text{-}N_2O$ m^{-2} h^{-1}. After this "Boost effect" the N_2O emissions of all treatments decreased. All gas fluxes of the treatments showed the same temporal pattern.

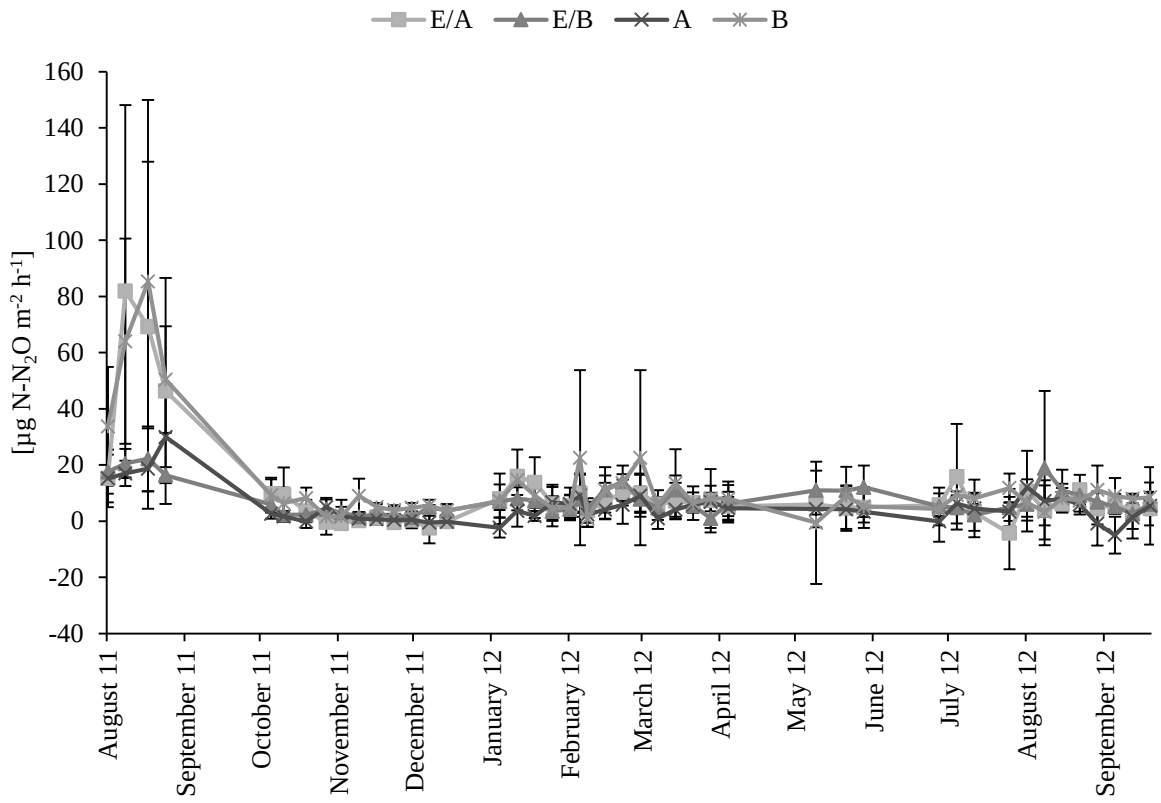

Fig. 4.2: Timescale (416 d) of the average fluxes of N_2O (µg $N\text{-}N_2O$ m^{-2} h^{-1}) and standard deviation (SD) of the treatments earthworms/ash-litter (E/A), earthworm/beech-litter (E/B), ash-litter (A) and beech-litter (B).

Generally, beech and ash saplings stop their vegetation period at the end of November and lose all leaves at the end of December. This could also observe during the experimental time by lower fluxes and an increase of the fluxes again at the end of January. Also in this experiment the fluxes were lower during this experimental time and increased again at the end of January with frondescence.

4.4.1.1 CUMULATIVE N_2O-FLUXES

Figure 4.3 shows the cumulative gas fluxes of N_2O. The treatment E/A had the highest N_2O emission (169 ± 68 mg $N\text{-}N_2O$ m^{-2}), followed by the treatment B with an emission of 112 ± 13 mg $N\text{-}N_2O$ m^{-2}. The treatments A and E/B had lower fluxes from 44 ± 11 – 64 ± 23 mg $N\text{-}N_2O$ m^{-2}. The interaction of the factors "litter" and earthworm" was significant. The post-hoc test showed that the in the presence of earthworms rhizothrons with ash litter had significantly higher fluxes. This pattern was reversed when earthworms were absent and the treatments E/B and B (P = 0.02). Furthermore, there was a significant difference between the both treatments without earthworms A and B (P = 0.02).

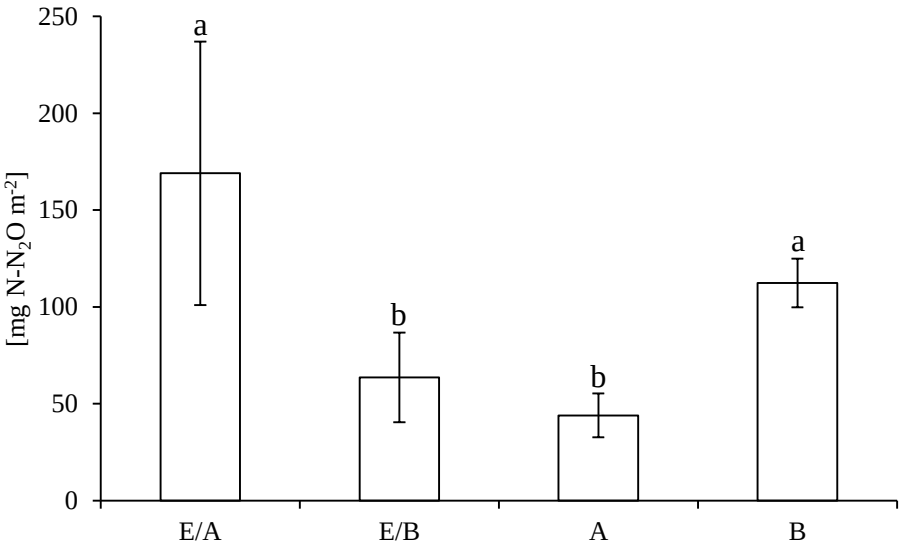

Fig. 4.3: Cumulative gas fluxes of N_2O (mg $N\text{-}N_2O$ m^{-2}) and standard deviation (SD) during experimental time (416 d). Interpolated measurements on days between the measurements been interpolated with building the mean of the measurement before and after to get closer to the fluxes. Earthworm/ash-litter (E/A), earthworms/beech-litter (E/B), ash-litter (A), beech-litter (B), Bars with the same letter are not significant different, using LSD-based pairwise comparison test.

4.4.2 CH_4 UPTAKE

At the beginning of the experiment a decreasing CH_4 uptake were observed and after ca. 3 month the CH_4 uptake in the soil nearly reached a steady state condition. During the experimental time, all treatments had nearly the same CH_4 uptake rate. The treatments with earthworms and beech-litter had the smallest uptake rate (-12.5 ± 4 µg $C\text{-}CH_4$ m^{-2} h^{-1}). The temporal development of the CH_4 uptake of the treatments showed several times increases and decreases. But the treatments with ash litter are nearly on the same level (-13 ± 5 to -13.1 ± 5 µg $C\text{-}CH_4$ m^{-2} h^{-1}). The treatment B showed the highest uptake of -13.4 ± 4 µg $C\text{-}CH_4$ m^{-2} h^{-1} (Fig. 4.4).

In this experimental time, during the end of the vegetation period (end of November), the uptake was lower and increased in January with frondescence.

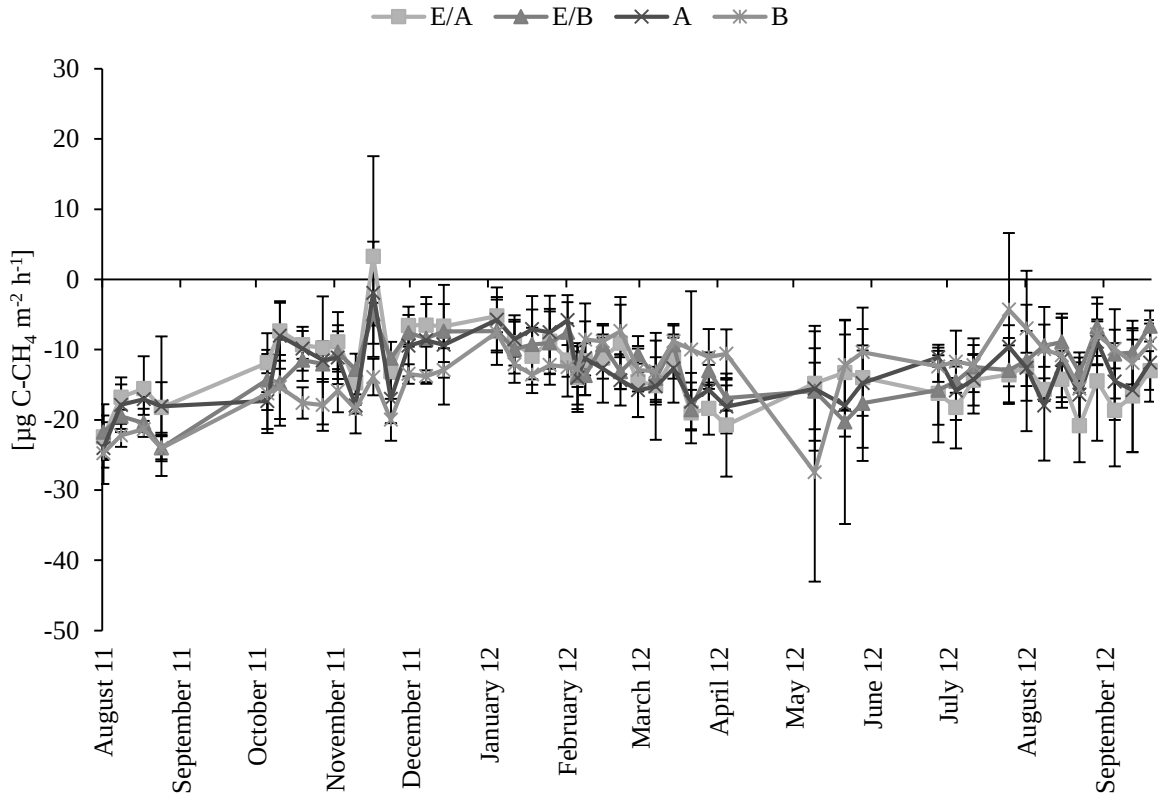

Fig. 4.4: Timescale of the average fluxes of CH_4 (µg C-CH_4 m^{-2} h^{-1}) and standard deviation (SD) from the rhizotrones of the treatments earthworms/ash-litter (E/A), earthworm/beech-litter (E/B), ash-litter (A) and beech-litter (B) on base of 45 measurements over 416 days.

4.4.2.1 CUMULATIVE CH_4-FLUXES

Figure 4.5 shows the cumulative CH_4 gas fluxes (mg C-CH_4 m^{-2}). The emission of the treatments E/B and A had a nearly same low cumulative uptake between -114 ± 24 / -104 ± 17 mg C-CH_4 m^{-2} in 416 days. The rhizotrones of the treatment E/A had the highest uptake rate of about -219 ± 57 mg C-CH_4 m^{-2}, followed by the treatment B with an uptake rate of about 178 ± 47 mg C-CH_4 m^{-2}. Significant differences were found between the treatments E/A and E/B (P = 0.003), E/A and A (P = 0.008) and between the treatments A and B (P = 0.02) on the cumulative CH_4 gas fluxes could be tested.

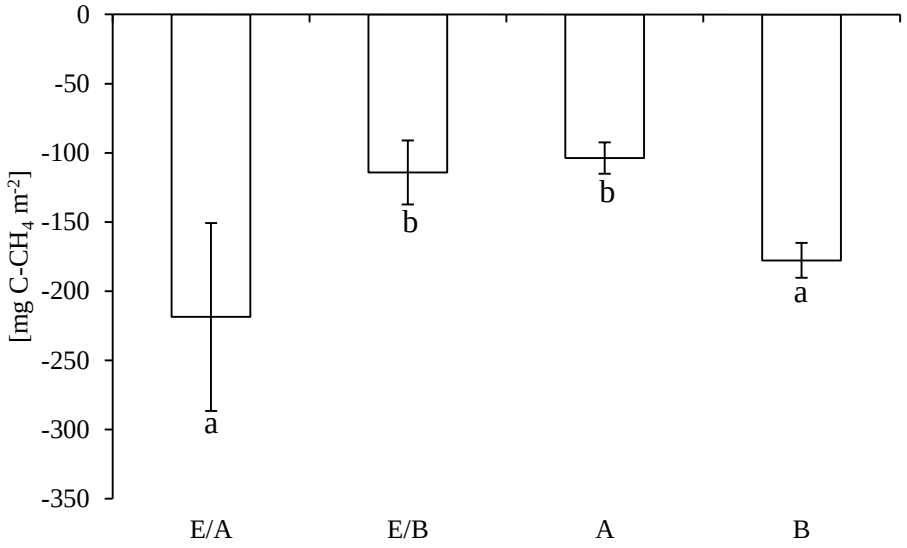

Fig. 4.5: Cumulative gas fluxes of CH_4 (mg C-CH_4 m^{-2}) and standard deviation (SD) while experimental time. Interpolated measurements on days between the measurements were interpolated with building the mean of the measurement before and after to get closer to the fluxes. Earthworm/ash-litter (E/A), earthworms/beech-litter (E/B), ash-litter (A), beech-litter (B), Bars with the same letter are not significant different, using LSD-based pairwise comparison test.

4.4.3 CO_2 EMISSION

Mean CO_2 emission rates of 45 gas measurements throughout the experimental period are shown in Fig. 4.6. The treatments applied with earthworms (E/A and E/B) showed a higher variability of the CO_2 fluxes. The CO_2 fluxes from the treatments applied with beech-litter showed the highest CO_2 fluxes.

The mean CO_2 emission for the treatment (B) showed the highest mean value of 37 ± 17mg C-CO_2 m^{-2} h^{-1} followed by the E/B treatment (30 ± 16 mg C-CO_2 m^{-2} h^{-1}). The CO_2-emission of the (A) treatment had a mean emission of 25 ± 14 mg C-CO_2 m^{-2} h^{-1}. The treatment E/A had similar low CO_2-emissions of 25 ± 18 mg C-CO_2 m^{-2} h^{-1}. Interesting is the fact, that the CO_2 emission rates peak of the fluxes at the beginning of the experiment, followed from decreased the CO_2 fluxes. Increased CO_2 fluxes after the depression were rather constant after the depression and reached a constant level. The decrease of the fluxes caused by the end of the vegetation period end of November and all leaves fallen end of December. In this experimental time the fluxes are lower and increased end of January with frondescence.

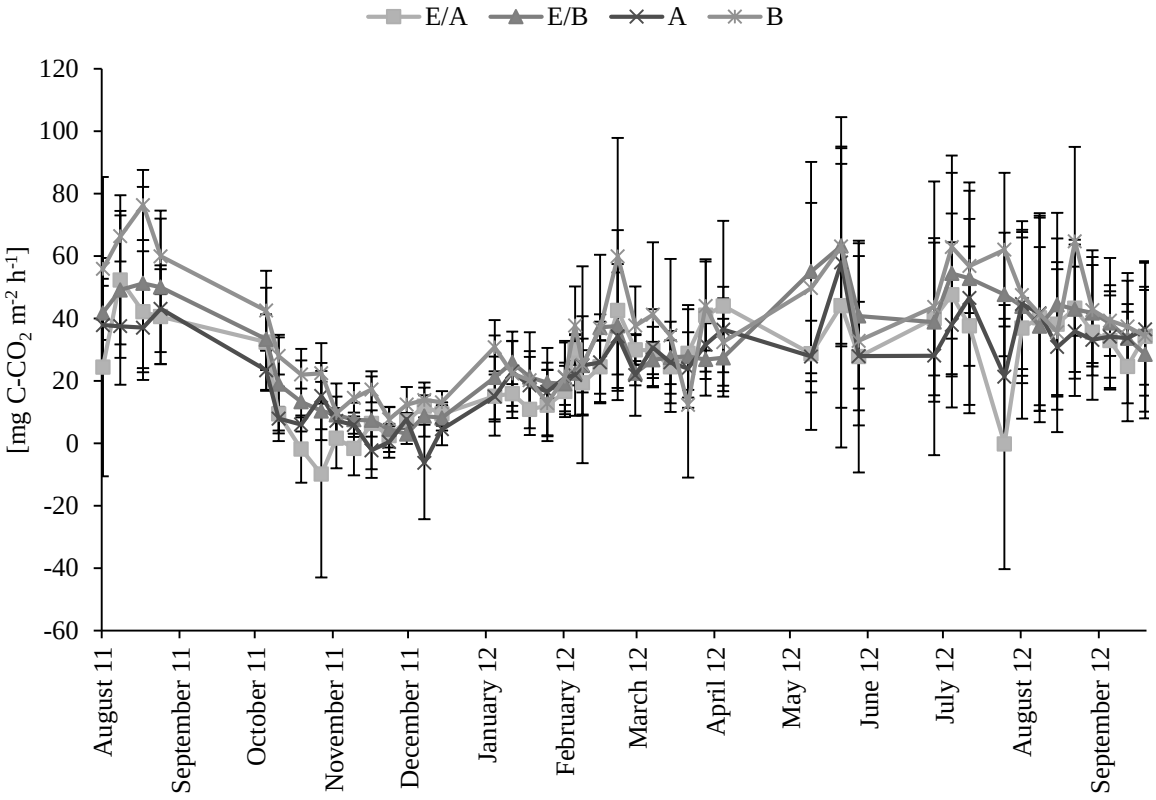

Fig. 4.6: Timescale of the average fluxes of CO_2 (mg C-CO_2 m^{-2} h^{-1}) and standard deviation (SD) from the rhizotrones of the treatments earthworms/ash-litter (E/A), earthworm/beech-litter (E/B), ash-litter (A) and beech-litter (B) on base of 45 measurements over 416 days.

4.4.3.2 CUMULATIVE CO_2-FLUXES

Figure 4.7 shows the cumulative gas fluxes of CO_2 (g C-CO_2 m^{-2}) during the 416 days of the experiment. The emissions of the treatments E/A and E/B were not significantly different (279 ± 120 and 273 ± 95 g C-CO_2 m^{-2}). The treatment B had the highest CO_2 fluxes of 368 ± 144 g C-CO_2 m^{-2} and the treatment A litter had the lowest CO_2 emission with a value of 193 ± 93 g C-CO_2 m^{-2}. No significant effects could detect between the treatments. However, the treatments A and B showed a *P*-value of 0.052.

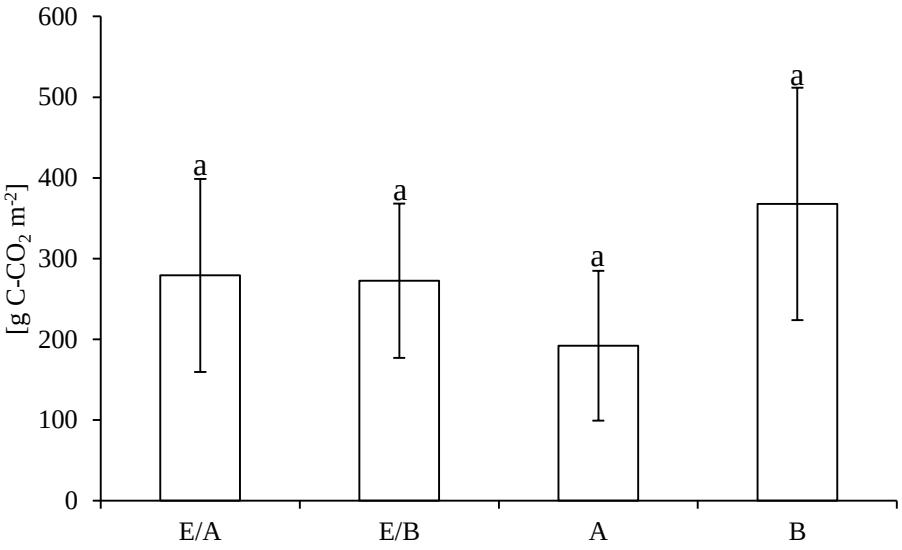

Fig 4.7: Cumulative CO_2 fluxes (g C-CO_2 m^{-2}) and standard deviation (SD) during the experimental time (416 d). Missing values on days between the measurements have been interpolated by calculating the average of the preceding and following measurement to get closer to the fluxes. Earthworm/ash-litter (E/A), earthworms/beech-litter (E/B), ash-litter (A), beech-litter (B), Bars with the same letter are not significant different, using LSD-based pairwise comparison test.

4.4.4 COMBINATION OF THE GAS FLUXES OF THE EXPERIMENTAL TIME

To combine the results of the treatments in terms of the Global Warming Potential (GWP) of N_2O, CH_4 and CO_2 released from soil, the CO_2-equivalent (CO_2e) was used. The results are shown in Tab. 4.2.

During the experimental time all treatments were net-sources for greenhouse gases. The treatment A had the lowest net-emission with a value of 136 g CO_2e m^{-2} and the other treatments were on a same level with net-emissions of 193 – 198 g CO_2e m^{-2}.

CO_2 dominated the relative contributions of emission from the rhizotrons. The treatment B had with 16% the highest N_2O percentage of the CO_2e emission, followed from the treatment E/A with a percentage of 14%.

Tab.4.2: Relative parts of carbon and nitrogen of the net emission (CO_2e) during the experimental time.

Treatment	Balance (CO_2e)	C-(CO_2e)		N-(CO_2e)	
	g/m^{-2}	g/m^{-2}	%	g/m^{-2}	%
E/A	194	186	86	7	14
E/B	193	187	89	6	11
A	136	132	94	4	6
B	198	190	84	8	16

4.4.5 AMMONIA/NITRATE AND CH_4-, N_2O-FLUXES

A significant difference between the cumulative N_2O emission and the salt-extractable NO_3^- concentration in the soil across the four treatments (P = <0.04, Fig. 4.8 a) existed. Also a significant difference existed between the N_2O flux and total fine root area in the rhizotron (P = <0.001, Fig. 4.8 b).

In relation to CH_4 all treatments showed significant differences between uptake fluxes and extractable NH_4^+ concentration (P = <0.001, Fig. 4.8 c) also the CH_4 fluxes were significant different to root biomass (P = <0.001, Fig. 4.8 d).

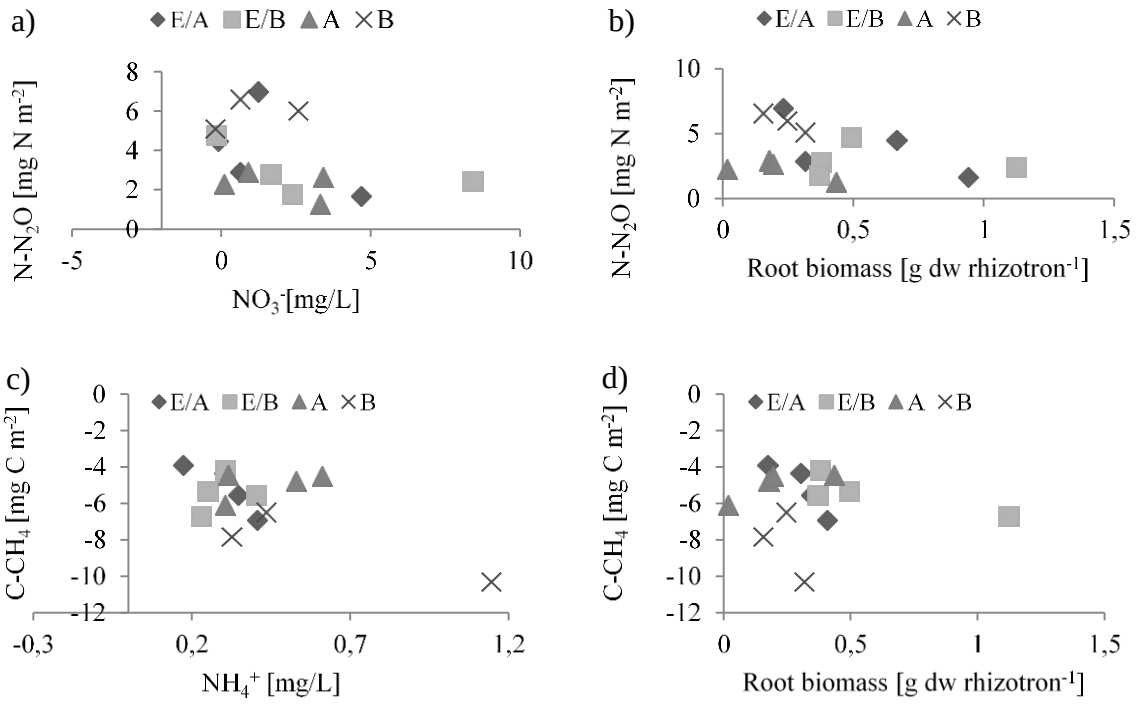

Fig. 4.8: Relationship between cumulative N_2O fluxes (416 d) in rhizotron treatments earthworms/ash-litter (E/A), earthworms/beech-litter (E/B), ash-litter (A) and ash/beech-litter (B) and (a) NO_3^- concentration of the upper 20 cm of the soil, (b) the total root biomass in the upper 20 cm of the soil. Relationship between the cumulative CH_4 uptake of soil (416 d) and(c) the NO_3^- concetration in the upper 20 cm of the soil or (d) total root biomass in the upper 20 cm of the rhizotrons.

4.5 DISCUSSION

The dynamics of N_2O, CH_4 and CO_2 fluxes are caused and affected by many factors. However, in a greenhouse experiment under controlled conditions the seasonal conditions can be manipulated and the effects on the fluxes from soil are measurable. The different tree-, earthworm- and litter-types have different impacts on the chemical and physical soil conditions which entails the influences on the GHG-fluxes. Litter, litter fall, bulk density, soil moisture and initial soil N and C content as well as the root-induced effect of different trees, affected N_2O, CH_4 and CO_2 fluxes from soil.

4.5.1 N_2O-EMISSION

N_2O fluxes from soil and the influences of ash (*Fraxinus excelsior*), beech (*Fagus sylvatica*), earthworms (*Lumbricus terrestris* and *Aporrectodea caliginosa*) and ash- and beech-litter are manifold. The measured N_2O fluxes from soil in the rhizotron experiment were lower than in the soil column experiments (Chapter 2 and 3). The measurement under field conditions in the SPLIDRHEX experiment (Chapter 5) resulted in even lower fluxes than in the rhizotron experiment. This is a common effect of the destruction of soil aggregates and a higher bio availability of carbon and nitrogen resources under laboratory or greenhouse conditions (JUNGKUNST et al., 2008). The nearly constant soil moisture and higher temperatures in the greenhouse chamber (10-20 °C vs. -10 – 20 °C) had an increasing effect on the GHG-fluxes and higher root-, earthworm- and microorganism-activity. Very problematic was the mortality of the earthworms, because it was not possible to control from outside how much earthworms were still alive, during harvesting it become sure how much earthworms survived the experiment.

At the beginning of the rhizotron experiment, the N_2O fluxes were very high, caused by the availability of nitrogen, carbon and oxygen in the soil "boost-effect". The bioturbation activity of earthworms caused also a higher N_2O emission.

The described circumstances of the N_2O emission caused a high variation across the measurements of all treatments and the standard deviation (SD) was for all treatments very high. During the first 1-3 weeks after earthworm application, the N_2O emissions of the treatments, excluding the treatment A, were on a relatively high level (46 ± 51 µg $N\text{-}N_2O\ m^{-2}\ h^{-1}$). A very fast peak, one week after application with 82 ± 66 µg $N\text{-}N_2O\ m^{-2}\ h^{-1}$ had the treatment E/A which indicates a related effect of earthworms and ash litter. The highest peak had the treatment B with 85 ± 65 µg $N\text{-}N_2O\ m^{-2}\ h^{-1}$. However on this measurement day the rhizotrones of this treatment had a very high SD. That effect was possibly initiated by the

soil setting effect and higher earthworm activity in the first weeks. The treatment E/B had no high N_2O emissions or a peak, which could be affected by a lower feeding activity of the earthworms from beech litter and a possible higher mortality of the earthworms. Since the end of September 2011 a constant level between the treatments with and without earthworms was observed.

The cumulative N_2O emission between the high N_2O emission treatments E/A and B had statistically a significant difference compared to the low N_2O emission treatments E/B and A (Fig 4.3).The results confirmed in part hypothesis 1, which stated that presence of earthworms will promote N_2O fluxes. This finding, however, depended on the litter type, which determined eating activity and survival rate of the earthworms. Although the differences between the treatments with earthworms (E/A, E/B) were statistically different (P=0.002), an influence of the earthworms on N_2O emission can be derived from the results: The fact that cumulative N_2O emissions were not at similar levels, depends on litter quality, associated with eating activity of earthworms, which could also lead to a higher mortality. Other studies on the influence of earthworms on microbial activity in soils provide evidence and agree with our assumption (SIMEK & PIZL, 2010; RIZHIYA et al., 2007; BERTORA et al., 2007; TIUNOV & SCHEU, 1999; PARKIN & BERRY, 1999; EDWARDS & BOHLEN, 1996; SVENSSON et al., 1986). According to these studies, a higher microbial activity and thus a higher greenhouse gas emission due to earthworm activity via incorporation of litter would be expected. Besides, the fact that cumulative N_2O fluxes of the treatment ash litter (A) were expected it was the treatment with the lowest emissions.

Comparing the proportions of N_2O on the net emission (CO_2e) of the treatments, lead to the assumption that *in vivo* emissions took place as reported by DRAKE & HORN (2007). The relative part of the net N_2O emission from the treatments beech litter (B) was the highest with a percentage of about 16%, the treatment earthworm/ash litter (E/A) had a percentage of N_2O of about 14%. The treatment ash litter (A) had with 6% N_2O a low percentage and the treatment earthworm and beech litter (E/B) had a percentage of 11%. Although it is clear from the data that presence of earthworms in the ash litter treatment increased the proportion of N_2O, but was lower as the treatment beech litter and the mechanistic cause of this effect remains speculative.

Across all 15 rhizotrons, there were no correlations of N_2O flux with the NH_4^+ or NO_3^- concentration. This could be caused by a more rapid NO_3^- reduction with higher denitrification rates, which is a main source of the N_2O released (BATEMAN & BAGGS, 2005; DAVIDSON et al., 2000). A significant difference was also found between root biomass and

the cumulative N_2O fluxes in the rhizotrons (R^2 = 0.18, *P* = 0.036). Ash has a more rapid root and shoot growth rate and this caused a higher nitrogen uptake as compared to slower growing beech trees. However a trend for greater reduction of the NO_3^- and N total pools in the soil by ash compared to slower growing beech was not found. All treatments are planted with one ash and one beech, so the interaction between the trees influenced themselves and also the soil of the treatments. However, in a ^{15}N-tracer field experiment, a larger uptake of NH_4^+ and glycin in ash compared to beech, maple, lime and hornbeam was found (JACOB et al., 2013). The NO_3^- concentration in the soil was not related to root mass, and no significant differences between the treatments were found. FENDER et al. (2012) indicated that certain broad-leaved tree species can have a substantial influence on the emission of N_2O from forest soils through their root systems.

4.5.2 CH_4 EMISSION

The measured mean CH_4 uptake during experimental time (416 d) in the rhizotrons (-3 ± 10 – -21 ± 6 µg C-CH_4 m^{-2} h^{-1}) showed a nearly similar magnitude as CH_4 fluxes measured under field conditions in the Hainich forest (0 – 78 µg C-CH_4 m^{-2} h^{-1}; GUCKLAND et al., 2009).

All treatments of the rhizotron experiment were on the same level (-12.5 ± 4 to -13.4 ± 5µg C-CH_4 m^{-2} h^{-1}). Cumulative CH_4 gas fluxes of the treatments have a significant difference between the treatments E/A and E/B (*P* = 0.003), E/A and A (*P* = 0.008) and between the treatments A and B (*P* = 0.02) (Fig. 4.5).

Hypothesis 1, that earthworms had a higher CH_4 uptake into the soil, could not be confirmed. Our assumption that the bioturbation of earthworms increases the oxygen concentration in the soil and thus supports CH_4 uptake via enhanced CH_4 oxidation did not prove true. The treatment without earthworms with beech litter had a higher methane uptake then the treatment with earthworms and beech litter. This result can be influenced by the 77% mortality of the earthworms in the treatment E/B, but it was not possible to find out at what time of the experiment the earthworm loss happends.

The major influence for CH_4 uptake in the soil was that the methanotrophic bacteria reduce the CH_4 concentration and thus enhanced the diffusive gradient between soil and atmosphere (BLUME et al., 2010). For this, sufficient oxygen availability is necessary, which is determined by soil structure and gas diffusivity (FIEDLER, 2001). The observed high CH_4 uptake rates at the start of the GHG measurement led to the assumption that a soil settling of the soil took place.

A possibility for the reduced CH_4 uptake could be a stimulation of microbial activity in the worm scat and drilosphere to such an extent that microbial oxygen consumption is higher than the oxygen supply by diffusive transport from the atmosphere. As a consequence a reduced activity of methanotrophic bacteria and even methanogenesis could be possible. Accounting for the low influence of earthworms on CO_2 fluxes during the experimental time, the processes mentioned above seem negligible. In particular the CO_2 emission from aerobe soils is equimolar to the consumption of oxygen (BLUME et al., 2010).

Hypothesis 2 that the described earthworm effect is an enduring effect could not be supported for the experimental time, a steady-state effect after a longer time occurs.

Beside this species effect, a negative correlation between CH_4 uptake and the amount of root biomass in the rhizotrons of all treatments were found. Methane oxidation is sensitive to NH_4^+ fertilisation either through competitive inhibition of methane monooxygenase by NH_4^+ or through a negative salt effect in fertilisation experiments (BODELIER, 2011; STEUDLER et al., 1989). A significant difference between CH_4 uptake rate and extractable NH_4^+ concentration was found (P = <0.001).

4.5.3 CO_2 EMISSION

It is difficult to separate the measured net CO_2 efflux from soils into the relevant sources, for example autotrophic respiration (root maintenance and growth respiration), the respiration of earthworms, bacteria, fungi and other animals in the soil matrix, and additional microbial respiration in the immediate closeness of roots that is stimulated by root exudation (root-induced respiration) (KUZYAKOV, 2006).

The mean CO_2 emission of the treatment beech-litter (B) had the highest value of 37 ± 17 mg C-CO_2 m^{-2} h^{-1} and the treatment earthworm and ash-litter (A) had the lowest emission of about 25 ± 18 mg C-CO_2 m^{-2} h^{-1}. The rhizotrones applied with earthworms were on nearly the same level (25 ± 18 to 30 ± 16 mg C-CO_2 m^{-2} h^{-1}. The cumulative CO_2-emissions were not significantly different to each other (Fig. 4.7). In this regard, our hypothesis that earthworms stimulate CO_2 release from soils could not be supported. The field study of BORKEN et al. (2000) showed similar results. The authors found no significant differences of CO_2 fluxes influenced by earthworms. However, they measured a significantly higher CO_2 emission in the first 4-5 weeks, which is explained by the construction of wormholes and the incorporation of detritus in the mineral soil. Nevertheless, a higher soil respiration due to earthworm activity would have been expected. The question arises, if this study underestimates the temporal dimension of the mineralization process. The contribution of

earthworms to soil respiration is small (EDWARDS & BOHLEN, 1996). So it is conceivable that the mineralization of litter needs a longer time to influence the CO_2 emission significantly.

After balancing of the gas fluxes of N_2O, CH_4 and CO_2, net emission of soil greenhouse gases expressed by the CO_2-equivalent (CO_2e) of the treatment earthworm/ash-litter (186 g C-CO_2e m^{-2}) which was higher than the treatment with ash litter without earthworm (132 g C-CO_2e m^{-2}). That indicates an influence of the earthworm on the CO_2 fluxes, however not significant. The treatments with the earthworm/beech-litter (187 g C-CO_2e m^{-2}) and the highest CO_2e emitter the treatment beech-litter (190 g C-CO_2e m^{-2}) are nearly on the same CO_2e emission level. BERGER et al., 2010 described the higher CO_2 emission from soil covered with beech litter compared to spruce needle. However, the ash litter turnover is faster (VESTERDAL et al., 2012) and JUDAS (1992) analysed the plant particles in earthworm gut of *Lumbricus terrestris* which showed that they prefer non-*Fagus sylvatica* L. leaves.

The view on the root biomass (Tab. 4.1) shows a difference of about 2 g dw^{-1} between the treatment earthworm/ash-litter (57 g dw^{-1}) compared to the treatment earthworm/beech-litter (55 g dw^{-1}). According to CURRY & SCHMIDT (2007) it is possible that the earthworms in the treatment with beech litter also use roots as a food source.

The higher CO_2 emission from the treatment beech-litter might be a root respiration effect. This treatment had a higher roots biomass, which caused a higher CO_2 emission trough root respiration (FENDER et al., 2012, CESARZ et al., 2013).

The harvest of the experiment showed how high the mortality of the earthworms was. The experiment had a losing of *Lumbricus terrestris* in the treatment with ash litter in mean -0.69 g fw^{-1} (16%) and of *Aporrectodea caliginosa* about -0.18 (10%). The treatment with beech litter had an earthworm loss of *Lumbricus terrestris* about -1.81 g fw^{-1} (77%) and a loss of *Aporrectodea caliginosa* about -0.25 g fw^{-1} (5%). The high mortality of the species *Lumbricus terrestris* in the earthworm treatment with beech litter could have a cause in the food preference and that could give a reason for the low CO_2 fluxes in comparison to the treatment E/A. The treatment with ash litter pasture showed a lower mortality. The treatment E/B showed a lower root biomass, which could be an indicator that the earthworm prefer roots instead of the beech litter (-1.93 g dw^{-1}).

The hypothesis 1, that earthworms support the net emission (CO_2e) from the soil columns could be supported but is statistically not significant.

The hypothesis 2, that the described earthworm effect is an enduring effect (for a longer period) could not be supported.

4.6 CONCLUSIONS

The present study investigated how earthworms, beech and ash saplings and beech- and ash-litter influence the greenhouse gas fluxes from soil by using novel double-split-root rhizotrons. The cumulative N_2O emissions showed a significant influence of earthworms in relation to the treatment with ash litter. The earthworm treatment with ash-litter was in relation to the treatment with ash-litter and without earthworm significant different.

The earthworm treatment with beech-litter was in relation to the treatment with beech-litter without earthworm significant different. The low N_2O emissions will be affected by the high earthworm mortality of the earthworm/beech-litter treatment. The study of EDWARDS & BOHLEN (1996) showed that the activity of earthworms and microorganism caused higher greenhouse gas fluxes. In our study at the first period the turnover of the soil-derived nitrogen and the influence of the earthworms increased when the ash and beech litter incorporated into the soil were measured. The earthworm effect on the GHG fluxes from soils is not an enduring effect, 3-4 weeks after earthworm application the fluxes decreased and reached a steady state level.

All treatments had a CH_4 uptake, however through reducing of NH_4^+ and NO_3^- in the soil the methanotroph microorganism inhibited. At the beginning of the experiment the CH_4 uptake decreased, caused from the soil setting effect. After three month the CH_4 uptake in the rhizotrons reached a steady state level. The end of the vegetation period caused a decrease of the CH_4 uptake and during frondescence.

The cumulative CO_2 emission of the treatments appliqued with earthworms showed no significant differences, however the treatment beech-litter showed an advanced emission than the other treatments. This emission initiated from the higher root biomass and was a root respiration effect. With the end of the vegetation period the CO_2 fluxes from soil decreased and increased again with the start of the vegetation period.

The balance of the cumulative gas fluxes of N_2O, CH_4 and CO_2 as CO_2e- equivalent showed that all soils of the treatments are resources of greenhouse gases. The treatment beech-litter had the highest fluxes (root respiration effect) followed from the treatments with earthworm and beech litter.

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CHAPTER 5

ON THE SPECIES-SPECIFIC INFLUENCE OF BEECH AND ASH SAPLINGS ON CO_2, CH_4 AND N_2O FLUXES FROM SOIL DURING FRONDESCENCE

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Submitted to

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5.1 ZUSAMMENFASSUNG

Bisher existieren nur wenige fundierte Kenntnisse über die regulierende Funktion terrestrischer Waldökosysteme, als Senken- oder Quellen für die Treibhausgase CO_2, CH_4 und N_2O. Die in den vergangenen Jahrzehnten intensivierte Landnutzung und damit verbundene Veränderung der Landoberfläche beeinflusst die Interaktionen zwischen der terrestrischen Biosphäre, Pedosphäre und Atmosphäre. Das Ziel des Freilandexperimentes bestand darin zu prüfen ob es unter natürlichen Bedingungen einen artspezifischen Einfluss von Jungbäumen der Rotbuche (*Fagus sylvatica* L.) und der Gemeinen Esche (*Fraxinus excelsior* L.) hinsichtlich der Treibhausgasflüsse zwischen Boden und Atmosphäre gibt. Es wird davon ausgegangen, dass eine hohe metabolische Aktivität der Feinwurzeln vor und während des Blattaustriebes einen starken artspezifischen Einfluss auf die Treibhausgasflüsse aus dem Boden hat. Dies ist auf charakteristische Unterschiede im phänologischen Zyklus und des Feinwurzelwachstums dieser Baumarten zurückzuführen.

Die Treibhausgasemissionen für beide Baumarten zeigten eine konsistent niedrige mittlere Flussrate während der blattlosen Phase (14 µg $N\text{-}N_2O$ m^{-2} h^{-1}). Kurz vor dem Blattaustrieb stiegen die Treibhausgasemissionen aus dem mit *F. sylvatica* bepflanzten Boden geringer an, als die aus dem Boden unter *F. excelsior*. In diesem Stadium waren die Emissionen unter gleichen Temperaturbedingungen bis zu 230 % höher (14 zu ca. 80 µg $N\text{-}N_2O$ m^{-2} h^{-1}). Während des Blattaustriebes sind die Treibhausgasflüsse aus dem Boden weiter angestiegen, jedoch konnten keine anhaltend hohe Emissionen nachgewiesen werden. Die N_2O Emissionen aus bepflanztem Boden waren stetig niedriger als die der Kontrolle (unbepflanzter Boden) und der Boden unter Esche wies die stärkste Reduktion der N_2O Emissionen auf. Die Gasmessungen während der blattlosen Phase zeigten eine konstante Aufnahme von CH_4 durch den Boden. Dabei war die CH_4-Aufnahme aus der Atmosphäre für Boden unter Esche höher als die des Bodens unter Buche. Im Verlauf des Messzeitraumes konnte für den bepflanzten Boden ein zunehmender Anstieg der CO_2-Emission mit durchschnittlich 30,4 ± 5,1 bis 85 ± 35,4 mg $C\text{-}CO_2$ m^{-2} h^{-1} gemessen werden. Während des Blattaustriebs konnte eine Reduzierung der Emission von 60-80% festgestellt werden, wobei der mit Buchen bepflanzte Boden im Vergleich zum Boden unter Esche, höhere Emissionen aufwies, die jedoch keinen signifikanten Unterschied zeigten.

Zum einen, gab es eine Zunahme der N_2O-Emissionen bei bewachsenen Boden während des Messzeitraumes, welcher nach Blattaustrieb wieder abnahm. Andererseits, waren nach dem Ende des Blattaustriebs die CO_2-Emissionen von Boden bepflanzt mit Buchen kontinuierlich erhöht.

Schlüsselworte: *Fraxinus excelsior* L., *Fagus sylvatica* L., Treibhausgasflüsse, Blattaustrieb.

5.1.2 ABSTRACT

Knowledge about the influence of terrestrial ecosystems and their regulating function as net sink or source for greenhouse-gas fluxes is limited. During the past decades, land-use and land-cover changed and thus the interactions between the terrestrial biosphere, pedosphere, and atmosphere were altered. One main objective of this experiment was to verify species-specific influences of European beech (*Fagus sylvatica* L.) and European ash (*Fraxinus excelsior* L.) saplings on greenhouse gas (GHG) fluxes between soil and atmosphere under near-natural conditions in a field experiment. The hypothesis was that high metabolic activity of fine roots induces strong species-specific effects on GHG fluxes before and during frondescence in early spring. This is due to characteristic differences in the phenological cycle of these tree species, also addressing fine root growth, which may lead to considerably different GHG fluxes. According to that the GHG emissions showed a consistent low fluxes for both tree species (14 µg $N\text{-}N_2O$ m^{-2} h^{-1}) during the leafless period. Before frondescence, the GHG emissions from soil planted with *F. sylvatica* increased less than from soil planted with *F. excelsior* which increased up to 230 % (14 to ca. 80 µg $N\text{-}N_2O$ m^{-2} h^{-1}) under the same soil temperature regime. During frondescence, the fluxes continued to increase and no constant emissions were observed. Generally emissions of planted soil plots were lower than those of the control. The strongest reduction of N_2O emission was observed for soils planted with ash. The five gas measurements during the leafless period showed that the CH_4 uptake by the soil remained constant over time. Uptake was higher for soil planted with ash than planted with beech. A trend of increasing CO_2 efflux from each plant treatment was observed. Mean fluxes ranged from 30.4 ± 5.1 to 85 ± 35.4 mg $C\text{-}CO_2$ m^{-2} h^{-1} during frondescence the measurement time. Declines of up to 60-80 %in fluxes were found. Fluxes of CO_2 from plots with *F. sylvatica* were higher than plots with *F. excelsior* but not significant.

On the one hand, the temporal increase of the N_2O emission from planted soil ended after frondescence. On the other hand, CO_2 emission of soils planted with beech continuously increased after the end of frondescence.

Keywords: *Fraxinus excelsior* L., *Fagus sylvatica* L. greenhouse gas fluxes, frondescence.

5.2 INTRODUCTION

The enrichment of greenhouse gases (GHG) in the atmosphere and the consequences on the radiative forcing are in the centre of research and discussions about climate change.

Thereby, an essential task is to determine the function of terrestrial ecosystems as sources and sinks for GHGs. The main focus in this study lies on the quantification of forest soils as sources and sinks for GHGs and their seasonal dynamics. Forests are main contributors to the carbon and nitrogen cycle and have received great attention with respect to the quantification of CO_2, CH_4 and N_2O fluxes during the past decade. Forests are considerable pools for carbon derived from photosynthetic CO_2 assimilation, and they sequester it aboveground and more importantly belowground in the pedosphere as well as in the rhizosphere. Especially forest soils in the northern hemisphere play an important role in the greenhouse gas balance (IPCC, 2007; JANSSENS & PILLEGARD, 2003; UNFCCC, 1997). In addition to their function as long-term carbon pools, temperate forest soils are the most relevant terrestrial sinks for CH_4 due to methane oxidizing microorganisms in soils. Furthermore, they function as a major source for N_2O emission – beside agricultural soils (JUNGKUNST ET AL., 2006; KESIK ET AL., 2005), however their contribution to the global N_2O emission is still unknown (PIHLATIE ET AL., 2005). While the effects of abiotic factors like soil temperature, soil moisture, bulk density or pH-value on GHG fluxes are well studied (CIARLO ET AL., 2008; LE MER & ROGER, 2001), knowledge of the effects of biotic variables is missing. Therefore the scientific task of this field study was to focus on biotic factors like tree species-specific effects and their interactions. This study aims to identity influences of European beech (*Fagus sylvatica* L.) and European ash (*Fraxinus excelsior* L.) saplings on GHG fluxes under near-natural conditions. These tree species are of high economic and ecological importance for Central European forests (ELLENBERG & LEUSCHNER, 2010).

5.2.1 STUDY AREA

The **S**pecies **L**itter Identity and **D**iversity effect on the **Rh**izosphere of trees **Ex**periment (SPLIDRHEX) was established in spring 2011 to differentiate the rhizosphere effects of below- and aboveground plant diversity and to explore their interactions in a two-factorial design (sapling identity and litter identity). The experiment was set up in a 150-year-old montane oak forest near Göttingen (Reinhäuser Wald, 51°26'N 10°01'E) 320 m a.s.l. (GRUBERT ET AL., 2011, Fig. 5.1).

Seedlings of four deciduous broad-leaved tree species (*Fraxinus excelsior, Fagus sylvatica, Tillia cordata, Acer pseudoplatanus)* differing in litter decomposability and mycorrhizal

associations were planted (GRUBERT ET AL., 2011). The plant species and litter treatments were manipulated independently and replicated four times. In total, 304 plots (180 x 120 cm) each containing 30 tree individuals were established in four blocks.

The hypothesis, that different functional traits in root biology may influence the GHG fluxes was investigated in a separate field experiment at the SPLIDRHEX – site in Reinhausen. The greenhouse gas measurement took place on the control-, ash- and beech- plots because the experiment in the greenhouse chamber has the same treatments. The SPLIDRHEX - site provides the condition for a comparison because the *Fagus sylvatica* and *Fraxinus excelsior* saplings are nearly the same age.

The soil type is a Regic Cambisol with a thickness of about 60-100 cm (NIBIS, 2012).

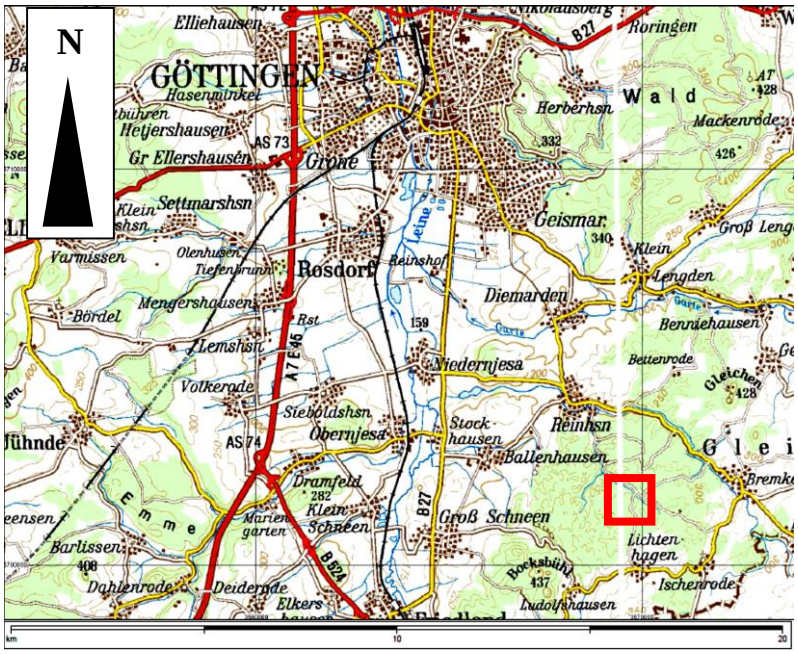

Fig. 5.1: Location of the study site in the Reinhäuser Wald (red box) ca. 10 km southeast of Göttingen.

5.2.2 CLIMATIC CONDITIONS

As there is no weather station in the Reinhäuser Wald, weather records were provided by a station located in the New Experimental Botanical Garden of the University of Göttingen (Fig. 5.2a), and corrected for local site conditions.

In 2012, the mean annual air temperature was 9.0 °C with a minimum mean temperature of 1 °C in January and the maximum of 17.4 °C in July (Wetterstation Göttingen, 2012). The annual precipitation was 628 mm, with a minimum in February (36 mm) and a maximum in June (74 mm). Continuous soil temperature (2 cm) of the experimental plots (Fig. 5.2b) was measured by use of data logging I-Buttons (DS1922L-F5, Maxim Integrated, San Jose, California, USA) and by own sporadically temperature measurements with a thermometer

(Testo 110, Lenzkirch,Germany). Soil water content was measured by use of a moisture meter (HH2, Delta-T Devices, Cambridge, UK).

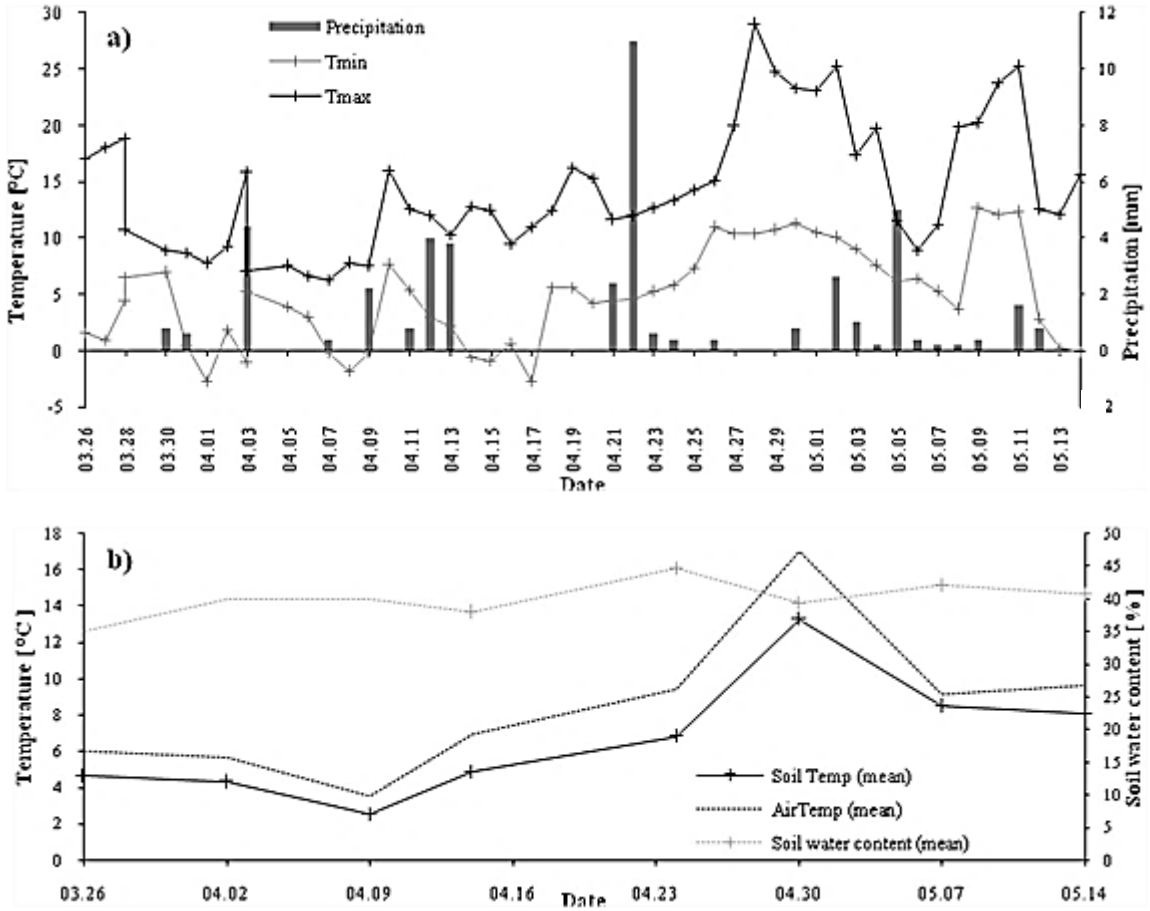

Fig. 5.2: (a) Air temperature (Tmin & Tmax) and precipitation (weather station Univ. Göttingen) during the experimental period 2012. b) Average mean air temperature (weather station Univ. Göttingen), mean soil temperature (2 cm), and mean soil water content at the measurement days.

5.3 OBJECTIVES & HYPOTHESES

One main objective of the SPLIDRHEX-experiment is to identity the species-specific influence of European beech (*Fagus sylvatica* L.) and European ash (*Fraxinus exelsior* L.) saplings on GHG fluxes between soil and atmosphere under near-natural conditions. It is hypothesized that leaf-litter decomposability and mycorrhizal associations can influence the GHG fluxes, particularly before and during frondescence, when both tree species induce different effects on biogeochemical soil processes driven by different metabolic activity in the rhizosphere (Fig. 5.3-5.5). During the setting with photosynthesis, NEE (net ecosystem exchange) was measured. R_{ECO} (ecosystem respiration) was measured, whereby gross ecosystem exchange could be calculated with GEE = NEE - R_{ECO}.

During the development of new fine roots before frondescence, growing plants need N resources from the soil. The reactive N resources are probably deprived from the reserve from the last vegetation period. If ash shows higher root growth rates with deeper rooting depths than *F. sylvatica* (FENDER ET AL., 2012; MEINEN ET AL., 2009), the following hypotheses were formulated:

- **CO_2:**

  H 1.1: The R_{ECO} fluxes increase before frondescence. Assuming that the root mass increases the R_{ECO} fluxes are generally higher for *F. excelsior* than for *F. sylvatica.*

  H 1.2: During frondescence the R_{ECO} fluxes are consistent. Assuming all carbohydrate resources are used for leaf growth and root mass does not change, R_{ECO} fluxes are generally higher for *F. excelsior* than for *F. sylvatica.*

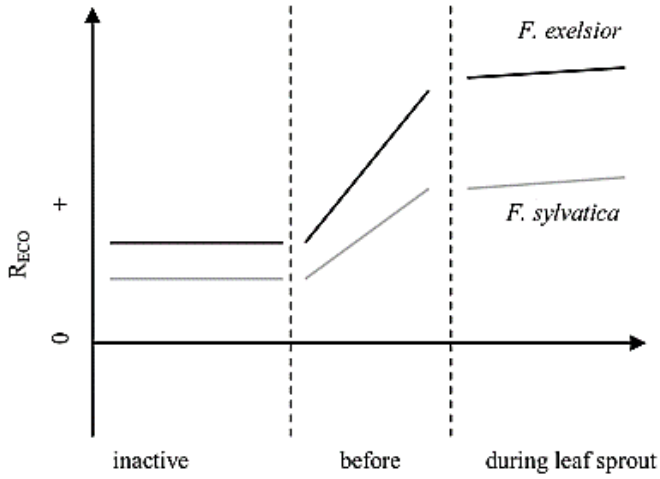

Fig. 5.3: Hypothesized relationship between R_{ECO} and root-growth stadium.

- **CH_4:**

  H 1.3: The CH_4 uptake is consistent in the inactive phase and higher for soils planted with *F. excelsior*.

  H 1.4: The CH_4 uptake increases before frondescence assuming the plant needs available N for plant growth and MMO uses CH_4 for oxidation. After that, the uptake decrease. The CH_4 uptake is generally higher for *F. excelsior* than for *F. sylvatica* planted soils.

  H 1.5: During the frondescence the CH_4 uptake is consistent. Assuming equilibrium has been adjusted between nonspecific use of CH_4 and NH_4^+, a constant rate

in uptake is reached. The CH_4 uptake is generally higher in soil-plant systems with *F. excelsior* than for systems with *F. sylvatica.*

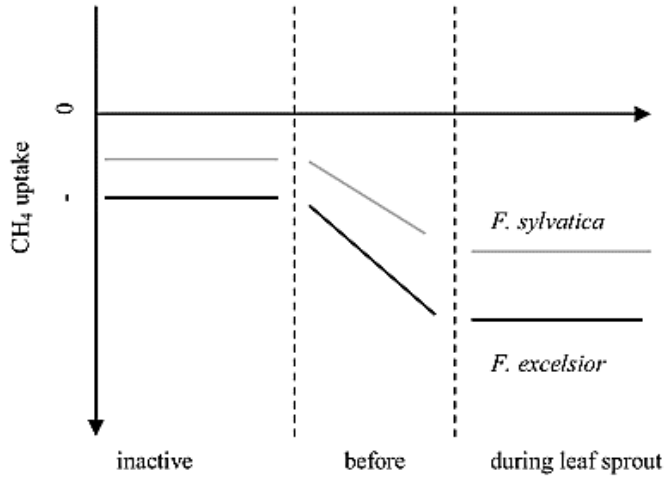

Fig. 5.4: Hypothesized relationship between CH_4 uptake and root growth stadium.

- **N_2O:**

H 1.6: The N_2O emissions are consistent in the inactive phase.

H 1.7: Before frondescence, emissions of *F. excelsior* planted soils are lower than soils planted with *F. sylvatica* and both are lower than control. Based on the assumption that plants use reactive N as a nutrient, less N is available for nitrifying or denitrifying.

H 1.8: During frondescence, the N_2O emissions still decrease, but the N_2O emissions are generally lower for *F. excelsior* than for *F. sylvatica.*

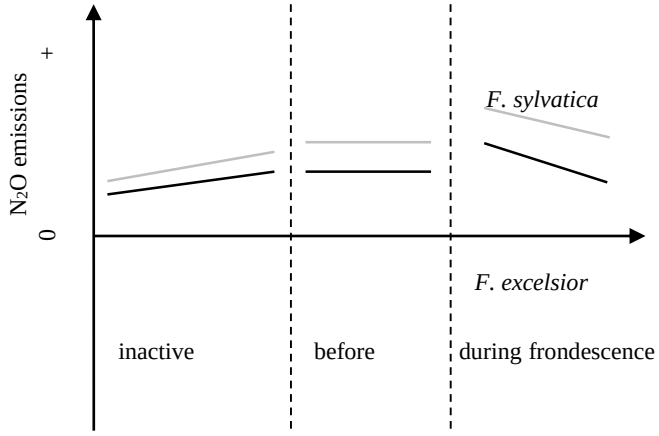

Fig. 5.5: Hypothesized relationship between N_2O emissions and root growth stadium.

5.4 MATERIAL AND METHODS

5.4.1 ANALYSIS OF TRACE GAS FLUXES

Trace gas fluxes were investigated from 26 March until 14 May, 2012. 12 out of 304 plots (180 x 120 cm), planted with ash and beech, and unplanted controls (Tab. 5.1, Fig. 5.6) were randomly selected.

In each center of a plot, a PVC-collar (10 cm in diameter) was installed towards a depth of 2 cm in the A_h horizon (Fig. 5.7). On each site soil temperature at 2 cm depth and relative soil water content were measured. GHG fluxes were measured by use of the 'closed-dynamic chamber' method (HOON ET AL., 2008; KUSA ET AL., 2008; NORMAN ET AL., 1997).

Tab. 5.1: Chosen plots on the study site.

Block	Plot No.	Tree-species
A	9	*F. excelsior*
	15	*F. sylvatica*
	30	Ctrl.
B	9	*F. excelsior*
	22	Ctrl.
	64	*F. sylvatica*
C	3	*F. sylvatica*
	65	Ctrl.
	76	*F. excelsior*
D	22	*F. sylvatica*
	27	*F. excelsior*
	43	Ctrl.

The chambers for gas accumulation are made of PVC (Fig. 5.7, right), 105 cm in height and 10 cm in diameter (volume: 8.2 L, collar area: 78.5 cm²). Air inside a chamber was circulated by using a small fan, and a tube which was linked to the atmosphere to prevent low pressure during gas sampling. On top, a valve was connected with a needle which was fixed with a septum. To take a gas sample, the syringe had to be connected with the valve. For this study 60 mL syringes were used, taking 50 mL gas per sampling. Immediately after installation of a chamber on a collar, the first gas sample was taken (T_0). The first measurement (T_0) was taken on Block B Plot 22, following a sampling route shown in Fig.5.6. One sampling route lasted 12 min (period 0-12 min). T_1 samples from each plot were taken from minute 15 to minute 27 and T_2 samples were taken from minute 30 to minute 42. This circumnavigation assured that each plot was sampled after 15 and 30 minutes after T_0.

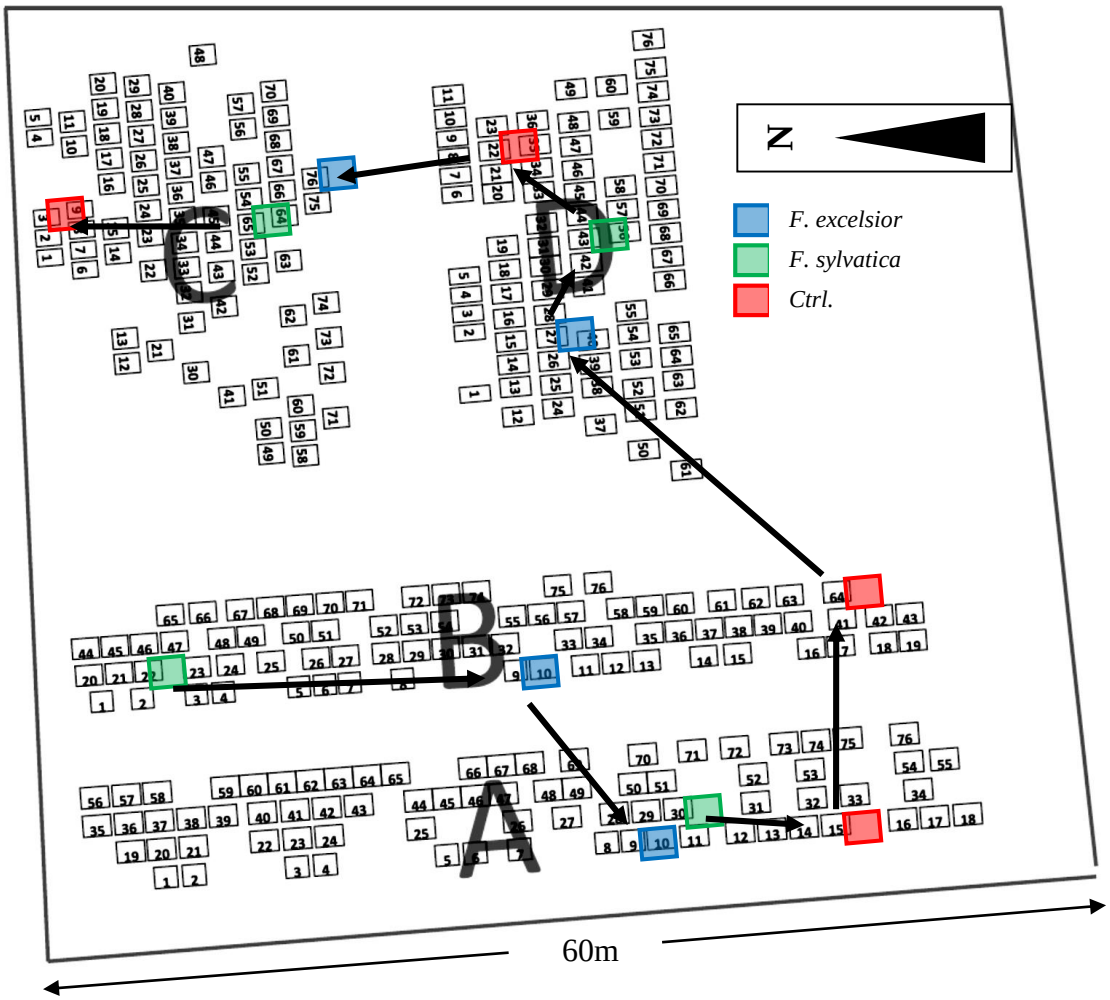

Fig. 5.6: Overview of the SPLIDRHEX site. A, B, C and D are the blocks. Plots used for trace gas measurements are marked by boxes and numbers. Arrows in the map mark the lap direction to taking the gas samples.

Fig. 5.7: Two plot examples. **To the left:** the red line shows the rectangular dimension of the plot (180 x 120 cm) and the PVC-collar in its center. To the right: closed PVC-tubes with access ports for gas sampling on the top and devices for maintenance of pressure balance at the bottom.

5.4.2 CHEMICAL SOIL ANALYSES

Chemical soil analyses for the SPLIDRHEX-site (Tab. 5.2) were conducted by the Department of Ecology and Ecosystems Research, Albrecht von Haller Institute for Plant Sciences, University of Göttingen.

Tab. 5.2: Chemical soil parameters of the blocks (A – D) in two soil depths.

Block	Horizon [cm]	pH (H_2O)	pH (KCl)	C total [%]	N total [%]	C:N	Base Saturation
		Mean / % ± SE					
A	0-10	5.3 ± 0.2	4 ± 0.1	3.1 ± 0.7	0.21 ± 0.06	14.1± 0.9	44 ± 11.9
	10-20	4.8 ± 0.2	3.9± 0.1	0.8 ± 0.2	0.09 ± 0.01	8.8± 1.7	10.5 ± 3.9
B	0-10	5.6 ± 0.2	4.3± 0.2	2.1 ± 0.4	0.16 ± 0.04	13± 1.0	58.6 ± 14.4
	10-20	5.7 ± 0.3	4.6± 0.3	1.5 ± 0.6	0.12 ± 0.05	11± 2.0	46.5 ± 17.4
C	0-10	5.8 ± 0.4	4.3± 0.2	3.4 ± 0.2	0.23 ± 0.03	14.6± 0.4	53.3 ± 17.0
	10-20	5.2 ± 0.2	3.9± 0.1	1 ± 0.1	0.1 ± 0.02	9.8± 0.8	35.4 ± 16.4
D	0-10	5.4 ± 0.3	4.3± 0.3	2.9 ± 0.5	0.21 ± 0.06	13.8± 0.5	18.4 ± 5.5
	10-20	4.7 ± 0.1	3.9± 0.1	0.9 ± 0.1	0.1 ± 0.01	8.4± 1.0	45.5 ± 17.1

5.4.3 STATISTICS

Statistical analyses were performed by R 2.15.0 (03/30/2012) for Microsoft Windows (The R Foundation for Statistical Computing) with the "agricolae", "coin" and "exactRankTests" packages. All data were tested for normal distribution with the Shapiro-Wilk test. If any factor like tree species or photosynthesis influenced the gas fluxes the data were tested by using the F-test.

All the data of measured gas fluxes showed no normal distribution. In order to identify significant differences among the gas fluxes and the treatments, means of the cumulative gas fluxes and the gas fluxes for each measurement day were calculated. Therefore the Least Significant Difference (LSD) – test of the "agricolae"-package, including the multiple comparisons through the method of the minimum significant difference, was used. For the single measurement days and for the cumulative gas fluxes the level of significance was defined at $P = 0.05$. For comparison with literature data, gas fluxes from the experiment were corrected for soil temperature and were converted with the Q_{10} based formula:

$$Q_{10} = = \left(\frac{f(T2)}{f(T1)}\right)^{\frac{10}{(Temp\ T2 - Temp\ T1)}}$$

T1 = gas flux on *T1*

T2 = gas flux on *T2*

Temp T1 = reference temperature [°C]

Temp T2 = increased temperature [°C]

5.5 RESULTS

5.5.1 CO_2 FLUXES

In 2012, frondescence of *F. excelsior* was observed between late April and early May. For *F. sylvatica* the onset of frondescence was also observed in late April but lasted about one week longer until mid-May. During the increasing trend (R^2=0.69) in CO_2 effluxes from soil (Fig. 5.8), highly variable fluxes from each treatment were observed. Mean fluxes ranged from 30.4 ± 5.1 to 85 ± 35.4 mg C-CO_2 m^{-2} h^{-1} during that time. Decreases in fluxes were found on Nº 3 and 6 with up to 60-80 %. Until 23 April, CO_2-efflux from plots with *F. sylvatica* was slightly, but not significantly higher than those from plots with *F. excelsior*, while the reverse was observed during the first week of May, when ash was in its advanced state of frondescence.

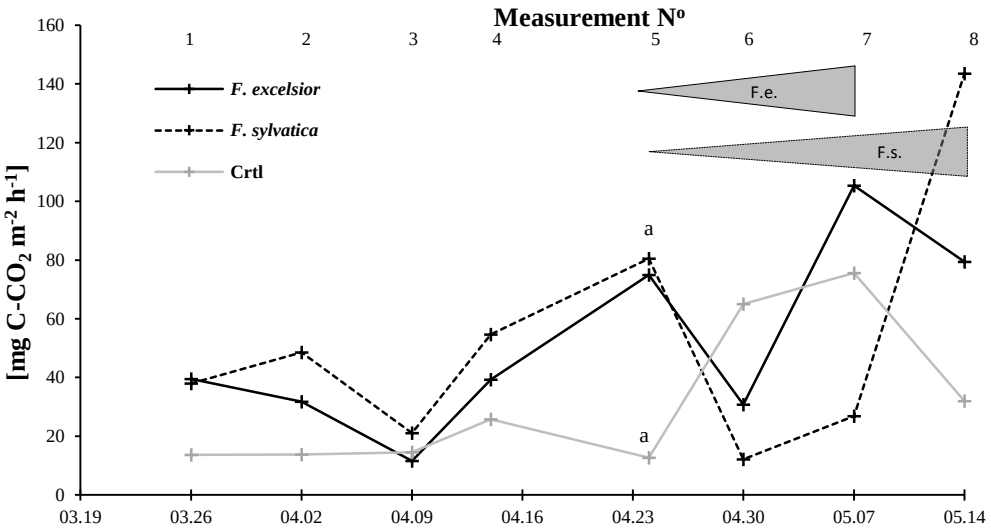

Fig. 5.8: Mean CO_2-efflux from soil for each measurement Nº (1-8), significant differences between the gas fluxes are indicated by different latters ($\alpha < 0.05$) using LSD-based pairwise comparisons test. Triangles mark the period of frondescence of both tree species.

5.5.2 CUMULATIVE C-CO_2 EFFLUX

At the end of the experimental period the cumulative CO_2 emission from tree-planted plots was nearly the same as the CO_2 emission from the control (Fig. 5.9).

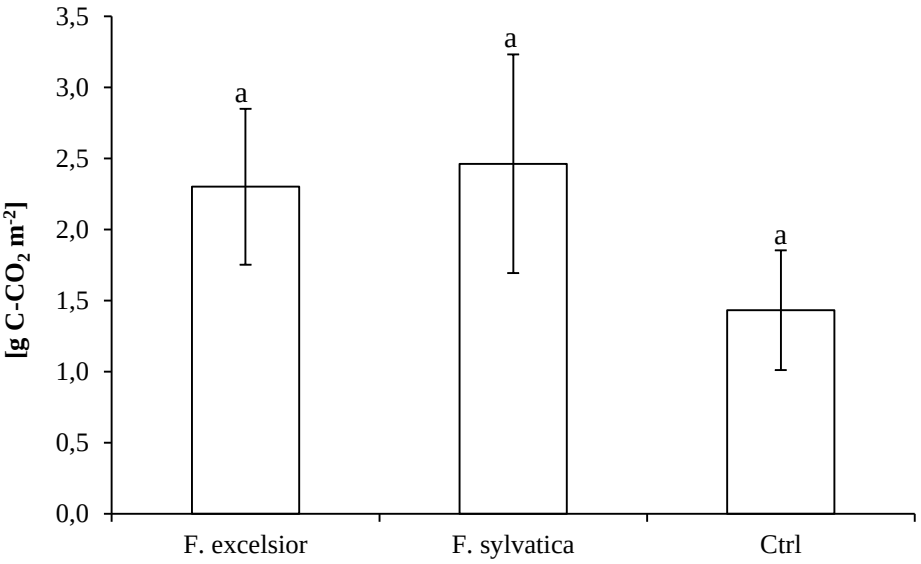

Fig. 5.9: Mean cumulative CO_2 emission (g C-CO_2 m^{-2}) over a period of 50 days. Gas fluxes with the same letter are not significantly different ($\alpha = 0.05$) using LSD-based pair wise comparisons test; for tree species n=4, means ± SE

5.5.3 CH_4 FLUXES

Methane fluxes into the soil were highly variable and showed no increasing trend (R^2 =0.08) during the experimental period (Fig. 5.10). Plots with *F. sylvatica* highly increased in uptake rates on N° 4 up to 400 % (from -6.5 to -27 µg C-CH_4 m^{-2} h^{-1}), afterwards uptake decreased until N° 7. Plots with *F. excelsior* showed a consistently increasing trend during the time. The uptake increased up to 250 % (from -12 to -30 µg C-CH_4 m^{-2} h^{-1}). Obviously, the peak in uptake on N° 6 was observed for all treatments. After that increased uptake rates for plots with *F. sylvatica* results in a value which was 600 % lower than on N° 5.

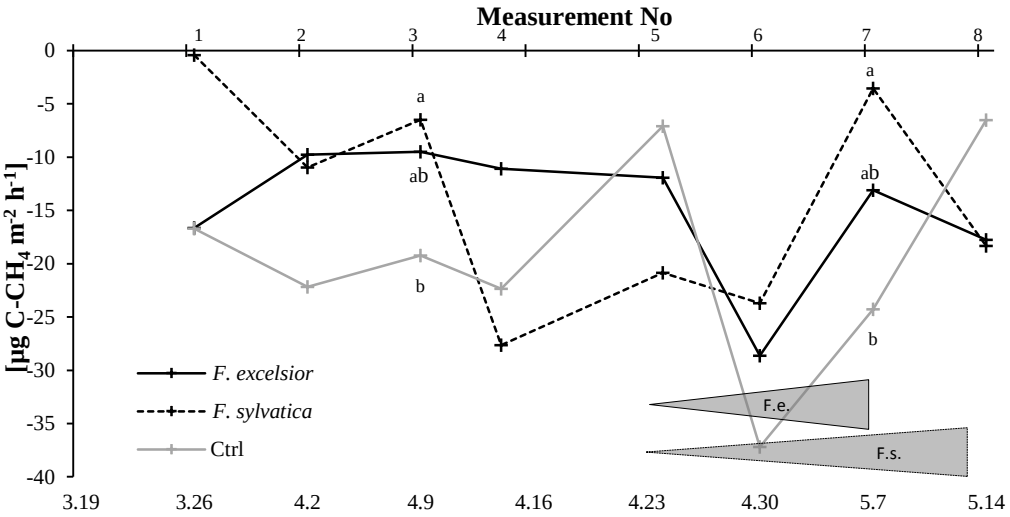

Fig. 5.10: Mean net C-CH_4 uptake for each measurement N° (1-8), significant differences between the gas fluxes are indicated by different letters ($\alpha < 0.05$) using LSD-based pairwise comparisons test. Explanations of symbols see Figure 5.8.

5.5.4 CUMULATIVE C-CH_4 UPTAKE

No significant differences of cumulative C-CH_4 uptake between the tree treatments were observed (Fig. 5.11).

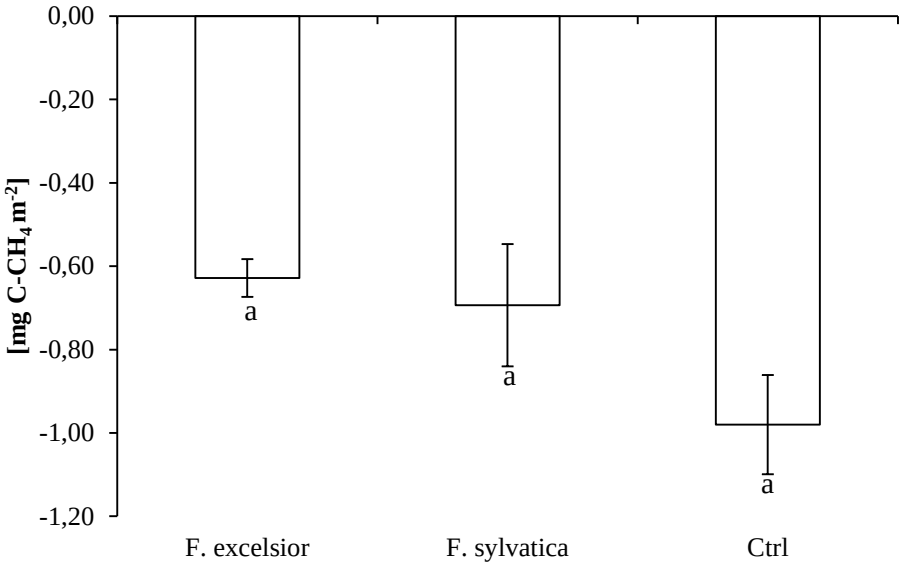

Fig. 5.11: Mean net cumulative CH_4 uptake (mg C-CH_4 m^{-2}) for the field study over a period of 50 days. Gas fluxes with the same letter are not significantly different ($\alpha = 0.05$) using LSD-based pairwise comparisons test; for tree species n=4, means ± SE

However, the planted plots showed the lowest C-CH_4 uptake compared with the uptake of the control plots: the uptake ranged from -630 ± 90 µg C-CH_4 m^{-2} h^{-1} for *F. excelsior*; and -690 ± 290 µg C-CH_4 m^{-2} h^{-1} for *F. sylvatica* to -930 ± 240 µg C-CH_4 m^{-2} h^{-1} for control.

5.5.5 N_2O FLUXES

Fig. 5.12 shows the amount and variation of mean N-N_2O fluxes under ash, beech, and pure soil during the phenological period of frondescence in spring 2012. From N° 4, N_2O fluxes from beech and ash planted soil increased up from 14 to ca. 80 µg N-N_2O m^{-2} h^{-1} until N° 6. Afterwards, fluxes decreased to the base level (15-20 µg N-N_2O m^{-2} h^{-1}). On N° 5, the control showed an N_2O-uptake at a rate of -32 µg N-N_2O m^{-2} h^{-1}. Additionally, fluxes of the controls reached a peak of N_2O-efflux at 150 µg N-N_2O m^{-2} h^{-1}. However no significant differences between the plant treatments were found, but the tendency of higher N_2O-efflux than from pure soil is visible.

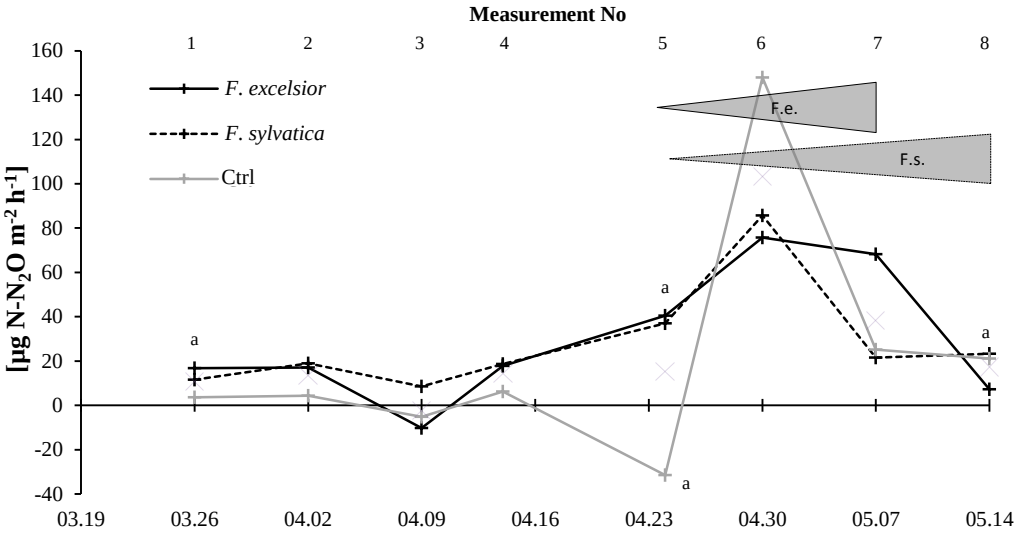

Fig. 5.12: Average net N-N_2O fluxes (n = 12 plots) of the SPLIDRHEX-experiment. Explanations of symbols see Fig.5.8.

5.5.6 CUMULATIVE N-N_2O EXCHANGE

During the period of frondescence, planted plots released more N-N_2O than pure soil (Fig. 5.13). Fluxes ranged from 1470 ± 480 µg N-N_2O m^{-2} h^{-1} (*F. excelsior*) to 1580 ± 760 µg N-N_2O m^{-2} h^{-1} (*F. sylvatica)*, while N-N_2O flux from unplanted soil was 1030 ± 880 µg N-N_2O m^{-2} h^{-1}. Accordingly, fluxes were not significantly different between each other.

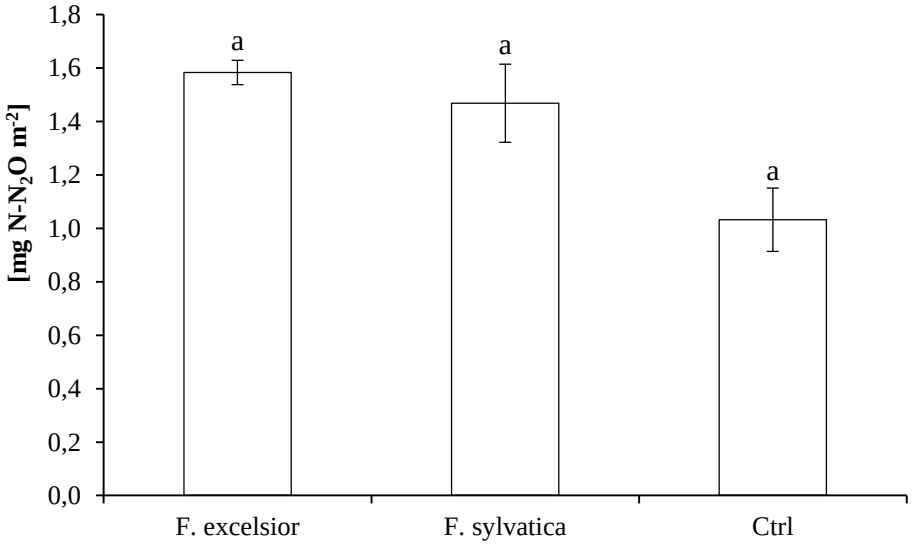

Fig .5.13: Mean net cumulative N-N_2O (mg N-N_2O m^{-2}) emission for the field study over a period of 50 days. Gas fluxes with the same letter are not significantly different ($\alpha = 0.05$) using LSD-based pairwise comparisons test; for tree species n=4, means ± SE

The statistical tests revealed an effect of tree species on the CO_2 (N° 1 and N° 6), CH_4 (N° 2 and N° 5), and N_2O (N° 7) fluxes (Tab. 5.3). For most of the measurements, block effects could be excluded (except CO_2 measurement N° 6 and N_2O measurement N° 7).

Tab. 5.3: *P*- values of F-tested influence of block design or tree species on GHG fluxes from soil.

		Measurement Nº							
		1	**2**	**3**	**4**	**5**	**6**	**7**	**8**
CO_2	Block	0.72	0.8	0.24	0.22	0.69	**0.05**	0.12	0.35
	Species	**0.1**	0.35	0.37	0.32	0.46	**0.1**	0.17	0.46
CH_4	Block	0.95	0.1	0.92	0.43	0.54	0.31	0.48	0.15
	Species	0.72	**0.02**	0.34	0.92	**0.08**	0.67	0.12	0.52
N_2O	Block	0.6	0.56	1	0.23	0.63	0.19	**0.01**	0.2
	Species	0.3	0.14	0.13	0.6	0.2	0.39	**0.01**	0.7

5.6 DISCUSSION

Species-specific root activity before frondescence and its influence on GHG-fluxes

5.6.1 CO_2 FLUXES

GHG-fluxes and Q_{10}-values in springtime matched in range with SAVAGE ET AL. (2009), JANSSENS & PILEGAARD (2003) and NGAO ET AL. (2012) (Tab.5.4). Smaller fluxes measured by BORKEN ET AL. (2002) showed higher consistency. Additionally, Q_{10} by BORKEN ET AL. (2002) for both sites suggest a consistency for forests dominated by *F. sylvatica*. For forests dominated by *F. excelsior*, values for effluxes and Q_{10} from NGAO ET AL. (2012) agreed with this study, but the authors used another gas measurement method.

To compare and arrange fluxes from this study with fluxes from other studies following table 5.4 was performed.

Tab. 5.4: C-CO_2 effluxes from other studies with occurring tree species.

Author	Location	Soiltype or characteristics	Dominant tree sp.	Method	C-CO_2 effluxes [C-CO_2 mg m^{-2} h^{-1}]	Q_{10}
Savage et al. (2009)	Massachusetts USA	"Canton fine sandy loam"	*Q. rubra*	automatic dynamic chamber	50 to 140 (April)	3.7-4.2
Janssens & Pilegaard (2003)	Denmark	Mollisol	*F. sylvatica*	closed dynamic chamber IRGA-Licor 6252	59 to 220 (April)	4.0-4.6
Ngao et al. (2012)	Hesse state forest eastern France	gleyic luvisol	*F. sylvatica, F.excelsior*	closed dynamic chamber IRGA-Licor 6252	40 to 122 (April)	2.4-2.9
Borken et al. (2002)	Unterlüß Lower Saxony, Germany	dystric Cambisols	*F. sylvatica, P. abies, P. sylvestris*	PVC-columns, GC	25 to 50 (April)	1.8-3.5 (0-5 soil depth [cm] for beech Stand)
Borken et al. (2002)	Solling Lower Saxony, Germany	dystric Cambisols	*F. sylvatica, P. abies, P. sylvestris*	PVC-columns, GC	25 to 30 (April)	1.7-2.97 (0-5 soil depth [cm] for beech Stand)
This study	**Reinhausen, Lower Saxony, Germany**	**regic Cambisol**	***Q. douglasii (Plots with F.sylcatica & F.excelsior)***	**closed dynamic chambers, syringes, GC**	**12 to 143 (F.s.) 16 to 85 (mean)**	**3.6±2.6 (F.s.) 2.9±0.9 (mean)**

CO_2 fluxes were tested if species or block design has any impact on emissions (Tab. 5.2). Gas fluxes were neither depending on tree species or block design. Cumulative effluxes from planted plots were larger than those from the control, but no significant differences were found.

Largest impact factors for increased emissions during the measuring time are soil temperature (Q_{10}, UVAROV ET AL. 2006; JANSSENS & PILEGAARD, 2003; BORKEN ET AL. 2002) and soil moisture (OTTOW, 2011). Each of them was correlated with CO_2 effluxes (Fig. 5.14). A multiple linear regression was performed to test the influence of both on CO_2 effluxes and showed high correlation between them (R^2= 0.93; p=0.0043; CO_2 effluxes = $(4.3771 \times T_{Soil}^{1.3432}) + (0.0715 \times Moisture_{Soil} + 36.606)$).

As a consequence, declines in CO_2 fluxes from soils were found on Nº 3 (04/09/12) and 6 (04/30/12). It could be suggested that the reduced CO_2 fluxes of Nº3 originated from a drop in air temperature to 0°C in the night before. The gas measurement was in the morning at 8.30 AM and the soil temperature was correspondingly low (Fig. 5.2). On Nº 6, air temperature reached up to 30°C (corresponding to a peak in the soil temperature around 13°C (Fig. 5.2) and soil moisture decreased to 40 %. These combined trends of both factors suggest affection on the strong decrease of CO_2 fluxes from soil. This effect superimposed possible impacts of frondescence from both tree treatments.

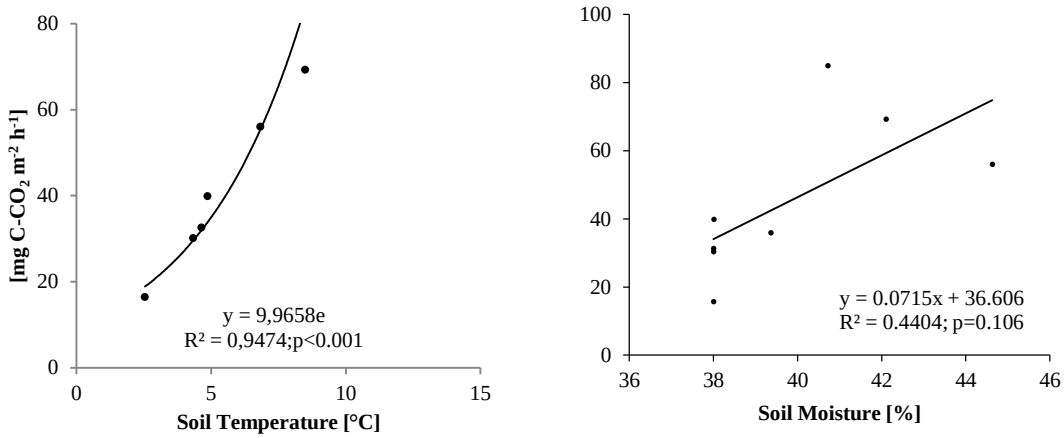

Fig. 5.14: Dependence of CO_2 emissions on soil temperature and soil moisture (without extreme value +).

5.6.2 CH_4 FLUXES

Uptakes are in a similar range like uptake rates observed by BORKEN ET AL. (2003, Unterlüß) and CHRISTIANSEN ET AL. (2012). Fluxes measured by CHRISTIANSEN ET AL. (2012) are in range, but fluxes were induced due to changes in soil water content (Tab. 5.5). Q_{10} determined by BUTTERBACH-BAHL & PAPEN (2002) is lower than in this study. This can be explained by a lower pH in their study site which reduced the CH_4 uptake (WESLIEN ET AL., 2009).

No significant influences of block design or tree species was observed (Tab. 5.3). Temperature (Q_{10}, VICCA ET AL., 2009) affected CH_4 uptake more than soil moisture (Fig.

5.15). In contrast to this study, positively influences of soil moisture on CH_4 uptake was observed by SMITH ET AL. (2000).

Based on these correlations, the peak in CH_4 uptake on N° 6 can be explained by high air temperature around 30°C (soil temperature reached up to 13°C). This effect also superimposed possible impacts of frondescence from both tree treatments.

Tab. 5.5: C-CH_4 uptake from other studies with occurring tree species.

Author	Location	Soiltype or characteristics	Dominant tree sp.	Method	C-CH_4 uptake [µg C-CH_4 m^{-2} h^{-1}]	Q_{10}
Borken et al. (2003)	Unterlüß Lower Saxony, Germany	dystric Cambisols	*F. sylvatica, P. abies, P. sylvestris*	PVC-columns, GC	-25 to -16 (April)	nD
Borken et al. (2003)	Solling Lower Saxony, Germany	dystric Cambisols	*F. sylvatica, P. abies, P. sylvestris*	PVC-columns, GC	-37.5 to -33 (April)	nD
Butterbach-Bahl & Papen (2002)	Höglwald, Bavaria, Germany	"acid Hapludalf"	*F. sylvatica site*	gas-probe within a soil profile, GC	-60 to -37 (April) -83 to -60 (average from 1994-1997)	1.48
Christiansen et al. (2012)	Denmark, Stødam	sandy loamy glacial till	*F. sylvatica*	closed static chambers, Syringes, GC	-11.1 to -9.7 (soil water content = 45%)	nD
Christiansen et al. (2012)	Denmark, Vestskoven	glacial origin with low variation in texture	*Q. robur*	closed static chambers, Syringes, GC	-2.7 to 0.5 (soil water content = 45%)	nD
this study	Reinhausen, Lower Saxony, Germany	regic Cambisol	*Q. douglasii (Plots with F.sylcatica & F.excelsior)*	closed dynamic chambers, syringes, GC	-24 to -0.4 (F.s.) -30 to -11 (mean)	5.1±2.1 (F.s.) 3.5±0.8 (mean)

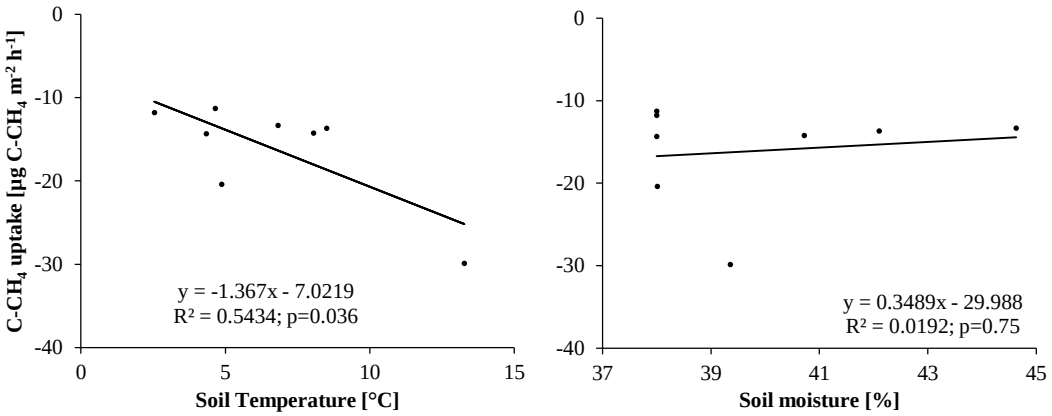

Fig. 5.15: Dependence of CH_4 uptake on soil temperature and soil moisture.

5.6.3 N_2O FLUXES

N_2O effluxes from this study are higher than other studies and are not in the same range (Tab. 5.6). Only lowest fluxes of mean matched into the range of CHRISTIANSEN ET AL. (2012). Nevertheless, uptake of N_2O was also observed in this study. Reasons for this are discussed in CHAPUIS-LARDY ET AL. (2007) who suggests that N_2O uptake is based on the consumption of nitrifiers and denitrifiers and it depends on availability of mineral N and physical and chemical soil properties.

Tab. 5.6: N-N_2O effluxes from other studies with occurring tree species.

Author	Location	Soiltype or characteristics	Dominant tree sp.	Method	N-N_2O uptake [µg N-N_2O m^{-2} h^{-1}]	Q_{10}
Borken & Beese 2006	Solling Lower Saxony, Germany	dystric Cambisols	*F. sylvatica, P. abies, P. sylvestris*	PVC-columns, GC	2 to 5 (April)	nD
Christiansen et al. (2012)	Denmark, Stødam	sandy loamy glacial till	*F. sylvatica*	closed static chambers, Syringes, GC	4 to 10 (soil water content = 45%)	nD
Christiansen et al. (2012)	Denmark, Vestskoven	glacial origin with low variation in texture	*Q. robur*	closed static chambers, Syringes, GC	8 to 13 (soil water content = 45%)	nD
this study	**Reinhausen, Lower Saxony, Germany**	**regic Cambisol**	***Q. douglasii (Plots with F.sylcatica & F.excelsior)***	**closed dynamic chambers, syringes, GC**	**9 to 86 (F.s.) 0.2 to 78 (mean)**	**25±21 (F.s.) 20±7 (mean)**

Temperature (Q_{10}, VICCA ET AL., 2009) affected N_2O emissions from soil more than soil moisture (Fig. 5.16). Soil temperature and N_2O emissions were positively correlated.

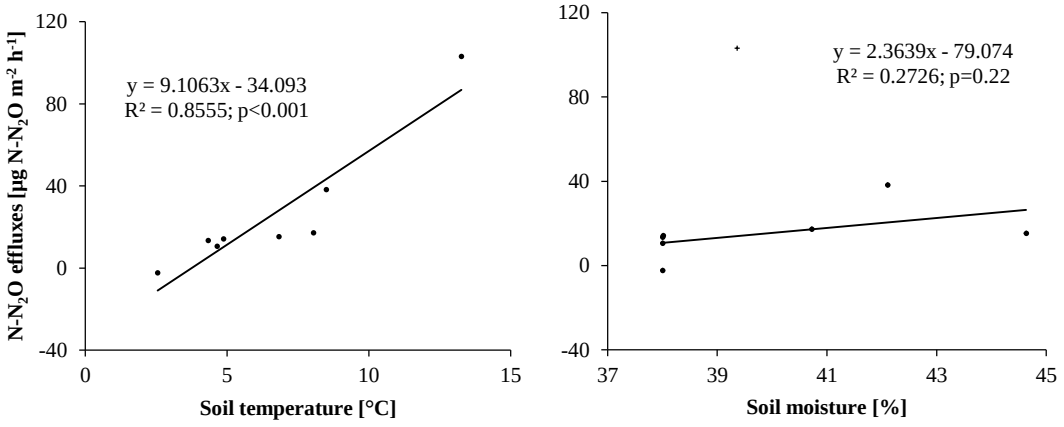

Fig. 5.16: Dependence of N_2O emissions on soil temperature and soil moisture (without extreme value +).

A multiple linear regression was performed to test the influence of both on N_2O effluxes and showed a high correlation between them (R^2= 0.92; p=0.001; N_2O effluxes = (9.1063×T_{Soil}-34.093) + (2.364 × $Moisture_{Soil}$-79.074)).

It can be assumed that the high peak in N_2O emissions is caused by climate conditions and is not induced by root growth.

5.7 CONCLUSION

Before frondescence emissions from soil planted with *F. sylvatica* increased less than those from soil planted with *F. excelsior*, confirming hypothesis 1.1. During frondescence, fluxes continued to increase and no constant emissions of the trace gases were observed. While the temporal increase of emissions from soil planted with *F. sylvatica* ended after frondescence fluxes from soil planted with *F. excelsior* continued to increase even after the end of frondescence. Focused on the trend of fluxes, hypothesis 1.2 was disapproved. Under natural conditions, an assertion about root growth is not possible because the amount of CO_2 effluxes from soil was superimposed by climate conditions (e.g. soil temperature and soil moisture).

The gas measurements before frondescence showed that CH_4 uptake into the soil remained constant over time. Soil planted with ash showed a slightly higher uptake of methane than soil planted with beech, supporting hypothesis 1.3. An increased uptake immediately before frondescence was not observed, and no significant differences were measured. Hence, hypothesis 1.4 could be rejected. During frondescence, a consistent uptake of methane was observed for soil planted with beech but not for soil planted with ash. Therefore hypothesis 1.5 was confirmed with respect to *F. sylvatica* but not for *F. excelsior*.

The gas measurements before frondescence showed that the N_2O emissions were consistent and no differences between both tree species were observed. Therefore, hypothesis 1.6 was confirmed. The strongest reduction of N_2O emission was observed for soil planted with *F. excelsior*. Generally N_2O emissions of planted soil treatments were nearly the same than those of the control (Fig. 5.12, no significant differences were found); this finding rejected hypothesis 1.7. During frondescence, fluxes increased, but are strongly depending on WFPS. N_2O effluxes for soils planted with *F. excelsior* were not significant lower than from soils planted with *F. sylvatica.* This rejected hypothesis 1.8.

Under natural conditions, temperature (Q_{10}) affected N_2O emissions from soil more than soil moisture. And based on these results, a species-specific influence on effluxes was not confirmed.

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Uni Goettingen = Climate conditions on the Forest Botanical Garden at the University of Göttingen.
URL: http://www.uni-goettingen.de/en/10232.html (visited on 08/19/2012)

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CHAPTER 6

SYNOPSIS

6. SYNOPSIS

The present study has the main objective to quantify the specific species effect of organisms on greenhouse gas fluxes from and into soils. Most current studies on GHG do not consider species specific effects or take biodiversity effects into account. These effects may very well explain differences in fluxes that were not explainable up-to-date. At the plant-soil system level, representing a simplified ecosystem level, such effects are detectable by manipulative experiments. For this PhD-Study the effects of earthworms (*Lumbricus terrestris* / *Aporrectodea caliginosa*), ash and beech saplings (*Fraxinus excelsior* L. / *Fagus sylvatica* L.), as well as litter and root induced effects on the N_2O, CH_4 and CO_2 fluxes from a temperate forest soil were investigated (Chapter 6.1). Further the investigation of the study was the species-specific influence of photosynthesis and root activity of ash and beech (*Fraxinus excelsior* L. / *Fagus sylvatica* L.) saplings on the N_2O flux from soil and identify influences on other greenhouse gas (GHG) fluxes of CH_4 and CO_2 between soil and atmosphere (Chapter 6.2). Additionally a field study under near-natural conditions was established to investigate, if a high metabolic activity of fine roots induces strong species-specific effects on GHG fluxes before and during frondescence in early spring.

6.1 THE INFLUENCE OF EARTHWORMS (*LUMBRICUS TERRESTRIS*, *APORRECTODEA CALIGINOSA*) ON THE SHORT TERM IN COMPARISON TO LONG TERMS EFFECTS ON GREENHOUSE GAS FLUXES (N_2O, CH_4 AND CO_2) FROM SOIL

(COMBINING THE SOIL COLUMN EXPERIMENT OF CHAPTER 2 WITH THE RHIZOTRON EXPERMENT OF CHAPTER 4)

The soil column experiment of Chapter 2 presented the results on the temporal dynamics of greenhouse gas fluxes between soil and atmosphere as influenced by earthworms and ash saplings. To investigate these trace gas fluxes, a laboratory experiment was constructed with soil and ash saplings (*Fraxinus excelsior* L.) and ash litter from a temperate mixed broad-leaved forest as forage to study the effects of earthworms (*Lumbricus terrestris* and *Aporrectodea caliginosa*) on the temporal pattern of greenhouse gas fluxes. The experimental time (90 days) of this soil column experiment showed that earthworms have an increasing effect on the N_2O emission and a decreasing effect on the CH_4 uptake. Ash showed a reducing effect of N_2O emission from soil and a higher CH_4 uptake; whereas a higher CO_2 emission caused by root respiration (FENDER et al., 2012[b]) was measured.

To investigate this earthworm effect at an extended experimental time of 416 days (Chapter 4), a rhizotron experiment was installed and planted with beech (*Fagus sylvatica* L.) and ash (*Fraxinus excelsior* L.) saplings. Two earthworm species, four *Lumbricus terrestris* and four *Aporrectodea caliginosa* where applied and beech- and ash-litter provide as forage. The experiment was established under defined climatic conditions in a greenhouse chamber and the incubated soil was layered (horizons $O/A_h/A_l/B_t$) in the rhizotrons.

During experimental time of the soil column experiment in Chapter 2, the treatment (A) planted with ash and without earthworms had decreased N_2O emissions and increased CH_4 uptake rates, while the other treatments had nearly the same level of emissions. A significant difference of the N_2O emissions was detected during the 90 days between the treatments planted with ash and the unplanted treatment supplied with earthworms (E).

The rhizotron experiment in Chapter 4 showed that the treatment without earthworms planted with ash and beech and applied ash litter had the lowest N_2O emission. A significant difference was found during 416 days between the treatment planted with beech/ash and ash-litter and the counterpart of this treatment with applied earthworms. But the time-scale showed that the N_2O peaks of the earthworm experiments occur in the first week after inserting the earthworms in the rhizotron experiment and after five weeks in the soil column experiment.

This emission effect of the soil column experiment was distinguished and extrapolated and it is important to know, whether identified impacts of earthworms on GHG dynamics from soils are solely inducing "hot moments" (CONRAD, 1996) and overall fluxes stay alike or if the effects are of prolonging nature. The N_2O emissions revealed 3 periods of the N_2O emission which was the reason why the total 90 days were additionally calculated as three 30 days periods.

The first period showed no significant differences between the treatments and had relative low N_2O emissions. The second period could be defined as a "hot moment" showing a rapid increase of the N_2O emissions for nearly all treatments. During the second period, treatments with earthworms were high emitter and the treatments without earthworms revealed lower emission levels. A significant difference between the treatments ash/earthworm (A/E) and ash (A) and between A/E and control (C) was found. Solely the control reacted delayed and its peak emission was found within the third period while all other treatments returned to low emissions. The significant difference between ash/earthworm and ash prevailed, but not between earthworm and control. The measured $N\text{-}N_2O$ fluxes are comparable to the results of BORKEN et al., 2000. The main question to be answered by this experiment was, if the

influence of earthworms on GHG fluxes prevails for planted soil representing a more complete ecosystem model experiment. The treatments showed a strong increase, but with different timing. The treatment ash/earthworm reacted 9 days prior to the earthworm treatment and their non-earthworm counterparts, whereas the treatments with ash reacted faster (8 days) than those without ash. Hence, an enduring earthworm effect was solely found for the plant-soil system, but not for the unplanted earthworm soil systems. During the "hot moment" phase of days 30 to 60 a temporal differentiation of the impact of earthworms on greenhouse gases from soil seems therefore to be appropriate. Consequently, earthworms support the release of N_2O; our results solely fully support this assumption for planted soils.

The rhizotron experiment (Chapter 4) showed that N_2O fluxes from soil were lower than in the soil column experiment (Chapter 2). This is a common effect of the destruction of soil aggregates and a higher bio availability of carbon and nitrogen resources (JUNGKUNST et al., 2008). At the beginning of the rhizotron experiment, the N_2O fluxes were very high, caused by the availability of nitrogen, carbon and oxygen in the soil ("boost-effect"). The bioturbation activity of earthworms also caused higher N_2O emissions. During the first week after earthworm insertion the N_2O emission of the treatments, excluding the treatment beech/ash and ash litter (A), was on a relatively high level. A very fast increase (first week) after application was shown by the treatment beech/ash/earthworm and ash litter (E/A) which indicates a related effect of earthworms and ash litter. The highest peak was shown by the treatment beech/ash/beech litter (B). That effect was initiated by the soil setting effect in the first weeks. The treatment beech/ash/earthworm and beech litter (E/B) showed neither high N_2O emissions nor an emission peak, which could be affected by a lower activity of the earthworms, foraged with beech litter and a possibly higher mortality of the earthworms. Four months after the start of the experiment a balanced effect between the treatments with and without earthworms was observed.

The cumulative N_2O emission between the high N_2O emission treatments E/A and B had a statistically significant difference compared to the low N_2O emission treatments E/B and A. The results showed that earthworms support the release of N_2O, the results did confirm this assumption; but only conditionally, it depends on the litter, associated with the forage activity and survival rate of the earthworms. The differences between the treatments with earthworms (E/A, E/B) were statistically different, an influence of the earthworms on N_2O emission can be derived from the results. The fact that cumulative N_2O emissions were not at similar levels, depends on litter quality, associated with forage activity of earthworms, which could also lead to a higher mortality. Besides, the circumstance that cumulative N_2O

fluxes of the treatment beech/ash/ash litter (A) were expected, it was the treatment with the lowest emissions.

The very high N_2O emission of the earthworm experiments ash/earthworm and earthworms in Chapter 2 and the treatment E/A in Chapter 4 are probably due to changes to the soil structure caused by the insertiont of the earthworms and the creation of burrows (tunnel effect) (BORKEN et al., 2000). A higher microbial activity and thus higher greenhouse gas emissions due to earthworm activity via incorporation of litter were to be expected. This proved to be very true for the high emission phase but not for the longer termed cumulative N_2O emissions.

In the soil column experiment of Chapter 2 the relative part of the net N_2O emission to CO_2-equivalents from the treatment ash only gets to 12% and the relative part of the treatment ash/earthworms had, with about 25%, a higher relative part of the net emission of N_2O. The relative parts of the unplanted group are higher at 35 – 37 %.

The relative parts of the rhizotron experiment (Chapter 4) on N_2O to the net emission (CO_2e) from the treatments beech/ash/earthworm and ash litter (E/A) was the highest with a percentage of about 7%, the treatment beech/ash/earthworm/beech litter (E/B) had a percentage of N_2O of about 4%. The treatment beech/ash/ash litter (A) had with 3% N_2O (percentage) a similar result to the treatment beech/ash/earthworm and beech litter (E/B).

The results from the two earthworm experiments on the N_2O fluxes support the suggestion that earthworms have an influence on the N_2O fluxes from soil. The rhizotron experiment supports this suggestion partially. The treatment E/A showed significantly increased N_2O fluxes to the counterpart without earthworms (A) and with the other earthworms treatment with beech litter (E/B). A reason for that result could be the high mortality (77%) of the earthworms during experimental time of the treatment with beech litter.

The CH_4 uptake of the soil columns in Chapter 2 showed an increased uptake over the time of the experiment. While the CH_4 uptake of the treatments ash and control increased continuously, the treatments with earthworms showed at the beginning of the study period a decreasing uptake. During the whole experimental time the treatments with earthworms (A/E and E) had a small CH_4 uptake rate and the treatment unplanted with earthworms (E) had the smallest CH_4 uptake rate. The temporal development of the CH_4 emission of the treatments showed increases and decreases several times. Significant differences were found between the planted soil columns with and without earthworms (A/E and A), planted with earthworm compared to the control (A/E and C), planted without earthworm and unplanted

with earthworms (A and E) and between the unplanted treatments (E and C). It was shown that earthworms apparently reduce the uptake rates of this soil. Cumulative CH_4 uptake fluxes of the treatment earthworms in comparison to the control were significantly lower by about 60%. For the planted treatments this difference was 42%.

That earthworms had a higher CH_4 uptake into the soil could not be confirmed for the treatments with applied earthworm as opposed to the N_2O results. The treatment ash/earthworm had a significant decreased CH_4 uptake referring to the ash treatment.

The rhizotron experiment (Chapter 4) showed that the cumulative CH_4 gas fluxes of the treatments have a significant difference between the treatments E/A and E/B, E/A and A and between the treatments A and B. That the described earthworm effect is an enduring effect could not be supported for the experimental time, a steady-state effect after a longer time occurs.

There are no studies describing earthworms as direct CH_4 emitters due to metabolic processes (KARSTEN & DRAKE, 1997; IHSSEN et al., 2003; DRAKE & HORN, 2007), consequently it is assumed that the reduced CH_4 uptake either refers to a decreased activity of methanotrophic bacteria in the soil columns or a reduced diffusion. The latter appears unlikely as earthworms create large holes and should therefore decrease the bulk density of the soil. During experimental time a progressive soil settlement in mean A/E -2 ± 0.3 cm 90 d^{-1} and E -2 ± 0.3 cm 90 d^{-1} of the earthworm treated soil columns of the Chapter 2 was observed, due to earthworm activity and thus reduced pore volume. The major prerequisite for the CH_4 uptake in the soil is that the methanotrophic bacteria decrease the CH_4 concentration and thus enhance the diffusive gradient between soil and atmosphere (BLUME et al., 2010). Sufficient oxygen availability is necessary for the CH_4 uptake and is determined by soil structure and ventilation (FIEDLER, 2001). To suppose that oxygen diffusion from the atmosphere into the soil was limited, thus leads to a relative inhibition of the methanotrophic bacteria in the soil columns. Another possibility could be the stimulation of microbial activity in the worm scat and drilosphere to such an extent that microbial oxygen consumption is higher than the oxygen supply by diffusive transport from the atmosphere. As a consequence a reduced activity of methanotrophic bacteria and even methanogenesis could be possible. Accounting for the low influence of earthworms on CO_2 fluxes during the experimental time, the processes mentioned above seem negligible. In particular the CO_2 emission from aerobe soils is equimolar to the consumption of oxygen (BLUME et al., 2010).

A desorption of NH_4^+ from cation exchange sites by high activities of H^+, Na^+ and K^+ cations is one possible mechanism reducing CH_4 oxidation (FENDER et al., 2012[a]) and the

excreta of the earthworms contain ammonia and urea nitrogen (EDWARDS & BOHLEN, 1996), which reduces the CH_4 uptake. That the described earthworm effect is an enduring effect could be supported for the experimental time, but a steady-state effect after a longer time is possible. This solely applies to CH_4 but not for N_2O that has to be rejected there.

The CO_2 fluxes of the soil columns experiment are in comparison to the other two gases relatively constant throughout the 90 days. Between the planted (A/E and A) and unplanted (E and C) treatments a significant difference was found. In this regard, our hypothesis that earthworms stimulate CO_2 release from soils could basically be supported. The field study of BORKEN et al. (2000) showed similar results. The authors found no significant differences of soil gas fluxes of CO_2 influenced by earthworms. However they measured a significantly higher CO_2 emission in the first 4-5 weeks, which is explained by the construction of wormholes and the incorporation of detritus in the mineral soil. The question arises, if this study underestimates the temporal dimension of the mineralization process. The contribution of earthworms to soil respiration is small (EDWARDS & BOHLEN, 1996). So it is conceivable that the mineralization of ash litter needs a longer time to significantly influence the CO_2 emission. But ash litter would anyhow influence the soil respiration regardless of earthworms present or not.

The rhizotron experiment in Chapter 4 showed that the CO_2 emission of the treatment beech/ash/beech-litter (B) had the highest value and the treatment beech/ash/earthworm and ash-litter (A) had the lowest emission. The rhizotrones applied with earthworms were on nearly the same emission level. The cumulative CO_2-emissions were not different to each other and in this regard, earthworms could not support a stimulation of CO_2 release from soils.

BERGER et al., 2010 described the higher CO_2 emission from soil covered with beech litter compared to spruce needle. However, the ash litter turnover is faster (VESTERDAL et al., 2012) and JUDAS, 1992 analysed the plant particles in earthworm gut of *Lumbricus terrestris* which showed that they prefer non-*Fagus sylvatica* L. leaves.

The view on the root biomass shows a difference of about 2 g dw^{-1} between the treatment earthworm with ash-litter (E/A) (57 g dw^{-1}) and the treatment earthworm with beech-litter (E/B) (55 g dw^{-1}). After CURRY & SCHMIDT, 2007 a possibility exists that the earthworms in the treatment with beech litter also use roots as forage instead of litter.

The higher CO_2 emission from the treatment beech/ash/beech-litter might be a root respiration effect. This treatment had a higher roots biomass, which caused a higher CO_2 emission (FENDER et al., 2012[b], CESARZ et al., 2013).

The harvest of the rhizotron experiment showed a high mortality of the earthworms. The experiment had a relative loss of *Lumbricus terrestris* in the treatment with ash litter of about 16% and of *Aporrectodea caliginosa* about 10%. The treatment with beech litter had an earthworm loss of *Lumbricus terrestris of* about 77% and a loss of *Aporrectodea caliginosa* of about 5%. The high mortality of the species *Lumbricus terrestris* in the earthworm treatment with beech litter could have a cause in the forage and that could give a reason for the low CO_2 fluxes in comparison to the treatment E/A. The treatment with ash litter forage showed a lower mortality. The treatment E/B showed a lower root biomass, which could be an indicator for the earthworm preferring roots instead of beech litter (-1.93g dw^{-1}).
The hypothesis 1, that earthworms support the net emission (CO_2e) from the soil columns could be supported but is statistically not significant.
The hypothesis 2, that the described earthworm effect is an enduring effect (for a longer period) could not be supported.

6.2 THE SPECIES-SPECIFIC INFLUENCE OF FRONDESCENCE, PHOTOSYNTHESIS AND ROOT ACTIVITY OF BEECH AND ASH SAPLINGS ON N_2O FLUXES FROM SOIL. A INVESTIGATION OF A LABORATORY EXPERIMENT IN COMPARISON TO A FIELD STUDY

(COMBINING THE RESULTS OF THE SOIL COLUMN EXPERIMENT OF CHAPTER 3 WITH THE RESULTS OF THE FIELD STUDY OF CHAPTER 4)

A laboratory experiment (Chapter 3) with incubated forest soil was conducted to investigate deciduous tree impacts on N_2O fluxes from soil. In a pre-experiment, a N_2O uptake of ash during photosynthetic activity was detected. This study tested three hypothesis related to the influence of photosynthesis from saplings of ash (*Fraxinus excelsior* L.) and beech (*Fagus sylvatica* L.).
The influence of photosynthesis on the cumulative N-N_2O emissions of ash is a reduction of roughly 55%. For beech, emissions were reduced by approximately 24%.
This study shows for the first time that photosynthesis has an instantaneous reduction effect of N_2O emissions from soils. These reductions were substantially larger for ash than for beech and the whole plant-soil system occasionally even switched from net emissions to net uptake. It was confirmed that N_2O emissions from ash–soil systems were lower than from beech–soil systems. The new aspect is that beech–soil systems show the same reduction behavior during photosynthesis as ash–soil systems. It is somehow puzzling that fluxes from

soils mainly mediated from bacteria react so instantaneously to illumination of the plants. It appears unlikely that the plant uptake of reactive N from soils has such an immediate impact.

Originating from the assumption that the reductions of N_2O emissions are a diurnal trend, the 24 hour experiment was conducted. Since the reduction of N_2O emissions was significantly larger for ash in the long-term experiment, the experiment was carried out only with this species. The general increasing trend of N_2O emissions during the 24h experiment was affected by declining WFPS as correlations between both indicated.

Contrary to the hypothesis that there would be a diurnal trend of the absolute and relative reduction of N_2O in the course of photosynthesis, there solely seems to be a minimum in the very early morning (5:00-8:00 AM).

Thereafter, reduction decreased during noon and afternoon. This observation supports the assumption about the photosynthesis effects of ash and according to KUZYAKOV (2006), a higher photosynthesis rate results in higher releases of root exudates. These exudates act as an energy source for nitrifying and denitrifying microorganisms (YANG & CAI, 2006). Therefore, the photosynthesis activity rate may affect N_2O production and consumption in planted soils in three possible ways: (a) release of root-exudates as energy source for nitrification and denitrification; (b) withdrawal of reactive N compounds by roots during photosynthetically active plants and (c) direct N_2O reduction by ash itself.

The result showed that there is an effect of photosynthesis on N_2O emissions from soils and there are differences between ashes and beeches in the case of this photosynthesis effect. As a consequence, photosynthesis activity of both species reduced the N_2O emissions with the same absolute rate which was significantly different to zero. Therefore, it is apparently important for ecosystems' GHG flux measurements to consider if plants receive light or not.

One main objective of the field study of Chapter 5 is to identify species-specific influences of European beech (*Fagus sylvatica* L.) and European ash (*Fraxinus excelsior* L.) saplings on greenhouse gas (GHG) fluxes between soil and atmosphere under near-natural conditions. The hypothesis is that high metabolic activity of fine roots induces strong species-specific effects on GHG fluxes before and during frondescence in early spring. This is due to characteristic differences in the phenological cycle of these tree species, also addressing fine root growth, mobilization of nonstructural carbohydrates and mycorrhizal metabolism which may lead to considerably different GHG fluxes. According to that the GHG emissions showed consistent low fluxes for both tree species (14 µg $N\text{-}N_2O\ m^{-2}\ h^{-1}$) during the leafless period. Before frondescence, the GHG emissions from soil planted with beech increased less

than from soil planted with ash which increased up to 230 % (14 to ca. 80 µg N-N_2O m^{-2} h^{-1}) under the same soil temperature regime. During frondescence, the fluxes continued to increase and no constant emissions were observed. Generally emissions of planted soil plots were lower than those of the unplanted control. The strongest reduction of N_2O emission was observed for soils planted with ash. The five gas measurements during the leafless period showed that the CH_4 uptake by the soil remained constant over time. Uptake was higher for soil planted with ash than planted with beech. A trend of increasing CO_2 efflux from each plant treatment was observed. Mean fluxes ranged from 30.4 ± 5.1 to 85 ± 35.4 mg C-CO_2 m^{-2} h^{-1} during the measurement time. Drops in fluxes of up to 60-80 % were found. Fluxes of CO_2 from plots planted with beech were higher than plots planted with ash but not significantly.

6.3 FINAL REMARKS

The present study indicated under laboratory and nearly natural conditions, that earthworms, ash and beech have species-specific influence on soil biogeochemistry, which have to be considered in addition to beech and ash litter. These species may relevantly affect the source/sink potential of terrestrial forest soils for N_2O, CH_4 and CO_2.

The effects of higher N_2O emission and lower CH_4 uptake from soil applied with earthworm were observed. Clear differences between ash and beech planted soil with and without photosynthetic activity were detected and showed that trees have a photosynthetic influence on the greenhouse gas fluxes from the atmosphere into the soil.

For future studies, the focus should be placed on N_2O and CH_4 because they have a longer residence time in the atmosphere than CO_2 and a larger global warming potential (GWP). Investigations of the earthworm influence on the sink and source function of soils should be observed for a longer experimental time. The potential of ash saplings to reduce N_2O emissions was even higher. This study showed that (a) global warming can decline by changing tree species during afforestation and (b) based on the confirmed photosynthesis effect on N_2O fluxes, calculations of N_2O ecosystem fluxes for deciduous forest and its potential impact on global warming should be rethought by scientists.

6.4 References

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APPENDIX

CHAPTER 2

Tab. A 2.1: Fluxes of the soil columns (SC) in N-N_2O µg m^{-2} h^{-1} of the experiment in Chapter 2

Date	SC 1	SC 2	SC 3	SC 4	SC 5	SC 6	SC 7	SC 8	SC 9	SC 10	SC 11	SC 12	SC 13	SC 14	SC 15	SC 16
19 May 2011	148.85	68.36	27.66	126.86	20.56	8.82	8.94	18.56	96.26	80.62	193.40	55.29	2.62	6.74	213.12	13.69
22 May 2011	26.05	27.93	17.72	62.35	8.30	12.36	26.64	10.20	27.91	38.48	37.96	31.72	9.35	6.26	122.14	58.91
24 May 2011	12.22	32.04	13.57	42.37	7.39	15.96	17.61	8.51	23.22	7.97	19.98	10.28	5.97	10.91	23.06	5.19
26 May 2011	33.23	24.20	3.18	31.58	3.24	8.23	49.47	7.58	40.94	9.31	31.00	13.46	6.55	7.78	11.24	9.76
31 May 2011	34.66	61.72	52.90	66.02	5.43	11.22	23.58	5.63	22.29	14.65	29.08	6.94	3.91	4.59	11.10	7.43
07 June 2011	21.71	21.97	120.21	47.03	4.04	2.76	13.19	12.12	18.63	13.18	6.29	7.97	6.16	8.14	2.84	3.36
09 June 2011	60.91	14.45	43.31	23.70	6.07	6.73	11.26	6.95	20.84	8.49	8.62	2.64	0.82	3.57	2.90	5.46
14 June 2011	205.91	31.43	151.54	80.63	14.50	15.34	14.61	6.55	105.31	29.95	48.69	28.17	7.17	8.35	7.77	6.76
16 June 2011	45.37	9.66	179.64	15.02	8.97	10.57	9.58	2.70	28.36	22.98	11.78	1.03	3.99	1.68	2.32	2.26
21 June 2011	69.38	14.47	177.01	59.71	9.44	7.59	7.17	-2.98	95.26	16.25	62.51	2.77	0.41	3.09	5.00	6.96
24 June 2011	13.85	15.45	18.52	15.45	3.84	12.43	6.02	0.90	6.04	6.85	11.43	10.31	68.10	24.78	11.15	6.92
28 June 2011	55.99	105.76	87.36	590.30	7.97	14.23	28.69	11.95	16.98	11.22	45.20	41.31	82.49	47.99	41.82	13.60
30 June 2011	45.50	192.37	62.30	100.96	7.98	20.13	39.23	3.00	28.27	9.02	73.13	76.60	45.10	43.12	98.45	7.46
05 July 2011	91.27	431.50	28.25	251.70	61.08	130.06	113.60	29.65	196.79	54.09	167.92	159.28	40.56	73.40	174.66	30.69
07 July 2011	172.17	367.27	36.05	264.31	113.46	134.20	212.55	53.29	232.10	91.96	166.42	162.87	56.27	76.53	190.14	64.93
12 July 2011	324.49	214.46	21.97	347.40	176.94	199.59	238.61	105.78	160.94	89.98	155.24	70.03	115.56	104.96	260.00	148.83
14 July 2011	274.90	118.95	17.54	210.50	233.03	245.55	416.34	139.90	70.59	60.75	90.34	44.62	128.55	114.74	281.71	178.50
19 July 2011	289.64	17.07	8.42	25.05	98.20	281.07	125.96	202.60	19.10	19.58	16.06	8.38	105.86	169.93	185.13	150.54
22 July 2011	341.61	19.60	10.74	35.55	62.84	342.24	47.87	246.36	12.43	5.42	50.16	6.39	202.23	241.52	135.77	177.72
26 July 2011	305.90	18.65	4.29	9.81	2.36	186.48	18.02	244.78	9.80	4.39	190.40	4.58	158.31	41.86	14.64	18.51
01 Aug 2011	384.56	15.12	9.90	19.72	9.19	97.56	16.01	298.95	5.28	17.51	8.38	5.13	88.40	13.58	12.41	9.26
06 Aug 2011	360.88	24.41	18.68	61.93	12.85	49.72	19.52	316.22	31.83	11.01	59.30	1.80	34.40	45.71	6.70	9.08
09 Aug 2011	213.69	15.47	7.18	32.81	9.29	61.56	9.07	187.85	45.47	9.53	89.01	11.51	9.49	50.86	7.96	3.76
15 Aug 2011	10.53	17.48	7.91	27.42	5.86	177.38	11.11	90.85	89.48	7.32	45.09	9.90	8.59	46.95	15.46	17.45
19 Aug 2011	7.34	15.08	8.69	8.83	-3.65	98.45	6.79	17.99	76.93	3.28	22.43	7.93	7.82	12.01	5.02	2.84
23 Aug 2011	-3.80	22.10	14.97	3.65	10.02	134.67	5.32	14.52	26.00	7.42	15.05	14.67	9.57	10.29	18.21	9.11
26 Aug 2011	2.09	12.12	13.49	3.42	6.25	41.34	15.10	5.64	20.50	8.53	11.61	2.87	15.27	5.27	4.82	-0.52
29 Aug 2011	-6.29	14.01	6.90	14.88	2.87	11.09	7.32	9.52	36.17	3.13	10.83	17.77	5.35	4.98	3.87	12.26

Tab A 2.2: Fluxes of the soil columns (SC) in C-CH_4 µg m^{-2} h^{-1} of the experiment in Chapter 2

Date	SC 1	SC 2	SC 3	SC 4	SC 5	SC 6	SC 7	SC 8	SC 9	SC 10	SC 11	SC 12	SC 13	SC 14	SC 15	SC 16
19 May 2011	-3.18	-5.44	-5.61	-5.69	-5.55	-4.13	-5.82	-5.16	-2.50	-3.23	-2.28	-1.09	-1.99	-3.35	-1.07	-0.56
22 May 2011	-3.15	-5.58	-6.37	-5.13	-6.14	-4.82	-5.03	-5.60	-2.09	-3.34	-0.97	-1.18	-3.70	-4.28	-1.46	-1.11
24 May 2011	-2.59	-4.82	-6.91	-5.52	-6.95	-2.90	-4.20	-6.39	-2.14	-4.17	-3.53	-1.62	-4.54	-1.94	-0.92	-2.04
26 May 2011	-2.08	-3.67	-5.52	-4.39	-5.37	-4.09	-2.56	-3.83	-1.67	-2.63	-1.70	-0.67	-3.35	-2.71	0.10	-0.31
31 May 2011	-2.69	-5.36	-8.85	-5.50	-6.84	-6.95	-2.85	-5.88	-2.62	-4.91	-4.12	-1.22	-4.47	-5.79	-0.95	-3.36
07 June 2011	-1.96	-1.79	-8.62	-2.90	-5.88	-3.37	-0.91	-4.61	-2.06	-4.73	-1.83	-0.69	-4.11	-4.16	-1.07	-0.36
09 June 2011	-2.86	-2.91	-10.07	-3.98	-6.72	-4.59	-1.08	-5.77	-2.65	-5.69	-2.54	-0.78	-3.87	-4.78	-1.27	-0.02
14 June 2011	-2.94	-3.05	-9.60	-4.42	-8.33	-4.97	-1.28	-6.01	-2.62	-5.00	-3.19	0.28	-4.40	-5.65	0.03	0.18
16 June 2011	-2.01	-2.18	-10.74	-3.28	-6.53	-3.75	-1.48	-4.22	-2.34	-5.18	-2.19	-1.25	-3.34	-4.31	-1.00	0.09
21 June 2011	-2.08	-2.56	-11.69	-3.96	-8.82	-5.39	-1.88	-5.62	-2.79	-7.76	-4.07	-0.46	-4.38	-4.97	-0.64	-0.67
24 June 2011	-2.56	-3.13	-9.33	-3.49	-6.44	-5.50	-1.37	-5.64	-2.64	-6.17	-1.94	-0.39	-7.55	-6.33	-1.66	-1.31
28 June 2011	-3.21	-4.48	-13.07	-5.57	-9.92	-7.64	-1.76	-7.23	-2.89	-8.82	0.15	-3.52	-8.65	-6.84	-1.77	-2.72
30 June 2011	-3.38	-4.99	-12.96	-4.41	-10.44	-7.25	-1.85	-7.40	-4.32	-8.49	-1.37	-0.70	-11.68	-6.71	-1.66	-3.68
05 July 2011	-3.89	-4.98	-12.73	-5.13	-11.89	-9.35	-3.17	-8.85	-4.28	-10.26	-4.62	-2.93	-9.58	-7.91	-2.26	-4.59
07 July 2011	-5.00	-3.62	-12.66	-5.70	-12.81	-8.68	-3.15	-8.46	-4.09	-10.01	-5.56	-2.75	-11.44	-8.44	-3.92	-5.21
12 July 2011	-4.27	-6.85	-13.63	-4.94	-13.61	-8.42	5.15	-9.15	-4.90	-12.82	-5.19	-4.25	-5.16	-8.43	-3.44	-4.27
14 July 2011	-7.14	-7.42	-14.77	-6.27	-12.64	-9.96	-3.97	-9.22	-6.91	-11.71	-5.17	-4.27	-10.72	-10.49	-5.46	-6.46
19 July 2011	-6.67	-6.96	-10.36	-5.61	-11.53	-10.03	-3.95	-9.43	-3.86	-11.61	-4.85	-1.06	-11.41	-9.69	-5.02	-7.16
22 July 2011	-7.01	-8.09	-14.19	-6.31	-11.90	-10.20	-4.79	-10.25	-3.71	-11.37	-5.54	-2.61	-9.98	-9.14	-4.46	-6.04
26 July 2011	-6.34	-6.53	-12.42	-4.56	-11.72	-8.69	-4.87	-10.37	-3.58	-9.62	-3.90	-1.45	-10.09	-10.10	-3.21	-6.42
01 Aug 2011	-7.84	-8.19	-15.37	-6.39	-14.13	-11.18	-6.83	-12.71	-7.21	-13.89	-7.64	-3.90	-11.55	-11.36	-4.52	-7.27
06 Aug 2011	-6.12	-8.80	-13.92	-4.90	-12.52	-11.83	-5.33	-11.94	-6.16	-12.02	-3.21	-3.27	-12.49	-11.19	-3.99	-2.05
09 Aug 2011	-8.37	-8.29	-10.64	-5.46	-13.40	-11.33	-4.69	-12.52	-5.16	10.85	-5.91	-2.94	-11.79	-11.47	-3.83	-7.74
15 Aug 2011	-9.69	-12.45	-14.47	-7.69	-13.40	-12.38	-5.27	-12.29	-8.00	-13.53	-8.56	-4.28	-13.84	-12.99	-5.64	-9.27
19 Aug 2011	-9.28	-9.63	-15.00	-7.58	-15.76	-12.00	-4.81	-12.63	-17.30	-12.70	-6.42	-1.68	-13.09	-11.64	-4.16	-7.65
23 Aug 2011	-9.87	-12.88	-15.88	-9.81	-13.90	-12.82	-5.87	-12.25	-4.76	-14.21	-8.89	-3.88	-12.35	-13.41	-5.29	-9.94
26 Aug 2011	-6.18	-7.31	-13.17	-5.22	-12.89	-11.91	-12.90	-4.57	8.30	-12.59	-6.92	-2.58	-11.63	-12.05	-4.81	-9.02
29 Aug 2011	-11.68	-10.67	-13.77	-4.78	-13.26	-10.85	-4.77	-12.33	5.22	-13.64	-8.27	-2.82	-12.42	-11.56	-5.37	-5.77

Tab. A 2.3: Fluxes of the soil columns (SC) in C-CO_2 mg m^{-2} h^{-1} of the experiment in Chapter 2

Date	SC 1	SC 2	SC 3	SC 4	SC 5	SC 6	SC 7	SC 8	SC 9	SC 10	SC 11	SC 12	SC 13	SC 14	SC 15	SC 16
19 May 2011	40.78	48.13	45.47	48.71	33.66	32.97	37.04	26.38	41.42	34.54	56.79	34.80	29.45	28.89	35.74	36.05
22 May 2011	38.25	49.45	48.88	65.42	37.90	27.03	34.36	25.08	47.58	33.30	51.92	28.96	27.42	26.67	29.58	37.34
24 May 2011	44.63	53.29	58.65	58.12	42.90	42.51	38.60	28.67	46.18	40.06	51.18	37.03	30.40	35.37	32.46	35.86
26 May 2011	25.95	39.25	45.87	42.62	35.58	33.20	37.99	24.04	37.65	38.76	40.90	38.50	23.65	30.20	40.47	34.29
31 May 2011	39.72	59.00	65.84	62.01	47.90	32.95	42.39	29.70	56.77	45.66	65.36	33.31	27.19	31.21	35.40	45.86
07 June 2011	35.63	31.69	63.05	39.92	43.64	36.51	32.59	32.63	40.88	38.65	43.75	29.98	28.44	34.43	29.92	38.17
09 June 2011	36.17	31.78	53.54	34.85	36.36	21.46	29.60	20.66	43.35	40.42	43.83	28.48	24.62	26.84	18.91	43.85
14 June 2011	39.63	45.04	73.02	50.29	53.51	37.52	34.68	24.69	53.15	46.20	61.72	34.01	26.31	31.17	24.03	40.53
16 June 2011	22.90	30.55	74.54	38.77	48.98	42.69	27.14	20.01	40.94	46.08	49.32	24.59	20.77	25.00	22.19	35.75
21 June 2011	28.13	47.38	74.06	45.17	43.08	26.08	30.09	20.52	50.46	49.85	64.12	26.86	22.08	26.95	24.72	41.22
24 June 2011	21.70	47.95	65.21	42.85	42.17	31.28	28.11	23.47	37.20	48.72	49.07	30.08	38.14	34.59	33.96	37.84
28 June 2011	33.35	61.47	82.51	69.46	47.10	25.32	40.67	21.18	51.36	47.09	70.26	34.54	21.45	25.89	36.94	35.17
30 June 2011	33.77	60.41	69.23	48.57	38.08	26.12	39.74	24.77	43.72	50.61	72.93	45.37	30.00	31.78	42.17	37.85
05 July 2011	25.42	52.51	52.82	31.43	37.42	25.04	32.10	8.21	47.82	56.15	58.47	45.38	22.94	31.33	34.59	35.50
07 July 2011	42.77	61.24	72.60	45.88	52.05	29.84	50.61	12.07	58.93	59.51	75.65	42.79	17.28	32.83	48.38	31.78
12 July 2011	38.99	66.01	73.71	46.29	58.60	31.78	33.37	27.84	62.16	56.33	65.44	35.98	27.27	31.08	42.67	39.54
14 July 2011	36.12	60.31	68.40	37.58	60.51	25.84	40.18	24.90	62.04	54.79	60.90	28.27	27.56	32.37	40.23	43.00
19 July 2011	36.91	62.03	67.52	37.30	58.01	34.24	35.42	32.04	52.61	58.40	60.84	20.90	30.22	30.15	40.01	34.72
22 July 2011	35.80	61.71	63.33	29.99	54.14	25.56	33.42	27.77	60.36	42.37	54.75	25.27	30.57	28.70	33.14	35.25
26 July 2011	41.62	60.43	66.17	31.73	47.10	25.99	32.81	32.43	52.84	48.80	50.55	20.97	35.26	34.24	26.01	32.63
01 Aug 2011	38.21	57.55	53.70	30.55	38.71	23.13	32.05	26.75	57.06	48.21	45.34	27.75	26.93	28.18	29.43	24.02
06 Aug 2011	36.37	77.90	75.08	31.26	35.04	19.00	31.65	20.61	84.27	40.66	54.55	18.47	18.90	13.53	25.85	6.48
09 Aug 2011	39.23	63.02	56.43	31.50	29.10	25.07	29.72	19.91	64.98	15.17	50.32	24.87	22.65	28.52	28.89	27.62
15 Aug 2011	31.36	70.96	57.38	25.18	30.82	21.62	20.85	15.91	47.44	37.13	47.69	22.12	19.60	16.80	21.64	24.46
19 Aug 2011	30.82	79.36	62.01	30.83	32.17	26.82	30.00	20.30	76.52	48.46	54.37	20.83	24.19	28.43	28.58	22.08
23 Aug 2011	23.89	75.60	58.31	25.65	31.48	28.81	28.76	18.79	62.84	36.99	52.81	24.95	21.05	26.18	29.99	27.05
26 Aug 2011	23.57	71.09	61.20	29.74	35.83	27.32	24.77	18.58	69.98	47.61	59.38	22.02	15.82	28.39	29.05	25.49
29 Aug 2011	30.65	69.84	61.42	29.32	18.56	21.94	26.76	19.02	80.77	42.66	66.44	30.98	23.80	26.49	28.92	18.59

Tab. A 2.4: Mean fluxes of the treatments and standard derivation (SC) of the experiment in Chapter 2

	mg C-CO_2 $m^{-2}h^1$			µg N-N_2O $m^{-2}h^{-1}$			µg C-$CH_4$$m^{-2}h^{-1}$		
Date	Treatment	Mean	SD	Treatment	Mean	SD	Treatment	Mean	SD
19 May 2011	A/E	48.76	3.15	A/E	121.22	26.86	A/E	-3.98	0.92
	A	37.43	2.72	A	35.63	15.26	A	-3.74	1.20
	E	37.09	1.31	E	106.55	45.92	E	-2.79	1.12
	C	29.42	1.36	C	9.19	3.38	C	-3.66	0.67
22 May 2011	A/E	53.59	4.04	A/E	39.04	8.12	A/E	-3.44	1.13
	A	39.36	3.34	A	30.85	11.28	A	-4.24	1.25
	E	32.79	2.18	E	51.64	23.54	E	-2.70	0.89
	C	26.55	0.51	C	9.54	1.26	C	-4.60	0.40
24 May 2011	A/E	52.19	2.48	A/E	29.40	5.02	A/E	-4.00	0.75
	A	44.37	4.98	A	8.53	1.78	A	-5.02	1.19
	E	38.18	2.51	E	15.79	2.88	E	-2.33	0.71
	C	34.24	3.10	C	10.34	2.13	C	-3.94	0.98
26 May 2011	A/E	40.11	1.07	A/E	31.93	3.44	A/E	-2.86	0.69
	A	38.62	2.59	A	6.37	1.83	A	-3.46	1.24
	E	35.72	3.30	E	26.85	9.02	E	-1.30	0.62
	C	27.77	2.35	C	7.54	0.36	C	-3.49	0.30
31 May 2011	A/E	60.79	1.87	A/E	44.78	11.14	A/E	-4.40	0.67
	A	51.32	4.87	A	20.10	11.11	A	-5.99	1.19
	E	37.70	2.05	E	19.07	6.29	E	-1.93	0.49
	C	30.26	1.22	C	6.34	1.66	C	-5.77	0.51
07 June 2011	A/E	39.06	2.59	A/E	23.48	8.54	A/E	-2.14	0.26
	A	45.88	5.86	A	35.20	28.43	A	-4.90	1.72
	E	32.03	1.35	E	11.43	4.03	E	-1.16	0.28
	C	33.00	1.72	C	7.29	1.96	C	-4.07	0.26
09 June 2011	A/E	38.45	3.03	A/E	16.90	3.37	A/E	-3.02	0.33
	A	43.54	3.67	A	15.83	9.18	A	-5.63	2.09
	E	28.29	3.56	E	19.43	13.97	E	-1.50	0.46
	C	23.39	1.43	C	4.52	1.45	C	-4.75	0.39
14 June 2011	A/E	52.55	3.49	A/E	66.51	16.46	A/E	-3.32	0.39
	A	53.32	7.08	A	50.69	33.96	A	-5.69	2.18
	E	33.09	3.27	E	64.12	47.45	E	-0.98	0.74
	C	29.92	2.88	C	9.35	2.03	C	-5.26	0.36
16 June 2011	A/E	39.90	3.86	A/E	16.21	4.20	A/E	-2.50	0.26
	A	51.34	8.24	A	53.46	42.28	A	-5.59	2.23
	E	24.21	1.10	E	14.57	10.44	E	-1.43	0.22
	C	27.12	5.31	C	4.74	2.00	C	-3.90	0.22
21 June 2011	A/E	51.78	4.25	A/E	57.99	16.60	A/E	-3.35	0.39
	A	52.05	7.57	A	52.41	41.58	A	-7.24	2.34
	E	27.45	1.13	E	21.08	16.13	E	-1.27	0.42
	C	23.91	1.55	C	2.03	2.23	C	-5.09	0.27
24 June 2011	A/E	44.27	2.72	A/E	12.09	2.23	A/E	-2.80	0.34

	mg C-CO_2 $m^{-2}h^{1}$			µg N-N_2O $m^{-2}h^{-1}$			µg C-$CH_4$$m^{-2}h^{-1}$		
Date	Treatment	Mean	SD	Treatment	Mean	SD	Treatment	Mean	SD
	A	48.49	6.01	A	9.03	3.24	A	-5.81	1.66
	E	28.46	2.56	E	10.33	1.62	E	-1.50	0.45
	C	31.87	3.13	C	26.55	14.68	C	-6.26	0.47
28 June 2011	A/E	63.14	4.40	A/E	189.56	134.86	A/E	-3.20	1.24
	A	52.97	10.24	A	30.04	19.14	A	-8.63	2.17
	E	36.37	1.61	E	41.95	5.58	E	-2.56	0.47
	C	23.46	1.25	C	39.16	16.63	C	-7.59	0.39
30 June 2011	A/E	56.41	6.53	A/E	98.68	34.63	A/E	-3.77	0.81
	A	48.94	7.39	A	21.69	13.54	A	-8.89	1.96
	E	40.26	2.45	E	64.95	13.84	E	-1.90	0.55
	C	28.17	1.64	C	27.84	10.03	C	-8.26	1.15
05 July 2011	A/E	47.56	5.80	A/E	261.98	59.12	A/E	-4.75	0.19
	A	45.47	5.26	A	43.53	8.26	A	-9.87	1.83
	E	34.37	4.15	E	134.70	19.43	E	-3.07	0.34
	C	21.88	4.89	C	68.42	22.55	C	-8.92	0.37
07 July 2011	A/E	60.43	6.10	A/E	257.52	41.87	A/E	-4.74	0.52
	A	53.99	8.53	A	76.60	16.77	A	-10.17	1.78
	E	46.14	1.99	E	184.43	10.95	E	-3.71	0.49
	C	23.01	4.96	C	80.07	18.77	C	-9.26	0.73
12 July 2011	A/E	59.97	4.64	A/E	219.51	44.67	A/E	-5.47	0.47
	A	57.05	6.99	A	109.43	34.32	A	-11.08	2.28
	E	37.75	2.00	E	223.28	54.25	E	-1.70	2.29
	C	29.49	1.13	C	131.47	22.83	C	-7.79	0.89
14 July 2011	A/E	55.21	5.89	A/E	122.60	30.94	A/E	-6.44	0.49
	A	56.68	5.34	A	122.46	50.15	A	-11.39	1.77
	E	36.20	2.81	E	254.39	77.14	E	-5.21	0.72
	C	27.67	1.66	C	157.19	29.90	C	-10.10	0.33
19 July 2011	A/E	53.19	5.70	A/E	19.32	2.01	A/E	-5.32	0.65
	A	54.66	7.00	A	69.19	33.68	A	-10.17	1.04
	E	33.31	4.24	E	152.27	58.70	E	-4.17	1.18
	C	31.66	0.96	C	189.87	36.44	C	-10.14	0.44
22 July 2011	A/E	51.70	7.39	A/E	29.43	8.43	A/E	-5.91	0.91
	A	48.77	6.22	A	64.18	40.00	A	-10.88	1.72
	E	31.91	2.29	E	132.91	74.61	E	-4.72	0.90
	C	28.15	1.04	C	258.09	29.74	C	-9.89	0.26
26 July 2011	A/E	48.89	6.10	A/E	57.17	44.46	A/E	-4.65	0.66
	A	48.68	6.87	A	7.38	3.74	A	-10.04	1.35
	E	30.35	4.47	E	85.79	73.43	E	-3.97	1.05
	C	31.98	2.08	C	157.86	42.65	C	-9.82	0.38
01 Aug 2011	A/E	47.62	6.35	A/E	12.12	3.26	A/E	-7.36	0.38
	A	41.16	6.50	A	11.46	2.02	A	-12.66	1.83
	E	31.86	2.29	E	104.53	93.37	E	-5.77	0.94
	C	26.25	1.09	C	124.62	61.08	C	-11.70	0.34

APPENDIX

	mg C-CO_2 $m^{-2}h^{1}$			µg N-N_2O $m^{-2}h^{-1}$			µg C-$CH_4$$m^{-2}h^{-1}$		
Date	Treatment	Mean	SD	Treatment	Mean	SD	Treatment	Mean	SD
06 Aug 2011	A/E	62.00	12.07	A/E	44.37	9.52	A/E	-5.77	1.18
	A	50.26	14.07	A	14.18	2.07	A	-12.82	2.72
	E	28.09	3.86	E	97.22	87.96	E	-4.68	0.64
	C	18.01	1.54	C	111.51	68.31	C	-11.86	0.27
09 Aug 2011	A/E	52.45	7.70	A/E	45.69	15.69	A/E	-6.21	0.71
	A	32.08	8.70	A	7.44	1.33	A	-5.23	5.48
	E	30.68	3.04	E	60.56	51.05	E	-4.96	1.19
	C	24.04	1.83	C	77.44	38.48	C	-11.78	0.27
15 Aug 2011	A/E	47.82	9.35	A/E	44.87	15.93	A/E	-9.17	1.11
	A	37.45	7.13	A	9.64	2.64	A	-12.67	1.16
	E	23.99	2.47	E	11.75	1.26	E	-6.22	1.19
	C	18.48	1.31	C	80.94	36.27	C	-12.87	0.36
19 Aug 2011	A/E	60.27	11.29	A/E	30.82	15.62	A/E	-10.24	2.45
	A	41.18	8.82	A	2.79	2.53	A	-12.78	1.83
	E	27.56	2.29	E	6.77	0.63	E	-4.98	1.58
	C	24.94	1.78	C	34.07	21.56	C	-12.34	0.32

CHAPTER 3

Tab. A 3.1: Measured fluxes of the soil columns (SC) of Chapter 3 µg $N\text{-}N_2O$ m^{-2} h^{-1} with photosynthesis

	SC 1	SC 2	SC 3	SC 4	SC 5	SC 6	SC 7	SC 8	SC 9	SC 10	SC 11	SC 12	SC 13	SC 14	SC 15
Date	Beech	Control	Beech	Control	Beech	Control	Beech	Ash	Ash	Ash	Ash	Ash	Control	Beech	Control
28 February 2012	28.09	16.67	12.50	58.00	-20.66	95.45	-19.48	5.13	2.95	-8.05	-6.19	23.94	80.23	-2.64	18.73
01 March 2012	61.93	72.71	16.12	88.75	43.13	370.83	32.36	-0.73	2.34	8.51	8.22	17.39	179.68	62.15	42.69
06 March 2012	-6.69	6.59	12.98	36.43	7.60	91.57	-7.57	-14.97	-8.49	-1.12	-6.98	2.77	92.63	41.25	11.39
08 March 2012	40.47	54.85	6.65	95.01	67.75	395.50	31.39	-6.87	-1.55	-3.51	-0.87	12.10	275.26	211.61	44.72
13 March 2012	-15.64	3.38	-3.22	4.53	-16.12	67.73	-15.11	-11.47	-25.67	-12.28	0.25	-7.72	27.07	-2.38	16.81
15 March 2012	-0.89	25.81	10.86	27.90	-1.29	317.57	-16.95	-11.88	-11.47	-8.40	12.13	-0.19	129.92	25.61	24.77
27 March 2012	-1.69	25.32	26.29	6.72	-9.10	56.24	-12.74	13.27	-0.04	-3.86	-6.51	-9.08	49.49	7.41	1.46
29 March 2012	72.89	31.95	98.64	41.50	-9.95	251.37	-5.83	338.56	26.86	-9.53	-0.87	-0.24	202.85	59.21	13.63
03 April 2012	16.05	13.07	11.72	30.65	-11.87	86.06	-3.50	-12.69	-10.25	-12.09	-16.75	6.33	62.17	19.92	14.41
05 April 2012	122.84	58.21	190.88	109.53	4.19	449.02	-4.36	46.57	80.93	-5.74	30.92	8.92	271.03	137.82	48.94
10 April 2012	34.52	19.78	81.88	12.97	-6.30	54.63	-11.79	-13.61	-20.39	-6.90	-18.79	-13.46	29.01	26.92	95.60
12 April 2012	357.90	39.90	285.28	66.02	-9.48	280.45	-7.49	35.37	141.29	1.32	18.80	28.87	207.46	164.05	41.63
24 April 2012	57.43	11.10	11.84	-0.76	0.18	51.39	-11.30	-13.42	-3.64	3.04	138.18	-6.41	63.46	4.67	12.06
26 April 2012	138.13	424.00	69.90	-34.09	-17.11	146.86	-21.71	1.68	3.99	-15.35	53.30	0.10	112.39	47.89	-3.05

Tab. A 3.2: Measured fluxes of the soil columns (SC) in Chapter 3 µg $N\text{-}N_2O$ m^{-2} h^{-1} without photosynthesis

	SC 1	SC 2	SC 3	SC 4	SC 5	SC 6	SC 7	SC 8	SC 9	SC 10	SC 11	SC 12	SC 13	SC 14	SC 15
Date	Beech	Control	Beech	Control	Beech	Control	Beech	Ash	Ash	Ash	Ash	Ash	Control	Beech	Control
28 February 2012	46.6	3.7	30.9	14.1	6.1	93.1	7.0	2.0	18.5	7.8	10.7	33.7	73.7	1.9	9.2
01 March 2012	78.5	69.6	42.3	104.7	65.2	390.6	48.7	-0.1	11.8	2.8	19.7	25.9	174.0	79.7	28.7
06 March 2012	20.0	13.0	24.4	38.0	15.5	117.7	17.2	10.0	12.6	7.7	-0.9	12.5	94.6	51.3	2.4
08 March 2012	51.6	47.3	30.2	82.6	80.5	405.4	46.1	-1.1	18.5	9.2	8.8	25.2	229.6	179.8	39.1
13 March 2012	7.1	4.9	15.6	2.6	3.8	86.7	4.7	4.1	13.4	2.6	6.8	9.3	36.3	12.5	6.2
15 March 2012	6.0	34.9	30.1	40.7	28.9	340.7	8.8	4.3	16.7	13.0	9.8	43.4	159.6	39.9	22.4
27 March 2012	24.3	23.2	43.0	7.3	-0.8	27.5	10.3	49.3	20.5	1.3	-1.5	3.5	47.9	7.6	21.1
29 March 2012	115.7	36.6	111.8	38.1	11.4	225.8	13.0	414.0	46.5	-1.7	16.6	15.3	265.5	58.5	19.3
03 April 2012	15.1	13.3	39.8	24.8	5.0	106.3	9.3	14.5	12.2	-0.6	-3.2	13.8	65.4	34.0	9.5
05 April 2012	132.3	58.6	204.1	102.0	16.5	411.0	2.9	86.7	133.5	21.2	48.0	36.4	280.0	165.1	32.9
10 April 2012	87.3	7.0	93.9	7.5	0.1	58.0	9.1	1.4	15.3	13.5	8.6	14.0	46.4	28.1	90.0
12 April 2012	538.0	60.2	318.0	61.9	1.0	269.5	3.6	67.3	187.2	23.7	23.5	43.4	215.1	166.0	30.9
24 April 2012	65.8	8.6	31.5	2.8	6.2	37.2	12.0	-4.8	4.2	20.7	39.1	208.6	222.2	7.9	30.7
26 April 2012	124.0	32.0	107.3	2.8	21.3	108.0	5.3	13.8	33.9	3.9	14.8	37.5	87.1	53.0	-0.6

Tab. A 3.3: Measured fluxes of the treatments in Chapter 3 µg $N\text{-}N_2O$ m^{-2} h^{-1} with photosynthesis (PS = 1), without photosynthesis (PS = 0) and the difference (Δ-delta)

Date	Ash PS = 1	Beech PS = 1	Control PS = 1	Ash PS = 0	Beech PS = 0	Control PS = 0	Δ-delta Ash	Δ-delta Beech	Δ-delta Control
28 February 2012	3.556	-0.438	53.817	14.536	18.538	38.764	-10.9794	-18.9754	15.0534
01 March 2012	7.146	43.137	150.932	12.023	62.889	153.526	-4.8772	-19.7517	-2.5935
06 March 2012	-5.759	9.513	47.723	8.390	25.696	53.149	-14.1488	-16.1822	-5.4259
08 March 2012	-0.141	71.577	173.068	12.140	77.630	160.800	-12.2809	-6.0535	12.2676
13 March 2012	-11.378	-10.495	23.904	7.235	8.766	27.344	-18.6130	-19.2602	-3.4397
15 March 2012	-3.961	3.468	105.194	17.463	22.738	119.686	-21.4244	-19.2707	-14.4917
27 March 2012	-1.245	2.034	27.846	14.625	16.888	25.381	-15.8694	-14.8544	2.4651
29 March 2012	70.958	42.990	108.258	98.138	62.093	117.066	-27.1801	-19.1025	-8.8083
03 April 2012	-9.089	6.462	41.271	7.335	20.630	43.845	-16.4238	-14.1678	-2.5741
05 April 2012	32.317	90.274	187.344	65.141	104.170	176.907	-32.8237	-13.8966	10.4370
10 April 2012	-14.630	25.047	42.396	10.554	43.712	41.761	-25.1836	-18.6647	0.6344
12 April 2012	45.132	158.053	127.090	69.027	205.318	127.538	-23.8947	-47.2644	-0.4477
24 April 2012	23.548	12.564	27.449	53.563	24.708	60.306	-30.0148	-12.1435	-32.8571
26 April 2012	8.743	43.419	129.222	20.763	62.161	45.865	-12.0197	-18.7414	83.3566

Tab. A.3.4: 24h-experiment - means of N-N2O fluxes for PS=0. PS=1. Δ. and relative differences ± SE

		time of day							
	Column	5:00 AM	8:00 AM	11:00AM	2:00 PM	5:00 PM	8:00 PM	11:00PM	2:00 AM
N-N_2O fluxes PS=0 [µg N-N_2O m^{-2} h^{-1}]	11	8.2	17.0	19.8	25.4	16.4	33.4	28.4	21.5
	12	30.3	32.7	37.2	39.4	50.4	43.8	59.9	47.6
	14	22.9	45.1	69.4	66.5	53.2	86.9	81.3	86.8
	16	43.7	55.2	76.2	81.6	96.3	97.8	121.4	118.6
	17	28.7	46.4	30.6	30.4	25.8	42.3	35.1	23.0
	Mean	26.8	39.3	46.6	48.7	48.4	60.8	65.2	59.5
	SE	6.4	7.4	12.4	12.2	15.5	14.6	18.9	21.2
N-N_2O fluxes PS=1 [µg N-N_2O m^{-2} h^{-1}]	11	-15.2	-13.6	4.3	-1.6	2.1	5.0	2.4	3.7
	12	13.2	3.2	-2.8	14.4	19.9	36.1	36.1	31.7
	14	12.8	22.5	24.9	38.4	43.9	57.4	68.5	63.1
	16	28.1	25.2	47.6	56.8	55.1	68.9	98.0	101.5
	17	25.3	25.0	14.5	18.1	2.5	15.5	27.7	24.1
	Mean	12.8	12.5	17.7	25.2	24.7	36.6	46.5	44.8
	SE	8.6	8.6	9.9	11.3	12.0	13.5	18.6	19.1
Δ-N_2O fluxes (PS1-PS0) [µg N-N_2O m^{-2} h^{-1}]	11	-23.4	-30.6	-15.6	-26.9	-14.3	-28.4	-26.0	-17.8
	12	-17.1	-29.5	-39.9	-25.0	-30.5	-7.7	-23.8	-15.9
	14	-10.1	-22.6	-44.5	-28.1	-9.4	-29.5	-12.7	-23.7
	16	-15.6	-30.0	-28.6	-24.8	-41.2	-28.9	-23.4	-17.1
	17	-3.4	-21.4	-16.1	-12.3	-23.3	-26.8	-7.5	1.1
	Mean	-13.9	-26.8	-28.9	-23.4	-23.7	-24.2	-18.7	-14.7
	SE	7.6	4.4	13.3	6.4	12.7	9.3	8.1	9.3
relative difference (PS1-PS0) [%]	11	-285.6	-179.7	-78.5	-106.1	-87.0	-85.0	-91.6	-82.6
	12	-56.5	-90.2	-107.4	-63.5	-60.6	-17.5	-39.7	-33.4
	14	-44.2	-50.1	-64.1	-42.3	-17.6	-33.9	-15.7	-27.3
	16	-35.7	-54.4	-37.5	-30.4	-42.8	-29.6	-19.3	-14.4
	17	-11.8	-46.2	-52.7	-40.5	-90.3	-63.4	-21.3	5.0
	Mean	-86.8	-84.1	-68.1	-56.6	-59.6	-45.9	-37.5	-30.5
	SD	112.4	56.2	26.6	30.2	30.6	27.6	31.6	32.6

CHAPTER 4

Tab. A 4.1: Fluxes of the rhizotrones (RT) in N-N_2O µg m^{-2} h^{-1} of the experiment in Chapter 4

Date	RT 1	RT 2	RT 3	RT 4	RT 5	RT 6	RT 7	RT 8	RT 9	RT 10	RT 11	RT 12	RT 13	RT 14	RT 15
01 August 2011	2.48	29.63	12.57	26.36	62.55	30.97	11.98	27.64	8.29	8.28	12.31	10.30	22.50	14.09	13.16
08 August 2011	180.81	9.87	17.13	107.10	67.20	27.59	13.82	30.46	22.35	13.42	17.85	18.55	102.82	17.76	22.95
17 August 2011	169.55	14.22	12.22	40.18	38.96	22.70	9.65	35.52	42.80	22.38	176.80	5.48	49.59	40.46	15.96
24 August 2011	112.44	17.68	12.89	29.09	46.85	16.87	14.78	21.93	44.41	7.63	75.25	44.86	43.24	20.78	13.07
05 October 2011	4.05	0.86	3.60	11.64	15.30	8.81	6.51	12.23	4.99	5.93	0.69	0.99	17.01	3.09	5.39
10 October 2011	25.32	1.70	-0.30	7.44	12.64	3.14	0.27	5.95	3.82	-0.74	-0.88	1.53	7.18	2.12	3.61
19 October 2011	-1.38	-1.50	-2.42	6.77	13.36	2.47	3.01	9.59	3.62	2.12	4.45	-0.34	4.10	2.95	0.74
27 October 2011	-7.91	2.16	5.80	2.26	2.31	8.40	1.12	0.55	2.00	3.07	0.07	10.02	2.94	6.85	0.54
02 November 2011	-3.01	3.35	1.32	-0.77	2.80	-0.18	6.28	-1.24	-3.22	-1.66	3.28	5.75	2.67	8.66	-2.63
09 November 2011	0.87	-0.13	2.66	5.24	17.60	4.12	-0.47	1.32	0.20	-2.36	4.24	0.59	0.97	2.14	0.56
16 November 2011	-1.94	-1.24	0.93	5.19	6.73	3.58	4.71	4.13	0.06	2.78	3.17	3.07	0.49	5.07	-3.68
23 November 2011	-1.42	-1.62	-0.92	3.46	5.72	6.39	1.93	-1.43	1.86	0.68	2.63	2.16	0.27	3.46	-3.27
30 November 2011	-2.19	-1.65	-3.20	3.00	7.04	2.13	3.28	-1.16	2.65	3.46	4.16	4.14	1.65	-0.76	0.57
07 December 2011	0.53	1.24	-4.47	8.19	5.23	5.32	6.06	-11.85	-0.72	0.16	3.36	1.78	1.58	4.22	4.24
14 December 2011	-1.48	0.05	0.59	3.71	0.85	6.40	4.63	-2.96	-0.12	3.11	6.50	-1.37	0.56	3.78	0.28
04 January 2012	8.12	1.29	-1.52	9.93	12.56	11.79	5.15	22.62	-0.84	1.39	-0.99	-8.21	-0.29	3.70	7.28
11 January 2012	25.38	2.49	-1.18	15.13	16.39	8.14	7.97	24.42	13.09	2.35	12.38	0.21	11.51	2.04	13.73
18 January 2012	21.66	0.93	4.03	11.58	10.03	5.73	3.34	23.47	3.04	2.30	5.69	-0.62	7.71	2.40	17.76
25 January 2012	7.76	2.63	-2.37	11.02	10.66	3.49	2.51	5.13	-1.97	2.27	12.88	0.01	7.26	1.85	16.37
01 February 2012	2.94	1.87	0.30	4.36	8.48	1.20	5.74	4.96	3.19	3.89	12.24	0.27	11.97	1.23	15.60
05 February 2012	2.44	0.72	2.43	17.08	13.32	76.47	5.42	3.66	5.68	7.66	16.25	6.67	3.37	6.67	21.67
08 February 2012	-0.11	0.16	4.01	5.01	7.08	1.89	1.82	5.54	-0.53	3.11	10.35	-1.91	-0.83	-2.51	9.79
15 February 2012	0.27	1.28	8.96	17.97	18.17	2.84	7.01	23.92	3.29	6.43	5.97	1.59	5.80	12.08	7.55
22 February 2012	1.32	14.04	10.96	12.35	17.28	8.71	8.13	24.28	2.35	14.11	11.94	-1.83	10.64	10.60	15.59
29 February 2012	2.44	0.72	2.43	17.08	13.32	76.47	5.42	3.66	5.68	7.66	16.25	6.67	3.37	6.67	21.67
07 March 2012	-1.80	2.53	2.49	4.66	3.73	14.76	-3.28	2.82	8.34	8.20	8.37	5.92	0.99	4.31	2.99
14 March 2012	0.27	1.28	8.96	17.97	18.17	2.84	7.01	33.54	3.29	6.43	5.97	1.59	5.80	12.08	7.55
21 March 2012	4.59	6.60	4.01	12.41	8.95	10.94	7.25	12.50	2.91	3.77	4.56	8.39	-2.73	5.06	3.34
28 March 2012	4.03	6.48	8.07	15.98	-2.92	20.40	8.58	-8.54	1.79	-2.15	5.31	3.35	9.29	11.17	11.34
04 April 2012	1.06	-1.73	0.90	12.09	15.65	10.46	4.06	16.82	7.97	2.08	2.87	2.01	3.22	1.39	11.33

APPENDIX

Date	RT 1	RT 2	RT 3	RT 4	RT 5	RT 6	RT 7	RT 8	RT 9	RT 10	RT 11	RT 12	RT 13	RT 14	RT 15
09 May 2012	-6.07	0.35	9.00	10.04	20.32	12.65	11.84	-35.94	7.92	3.73	5.70	6.12	21.01	-0.11	5.43
21 May 2012	12.98	-3.78	4.39	18.03	22.80	13.01	5.74	11.56	3.04	5.42	1.30	4.87	6.13	5.00	-6.67
28 May 2012	3.71	-4.48	3.23	13.26	22.06	9.01	4.27	8.84	0.27	10.86	10.43	4.90	-4.57	7.77	0.27
27 June 2012	-1.17	2.75	5.36	9.80	13.38	2.76	3.27	8.48	9.94	-3.08	0.62	8.91	2.70	3.30	-11.15
04 July 2012	9.56	3.81	3.36	8.00	12.41	19.78	2.04	10.98	3.22	-1.20	48.25	5.57	2.25	4.27	8.15
11 July 2012	14.94	-7.13	1.61	6.00	3.24	7.89	3.10	5.31	11.05	1.75	2.69	11.54	8.24	10.94	-11.60
25 July 2012	4.11	2.86	3.21	-25.98	13.61	17.55	6.78	12.39	-0.80	-2.22	6.90	-2.11	3.39	13.83	4.85
01 August 2012	8.92	-0.85	10.37	13.05	9.99	11.98	15.68	-1.68	-2.74	-2.28	33.29	11.86	8.76	7.55	
08 August 2012	16.73	19.59	57.02	-10.04	-6.45	10.00	2.74	-3.18	4.62	6.06	1.76	5.21	1.60	4.47	3.85
15 August 2012	13.01	8.55	12.88	7.95	18.75	13.82	4.58	12.60	1.92	0.97	6.01	10.32	3.67	2.42	4.66
22 August 2012	9.80	9.32	11.47	6.60	5.54	11.50	2.92	1.04	8.30	10.59	20.29	8.84	9.22	7.37	1.87
29 August 2012	-2.90	5.03	4.31	10.43	12.06	5.02	3.02	26.11	-4.70	4.09	7.06	8.74	6.25	7.00	-12.36
05 September 2012	-1.22	1.97	4.38	11.47	7.67	2.44	-2.22	19.50	5.20	3.47	6.40	-0.14	6.94	7.07	-16.32
12 September 2012	-2.60	-3.92	4.62	8.84	1.97	9.36	7.06	9.97	-1.41	1.32	10.54	9.89	6.19	6.47	-8.91
19 September 2012	19.36	4.12	8.09	6.42	9.50	8.07	11.70	16.99	-4.66	0.56	12.01	8.08	6.23	2.57	-17.41

Tab. A 4.2: Mean fluxes of the treatments and standard derivation (SC) in N-N_2O µg m^{-2} h^{-1} of the experiment in Chapter 4

Date	E/A	SD	E/B	SD	A	SD	B	SD
01 August 2011	15.23	10.22	17.55	7.78	15.19	8.47	33.74	21.16
08 August 2011	81.88	66.25	20.53	5.21	16.98	4.53	64.05	36.50
17 August 2011	69.26	58.70	22.20	11.51	18.68	14.30	85.32	64.69
24 August 2011	46.31	40.23	16.37	2.88	29.96	14.77	50.39	19.01
05 October 2011	9.80	5.15	5.95	2.06	2.61	1.76	9.21	6.21
10 October 2011	9.43	9.66	2.29	1.28	1.69	1.46	6.40	5.57
19 October 2011	3.61	3.97	2.30	0.92	-0.16	2.30	8.19	3.77
27 October 2011	-0.34	4.49	4.23	3.45	5.00	3.27	1.54	1.04
02 November 2011	-0.81	2.11	3.03	4.60	1.80	3.30	1.77	1.81
09 November 2011	0.20	1.49	1.59	1.73	0.83	1.08	9.03	6.07
16 November 2011	1.37	2.31	2.42	3.57	0.70	1.57	5.03	1.46
23 November 2011	-0.48	0.96	2.13	3.51	0.37	1.66	3.93	1.30
30 November 2011	0.44	2.24	1.30	1.53	0.49	3.01	4.73	1.70
07 December 2011	-2.40	5.49	4.96	0.77	-0.54	2.45	5.59	1.99
14 December 2011	-0.19	2.28	3.77	2.23	-0.21	0.72	3.69	2.31
04 January 2012	7.96	9.03	6.98	3.05	-2.32	3.56	7.17	5.87
11 January 2012	15.92	9.56	7.97	4.13	3.65	5.61	14.63	1.68
18 January 2012	13.79	9.01	7.31	6.16	1.84	1.81	9.10	2.49
25 January 2012	6.14	6.07	3.52	5.39	6.66	6.27	4.43	2.00
01 February 2012	5.42	4.04	4.22	3.35	6.14	5.80	4.84	4.39
05 February 2012	9.93	6.96	7.80	4.45	9.05	7.45	22.54	31.16
08 February 2012	3.75	4.37	4.73	1.70	2.40	4.47	1.02	3.05
15 February 2012	7.13	6.48	11.19	5.04	4.10	3.21	11.16	8.09
22 February 2012	10.17	4.58	14.12	2.58	5.80	6.70	13.56	6.24
29 February 2012	9.93	6.96	7.80	4.45	9.05	7.45	22.54	31.16
07 March 2012	5.97	2.50	4.81	2.45	0.95	3.69	5.72	5.35
14 March 2012	7.13	6.48	11.19	5.04	4.10	3.21	13.56	12.01
21 March 2012	6.62	3.59	5.58	2.39	5.89	2.02	6.44	5.98
28 March 2012	7.39	5.25	1.00	5.01	6.82	3.29	8.08	10.47
04 April 2012	5.30	5.21	6.21	6.69	4.61	4.03	7.97	6.13
09 May 2012	6.00	3.61	11.02	6.92	4.33	6.50	-0.60	21.75
21 May 2012	4.65	8.12	10.87	8.45	4.23	7.03	8.92	3.42
28 May 2012	4.87	7.25	12.05	7.73	3.29	1.79	5.26	5.70
27 June 2012	5.78	4.16	5.22	6.72	-0.04	7.35	4.31	2.42
04 July 2012	15.82	18.81	4.86	5.66	6.33	2.86	9.32	6.85
11 July 2012	3.15	6.64	2.20	0.74	4.50	10.25	8.09	1.99
25 July 2012	-4.26	12.84	4.87	6.57	3.41	3.33	11.79	5.20
01 August 2012	10.69	14.40	6.03	5.87	12.15	2.77	6.65	5.08
08 August 2012	3.98	10.55	18.88	27.45	7.13	5.61	3.22	4.77
15 August 2012	6.11	2.59	10.87	7.39	8.14	3.65	8.13	5.12
22 August 2012	11.13	5.38	9.20	2.61	5.85	3.50	7.28	3.89
29 August 2012	4.45	5.63	6.82	3.71	-0.87	7.80	11.09	8.70
05 September 2012	6.26	3.42	5.17	1.80	-4.97	6.59	8.99	6.35
12 September 2012	3.51	6.27	2.64	1.43	1.36	7.53	8.00	1.68
19 September 2012	4.48	6.00	6.05	3.93	5.43	13.80	8.46	5.30

Tab. A 4.3: Fluxes of the rhizotrones (RT) in C-CH_4 µg m^{-2} h^{-1} of the experiment in Chapter 4

Date	RT 1	RT 2	RT 3	RT 4	RT 5	RT 6	RT 7	RT 8	RT 9	RT 10	RT 11	RT 12	RT 13	RT 14	RT 15
01 August 2011	-25.16	-19.98	-24.43	-27.31	-28.38	-21.74	-16.88	-25.54	-27.77	-18.27	-18.52	-23.99	-20.77	-27.89	-20.56
08 August 2011	-13.95	-12.99	-16.43	-20.25	-24.27	-21.03	-17.87	-18.60	-23.74	-18.03	-22.15	-18.26	-16.49	-21.52	-17.46
17 August 2011	-19.43	-13.89	-18.01	-21.49	-20.86	-23.58	-18.39	-20.77	-16.36	-10.05	-21.66	-19.98	-12.00	-20.77	-18.97
24 August 2011	-19.96	-24.10	-25.01	-26.04	-24.53	-21.80	-26.33	-22.23	-0.92	-12.44	-21.56	-22.19	-18.33	-24.42	-23.39
05 October 2011	-12.66	-14.10	-14.74	-19.41	-20.98	-11.97	-18.01	-4.80	-24.07	-15.18	-8.34	-16.38	-14.85	-8.49	-18.80
10 October 2011	-2.79	-1.21	-8.25	-15.28	-20.92	-6.94	-23.94	-8.12	-14.45	-4.59	-9.78	-8.21	-13.87	-12.65	-15.31
19 October 2011	-12.49	-4.74	-11.90	-16.35	-20.75	-7.06	-15.31	-9.13	-12.81	-7.08	-15.70	-10.01	-8.56	-12.09	-11.58
27 October 2011	-10.81	3.26	-12.79	-17.30	-22.65	-8.41	-14.19	-10.00	-15.20	-8.20	-13.69	-21.42	-10.04	-10.94	-14.61
02 November 2011	-12.77	-6.26	-16.43	-17.24	-18.72	-4.67	-10.80	-5.99	-9.36	-3.53	-11.60	-12.54	-13.34	-10.56	-15.45
09 November 2011	-17.39	-21.49	-22.25	-17.61	-19.08	-10.35	-14.98	-14.73	-12.98	-13.06	-18.77	-15.13	-13.83	-15.19	-10.78
16 November 2011	-6.67	-1.50	-11.58	-11.67	-17.53	-2.95	-6.57	27.66	-3.32	-0.85	-12.51	8.81	-7.11	-6.50	-3.76
23 November 2011	-14.58	-16.31	-21.82	-17.09	-24.10	-8.07	-12.90	-13.33	-12.18	-12.42	-18.79	-17.75	-12.24	-14.00	-9.97
30 November 2011	-9.02	-7.20	-16.11	-11.86	-15.25	-5.10	-7.35	-4.65	-4.29	-3.23	-13.28	-10.23	-9.36	-10.63	-7.41
07 December 2011	-9.30	-2.07	-17.70	-12.75	-14.83	-6.29	-9.27	-4.34	-3.98	-2.83	-13.76	-10.98	-9.62	-9.01	-8.96
14 December 2011	-10.54	-1.71	-22.98	-12.03	-14.46	-4.71	-8.25	-4.41	-2.53	-2.87	-12.16	-10.00	-8.85	-8.71	-7.89
04 January 2012	-8.57	-4.11	-13.69	-5.38	-11.17	-9.10	-14.15	-4.44	-2.28	-2.13	-6.10	-2.95	-5.70	-1.23	-4.91
11 January 2012	-13.07	-8.05	-11.68	-11.16	-13.93	-10.03	-17.52	-4.09	-9.50	-8.59	-11.23	-4.83	-10.31	-4.43	-7.75
18 January 2012	-17.30	-10.69	-12.73	-13.91	-16.56	-7.79	-16.95	-9.64	-2.65	-6.10	-10.21	-2.22	-10.68	-3.15	-9.17
25 January 2012	-16.54	-8.31	-15.63	-12.89	-15.24	-9.04	-15.64	-5.19	-2.03	-7.96	-8.46	-4.15	-5.46	-3.05	-8.39
01 February 2012	-20.39	-8.95	-9.77	-13.20	-13.71	-6.44	-11.26	-9.24	-2.31	-9.30	-10.57	-2.23	-6.96	-0.93	-11.56
05 February 2012	-19.86	-21.87	-13.78	-11.30	-10.71	-15.20	-19.31	-15.46	-8.63	-7.48	-16.36	-11.69	-13.18	-7.86	-12.28
08 February 2012	-14.79	-12.80	-12.73	-13.81	-17.49	-9.75	-15.79	-15.64	-7.31	-10.83	-12.37	-2.51	-7.46	-1.37	-11.78
15 February 2012	-20.30	-15.88	-13.08	-9.67	-8.28	-9.47	-10.58	-11.24	-8.13	-6.59	-11.22	-7.07	-4.66	-9.89	-12.82
22 February 2012	-18.07	-8.24	-12.40	0.85	-10.53	-2.33	-10.18	-11.16	-11.72	-16.49	-17.10	-11.33	-5.11	-10.78	-17.82
29 February 2012	-19.86	-21.87	-13.78	-11.30	-10.71	-15.20	-19.31	-15.46	-8.63	-7.48	-16.36	-11.69	-13.18	-7.86	-12.28
07 March 2012	-25.75	-18.31	-16.09	-14.25	-16.40	-19.43	-17.27	-14.51	-11.25	-9.83	-16.73	-4.61	-10.55	-7.84	-13.33
14 March 2012	-20.30	-15.88	-13.08	-9.67	-8.28	-9.47	-10.58	-11.24	-8.13	-6.59	-11.22	-7.07	-4.66	-9.89	-12.82
21 March 2012	-23.39	-16.80	-19.93	-24.60	-21.06	-20.35	-18.78	2.77	-13.25	-14.64	-21.45	-14.98	-10.26	-12.07	-12.55
28 March 2012	-20.29	-16.27	-11.19	-22.40	-16.70	-7.17	-18.00	-10.62	-13.38	-11.11	-21.51	-11.77	-17.67	-8.83	-12.81
04 April 2012	-24.42	-8.46	-15.07	-27.47	-19.32	-11.03	-14.23	-11.09	-22.25	-16.32	-24.89	-17.61	-14.96	-5.25	-16.23
09 May 2012	-18.33	-2.02	-9.42	-23.13	-27.87	-35.15	-18.80	-49.32	-13.51	-10.38	-20.55	-5.58	-12.79	-12.55	-19.57
21 May 2012	-24.99	-4.04	-9.89	-16.81	-40.86	-12.76	-18.52	-21.62	-17.63	-10.10	-14.59	-13.71	-3.90	-10.46	-14.46

Date	RT 1	RT 2	RT 3	RT 4	RT 5	RT 6	RT 7	RT 8	RT 9	RT 10	RT 11	RT 12	RT 13	RT 14	RT 15
28 May 2012	-13.99	-5.10	-10.59	-16.14	-29.15	-9.87	-14.06	-13.63	-5.31	-13.15	-29.44	-9.01	-5.18	-12.82	-21.98
27 June 2012	-9.22	-10.69	-16.30	-28.07	-21.54	-9.85	-13.02	-15.75	-14.32	-9.46	-11.89	-10.70	-12.92	-11.00	-11.40
04 July 2012	-17.56	-14.58	-15.17	-28.33	-14.32	-16.77	-21.83	-15.30	-14.87	-14.06	-15.12	-12.81	-6.31	-8.46	-11.10
11 July 2012	-18.98	-13.37	-13.11	-20.45	-14.33	-15.49	-19.09	-16.56	-12.21	-9.95	-11.42	-8.11	-8.61	-8.22	-10.82
25 July 2012	-11.65	-13.59	-17.46	-20.35	-14.71	-10.01	-13.56	-13.53	-9.84	-6.64	-10.51	-6.77	14.31	-7.98	-6.40
01 August 2012	-21.59	-7.03	-12.51	-20.26	-12.13	-13.59	-20.62	-14.74	-9.52	-10.00	-12.44	-8.22	5.74	-5.35	0.00
08 August 2012	-27.01	-14.48	-11.84	-18.26	-11.29	-2.22	-24.10	-13.01	-14.20	-5.22	-15.90	-8.04	-17.98	-6.58	-12.69
15 August 2012	-20.06	-9.97	-13.04	-20.74	-9.05	-7.39	-14.03	-20.61	-12.04	-4.65	-14.16	-6.54	-10.34	-4.98	-5.11
22 August 2012	-22.36	-18.53	-13.65	-29.79	-16.61	-20.02	-19.47	-14.69	-17.03	-9.59	-17.93	-11.60	-18.78	-8.67	-12.26
29 August 2012	-10.75	-6.86	-6.83	-28.88	-11.77	-10.25	-12.20	-12.57	-11.26	-1.59	-10.87	-3.81	-7.76	-0.88	-8.81
05 September 2012	-21.80	-12.50	-8.04	-32.25	-19.37	-12.60	-17.48	-10.12	-13.68	-4.45	-16.16	-7.62	-11.54	-5.40	-11.27
12 September 2012	-31.02	-9.54	-9.80	-30.21	-16.23	-18.61	-11.78	-8.60	-14.34	-5.21	-12.32	-10.36	-13.72	-6.66	-9.90
19 September 2012	-17.54	-13.27	-5.99	-16.43	-9.61	-8.92	-17.29	-6.72	-13.48	-4.34	-8.73	-5.76	-14.66	-6.21	-6.88

Tab. A 4.4: Mean fluxes of the treatments and standard derivation (SC) in C-CH_4 µg m^{-2} h^{-1} of the experiment in Chapter 4

Date	E/A	SD	E/B	SD	A	SD	B	SD
01 August 2011	-22.43	3.05	-21.77	3.97	-24.04	2.76	-24.74	4.42
08 August 2011	-16.77	1.80	-19.47	1.82	-17.86	3.89	-22.22	1.64
17 August 2011	-15.56	4.61	-20.43	2.02	-17.06	2.24	-21.34	0.35
24 August 2011	-18.24	3.62	-23.98	1.64	-18.06	9.94	-24.04	1.86
05 October 2011	-11.87	4.20	-14.32	4.28	-17.32	3.98	-16.24	5.63
10 October 2011	-7.34	4.23	-14.71	6.13	-8.03	4.68	-15.33	4.55
19 October 2011	-9.32	1.98	-11.51	2.94	-9.87	3.13	-17.60	2.24
27 October 2011	-9.76	0.96	-12.04	2.53	-11.54	9.11	-17.88	3.68
02 November 2011	-8.91	4.24	-10.37	3.83	-11.15	3.77	-15.85	3.07
09 November 2011	-14.75	1.63	-12.83	2.27	-17.96	3.99	-18.49	0.63
16 November 2011	3.26	14.30	-4.94	1.62	-1.90	7.26	-13.90	2.59
23 November 2011	-13.14	0.93	-11.24	2.35	-17.01	3.45	-19.99	2.99
30 November 2011	-6.56	2.68	-7.62	1.97	-9.46	4.38	-13.47	1.39
07 December 2011	-6.52	2.99	-8.38	1.21	-8.68	6.18	-13.78	0.85
14 December 2011	-6.67	3.14	-7.39	1.57	-9.31	8.53	-12.88	1.12
04 January 2012	-5.21	2.32	-7.35	4.81	-5.76	4.63	-7.55	2.57
11 January 2012	-9.01	3.26	-9.93	4.81	-8.52	2.49	-12.11	1.29
18 January 2012	-10.93	4.05	-9.26	4.97	-7.07	4.69	-13.56	2.61
25 January 2012	-8.79	4.60	-9.03	4.47	-7.53	5.19	-12.20	2.81
01 February 2012	-11.47	5.23	-7.55	4.33	-5.81	3.56	-12.49	1.37
05 February 2012	-13.99	4.46	-13.66	4.18	-13.99	4.90	-12.79	2.54
08 February 2012	-11.57	2.52	-13.68	2.80	-11.22	5.24	-8.56	5.11
15 February 2012	-11.22	2.90	-9.32	2.75	-12.70	4.85	-8.82	2.49
22 February 2012	-9.05	6.53	-13.14	2.49	-14.35	3.62	-7.34	3.76
29 February 2012	-14.54	5.06	-10.66	2.57	-15.78	3.81	-12.92	3.05
07 March 2012	-15.14	2.67	-14.11	3.02	-15.24	7.60	-13.08	4.36
14 March 2012	-11.22	2.90	-9.32	2.75	-12.70	4.85	-8.82	2.49
21 March 2012	-19.02	4.34	-18.54	2.80	-17.43	4.10	-9.98	8.28
28 March 2012	-18.39	3.72	-13.00	2.62	-15.72	3.54	-11.07	4.00
04 April 2012	-20.77	7.34	-16.90	1.79	-18.12	3.83	-10.58	3.46
09 May 2012	-14.80	8.18	-15.89	8.48	-15.57	5.78	-27.45	15.61
21 May 2012	-13.27	5.44	-20.28	14.55	-17.92	4.48	-12.19	6.34
28 May 2012	-14.00	9.97	-17.63	8.21	-14.76	4.64	-10.37	3.31
27 June 2012	-16.24	6.95	-15.77	4.95	-11.08	1.37	-12.38	2.23
04 July 2012	-18.23	5.84	-14.52	0.47	-15.82	4.20	-11.71	4.42
11 July 2012	-14.36	3.58	-12.46	1.85	-14.25	4.88	-12.22	3.83
25 July 2012	-13.57	4.16	-12.94	4.59	-9.59	3.09	-4.30	10.93
01 August 2012	-12.31	4.97	-11.55	1.10	-12.61	8.99	-6.98	8.19
08 August 2012	-15.71	1.61	-9.45	3.00	-17.96	7.84	-9.95	6.02
15 August 2012	-14.23	4.04	-8.91	3.43	-11.44	6.02	-10.83	5.96
22 August 2012	-20.82	5.21	-13.28	2.88	-16.42	4.61	-15.54	4.43
29 August 2012	-14.47	8.50	-6.73	4.15	-8.89	3.17	-7.86	4.38
05 September 2012	-18.65	7.97	-10.62	6.36	-14.54	5.48	-9.91	2.75
12 September 2012	-16.60	8.04	-10.41	4.52	-15.76	8.83	-11.90	4.65
19 September 2012	-12.98	2.75	-6.65	2.20	-11.87	5.56	-9.13	3.35

Tab. A 4.5: Fluxes of the rhizotrones (RT) in C-CO_2 mg m^{-2} h^{-1} of the experiment in Chapter 4

Date	RT 1	RT 2	RT 3	RT 4	RT 5	RT 6	RT 7	RT 8	RT 9	RT 10	RT 11	RT 12	RT 13	RT 14	RT 15
01 August 2011	40.94	47.70	57.03	68.99	83.49	49.29	34.55	71.06	23.20	-22.25	15.00	23.50	7.75	51.36	31.84
08 August 2011	47.92	31.16	49.51	65.87	94.52	56.85	49.98	75.11	44.76	20.72	38.59	24.44	65.45	54.40	35.32
17 August 2011	38.04	37.33	56.49	70.90	93.38	60.80	47.85	71.92	34.20	17.65	64.68	20.20	40.75	60.71	35.55
24 August 2011	55.48	38.86	54.00	64.02	83.07	57.23	51.22	55.86	57.24	22.86	32.56	22.19	28.01	54.59	36.94
05 October 2011	34.18	12.91	25.46	55.23	62.34	48.49	33.17	20.44	29.96	29.60	9.95	25.27	45.35	22.54	29.07
10 October 2011	0.78	1.47	8.69	28.53	40.54	16.37	27.00	7.14	11.50	5.77	14.78	9.86	23.89	17.41	15.00
19 October 2011	-17.04	2.61	5.48	18.80	33.52	18.10	16.39	6.72	8.65	-6.95	13.76	7.36	9.77	15.38	3.35
27 October 2011	-64.85	3.25	16.44	22.76	33.12	13.81	13.53	-5.90	9.09	11.20	11.28	31.63	19.86	12.93	1.18
02 November 2011	-6.89	2.85	9.01	13.69	13.21	5.69	6.40	-3.81	3.98	-0.83	1.95	12.96	17.88	19.48	4.66
09 November 2011	-16.02	5.06	10.44	16.97	17.08	10.32	7.63	-0.34	3.11	3.58	9.54	4.80	6.27	12.01	0.17
16 November 2011	12.10	0.08	-17.22	17.56	21.17	11.10	7.26	0.96	5.03	4.11	13.01	3.14	8.15	11.03	-0.09
23 November 2011	-1.11	2.68	-6.97	7.11	10.49	4.54	5.75	7.92	6.62	-1.18	5.55	-0.78	4.00	13.61	-6.13
30 November 2011	2.97	7.84	10.91	11.21	16.46	-5.02	9.13	8.11	5.75	8.90	9.37	6.33	8.45	7.38	0.44
07 December 2011	17.03	0.97	17.91	19.81	10.99	1.52	9.32	15.21	-30.97	1.71	10.81	-13.17	13.55	14.46	9.66
14 December 2011	8.89	0.91	13.22	11.69	14.94	6.53	6.96	15.49	0.80	5.68	12.74	2.86	7.38	11.37	7.59
04 January 2012	22.97	8.34	18.89	20.65	28.96	27.54	17.51	36.54	-2.94	8.62	7.61	5.21	11.24	6.87	27.84
11 January 2012	37.84	10.17	23.27	29.19	35.41	26.15	29.66	35.30	10.06	18.95	14.13	3.28	21.31	6.59	20.95
18 January 2012	24.53	9.80	25.95	24.41	28.14	15.84	17.47	44.82	4.74	9.50	4.30	4.03	17.44	2.50	27.97
25 January 2012	36.53	9.23	23.62	29.16	24.28	5.87	5.43	30.45	-2.95	10.43	13.08	1.57	11.63	3.40	22.52
01 February 2012	37.38	15.15	19.80	27.39	26.87	17.17	17.55	39.77	4.53	10.36	19.19	4.88	17.72	10.52	24.54
05 February 2012	12.55	23.99	24.87	32.75	25.57	25.86	16.28	57.66	35.99	16.95	27.06	14.13	39.00	28.17	44.41
08 February 2012	33.46	15.32	26.62	36.66	34.52	17.52	22.18	69.02	8.47	13.60	16.93	0.89	32.88	-18.85	43.15
15 February 2012	33.31	19.82	39.49	38.64	40.66	30.46	15.05	76.06	23.33	31.21	16.03	11.71	13.16	27.62	43.49
22 February 2012	37.00	80.42	57.71	51.82	44.45	86.57	36.98	105.79	16.16	10.55	21.70	2.90	11.47	35.85	60.18
29 February 2012	12.55	23.99	24.87	32.75	25.57	25.86	16.28	57.66	35.99	16.95	27.06	14.13	39.00	28.17	44.41
07 March 2012	43.84	22.57	31.85	30.00	29.69	34.65	21.68	80.78	41.90	18.64	24.41	15.50	22.85	26.38	41.72
14 March 2012	33.31	19.82	39.49	38.64	21.60	21.23	15.05	76.06	23.33	21.32	16.03	11.71	13.16	27.62	43.49
21 March 2012	31.76	33.96	28.75	48.70	47.47	43.41	22.02	-19.87	10.45	7.19	22.22	13.78	3.50	22.06	28.21
28 March 2012	38.54	35.12	43.16	71.76	17.60	68.16	29.55	33.36	27.13	19.72	29.82	14.70	41.01	33.43	43.66
04 April 2012	53.72	10.87	22.97	86.64	44.39	41.71	26.06	50.16	36.31	14.86	42.20	20.35	22.35	15.53	45.62
09 May 2012	34.75	2.17	43.72	67.69	102.58	95.94	36.34	41.85	16.19	18.76	28.66	8.09	25.86	35.18	32.08
21 May 2012	135.43	8.14	56.21	122.03	104.60	86.15	52.92	100.67	24.15	28.83	22.05	23.11	20.25	45.27	20.11

Date	RT 1	RT 2	RT 3	RT 4	RT 5	RT 6	RT 7	RT 8	RT 9	RT 10	RT 11	RT 12	RT 13	RT 14	RT 15
28 May 2012	43.50	-6.03	26.05	85.28	73.63	43.42	34.25	23.81	-3.93	22.70	35.61	-1.59	-5.07	69.18	35.38
27 June 2012	40.35	15.40	45.11	113.66	66.42	28.88	13.31	80.76	30.70	4.87	0.31	17.51	39.37	25.83	41.09
04 July 2012	83.63	21.79	83.49	90.40	70.28	99.49	19.65	82.20	32.54	9.44	45.34	26.46	43.63	26.12	22.04
11 July 2012	109.78	15.42	76.66	75.52	68.37	77.22	20.40	59.21	46.12	13.43	13.57	21.00	55.85	34.79	35.11
25 July 2012	58.87	30.74	66.00	-68.55	56.72	74.59	13.48	96.12	25.50	20.16	11.45	16.42	35.91	41.40	-3.39
01 August 2012	77.17	17.18	60.21	87.03	62.24	85.81	27.56	45.93	20.22	9.11	23.16	29.09	36.34	21.82	
08 August 2012	94.51	16.15	62.80	96.34	46.97	94.13	34.43	32.04	35.09	2.88	13.22	21.24	20.32	18.93	16.29
15 August 2012	77.51	31.36	79.33	84.71	46.46	58.28	17.52	53.00	15.69	7.39	20.92	19.36	14.12	16.93	8.91
22 August 2012	70.74	33.56	67.57	78.25	47.66	105.16	31.18	65.89	27.08	13.59	34.21	17.59	67.85	19.79	23.85
29 August 2012	34.52	24.25	51.60	72.92	59.87	48.39	36.59	61.49	21.67	13.77	23.33	19.24	45.69	15.15	42.13
05 September 2012	53.96	20.88	57.75	59.46	48.16	33.20	31.44	49.44	21.32	9.61	30.03	16.95	50.73	23.76	34.26
12 September 2012	51.51	8.67	58.90	52.28	34.43	40.28	23.83	22.14	10.18	7.67	27.26	25.68	60.14	26.94	33.66
19 September 2012	72.32	38.77	49.10	71.68	36.05	50.41	32.59	45.37	10.03	0.44	16.55	22.84	31.96	9.88	18.37

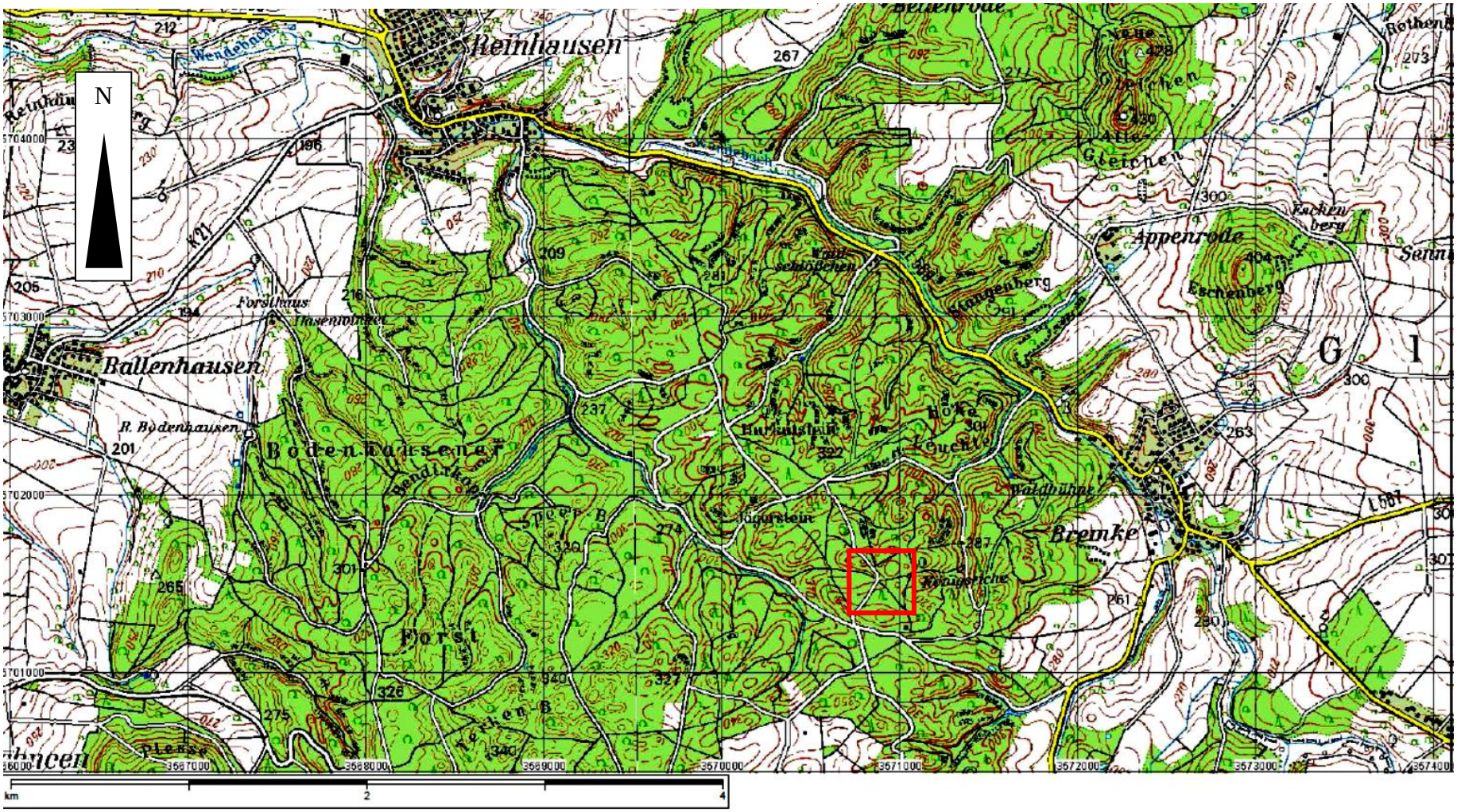
Tab. A 4.6: Mean fluxes of the treatments and standard derivation (SC) in C-CO_2 mg m^{-2} h^{-1} of the experiment in Chapter 4

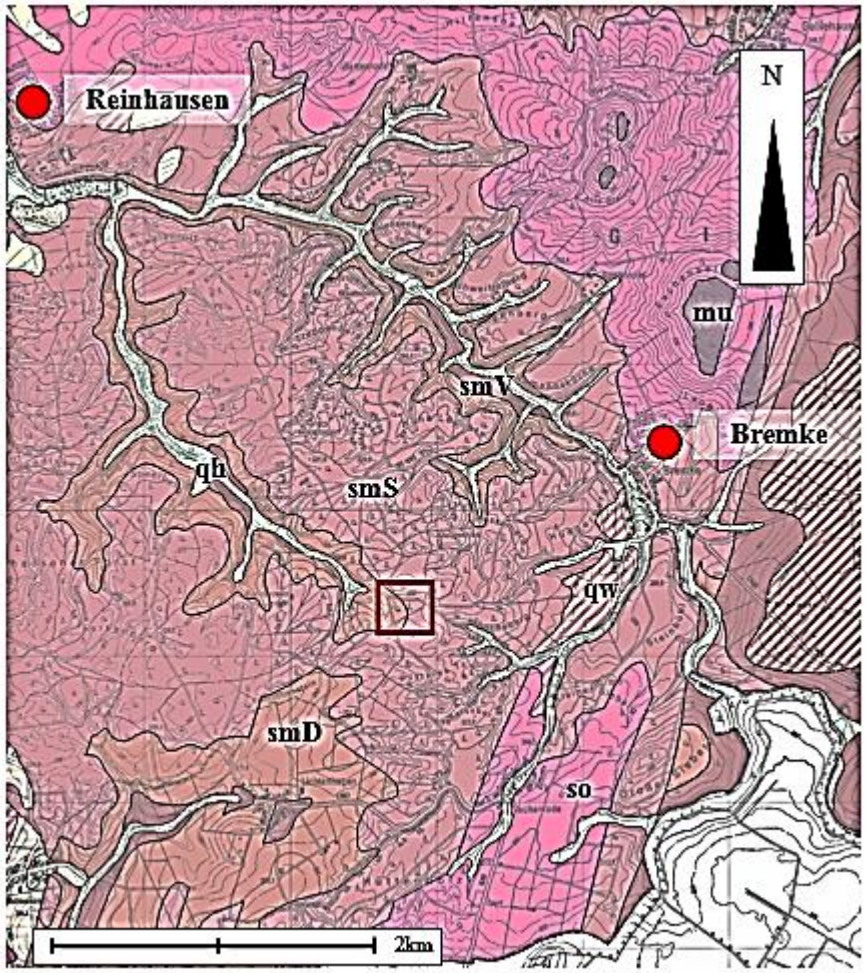
Date	E/A	SD	E/B	SD	A	SD	B	SD
01 August 2011	24.38	35.02	41.76	8.65	37.86	14.88	55.83	29.47
08 August 2011	52.30	20.67	49.14	30.37	37.47	10.10	66.33	8.13
17 August 2011	42.09	19.40	51.23	30.92	37.05	12.94	76.32	11.24
24 August 2011	40.55	15.23	49.99	24.59	43.07	13.91	59.88	12.11
05 October 2011	32.39	8.97	33.32	16.50	23.40	6.34	42.51	12.78
10 October 2011	9.39	8.70	18.95	15.75	7.88	3.83	27.95	5.97
19 October 2011	-1.87	10.79	13.31	16.93	6.02	2.27	22.03	4.49
27 October 2011	-9.92	33.04	10.36	9.35	15.10	10.63	22.39	9.66
02 November 2011	1.58	9.65	9.06	5.88	7.20	4.05	9.62	9.50
09 November 2011	-1.63	8.64	7.53	5.51	5.85	2.75	14.53	4.76
16 November 2011	6.33	4.19	7.33	15.71	-2.24	8.83	17.25	4.13
23 November 2011	2.41	3.81	4.44	7.26	0.39	4.99	7.72	3.83
30 November 2011	7.11	2.40	2.98	3.20	7.71	2.00	12.34	5.64
07 December 2011	11.87	6.00	8.74	6.64	-6.31	17.99	13.87	5.61
14 December 2011	9.36	3.72	8.12	4.02	4.45	5.13	13.12	3.56
04 January 2012	15.09	12.68	21.08	13.42	14.99	8.04	30.78	8.73
11 January 2012	15.89	7.85	25.88	6.97	22.93	12.82	22.34	10.39
18 January 2012	10.81	8.14	21.20	8.32	18.50	9.17	20.15	15.38
25 January 2012	12.13	11.47	19.44	6.38	16.51	13.99	12.84	10.60
01 February 2012	16.57	8.23	19.01	6.76	21.09	11.75	21.30	11.03
05 February 2012	29.95	4.70	22.46	3.91	21.84	13.10	37.67	12.56
08 February 2012	19.34	10.49	24.91	8.63	24.92	15.73	25.14	31.54
15 February 2012	24.45	8.59	37.12	4.21	25.89	13.07	36.82	23.58
22 February 2012	42.53	25.74	37.57	19.86	34.27	20.44	59.92	37.88
29 February 2012	29.95	4.70	22.46	3.91	21.84	13.10	37.67	12.56
07 March 2012	29.72	7.55	26.73	5.79	30.69	12.32	41.17	23.27
14 March 2012	24.45	8.59	27.47	8.50	25.89	13.07	34.52	24.53
21 March 2012	28.83	14.16	27.80	16.46	23.94	6.83	12.27	23.32
28 March 2012	40.96	18.02	26.83	11.58	31.61	10.99	43.99	14.29
04 April 2012	44.00	27.29	27.41	12.46	36.44	13.69	32.44	14.03
09 May 2012	28.68	24.40	55.02	35.14	27.82	11.49	49.71	27.29
21 May 2012	44.09	45.42	63.21	31.33	57.89	46.57	63.08	32.01
28 May 2012	27.73	37.13	40.79	23.26	27.89	17.39	32.84	27.16
27 June 2012	40.01	43.85	38.80	25.52	28.07	12.74	43.71	21.97
04 July 2012	47.52	26.12	54.41	32.25	37.94	26.49	62.86	29.31
11 July 2012	37.66	25.40	52.82	28.06	46.57	36.96	56.77	15.07
25 July 2012	-0.21	40.08	47.63	19.79	21.34	22.95	62.01	24.64
01 August 2012	36.89	29.02	43.85	24.58	44.60	23.04	47.47	23.74
08 August 2012	40.20	33.48	37.55	25.35	41.62	31.25	41.35	30.89
15 August 2012	38.17	27.46	44.39	29.40	30.83	27.24	35.58	20.17
22 August 2012	43.28	20.38	42.94	22.29	35.84	20.71	64.67	30.27
29 August 2012	35.54	21.60	41.75	20.07	33.12	8.49	42.68	16.98
05 September 2012	32.92	15.75	38.51	20.80	34.15	13.19	39.28	11.31
12 September 2012	24.60	17.57	33.67	20.92	33.67	10.94	37.37	14.73
19 September 2012	34.26	24.09	28.53	20.57	36.53	21.30	34.41	15.68

CHAPTER 5

Maps of the SPLIDRHEX-Site

Map 1: Location of the study site in Reinhäuser Wald (red box) (Map from GeoGrid-Viewer).





Holocene

qh = holocene

qw = Weichsel-cold stage

Middle Trias

mu = lower Muschelkalk

Lower Trias

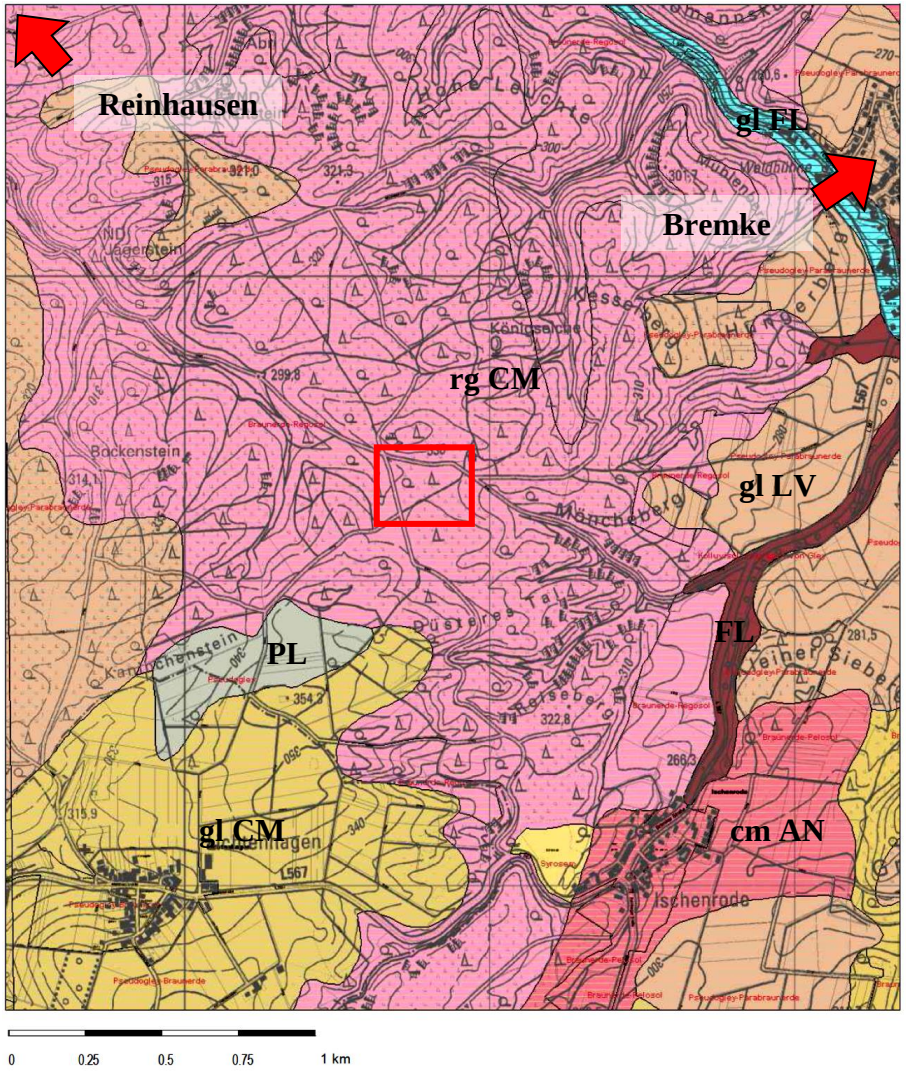
so = upper Buntsandstein

smS = middle Buntsandstein (Solling)

smD = middle Buntsandstein (Detfurth)

smV = middle Buntsandstein (Volpriehausen)

Map 2: Geological properties in the Reinhäuser Wald. The red box marks the study site (Map from NIBIS-MAPSERVER, LBEG 2012).



Soil types (after WRB. 2007)

cm AN = cambic Andosol
rg CM = regic Cambisol
gl CM = gleyic Cambisol
gl FL = gleyic Fluvisol
gl LV = gleyic Luvisol
FL = Fluvisol
PL = Planosol

Map 3: Pedological properties in the Reinhäuser Wald. The red box marks the study site (Map from NIBIS-MAPSERVER. LBEG 2012).

Tab. 5.1: Gas fluxes between soil and atmosphere and Q_{10} for the field study - SPLIDRHEX (means ± SE)

Gas	Treatment	Date								Q_{10}
		03/26	04/02	04/09	04/14	04/24	04/30	05/07	05/14	
Temperature [°C]		4.6	4.3	2.5	4.9	6.8	13.3	8.5	8.1	
$C\text{-}CO_2$ [mg $C\text{-}CO_2$ m^{-2} h^{-1}]	*F. excelsior*	39.5 ± 10.7	31.8 ± 8.6	11.6 ± 5.2	39.3 ± 11.2	74.9 ± 28.1	30.7 ± 9.5	105.3 ± 50.8	79.4 ± 24.4	3.9 ± 1.6
	F. sylvatica	38.0 ± 19.0	48.6 ± 24.3	21.0 ± 10.5	54.6 ± 27.3	80.5 ± 40.2	12.1 ± 6.1	26.9 ± 13.4	143.5 ± 71.8	3.6 ± 2.6
	Crtl	13.6 ± 6.8	13.7 ± 6.9	14.5 ± 7.2	25.7 ± 12.9	12.7 ± 6.3	65.1 ± 32.5	75.6 ± 37.8	31.9 ± 16.0	4.1 ± 2.2
	Mean	**30.4 ± 5.1**	**31.4 ± 8.4**	**15.7 ± 2.9**	**39.9 ± 8.3**	**56.0 ± 21.2**	**36.0 ± 13.5**	**69.3 ± 19.5**	**85.0 ± 35.4**	**2.9 ± 0.9**
$C\text{-}CH_4$ [µg $C\text{-}CH_4$ m^{-2} h^{-1}]	*F. excelsior*	-16.6 ± 6.2	-9.8 ± 3.5	-9.5 ± 2.2	-11.1 ± 4.6	-11.9 ± 3.9	-28.6 ± 2.0	-13.1 ± 3.9	-17.8 ± 4.0	3.5 ± 1.0
	F. sylvatica	-0.4 ± 0.2	-11.0 ± 3.2	-6.5 ± 2.3	-27.7 ± 7.3	-20.9 ± 8.5	-23.7 ± 3.1	-3.6 ± 4.5	-18.3 ± 9.1	5.1 ± 2.1
	Crtl	-16.7 ± 7.5	-22.2 ± 6.9	-19.2 ± 4.2	-22.4 ± 3.8	-7.1 ± 1.7	-37.2 ± 6.4	-24.3 ± 5.3	-6.5 ± 2.4	2.1 ± 0.5
	Mean	**-11.3 ± 3.7**	**-14.3 ± 3.0**	**-11.7 ± 2.3**	**-20.4 ± 3.5**	**-13.3 ± 3.3**	**-29.8 ± 2.8**	**-13.7 ± 3.5**	**-14.2 ± 3.5**	**3.5 ± 0.8**
$N\text{-}N_2O$ [µg $N\text{-}N_2O$ m^{-2} h^{-1}]	*F. excelsior*	16.8 ± 8.5	17.1 ± 5.3	-10.2 ± 5.6	17.9 ± 11.0	40.5 ± 10.3	75.7 ± 32.6	68.2 ± 17.4	7.3 ± 19.7	13.0 ± 4.8
	F. sylvatica	11.6 ± 0.6	19.0 ± 5.0	8.6 ± 2.3	18.7 ± 12.1	37.0 ± 14.5	85.7 ± 48.5	21.5 ± 8.6	23.4 ± 12.0	25.0 ± 21.8
	Crtl	3.6 ± 4.0	4.3 ± 3.1	-5.1 ± 5.3	6.3 ± 7.0	-31.5 ± 40.7	148.0 ± 49.1	25.2 ± 18.6	21.2 ± 16.6	21.4 ± 2.7
	Mean	**8.2 ± 3.3**	**10.2 ± 3.1**	**0.2 ± 3.4**	**13.2 ± 5.6**	**14.2 ± 16.7**	**78.1 ± 25.0**	**28.2 ± 10.3**	**16.7 ± 8.8**	**19.8 ± 7.0**

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EIDESSTATTLICHE ERKLÄRUNG

Hiermit versichere ich die vorliegende Arbeit mit dem Titel „EFFECTS OF EARTHWORMS AND TREE SPECIES (*FAGUS SYLVATICA* L., *FRAXINUS EXCELSIOR* L.) ON GREENHOUSE TRACE GAS FLUXES IN MIXED DECIDUOUS BROAD-LEAVED FORESTS" selbstständig und unter ausschließlicher Verwendung der angegebenen Literatur, Verweise und Hilfsmittel erstellt zu haben. Verwendete Quellen wurden als solche gekennzeichnet.

Landau, 11. Februar 2015

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Oct. 2008 March 2009	University Goettingen student scientist Key aspects of activity: Gaschromatography for the department of landscape ecology and the department of plant ecology and ecosystem research University Goettingen.
July 2007 Oct. 2008	Real estate surveyor and value Rinne und Partner GbR
June 2007 Feb. 2007	Engineer community for agriculture and environment IGLU
Sep. 2003 Jan. 2002	Military service 4. /Anti-aircraft tank battalion 6 Lütjenburg 2. /Anti- aircraft tank battalion 6 Lütjenburg

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10th Österreichischer Klimatag, Vienna, Austria, March 13-14, 2008

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