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**Influence of ozone on carbon transformation processes in plant–soil systems:
Changes in rhizosphere microbial community patterns of woody plants**

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J. Esperschütz, J. B. Winkler, A. Gattinger, J. C. Munch and M. Schloter

Recovery of photosynthate ^{13}C in plant parts and rhizosphere organisms of beech (*Fagus sylvatica* L.) at two different growth stages in an open-top chamber experiment.

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Rhizosphere microbial community structure in beech (*Fagus sylvatica* L.) and spruce (*Picea abies* (L.) Karst.) rhizosphere and its response to elevated ozone: A phytotron experiment.

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Influence of long term elevated ozone exposure on rhizosphere microbial communities of mature beech trees (*Fagus sylvatica* L.) on a free-air lysimeter device.

*You will die but the carbon will not;
its career does not end with you.
It will return to the soil,
and there a plant may take it up again
in time, sending it once more
on a cycle of plant and animal life.*

(Jacob Bronowski, 1908 – 1974)

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I Summary

Especially in the aspect of climate change, carbon plays an important role in ecosystems. One of the most important exchange processes between atmospherical carbon and terrestrial ecosystems is the photosynthesis of plants. Carbon compounds are immediately translocated via roots into soil and soil microorganisms, indicating the function of plants as an important link between atmosphere and soil. Carbohydrates leaving plants contribute to the pool of dissolved organic carbon in soil, postulated as a very attractive carbon source for microbial growth. High amounts of recent photosynthate carbon within plant exudates suggest the influence of plants and hence the response to environmental conditions by microbial communities in soil. Since plants respond to environmental changes like increasing tropospheric concentrations of O₃, carbon flux into soil and soil processes are altered, which again affects the global carbon cycle. In the present thesis, several experiments have been carried out to investigate direct carbon fluxes from plants into the soil and to determine how environmental changes like elevated O₃ concentrations alter these processes. By reason of increasing concern of tropospheric ozone damage on forest trees, this study focused on European beech (*Fagus sylvatica* L.) and Norway spruce (*Picea abies* (L.) Karst.) as experimental plants, since these are common in forests of Western Europe. Compound specific stable isotope analyses were chosen to trace photosynthetically fixed carbon through the plant into the soil and soil microbial communities. Using different ¹³C-labelling techniques, individual groups of organisms were identified to be involved in the utilization of exudates, indicating a microbial food web in the rhizosphere. Different groups of organisms within the soil microbial biomass were investigated by phospholipid fatty acid (PLFA) profiling. Higher abundances of microorganisms were detected in the rhizosphere of spruce compared to beech trees but also in rhizosphere soil compared to bulk soil, indicating the influence of plant and plant species on microbial communities in soil. Differences within the microbial community composition in the rhizosphere of saplings compared to mature trees but also changes of the microbial community structure within a vegetation period indicate the influence of plant age and stage of plant development. Irrespective these biological factors, microbial communities respond to environmental influences like elevated ozone. Investigating beech and spruce rhizosphere microbial community structures, the latter causes changes in the microbial community structure via the carbohydrate composition within plants and rhizodeposition.

II Zusammenfassung

Kohlenstoff spielt eine wichtige Rolle in Ökosystemen, insbesondere angesichts des Klimawandels. Die photosynthetische Kohlenstofffixierung stellt dabei einen der wichtigsten Austauschprozesse zwischen atmosphärischem Kohlenstoff und terrestrischen Ökosystemen dar. Kohlenstoffverbindungen werden umgehend über Wurzeln in den Boden abgegeben und somit Bodenmikroorganismen zur Verfügung gestellt, was die Funktion der Pflanze als wichtiges Verbindungsglied zwischen Atmosphäre und Boden verdeutlicht. Kohlenstoffverbindungen aus Pflanzen gehen in den Pool der gelösten organischen Substanz im Boden ein, welcher als attraktive Kohlenstoffquelle für mikrobielles Wachstum gilt. Große Mengen an jüngst photosynthetisch fixiertem Kohlenstoff in den Pflanzenexsudaten verdeutlichen den Einfluss der Pflanze, und folglich deren umweltbedingte Reaktion auf mikrobielle Gemeinschaften im Boden. Pflanzen reagieren auf Klimaveränderungen wie etwa die Erhöhung der troposphärischen Ozonkonzentrationen, was eine Veränderung im Kohlenstofffluss in den Boden und den damit verbundenen Prozessen zur Folge hat, und wiederum den globalen Kohlenstoffkreislauf beeinflusst. In der vorliegenden Arbeit wurden verschiedene Experimente durchgeführt, um direkte Kohlenstoffflüsse über Pflanzenwurzeln in den Boden zu untersuchen, und um zu determinieren, wie sich Klimaveränderungen wie erhöhte Ozonkonzentrationen auf diese Prozesse auswirken. Aufgrund zunehmender Bedenken bezüglich der Ozonschädigung von Waldbäumen stehen in der vorliegenden Arbeit die Versuchspflanzen Rotbuche (*Fagus sylvatica* L.) und die Gemeine Fichte (*Picea abies* (L.) Karst.) als typische Vertreter in den Wäldern Westeuropas im Fokus. Anhand komponentenspezifischer Isotopenanalysen wurde die Verlagerung von photosynthetisch fixiertem Kohlenstoff in Pflanzen, Boden sowie Bodenorganismen verfolgt. Mittels verschiedenen ¹³C-Markierungstechniken wurden unterschiedliche Beteiligungen solcher Organismengruppen am Abbau von Pflanzenexsudaten detektiert und mikrobielle Nahrungsnetze in der Rhizosphäre aufgezeigt. Unterschiedliche Organismengruppen konnten anhand ihrer Phospholipid-Fettsäuremuster (PLFA) identifiziert werden. Höhere mikrobielle Biomassen in der Rhizosphäre von Fichten im Vergleich zu Buchen, sowie höhere mikrobielle Biomassen in der Rhizosphäre im Vergleich zum wurzelfernen Boden verdeutlichen den Einfluss von Pflanze und Pflanzenart auf die Mikrobengemeinschaften im Boden. Sowohl Unterschiede in der Zusammensetzung mikrobieller Gemeinschaften in der Rhizosphäre von

jungen und älteren Bäumen, als auch Veränderungen in deren Struktur im Verlauf einer Vegetationsperiode zeigen den Einfluss von Pflanzenalter und Entwicklungsstand auf mikrobielle Gemeinschaften im Boden an. Abgesehen von solchen biologischen Faktoren reagieren mikrobielle Gemeinschaften in der Rhizosphäre auf Umwelteinflüsse wie erhöhte Ozonkonzentrationen. Lang anhaltend erhöhte Ozonkonzentrationen verursachen Änderungen in der Struktur mikrobieller Gemeinschaften über die Kohlenstoffverbindungen von Pflanzen und Exsudaten.

III Introduction

1 Carbon and the role of climate change

Carbon is one of the most important elements. It is a main constituent in every life on earth, present in numerous geological formations and also involved in many active exchange processes within the atmosphere and between ecosystems. In the latter one, carbon in form of CO₂ plays a major role in exchange processes, as CO₂ is fixed by autotrophic plants and resulting carbon compounds are allocated into terrestrial ecosystems. Carbon fixed by photosynthesis moves through the plant into the soil (Curl & Truelove, 1986; Muller *et al.*, 1993), where it represents an attractive carbon source for soil microorganisms (Bowen & Rovira, 1991), and is again released into the air by respiration. As a result of these processes, soil is known to implement the largest stock of carbon in terrestrial ecosystems (Cardon *et al.*, 2001). Therefore one of the key issues in climate change research is to understand future dynamics of organic carbon in soils (Bottner *et al.*, 2000). Carbon input into soil is dependent on plants and therefore, stresses that alter plant growth and hence carbon fluxes to soil may influence carbon dynamics in soil (Andersen, 2003).

Mainly due to excessive burning of fossil fuels, tropospheric concentrations of CO₂ and O₃ have steadily increased over the past century (Krupa & Kickert, 1993) and further increases are predicted (Kirschbaum, 2003). Especially rising concentrations of O₃, produced photochemically from nitrous oxides and hydrocarbons, have caused concern in recent years (Lippert *et al.*, 1996; Ashmore, 2005). Ozone may act as phytotoxic air pollutant and causes (acute and chronic) damages in plants (Matyssek & Innes, 1999), which subsequently alter carbon fluxes to roots (Andersen, 2003). A decrease in root growth and root carbohydrate concentration may in turn influence root exudation and hence available substrates for microbial communities. This may cause altered living conditions in soil influenced by roots (McCool *et al.*, 1982; Mulchi *et al.*, 1992; Islam *et al.*, 2000; Andersen, 2003). Taken together, plants may respond to O₃ with altered productivity and a change in distribution of assimilates. Subsequently carbon fluxes into soil may change and probably alter soil processes, which again affects the global carbon cycle (Islam *et al.*, 2000; Andersen, 2003).

2 Forest ecosystems and carbon dynamics within plants and soil

With an amount of 80% of terrestrial biomass (Saugier *et al.*, 2001), forests represent the major natural vegetation of European landscapes (Ellenberg, 1996). Carbon storage in forest ecosystems is large and therefore the important role of carbon in the global C-cycle is obvious (Lal, 2005). Changing climate conditions have drawn much attention towards the functioning of carbon dynamics in forest ecosystems (Wiemken *et al.*, 2001) since trees face such altered conditions throughout their lifetime (Saxe *et al.*, 2001). Persistent trees, representing the majority of the above-ground part of a forest ecosystem, determine the quantity and quality of resources translocated (in form of plant litter and exudation) into the below-ground parts of forest ecosystems: plant roots and soil. Therefore environmental influences on trees indirectly affect the soil organic carbon stock (Overby *et al.*, 2003; Lal, 2005). Allocation and distribution of carbon compounds in plants and soil was frequently studied (e.g. Bauhus & Barthel, 1995; Wiemken *et al.*, 2001; Dyckmans *et al.*, 2002; Hackl *et al.*, 2004), but inquisitiveness of carbon dynamics between plant and soil is still high. In this context, microbial communities in soils became of high importance. They play a key role in soil organic matter and nutrient transformation processes (Wiemken *et al.*, 2001) and thus are strongly influenced by root C inputs (Brant *et al.*, 2006). Such transformation processes are influenced indirectly via the plant by different environmental factors (Grayston *et al.*, 1996) and it is therefore of growing interest how changing climate conditions alter microbial community structures in the rhizosphere.

3 Rhizosphere and rhizodeposition

The volume of soil influenced by plant roots was first termed “rhizosphere” by Hiltner in 1904 and is reported as a zone of high microbial activity due to large quantities of carbon and other nutrients. These carbon compounds and nutrients are released by plant roots into the rhizosphere by “rhizodeposition”, which describes the total carbon entering the soil in form of water-soluble exudates, secretions, lysates, gases and mucilage (Grayston *et al.*, 1996). Within rhizodeposits, water soluble exudates, mainly carbohydrates, carboxylic acids and amino acids (Lynch & Whipps, 1990), are probably the most attractive components for microorganisms and therefore highly responsible for microbial growth (Lynch & Whipps, 1990). Water soluble exudates are extractable from the rhizosphere soil, together with soil

carbon within the pool of total dissolved organic carbon (DOC). Extracting DOC from rhizosphere soil gives an idea about the amount of water extractable organic carbon in soil, but the contribution of plant derived carbon to DOC is still unknown. Recently it was postulated that large amounts of exudates were stabilized in non-water extractable organic fractions (Marx *et al.*, 2007), which has to be taken into account when interpreting results obtained from DOC analyses. However, dissolved organic carbon in the rhizosphere is known to be very attractive for microorganisms (Meyer *et al.*, 1987; Paterson, 2003) and hence, lower amounts of carbohydrates and a lack of root exudates create less attractive living conditions for microbial communities in soil that is not directly influenced by plant roots (bulk soil). Due to this lack of root exudates, but also differences in chemical, physical and biological characteristics (Bertin *et al.*, 2003) may lead to differences in the microbial community structure and microbial activity in bulk soil compared to the rhizosphere (Schloter *et al.*, 2005).

Rhizodeposition may vary in response to environmental parameters (water potential, light, soil compaction, temperature) and biological parameters (plant species, stage of development; Baudoin *et al.*, 2003), but also to the presence of microorganisms (Grayston *et al.*, 1996). An increase in the amount of different microbial communities is a result of exudates-consumption in the rhizosphere and hence an increase in sink strength. Also the production of plant hormones, which increase root cell permeability was reported (Bowen, 1994). Since the rhizosphere and microbial communities are strongly influenced by root exudates (Brant *et al.*, 2006), it was even hypothesised that plants select beneficial microbial communities in their rhizosphere (Singh *et al.*, 2007). In temperate forests, ectomycorrhizal fungi live in close symbiosis with fine roots of deciduous and evergreen trees. Ectomycorrhizal fungi decompose organic substances obtained from the plant and in turn provide water, nutrients and mobilized minerals from rocks to their host (Smith & Read, 1997). It has been postulated recently that utilization of plant derived carbon by mycorrhizal fungi is very high (Högberg, 2006). However, the availability of plant exudates in soil may either stimulate or limit microbial growth and activity in the rhizosphere (Wardle, 1992) and consequently provide a linkage between plant and microbial community structure in the rhizosphere (Paterson, 2003). It is therefore inevitable to understand such complex dynamics between plants and rhizosphere microbial communities for a proper investigation of global carbon processes.

Hence reliable methods for structural and functional characterization of soil microbial communities are necessary.

4 Characterization of microbial biomass in soil

4.1 Microbial biomass and microbial communities in soil

Jenkinson (1978) quoted the soil microbial biomass as “the eye of the needle through which all the natural organic material that enter the soil must pass”. The whole microbial biomass may serve as a “transformation station”, converting materials into new products with subsequent release to the soil (Veen *et al.*, 1984). Therefore it is responsible for the mineralization and cycling of nutrients in soil (Lynch & Whipps, 1990). Several methods have been established to quantify this pool of soil microbial biomass via its carbon content (C_{mic}). Among others, the methods of fumigation-incubation (Jenkinson & Powlson, 1976), substrate-induced respiration (Anderson & Domsch, 1978) and fumigation-extraction (Vance *et al.*, 1987) are commonly used. The latter one has become as a useful tool in acidic (forest) soils (Vance *et al.*, 1987), but the description of total microbial biomass in more detail causes methodological challenges. Since a large number of microorganisms are unknown and uncultivable (Amann *et al.*, 1995), culture independent methods are very useful for studying the microbial community in soil. Reviewed by Leckie *et al.* (2004), on the one hand, nucleic acid-based methods based on extracting and purifying DNA and mRNA from soil have been improved rapidly within recent years. Nucleic acid-based techniques like quantitative polymerase chain reaction (qPCR) or fingerprinting increased the knowledge of below-ground live in soil, but still have to face problems (Soederberg *et al.*, 2004): as reproducibility of nucleic acid extraction and selectivity of the polymerase chain reaction (PCR). Thus, the need for conventional methods studying the microbial diversity remains unchanged. Apart from molecular methods characterizing genotypic criteria, microbial communities have been investigated indirectly via phenotypic characteristics. Probably the most common phenotypic method to characterize microbial communities in soil is the use of phospholipid fatty acids. Recently, phospholipid fatty acids (PLFA) were postulated to maximize power investigating soil microbial communities compared to PCR-based methods (Ramsey *et al.*, 2006).

4.2 Phospholipid fatty acids (PLFA) in soil

PLFA are essential membrane components of all living cells (Zelles, 1999). Since they are not synthesized in storage compounds and are rapidly degraded after cell death, PLFA serve as good indicators for living organisms (White *et al.*, 1979). As reviewed by Kaneda (1991), membrane fatty acids can be divided into two major groups, based on their biosynthetic relationships: Straight-chain fatty acids and branched-chain fatty acids. Due to different synthetic pathways, microorganisms differ regarding their fatty acid compilation. The extraction of PLFA from soil samples comprises all fatty acids of the whole microbial population, for which reason an interpretation of data is exceedingly difficult. Table 1 summarizes the main groups of fatty acids also according to the interpretation of a soil PLFA profile.

Tab. 1: Phospholipid fatty acid biomarkers commonly used for specific groups of microorganisms (according to Zelles, 1997; Zelles, 1999; Leckie *et al.*, 2004).

PLFA type	Indicator value	Reference
SATFA	bacteria, eucaryotes	Zelles, 1999
- <i>br</i>	Gram-positive bacteria	Lechevalier, 1977; Kroppenstedt, 1992;
- <i>iso / ant</i>	Gram-positive bacteria	Lechevalier, 1977; Kroppenstedt, 1992;
- <i>cyc</i>	Gram-negative bacteria	Ratledge & Wilkinson, 1989
- <i>br10</i>	actinomycetes	Lechevalier, 1977; Kroppenstedt, 1992;
MUFA	Gram-negative bacteria	Ratledge & Wilkinson, 1989;
16:1 ω 9 18:1 ω 9	fungi	Frostegard & Bååth, 1996; Klamer & Bååth, 2004
PUFA	eucaryotes	Zelles, 1999
18:2 ω 6,9	fungi	Ratledge & Wilkinson, 1989
18:3	fungi, plants	Ratledge & Wilkinson, 1989; Zelles, 1999
20:4 ω 6,9,12,15	microeucaryotes,	Lechevalier, 1977
PLOH	Gram-negative bacteria, fungi, plants	Zelles, 1997; Zelles, 1999
NEL-PLFA	anaerobic bacteria	Zelles, 1999

Saturated fatty acids (SATFA) comprise straight-chain fatty acids (nor), branched-chain fatty acids (br) and cyclopropyl fatty acids (cyc). Straight-chain fatty acids are ubiquitous in cell membranes (Zelles, 1999) and especially long straight chain fatty acids (indicating more than 20 carbon atoms) are main characteristics for eukaryotes and higher plants. Branched-chain fatty acids (iso and anteiso methyl branching, unknown methyl branching) are very common in cell walls of Gram-positive bacteria, whereas a methyl-branching at the tenth carbon atom (br10) was mainly detected in actinomycetes (Lechevalier, 1977; Kroppenstedt, 1992). Cyclopropyl fatty acids are common in some Gram-negative organisms, but also in anaerobic representatives of Gram-positive bacteria (Ratledge & Wilkinson, 1989). Cyclopropyl and br10-fatty acids are derivatives of straight chain mono unsaturated fatty acids and therefore an interpretation must be carried out with respect to this group of fatty acids.

Mono unsaturated fatty acids (MUFA) have been shown to be characteristic for Gram-negative bacteria (Ratledge & Wilkinson, 1989). Although MUFA can occur in Gram-positive bacteria as well, their relative contribution to total PLFA content therein is typically very small (less than 20%; Zelles, 1999). Previous studies indicate that physiological stress in bacteria as a consequence of changing environmental conditions lead to increasing contents of MUFA (Guckert *et al.*, 1986; Ratledge & Wilkinson, 1989; Heipieper *et al.*, 1996).

In contrast to SATFA and MUFA, poly unsaturated fatty acids (PUFA) were rarely detected in bacteria but in fungi, algae and protozoa (Ratledge & Wilkinson, 1989). PUFA 18:2 ω 6,9 (linoleic acid) were detected in rather high amounts in fungi, for which a positive correlation with the fungal biomarker ergosterol (Frostegard & Bååth, 1996) has been postulated. In general, linoleic as well as linolenic acid (18:3 ω 9,12,15) are widespread among eukaryotes, and therefore interpretation must be carried out with care.

Further, hydroxy-substituted fatty acids (PLOH) and non ester-linked (NEL-PLFA) fatty acids are present in environmental samples, but have not been engaged in the extraction protocol used for the experiments in this study. NEL-PLFA can be used as biomarkers for anaerobic bacteria, since sphingolipids, plasmalogens and other aminolipids are mainly present in this fatty acid fraction (Zelles, 1999). PLOH has been suggested to be used indicatively for Gram-negative bacteria in environmental samples, but was detected as well in fungi and plants (Zelles, 1997).

5 Carbon transformation processes in plant-soil systems

5.1 Tracing carbon fluxes into microbial communities

A very common method investigating carbon fluxes through plants into soil microbial biomass is to grow plants in an atmosphere with an altered carbon signature of CO₂ compared to the ambient one (Kuzyakov, 2001). By following this carbon signature through the plant into soil and microbial communities, one can gain knowledge about where photosynthetically assimilated carbon is located and transported within the plant (Ekblad & Högberg, 2001; Steinmann *et al.*, 2004). Furthermore, characterization of microbial communities which utilize carbon substrates exudated from plant roots into the rhizosphere is possible (Butler *et al.*, 2003; Lu *et al.*, 2004; Ostle *et al.*, 2007). Pulse labelling experiments allow the tracking of recently assimilated carbon into microorganisms (Thornton *et al.*, 2004) and show a fast incorporation of assimilated plant derived carbon into microbial communities (Rattray *et al.*, 1995). To gain further information about carbon incorporation and carbon transfer within the microbial food-web, continuous labelling periods are necessary to achieve a more homogeneously labelled carbon pool (Paterson *et al.*, 2007). In order to accomplish labelling techniques under ambient air conditions, where ¹³C-labelling is associated with high costs and extraordinary facilities, studies have been carried out using CO₂ derived from fossil-fuel burning to alter the ambient carbon isotopic signature of CO₂ (Steinmann *et al.*, 2004; Billings & Ziegler, 2005; Klumpp *et al.*, 2005).

Boschker *et al.* (1998) were probably the first scientists linking the use of ¹³C-labelled substrates with microbial PLFA. PLFA analyses have become a powerful tool investigating microbial community structure in soil (e.g. Zelles *et al.*, 1995; Frostegard & Bååth, 1996; Bai *et al.*, 2000; Gattinger *et al.*, 2002; Gattinger *et al.*, 2003; Esperschütz *et al.*, 2007; Nilsson *et al.*, 2007), and ¹³C tracking into PLFA has become more and more popular in answering ecological questions with respect to different environmental conditions (e.g. Pombo *et al.*, 2002; Butler *et al.*, 2003; Lu *et al.*, 2004; Leake *et al.*, 2006; Ostle *et al.*, 2007). Recent techniques also allow the tracking of plant derived carbon into dissolved organic carbon (DOC) and total microbial biomass (C_{mic}) and hence the identification of plant derived carbon within these carbon pools (Potthoff *et al.*,

2003; Marx *et al.*, 2007). However, it is possible that only a minor part of the labelled carbon is present in microbial communities at the time of sampling.

5.2 Carbon loss via respiration

A major part of recently fixed carbon may be lost via respiration (Damesin & Lelarge, 2003; Leake *et al.*, 2006). Especially respiration of woody tissue is a major component of the carbon balance of forests (Damesin & Lelarge, 2003), and, according to Damesin *et al.* (2002), about 25% of the total carbon assimilated by leaves in a beech forest were respired before entering the soil and microorganisms therein. Nevertheless, the rest of fixed carbon is distributed and translocated within the plant-soil system, incorporated into soil microbial biomass and, according to metabolic transformation processes of soil microorganisms, sequestered into non-living soil organic matter (Kindler *et al.*, 2006). However, according to endogenous respiration processes of living microorganisms in soil, as well as exoenzyme activities, carbon is slowly but continuously released from soil in form of CO₂ (Kindler *et al.*, 2006). As a consequence of microbial respiration in soil, also labelled carbon is lost again into the atmosphere and therefore is no more detectable in soil organic carbon or the microbial biomass. Taken together, a certain part of labelled carbon fixed via photosynthesis is respired into the atmosphere again by plant and microbial respiration processes, and therefore not detectable in soil and soil microorganisms.

5.3 Incorporation of plant derived ¹³C into different microbial groups

The ratio between fixed and respired carbon in microbes differs within groups of microbes. Differences in recent photosynthate ¹³C-incorporation may be due to metabolic differences (Ostle *et al.*, 2007). Fungi for example, comprise different metabolic properties compared to bacteria (Gunsalus *et al.*, 1955; Fraenkel & Vinopal, 1973; Romano & Conway, 1996), resulting in different amounts of respired carbon and subsequently fixed carbon. Comparing fast growing r-strategists to slow growing K-strategists, differences in carbon incorporation in these organisms also occur: r-strategists utilize high amounts of plant derived carbon and grow quickly using such easily degradable substrates (Fontaine *et al.*, 2003) and, as a consequence, less of these substrates remain for slow growing K-strategists. Furthermore, a

different utilization of carbon compounds as energy source or for purposes of maintenance may result in different labelling incorporation into different groups of microorganisms (Anderson & Domsch, 1985). However, detailed knowledge about the pathways for carbon incorporation or carbon respiration in different microbial groups is still missing.

5.4 Carbon isotope discrimination within the plant-soil system

Several biochemical reactions within a plant-soil system alter the equilibrium distribution of the carbon isotopes (Farquhar & Ehleringer, 1989). These processes, commonly described as “isotopic fractionation”, discriminate against one carbon isotope (e.g. the heavy ^{13}C), resulting in an accumulation of the other one (e.g. the light ^{12}C) and hence an enriched or depleted $\delta^{13}\text{C}$ value. Fractionation occurs first during photosynthesis, when glucose is produced from atmospheric CO_2 . The $\delta^{13}\text{C}$ value of leaves therefore is lower compared to the $\delta^{13}\text{C}$ value of the surrounding atmosphere, which is due to the isotopic fractionation process that occur in the photosynthetic carbon fixation step (Damesin & Lelarge, 2003). Between leaves and woody tissues, the isotopic signature may change further due to biochemical pathways within carbon translocation (Francey *et al.*, 1985). When carbon is transferred to sinks in form of mainly sucrose, this may lead in turn to an enriched $\delta^{13}\text{C}$ value, probably due to discrimination during loading or unloading of the phloem (Damesin & Lelarge, 2003). As a result, DOC and total organic carbon in soil reflects similar or slightly enriched ^{13}C signatures as the dominant vegetation (Fry, 2006). Dissolved organic carbon in the rhizosphere is known to be very attractive for microorganism (Meyer *et al.*, 1987; Paterson, 2003). By degrading exudates and incorporating carbon into cell wall components, again fractionation might occur, resulting in altered $\delta^{13}\text{C}$ values in C_{mic} . Incorporation of carbon into cell membranes of organisms occurs via different pathways of PLFA synthesis (White *et al.*, 1979). Coherently, carbon isotopic discrimination differs within individual PLFA extracted from the same substrate (Cifuentes & Salata, 2001). Against this background, different isotopic signatures of individual fatty acids within the same PLFA pattern are not unusual. Taken together, carbon discrimination, respiration and metabolic properties have to be taken into account when tracing carbon fluxes in plant-soil systems.

6 Working hypotheses

Rhizodeposition sustains a complex microbial food web in the rhizosphere (Singh *et al.*, 2007), but little is known about the activity of microbial groups using plant derived carbon. It is hypothesized that within rhizosphere microbial communities, different groups of organisms are involved in carbon utilization processes of rhizodeposits in distinct temporal patterns (I). Since the bulk soil compartment differs statistically significant from rhizosphere soil in chemical, physical and biological characteristics (Bertin *et al.*, 2003), between rhizosphere and bulk soil, microbial community abundances and compositions are expected to be different (II). In general, the rhizodeposition of plants is influenced by many environmental factors (water potential, light, soil compaction, temperature) and biological parameters (plant species, stage of development; Baudoin *et al.*, 2003). Therefore it is suggested that environmental and biological factors influence indirectly the microbial biomass and microbial community composition in the rhizosphere of plants (III).

Forests' ecosystems play a large role within the global carbon cycle and the part of microbial communities is essential for the functioning of these ecosystems. European beech (*Fagus sylvatica* L.) and Norway spruce (*Picea abies* (L.) Karst.) are two of the most common tree species in forests of Western Europe. It has been suggested that environmental and biological factors influence indirectly the microbial biomass and microbial community composition in the rhizosphere of plants, and it is therefore hypothesized that beech and spruce sustain a different microbial community structure in the rhizosphere (IV). By the reason of increasing concern regarding tropospheric ozone influence on trees, it is further hypothesized that chronic exposure to elevated ozone influences the rhizosphere microbial community structure of beech and spruce (V). A different microbial community structure in trees of different age was suggested to respond in a diverse way to long term chronic elevated ozone exposure (VI).

In the present study, four experiments (A – D) have been carried out under different environmental conditions to investigate carbon translocation processes from the plant into different soil compartments and microbial communities with respect to elevated ozone exposure. Table 2 presents the four experiments and their contribution to the individual working hypotheses.

Tab. 2: Labelling experiments and the corresponding working hypotheses carried out in the present thesis.

Experiment	contribute to working hypothesis	
A	Temporal dynamics of photosynthate ^{13}C distribution in young beech trees (<i>Fagus sylvatica</i> L.): A model plant-soil ecosystem under continuous labelling atmosphere.	(I) (II)
B	Recovery of photosynthate ^{13}C in plant parts and rhizosphere organisms of beech (<i>Fagus sylvatica</i> L.) at two different growth stages in an open-top chamber experiment.	(I) (II) (III)
C	Rhizosphere microbial community structure in beech (<i>Fagus sylvatica</i> L.) and spruce (<i>Picea abies</i> (L.) Karst) rhizosphere and its response to elevated ozone: A phytotron experiment.	(III) (IV) (V)
D	Influence of longterm elevated ozone exposure on rhizosphere microbial communities of mature beech trees (<i>Fagus sylvatica</i> L.) on a free-air lysimeter device.	(I) (III) (V) (VI)

IV Materials and Methods

The following section comprises the setup of four labelling experiments (A – D) as well as a detailed description of instruments, methodologies and calculations, necessary for accurate interpretation of the obtained results. A list of used chemicals and gases is provided in the Appendix (Tab. VIII-1). To assure comparability, soil and plant material was generally taken from the same sites and tree nursery.

The δ -notation, appearing several times in combination with labelling facilities and labelling gases as well as for the illustration of results, is commonly used to denote a difference relative to an international standard. Here, $\delta^{13}\text{C}$ values, relating to the international Vienna - Pee Dee Belemnite (V-PDB) standard, were calculated as follows (Werner & Brand, 2001):

$$\delta^{13}\text{C} (\text{‰}) = [(R_{\text{Sample}} - R_{\text{V-PDB}}) / R_{\text{V-PDB}}] * 1000 \quad (1)$$

where R_{Sample} and $R_{\text{V-PDB}}$ represent the ^{13}C to ^{12}C ratios of sample and international standard V-PDB (0.0111802), respectively. According to this definition, negative δ -values indicate relatively less heavy isotope than present in the standard, whereas a positive δ -value indicates more heavy isotopes than in the standard.

In the present thesis, labelling of the plants' surrounding atmosphere was performed in two different ways: Accumulation of heavy ^{13}C isotope by adding ^{13}C enriched CO_2 (A, C), and depletion of the heavy ^{13}C isotope by the addition of CO_2 derived from fossil-fuel burning (with relatively low amounts of heavy ^{13}C isotope (B, D). Incorporation of carbon derived from such an atmosphere into biomarker is indicated by an increase in its $\delta^{13}\text{C}$ signature if the first technique is applied, or by a decrease when using the second one.

1 Soil material

The soil used in the following experiments (34% sand, 46% silt and 20% clay) was taken from Höglwald (0 – 40 cm), a mixed forest stand in Bavaria, Germany (48°17' N11°04' O). According to Kreutzer & Bittersohl (1986) the pF-value of undisturbed soil from this site ranged between 1.7 and 2.3 at a watercontent between 30% and 40%. The main soil parameters are summarized in Table 3.

Tab. 3: Main soil parameters of a natural forest soil (0 – 40 cm; dystric Cambisol derived from Pleistocene Loess above tertiary sediments) originating from the Höglwald (Bavaria, Germany, 48°17' N 11°04' O).

	pH (H ₂ O)	C _{total} [%]	N _{total} [%]	C / N	δ ¹³ C in C _{total} [‰ V-PDB]
	3.9	6.4	0.3	19.9	-26.7
± stdev	0.10	0.64	0.02	0.38	0.15

2 Experimental design of the four individual labelling experiments

2.1 Temporal dynamics of photosynthate ¹³C distribution in young beech trees (*Fagus sylvatica* L.): A model plant-soil ecosystem under continuous labelling atmosphere (A)

To investigate carbon dynamics within the plant-soil system and into microbial communities in rhizosphere and bulk soil, a labelling experiment has been set up as described in the following.

2.1.1 Experimental setup

Three-year-old nursery-grown beech trees (*Fagus sylvatica* L.; Staatliche Samenklänge Laufen, Germany) were grown in 101 pots, one plant per pot. During the winter months the plants were kept at ambient air conditions to fulfil dormancy. In spring, 27 planted and 6 unplanted pots were placed into a greenhouse at a photoperiod of 14 hours daylight (additional light by sodium vapour discharge lamps, SON-T Agro 400, Philips, NL) and temperatures of 25°C (day) and 18°C (night). Relative humidity was maintained between 75% and 85% by a sprinkler system. Plants were irrigated every 96 hours; fertilization was performed based on a Hoagland nutrient solution (Appendix, Tab. VIII-2) one week after placement into the greenhouse. Irrigation was performed via irrigation-tubes. During the experimental period, pH did not change statistically significant. The water content in soil varied between 0.60 and 0.80g g⁻¹ dry matter.

2.1.2 Labelling facilities and harvesting procedure

A total of 3 planted and 3 unplanted pots were harvested serving as unlabelled controls, immediately after the uppermost leaves were fully developed. The remaining 24 planted and 3 unplanted pots were placed into an airtight tent, built of transparent plastic foil, to separate the plants from the outer greenhouse atmosphere (according to Marx *et al.*, 2007): CO₂ from the tent atmosphere was reduced by plant photosynthesis as well as scrubbing the tent atmosphere through vials containing soda lime (contains sodium and calcium hydroxide). The CO₂ depleted air was again pumped into the closed tent. In case the CO₂ concentration in the tent dropped below a minimum level of 350 μl l⁻¹, enriched ¹³CO₂ (δ¹³C_{13CO₂} = +170‰ V-PDB) was added to the tent atmosphere, until CO₂ concentration reached again 400 μl l⁻¹. At night time, the pump and the CO₂-absorption system managed to keep a stable CO₂-concentration of 350 μl l⁻¹.

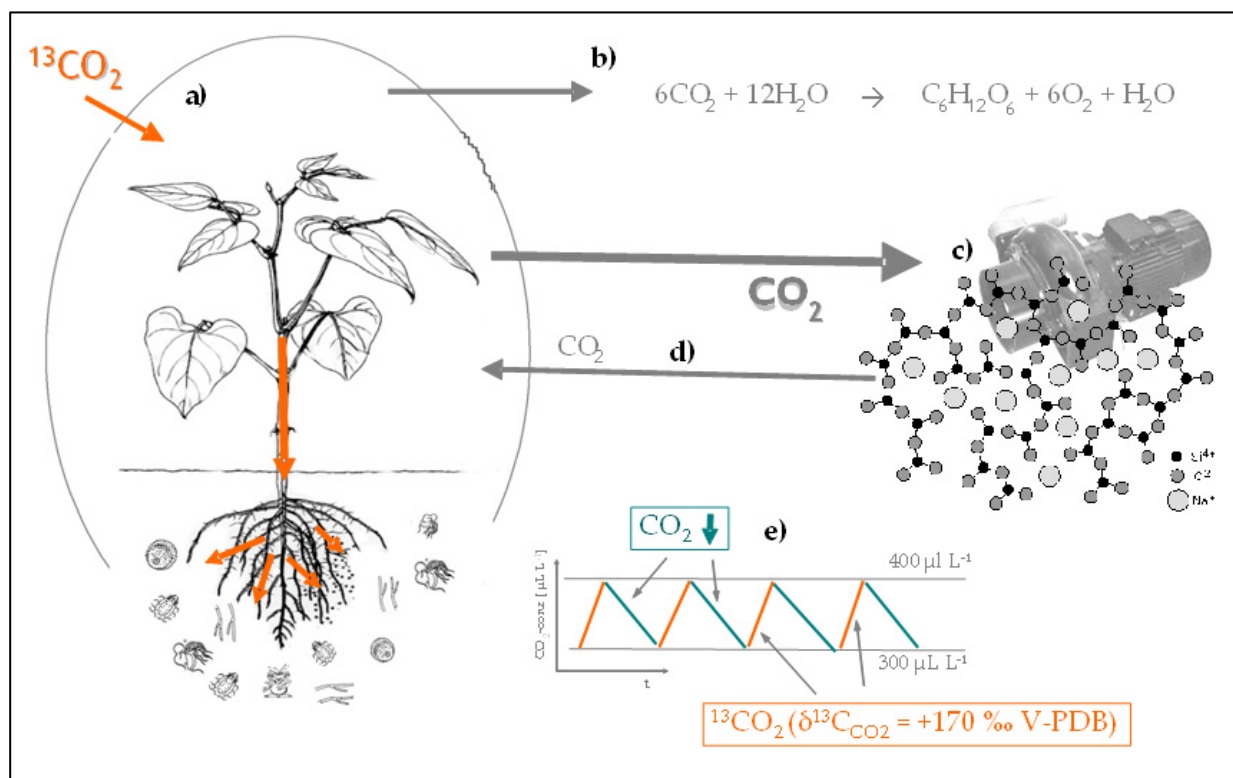


Fig. 1: Experimental design of the greenhouse pot experiment (A). Three-year-old beech trees in closed tents (a) were labelled with ¹³CO₂ over a period of three weeks: The CO₂ concentration in the tent was reduced by plant photosynthesis (b) and scrubbing the tent atmosphere through vials containing soda lime (c). The air with poor CO₂ content was again pumped into the closed tent (d). When the CO₂ concentration in the tent dropped below a minimum level of 350 μl l⁻¹, enriched ¹³CO₂ (δ¹³C_{13CO₂} = +170‰ V-PDB) was added to the tent atmosphere, until CO₂ concentration reached again 400 μl l⁻¹ (e). At night time, the pump and the CO₂-absorption system managed to keep a stable CO₂-concentration of 350 μl l⁻¹.

Using this experimental setup (Fig. 1), an enriched ^{13}C -atmosphere of between +20‰ to +40‰ V-PDB at the beginning, and between +60‰ to +80‰ V-PDB at the end of the experiment was established in the labelling tent. The CO_2 concentration of the atmosphere in the tent was measured continuously and air samples were collected for analysing the ^{13}C -enrichment of the CO_2 (see IV-3). To estimate the amount of soil autotrophic CO_2 -fixation, unplanted pots were analysed at the beginning and the end of the experiment. Plants were harvested in triplicates at given time points (0 days, 0.5, 1, 1.5, 2.5, 3.5, 5.5, 10.5 and 20.5 days). A higher harvesting frequency at the beginning of the experiment (within the first 5 days of labelling) was chosen according to a fast carbon transport through the plants into rhizosphere organisms, suggested in other studies (Butler *et al.*, 2004; Jones *et al.*, 2004; Leake *et al.*, 2006). The soil that stucked directly to the roots (≤ 5 mm) was defined as rhizosphere soil; bulk soil was taken at > 5 mm root distance. Rhizosphere soil and bulk soil was sieved < 2 mm and stored at $+4^\circ\text{C}$ for microbial biomass analyses and at -20°C for PLFA extraction.

2.2 Recovery of photosynthate ^{13}C in plant parts and rhizosphere organisms of beech (*Fagus sylvatica* L.) at two different growth stages in an open-top chamber experiment (B)

In the following experiment, investigation of carbon fluxes in beech trees at different stages of physiological plant development was carried out using CO_2 derived from fossil-fuel burning (Air Liquide, Düsseldorf, Germany) depleted in its carbon isotopic signature ($\delta^{13}\text{C}_{\text{fossil-fuel-CO}_2} = -40\text{‰}$ V-PDB) compared to ambient CO_2 ($\delta^{13}\text{C}_{\text{ambient CO}_2} = \text{ca. } -11\text{‰}$ V-PDB).

2.2.1 Experimental setup

Three-year-old nursery-grown beech trees (*Fagus sylvatica* L.; Staatliche Samenklengle Laufen, Laufen, Germany) were grown in 10 l pots. The soil was taken from a mixed beech/spruce stand in Höglwald (see IV-1). The water content in soil varied between 0.20 and 0.40 g g^{-1} dry matter.

2.2.2 Labelling system and harvesting procedure

A total number of 16 plants were placed into two different open-top chambers (eight plants per chamber) of 2 m height and 2 m in diameter, where plants were exposed to either ambient ($\delta^{13}\text{C}_{\text{atmosphere}} = -11\text{‰ V-PDB}$) or altered ($\delta^{13}\text{C}_{\text{labelling}} = -16\text{‰ V-PDB}$) CO_2 -conditions (Fig. 2).

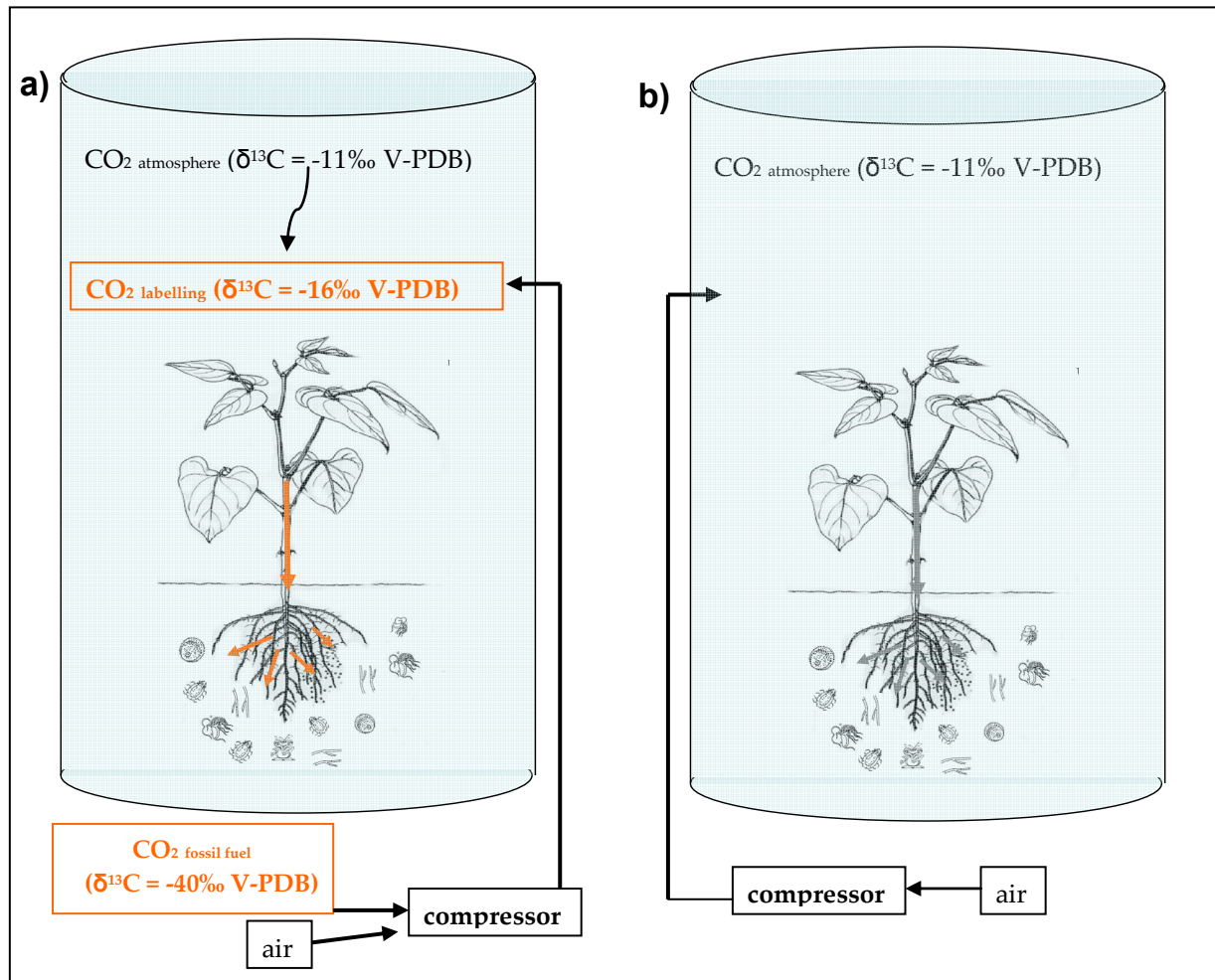


Fig. 2: Experimental design of the open-Top chamber (OTC) labelling experiment (B). Plants were exposed to a labelling atmosphere, where CO_2 concentration was increased at $75 \mu\text{l l}^{-1}$ by the injection of small amounts CO_2 derived from fossil-fuel burning (a). $\text{CO}_2_{\text{fossil fuel}}$ was distributed into the chamber together with ambient air via a compressor. Parallel measurements were carried out using the same number of plants exposed to ambient CO_2 atmosphere (b), where only ambient air was distributed via the compressor.

Altered CO_2 -conditions were achieved by increasing the CO_2 concentrations at approximately $75 \mu\text{l l}^{-1}$ using CO_2 derived from fossil-fuel burning ($\delta^{13}\text{C}_{\text{fossil-fuel-}\text{CO}_2} = -40\text{‰ V-PDB}$). Both chambers CO_2 -concentrations and isotopic signatures were monitored throughout the experiment (see IV.3). The labelling started after leaf expansion was finished (mid-June). At two different stages of growth (T1 = physiological active stage in mid-August; T2 = senescent stage in mid-October) four trees of each chamber were harvested. The plants were separated

in leaves, twigs, stem, fine roots and coarse roots; soil was taken from rhizosphere (< 5 mm root distance) and bulk fractions (> 5 mm root distance) for PLFA analyses.

2.3 Rhizosphere microbial community structure in beech (*Fagus sylvatica* L.) and spruce (*Picea abies* (L.) Karst.) rhizosphere and its response to elevated ozone: A phytotron experiment (C)

With respect to chronic ozone exposure, carbon allocation into microbial communities of beech and spruce rhizosphere was investigated in collaboration with the Department for Ecophysiology of Plants, Technical University of Munich. The setup was based on Grams *et al.* (2002) and Kozovits *et al.* (2005). Plant analyses and additional measurements (e.g. photosynthetic activity, stem respiration, soil respiration, mycorrhizal enzyme activities) were carried out by contributing working groups for their purpose and are not discussed in the present thesis.

2.3.1 Setup and plant material

In spring 2004, two-year-old beech trees (*Fagus sylvatica* L.; seed source 810-24, Bad Griesbach, Germany) and three-year-old spruce trees (*Picea abies* (L.) Karst., seed source 840-27, Altötting, Germany) were planted in containers of 0.7 x 0.4 x 0.3 m. The different ages of trees were chosen to obtain a unique tree height (about 20 cm) for the experimental setup. The water content of the soil ranged between 0.40 and 0.70 g g⁻¹ dry matter. Prior filling into the containers the soil was sieved ≤ 10 mm. Twenty plants per container were arranged in four rows of five individuals. A total number of 42 containers were planted with beech and spruce monocultures and beech/spruce mixtures, 14 containers for each treatment. To exclude edge effects of the container, only the six central plants of each container were harvested. For microbial investigation, the rhizosphere soil of the six central plants was pooled prior to analyses (Fig. 3, b).

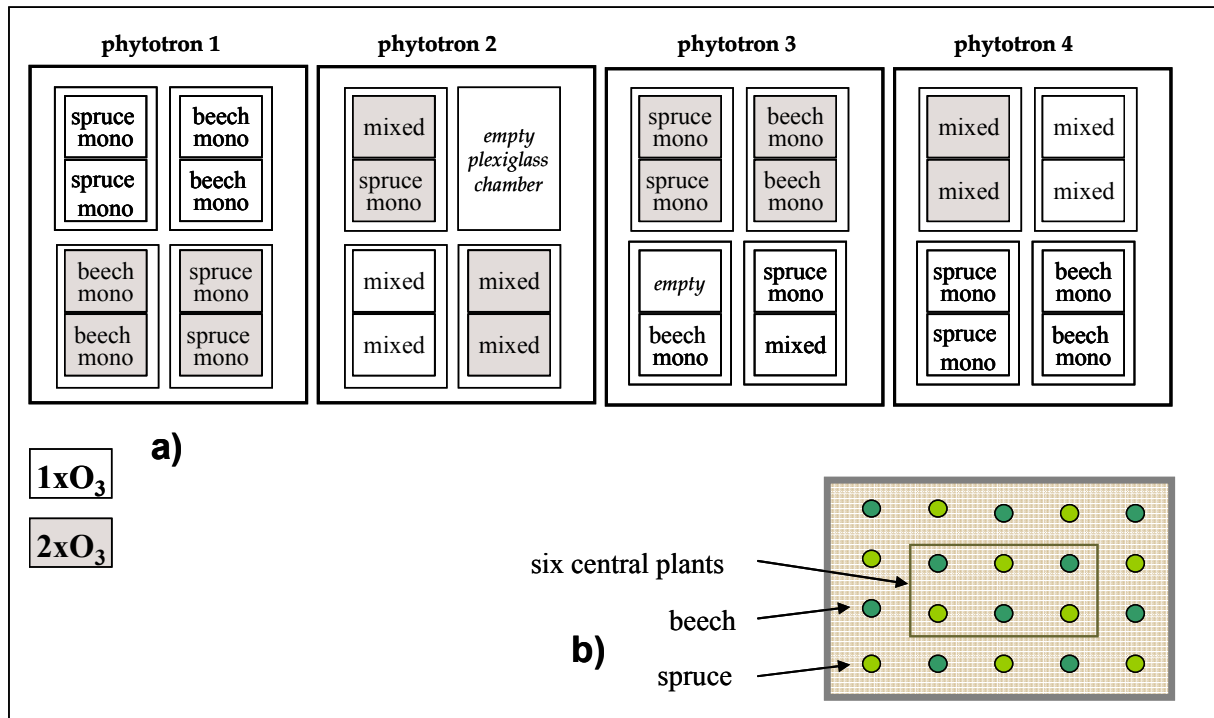


Fig. 3: Arrangement of containers in the four walk-in phytotrons (experiment C) maintained by the GSF – National Research Center for Environment and Health (Neuherberg, Germany). (a) Five containers per treatment were exposed to ambient ozone concentrations ($1 \times O_3$) measured in the Kranzberg Forest during the vegetation period 1998. Another five containers (four containers for beech monocultures) were treated with twice-ambient ozone concentrations ($2 \times O_3$). An empty plexiglass chamber was monitored for CO_2 and H_2O gas exchange throughout the experiment. Containers were planted with 20 trees (b) in mono and mixed cultures. To exclude edge effects of the container, only the six central plants of each container were harvested.

2.3.2 Experimental design and harvesting procedure

During the vegetation period 2004, plants were exposed to either ambient ($1 \times O_3$) or twice of the current ambient ($2 \times O_3$) ozone concentrations in a greenhouse. $2 \times O_3$ concentrations were given according to the corresponding ambient ozone concentration, restricted at $150 \text{ nmol mol}^{-1}$ to avoid acute ozone damage. During the winter months, containers were kept under ambient air conditions. After bud break in May 2005, two containers of each treatment were harvested destructively. Rhizosphere soil ($< 5 \text{ mm}$ root distance) was sieved $\leq 2 \text{ mm}$ and stored at $+4^\circ\text{C}$ for microbial biomass analyses and at -20°C for PLFA extraction. The remaining containers were placed into four walk-in phytotrons (Fig. 3, a) located at the GSF – National Research Center for Environment and Health (Neuherberg, Germany; Payer *et al.*, 1993). In these chambers, a typical forest climate, reproduced according to measurements in 1998 at the study site “Kranzberg Forest” near Freising (Bavaria, Germany, 490 m above sea level; Pretsch *et al.*, 1998) was run. The plants were exposed to $1 \times O_3$ and $2 \times O_3$ ozone concentrations (restricted to $150 \text{ nmol mol}^{-1}$). $2 \times O_3$ ozone concentrations were given according to corresponding ambient ozone concentrations measured during the vegetation period 1998 in

the Kranzberg Forest. Throughout the experiment, fertilization based on a Hoagland nutrient solution (Appendix, Tab. VIII-2) was carried out once every two months to ensure non-limiting nutrient supply. Irrigation was performed automatically via irrigation tubes and tensiometers. Containers were irrigated with deionized water whenever soil water tension reached 350 hPa. Soil pH did not change statistically significant during the vegetation period.

Preceding the final harvest of all containers during the first two weeks of September 2005, a five-day $^{13}\text{CO}_2$ labelling was performed in the phytotrons. Consecutively low amounts (2 ml min^{-1}) of $^{13}\text{CO}_2$ (99.9 atom%) were injected into the air-stream ($45 \text{ m}^3 \text{ h}^{-1}$) of each chamber from sunrise (6.00 a.m.) to sunset (20.00 p.m.). Using this labelling technique, $\delta^{13}\text{C}$ of each phytotron was raised up to average values of +130‰ V-PDB (due to a technical problem, in phytotron 1 (Fig. 3, a) only +25‰ V-PDB were measured within the first three days of the labelling period and therefore the amount of $^{13}\text{CO}_2$ -injection was raised (4 ml min^{-1}) to compensate for the mean $\delta^{13}\text{C}$ in the atmosphere over the five-day labelling period). Subsequently the containers were harvested destructively; soil samples were taken and stored prior to analyses as described above.

2.4 Influence of long term elevated ozone exposure on rhizosphere microbial communities of mature beech trees (*Fagus sylvatica* L.) on a free-air lysimeter device (D)

2.4.1 Experimental setup

The following experiment was accomplished on a lysimeter area in the GSF - National Research Centre for Environment and Health (Neuherberg, Germany) to investigate the influence of chronic ozone exposure on beech trees. Since it was not possible to harvest the lysimeter plants destructively, analyses were performed on plants growing in areas with the same soil and conditions between the lysimeters. In March 1999, natural forest soil from the Höglwald stand (Bavaria, Germany, see IV-1) was filled into eight lysimeters (of a surface area of 1 m^2 and a depth of 2 m) and the area between the lysimeters, retaining the natural horizons. In November 2002, four three-year-old beech seedlings were planted into each lysimeter (for details see Schloter *et al.*, 2005). Between the lysimeters further tree seedlings were planted at the same density. The latter ones were used for this experiment. Since June 2003, four of the

eight lysimeters were exposed to ambient ozone concentrations ($1 \times O_3$), while the other four lysimeters were treated with twice-ambient ($2 \times O_3$) ozone concentrations, restricted to $150 \text{ nmol mol}^{-1}$ to avoid acute ozone damage. $2 \times O_3$ concentrations were given according to corresponding ambient ozone concentrations on the lysimeter field. To inhibit atmospherical exchange between the two treatments, plexiglass walls of 2 m height were installed between the treatment areas and at the borders of the experimental field (Fig. 4). Ozone fumigation was performed using O_3 -generators (OZ-500, Fischer, Meckenheim, Germany) and the O_3 concentration was monitored by O_3 -analysers (CSI-3100, Columbia Scientific Industries, Austin, Texas, USA). Distribution of ozone within the lysimeter area was achieved via compressors and “curtains” of perforated tubes (Fig. 4). Additional measurements on the lysimeter device (mean air temperature, sum of precipitation, global radiation, photosynthetic photon flux density) were carried out as described recently (Schloter *et al.*, 2005; Pritsch *et al.*, 2008).

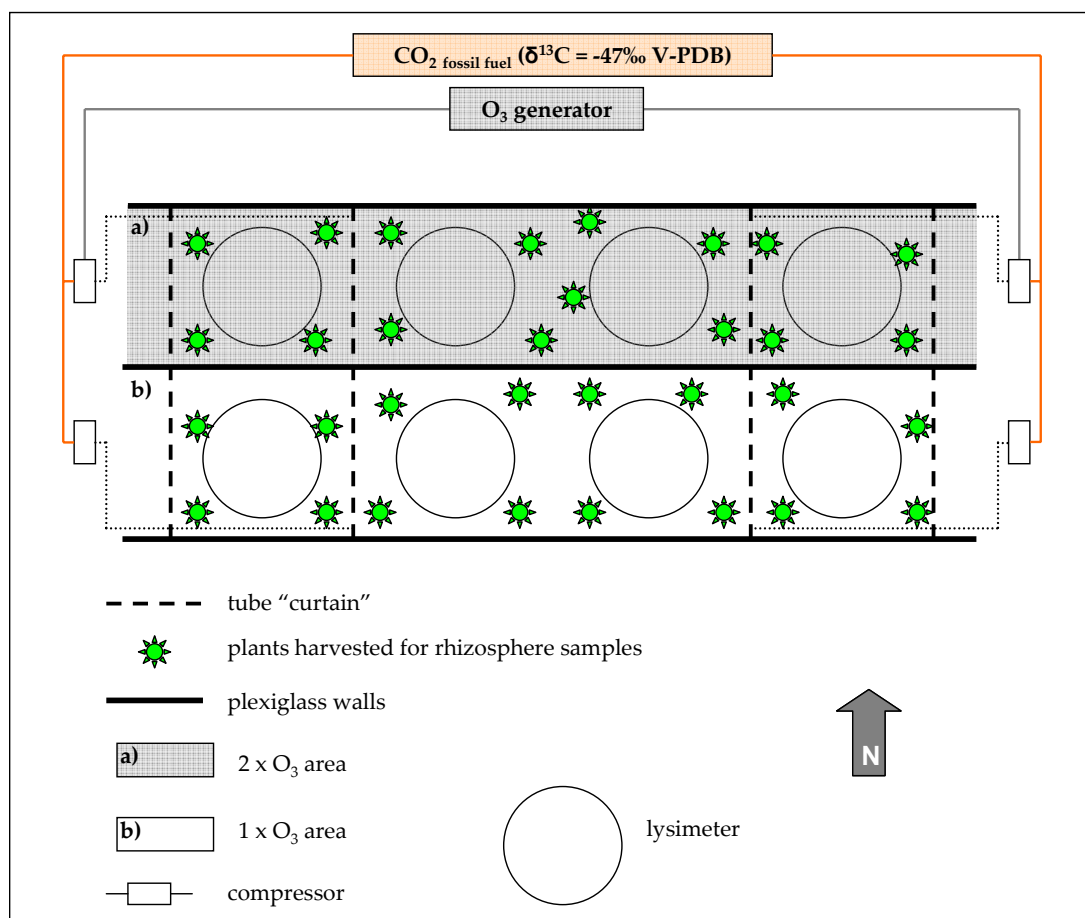


Fig. 4: Lysimeter field area (experiment D) at the GSF Research Centre for Environment and Health (Neuherberg, Germany). Four plants (one plant per lysimeter surrounding field) per ozone treatment were harvested monthly since initiation of “fossil fuel” labelling after leaf expansion.

2.4.2 Labelling facilities and harvesting procedure

At the beginning of the vegetation period 2006, the CO₂-labelling, established for the open-top chamber experiment (see IV-2.2) was adapted to the lysimeter device. After leaf expansion was finished (first week of June), CO₂ derived from fossil-fuel burning ($\delta^{13}\text{C}_{\text{fossil-fuel}} = -47\text{‰}$ V-PDB; Air Liquide, Düsseldorf, Germany) was additionally distributed via the tube curtains into both ozone treatments. The labelling was applied over the whole vegetation period until September. Additionally, infection with *Phytophthora citricola* and supply with ¹⁵N-labelled beech litter were carried out on the lysimeters, but these experiments did not affect the plants, used for this experiment. After start of “fossil-fuel” fumigation, four trees per treatment were harvested monthly from the lysimeter area (T0 = May 31st; T1 = July 3rd; T2 = July 31st; T3 = August 24th). The water content in rhizosphere soil was around 0.30 g g⁻¹ dry matter at T0, T1 and T3 but was only around 0.15 g g⁻¹ dry matter at T2. Rhizosphere soil (< 5 mm root distance) was harvested and sieved ≤ 2 mm prior storing at 4°C for microbial biomass analyses and at -20°C for PLFA extraction.

3 Monitoring of CO₂ atmosphere in the four experiments (A – D)

In the course of the experiment, CO₂-concentrations were monitored on-line by CO₂ analyser (photo-acoustic CO₂ controller 7MB1300, Siemens, Germany). The $\delta^{13}\text{C}$ values of CO₂ were determined using gas chromatography / isotope ratio mass spectrometry (GC/IRMS, Finnigan MAT DeltaPlus, Bremen, Germany). The gaseous samples were collected in glass vials, closed air-tight with a plastic lid and a butyl rubber septum (Labco Limited, High Wycombe, UK) and injected into the IRMS after CO₂ was separated on a GC column (Poraplot, 25 m) as described previously by Marx *et al.* (2007).

4 Sampling, preparation and analysis of plant parts

After harvest, plant parts were immediately separated into leaves, twigs (annual growth), stem (perennial growth), fine roots (< 2 mm) and coarse roots (> 2 mm). The plant material was dried at 65°C for 48 h, ball-milled (Retsch MM2, Retsch GmbH, Haan, Germany) and weighted into tin capsules (3,5 mm x 5 mm, HEKAtech GmbH, Wegberg, Germany). Analyses of C-content and $\delta^{13}\text{C}$ signatures therein were performed by EA-IRMS (Fig. 5). This device

consists of an elemental analyser Euro EA (Eurovector, Milan, Italy) coupled to an isotope ratio mass spectrometer (MAT 253, Thermo Electron, Bremen, Germany). Samples (in tin capsules) were completely oxidized under O₂ in the combustion furnace (C) and afterwards in a copper reduction furnace (R), emerging nitrogen oxides are transformed into N₂ and O₂ to CuO, respectively. H₂O was absorbed at magnesium perchlorate. CO₂ and N₂ were separated on a packed column (P) and were introduced to the IRMS consecutively (via an open split) to measure the carbon isotopic signatures.

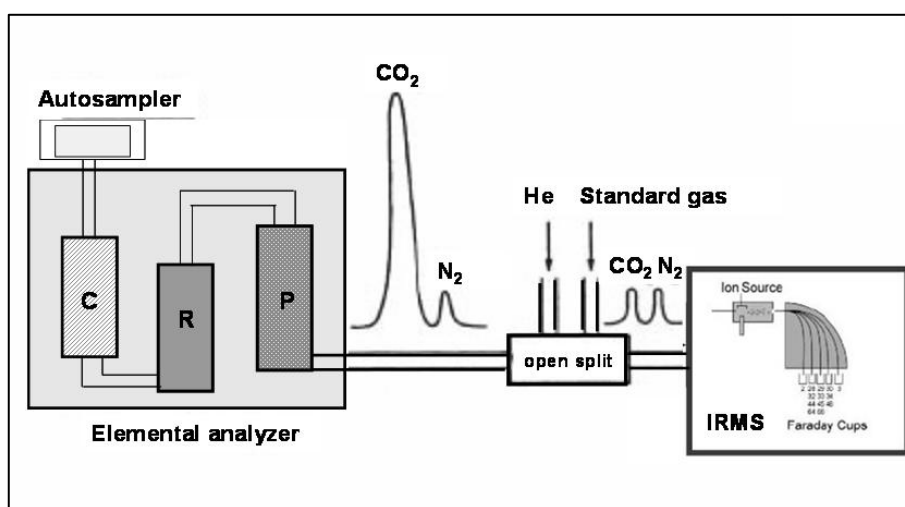


Fig. 5: Principle of an elemental analyzer - isotope ratio mass spectrometry (EA-IRMS, according to Glaser, 2005).

5 Analysis of microbial biomass carbon and dissolved organic carbon

5.1 Extraction procedure

Within 3 days after harvest, microbial biomass (C_{mic}) was estimated by chloroform-fumigation extraction according to Vance *et al.* (1987). Soil samples were divided into two parts equivalent to 5 g oven-dried soil. For chloroform-fumigation, one part was placed in a desiccator together with 25 ml of ethanol free chloroform (for chromatography). The desiccator was evacuated until the chloroform had boiled for 2 min, then it was sealed and the samples were incubated for 24 hours. Subsequently, chloroform was removed from the desiccator and evacuation was carried out (6 times) to remove all traces of chloroform from the soil. Fumigated samples and

non-fumigated controls were extracted with 20 ml of 0.5 M K₂SO₄ (extraction ratio 1:4, w/v) using a rotary shaker. Subsequently soil suspensions were filtered through a paper filter (Schleicher & Schuell, 595½). The extracts were stored at -20°C until measurement. Total organic carbon contents in the extracts were measured as CO₂ (non-dispersive infrared gas analyzer) in a Total Carbon Analyzer (TOC 5050, Shimadzu Corporation, Tokyo, Japan). Microbial biomass was calculated using a *k*_{EC}-factor of 0.45 (Wu *et al.*, 1990).

Dissolved organic carbon (DOC) was preserved by shaking soil samples (equivalent to 5 g oven-dried soil) in 0.01 M CaCl₂ solution (1:5; w/v) on a rotary shaker for 30 minutes. Subsequently, the soil suspension was centrifuged, the supernatant filtered through polycarbonate filters of 0.4 µm pore-size (Whatman Nucleopore Track-Etch Membrane filters). The filtered extracts were stored at -20°C until measurement. Total organic carbon contents in the extracts were determined on the Shimadzu TOC 5050.

5.2 Measurement of δ¹³C ratios in aqueous extracts

Measurement of δ¹³C in K₂SO₄ and CaCl₂ extracts was done by on-line coupling of liquid chromatography and stable isotope ratio mass spectrometry (LC-IRMS, Fig. 6): Analytes are injected into a Finnigan LC Isolink (Thermo Electron, Bremen, Germany) with a needle port (A) into a sample loop (B) and transferred via a six-port valve (C) together with the oxidation reagents and acid (phosphoric acid 8.5%) into the oxidation reactor (G). Oxidation reagents are dosed using two-head-pumps (E) and a pulse damper (F) at a T-piece (D). After all organic compounds had been converted to CO₂, the mobile phase is cooled (H) and CO₂ is separated from the liquid phase by semi-permeable membranes (I, J) and introduced into the isotope ratio mass spectrometer (MAT 253, Thermo Electron; Bremen, Germany) via an open split (K).

The δ¹³C in microbial biomass (δ¹³C_{Bio}) was calculated as follows (Marx *et al.*, 2007):

$$\delta^{13}\text{C}_{\text{Bio}} (\text{‰}) = (\delta^{13}\text{C}_{\text{fum}} * C_{\text{fum}} - \delta^{13}\text{C}_{\text{n-fum}} * C_{\text{n-fum}}) / C_{\text{Bio}} \quad (2)$$

where δ¹³C_{fum} and δ¹³C_{n-fum} are δ¹³C values in fumigated (fum) and non-fumigated (n-fum) extracts, respectively; C_{fum} and C_{n-fum} are carbon concentrations (in mg C l⁻¹) of fumigated and non-fumigated extracts, and C_{Bio} represents the microbial carbon concentration [mg C l⁻¹].

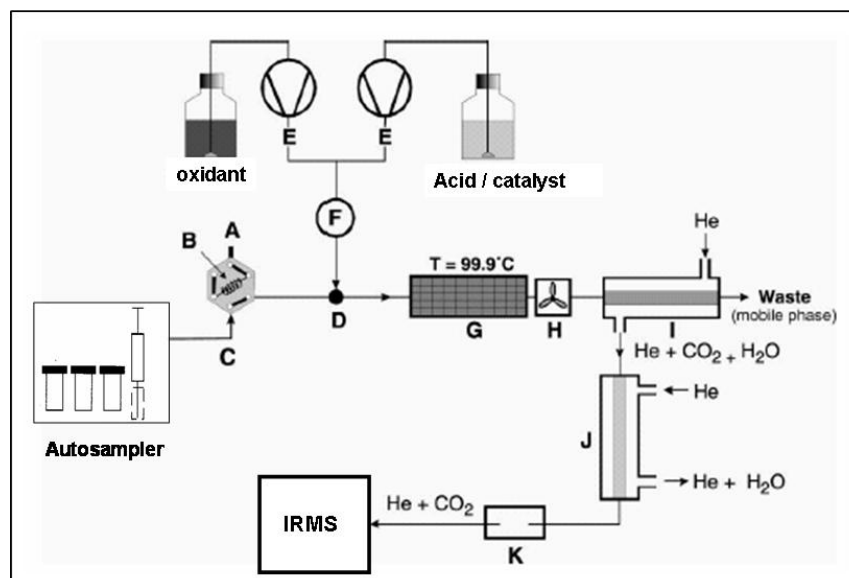


Fig. 6: Schematic illustration of liquid chromatography – isotope ratio mass spectrometry (LC-IRMS; see Krumpal *et al.*, 2004 for further details).

6 PLFA analysis

6.1 Lipid extraction

Lipid analyses of saturated (SATFA), monounsaturated (MUFA) and polyunsaturated (PUFA) fatty acids were based on Zelles *et al.*, (1995): An aliquot of fresh soil sample, equivalent to a dry weight of 10 g was extracted with 125 ml methanol, 63 ml chloroform and 50 ml phosphate buffer (0.05 M, pH 7; 50 ml minus H₂O content in soil). After 2 hours of horizontal shaking, 63 ml water and 63 ml chloroform were added for phase separation. The suspension was kept for 24 h, afterwards the water phase was removed and discarded. The lower phase was recovered, filtrated to remove soil particles and after 24 h phase separation it was concentrated to approximately 1 ml in a rotavapor (Rotavapor R-200, Büchi, Switzerland).

6.2 Lipid separation

The lipid material was fractionated into neutral lipids, glycolipids and phospho-(polar) lipids on a silica-bonded phase column (SPE-SI 2 g/12 ml; Bond Elut, Analytical Chem International, CA, USA) by elution with 1 volume of chloroform, acetone and methanol,

respectively. The phospholipid fraction was used for PLFA analysis according to Zelles *et al.* (1995).

6.3 Formation of fatty acid methyl esters (FAME)

In a mild alkaline hydrolysis (plus methylation), ester bonds between glycerol backbone and the fatty acid side chains were cleaved and fatty acid methyl esters (FAME) were formed from the released fatty acids. The residue of phospholipids was dissolved in 1 ml of methanol : toluene (1:1, v/v) and then 5 ml of 0.2 M KOH in methanol (freshly prepared) were added. This solution was incubated for 15 min at 37°C. Afterwards, the pH was adjusted to approximately pH 6 with 1 M acetic acid. 10 ml of chloroform and 10 ml of water were added and transferred to a centrifugation tube. After a 10-minute centrifugation step, the chloroform phase (lower phase) was removed and the water phase extracted once more with 5 ml of chloroform. The combined chloroform phases were dried over sodium sulphate and reduced to a small volume of approximately 1 ml.

6.4 Separation of unsubstituted FAME

Fatty acid methyl esters were separated on a NH₂ column from OH-substituted FAME and unsaponifiable lipids. NH₂ columns were prepared in glass columns using 0.5 g (\pm 0.05 g) of Sorbenz NH₂ (Chromabond) between 2 filter elements (Chromabond filter elements for glass columns). The FAME generated during step 6.3 were separated on a NH₂ column (column size: 0.5 g / 3 ml) after column conditioning with 1 volume of hexane : dichlormethane (3:1; v/v). Unsubstituted FAME were eluted with hexane : dichlormethane (3:1; v/v).

6.5 Separation of unsubstituted esterlinked PLFA (EL-PLFA)

Unsubstituted esterlinked PLFA obtained during step 6.4 were separated via an Ag-impregnated SCX column (column size: 0.5 g / 3 ml). Column conditioning was performed with 0.1 g of silvernitrate in 1.5 ml of acetonitril : water (10:1, v/v), followed by 2 volumes of acetonitril, 2 volumes of acetone and 4 volumes of dichlormethane. The sample was dissolved in dichormethane : hexane (7:3, v/v) and applied onto the column. Saturated fatty acids

(SATFA) were eluted with 2 volumes of dichloromethane : hexane (7:3, v/v), mono unsaturated fatty acids (MUFA) with 2 volumes of dichloromethane : acetone (9:1, v/v) and poly unsaturated fatty acids (PUFA) with 4 volumes of acetone : acetonitril (9:1, v/v), respectively. All liquids passed the column without pressure.

6.6 Derivatization of MUFA

MUFA obtained as described in section 6.5 were derivatized to identify the position of the double bond. The sample was dissolved in 0.05 ml of hexane and 0.1 ml of dimethyl-disulfide. After addition of 3 to 5 drops of I₂ (6% in diethylether, w/v) the solution was incubated at 60°C for 72 h. The excess I₂ was removed by addition of 1 ml of 5% sodium thiosulfate and the adduct was extracted 3 times with 1.5 ml of hexane. The hexane phases were combined, dried with sodium sulfate and evaporated to nearly dryness. Since heavy isotopic fragmentation might occur during the derivatization step of MUFA, samples were measured underivatized (Kramer, personal communication) to receive the correct isotopic signature. Afterwards, samples were measured again to identify the position of the double bond.

6.7 Identification of fatty acids

PLFA were analyzed as fatty acid methyl esters (FAME) using GC/MS-C-IRMS (Fig. 7): Separation and detection of fatty acids was done in a 5973MSD GC/MS (Agilent Technologies, Palo Alto, USA), isotopic composition of fatty acids was detected in a DeltaPlus^{Advantage} IRMS (Thermo Electron Cooperation, Bremen, Germany) after combustion (GC Combustion III, Thermo Electron Cooperation, Bremen, Germany).

Individual PLFA fractions obtained as described in sections 6.5 and 6.6 were measured in isooctane containing an internal standard (nonadecanoic acid methyl ester and myristic acid methyl ester for PUFA). For individual groups of fatty acids different temperature programs on the Agilent MSD were used to obtain an ideal separation of fatty acids: For SATFA and underivatized MUFA, an initial temperature of 50°C was kept for 2 minutes, then increased at 55°C min⁻¹ to 136°C, and subsequently at 2°C min⁻¹ to 250°C. To separate PUFA, an initial temperature of 150°C was raised at 1.5°C min⁻¹ to 210°C. The program for the identification of derivatized MUFA raised from 60°C for 2 minutes followed by several ramps (120°C min⁻¹ to

200°C, 20°C min⁻¹ to 203°C, 0.13°C min⁻¹ to 210°C and finally 5°C min⁻¹ to 250°C) until 250°C. The final temperature of each program was held for 10 minutes. All PLFA were separated on a polar column (BPX-70, SGE GmbH, Griesheim, Germany), 60 m x 0.25 mm x 0.25 µm, coated with 70% of cyanopropyl polysilphenylene-siloxane. The mass spectra of the individual fatty acids were obtained using the Quadrupol mass spectrometer (Fig. 7): Fatty acids were identified by comparing the obtained mass spectra with established fatty acid libraries (Solvit, CH 6500 – Luzern, Switzerland) using MSD Chemstation (Version D.02.00.237).

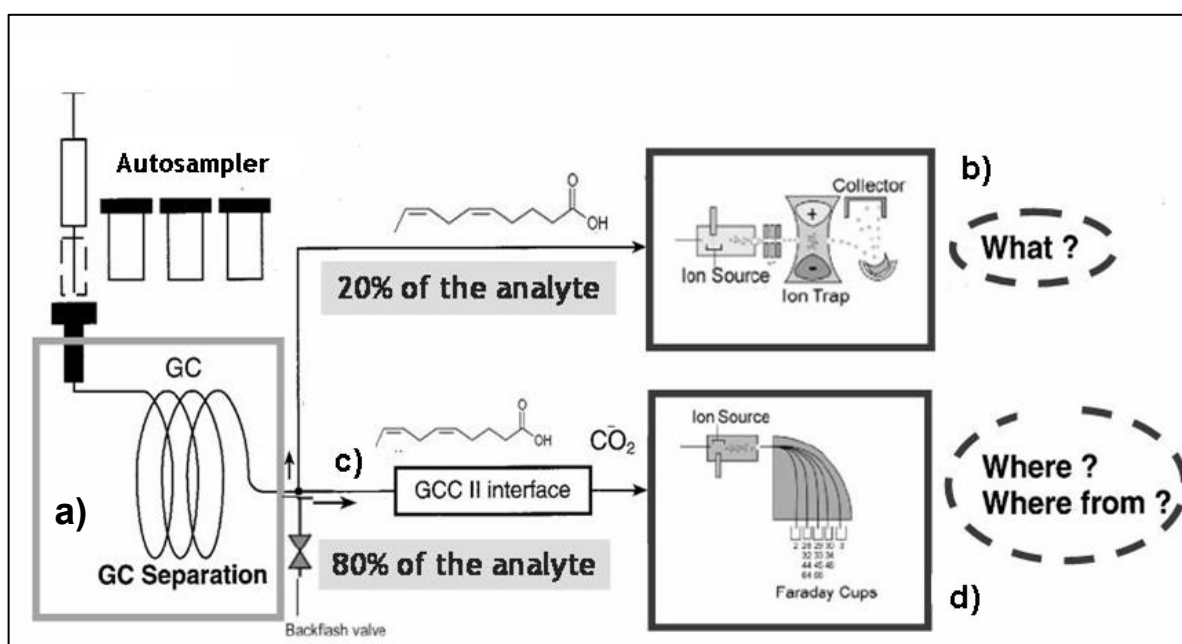


Fig. 7: Separation and detection of fatty acids and their contributing isotopic signature using gas chromatography /mass spectrometry – combustion – isotope ratio mass spectrometry (GC/MS-C-IRMS; Evershed *et al.*, 2006 modified). The extract of fatty acids is separated gas chromatographically (a) and subsequently splitted at a cross piece: 20% of the analyte served for the identification of the fatty acid in a quadrupol mass spectrometer (b), while 80% were oxidized at 940°C (c) and fed into an isotope ratio mass spectrometer (d) for simultaneous measurements of the fatty acids carbon isotopic composition.

Standard nomenclature was used for PLFA (Frostegard *et al.*, 1993), where the number before the colon represents the number of C-atoms, the number after the colon gives the number of double bonds and their location (ω). The prefixes “cy”, “i” and “a” indicate cyclopropyl-groups, and iso- and anteiso- branching, respectively. Saturated straight-chained fatty acids were indicated by “nor” and dicarboxylic fatty acids by the prefix “dic”. The “br” and the number before a fatty acid indicate methyl-branching at the individual C-atom.

6.8 Carbon signature in identified PLFA

The actual $\delta^{13}\text{C}$ ratio of the identified fatty acid was obtained by oxidizing 80% of the analyte in a combustion reactor (940°C) and subsequent introduction of the combustion products into an isotope ratio mass spectrometer (Fig. 7). Samples were measured in duplicates and measurements were repeated when a fluctuation of $> 0.5\%$ $\delta^{13}\text{C}$ V-PDB in the internal standard occurred. The $\delta^{13}\text{C}$ ratio of individual fatty acid methyl ester peaks (FAME; Fig. 8) obtained from the measurement (using mass spectrometer software Isodat 2.5) was corrected by the correction value resulting from the measurement of the internal standard by EA-IRMS and GC/MS-C-IRMS (nonadecanoic acid methyl ester, $\delta^{13}\text{C} = -30.5\%$ V-PDB or myristic acid methyl ester in PUFA fractions, $\delta^{13}\text{C} = -28.7\%$ V-PDB).

The actual PLFA ratio ($\delta^{13}\text{C}_{\text{PLFA}}$) was calculated by correcting the carbon isotope ratios of the FAME ($\delta^{13}\text{C}_{\text{FAME}}$) for the one carbon atom in the methyl group that has been added during derivatisation (6.3). Since no isotopic fragmentation in this step is known (Abrajano *et al.*, 1994), the calculation was done as follows:

$$\delta^{13}\text{C}_{\text{PLFA}} = [(n + 1) * \delta^{13}\text{C}_{\text{FAME}} - 1 * \delta^{13}\text{C}_{\text{Methanol}}] / n \quad (3)$$

where n is the number of carbon atoms in the PLFA and $\delta^{13}\text{C}_{\text{Methanol}}$ the $\delta^{13}\text{C}$ ratio of methanol used for derivatization (-38.5% V-PDB, determined by LC-IRMS).

7 Data analyses

Statistical analyses were performed with SPSS 15.0 for windows. Comparison of mean values was carried out using Student's t-test ($p < 0.05$) for paired (rhizosphere soil and bulk soil in the same planted pot) and unpaired samples. Differences ($p < 0.05$) within temporal dynamics have been tested against the control group (Dunnett) using a univariate analysis of variance (ANOVA). To determine statistically significant differences ($p < 0.05$) between the means of individual tree species and between different ozone treatments, ANOVA were used, followed by Duncan's t-test. Results were illustrated with S-Plus 6.2 for windows.

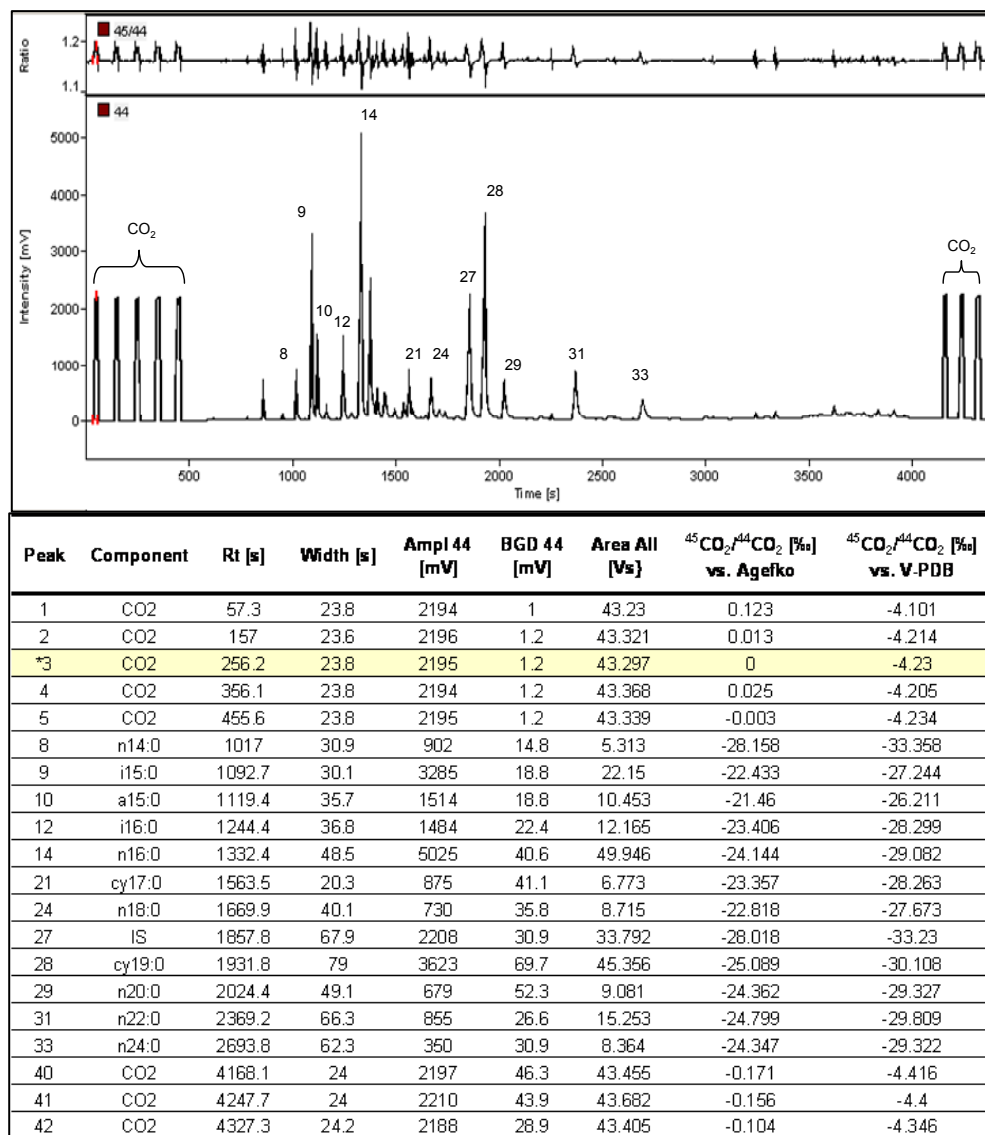


Fig. 8: Typical chromatogram of saturated fatty acids (SATFA; example taken from experiment A), visualized using the software Isodat 2.5. After five reference CO₂-peaks, fatty acid peaks occur in order of their chain length separated on the GC column. Carbon isotopic signatures of individual components were calculated against reference peaks (vs. Agefko) and against the international carbon standard V-PDB. The upper part of the chromatogram shows the isotopic trace of mass 45 (¹³CO₂) against mass 44 (¹²CO₂).

V Results

1 Temporal dynamics of photosynthate ^{13}C distribution in young beech trees (*Fagus sylvatica* L.): The model plant-soil ecosystem under continuous labelling atmosphere (A)

1.1 Carbon signature in plant parts of young beech trees

Figure 9 illustrates the incorporation of ^{13}C -carbon into plant parts of incubated beech trees: Label was immediately detected in leaves ($p < 0.05$) after $\frac{1}{2}$ day. In twigs, statistically significant incorporation was detected after $1\frac{1}{2}$ days. Since the beginning of labelling, ^{13}C in fine roots increased steadily, until a statistically significant $\delta^{13}\text{C}$ enrichment compared to day 0 was detected after 20 days. Perennial plant parts like coarse roots and stems showed a statistically significant ^{13}C enrichment after 10 days and 5 days, respectively. The highest increase of $\delta^{13}\text{C}$ in plant parts at the end of the experiment (around 7‰ V-PDB) was detected in fine roots.

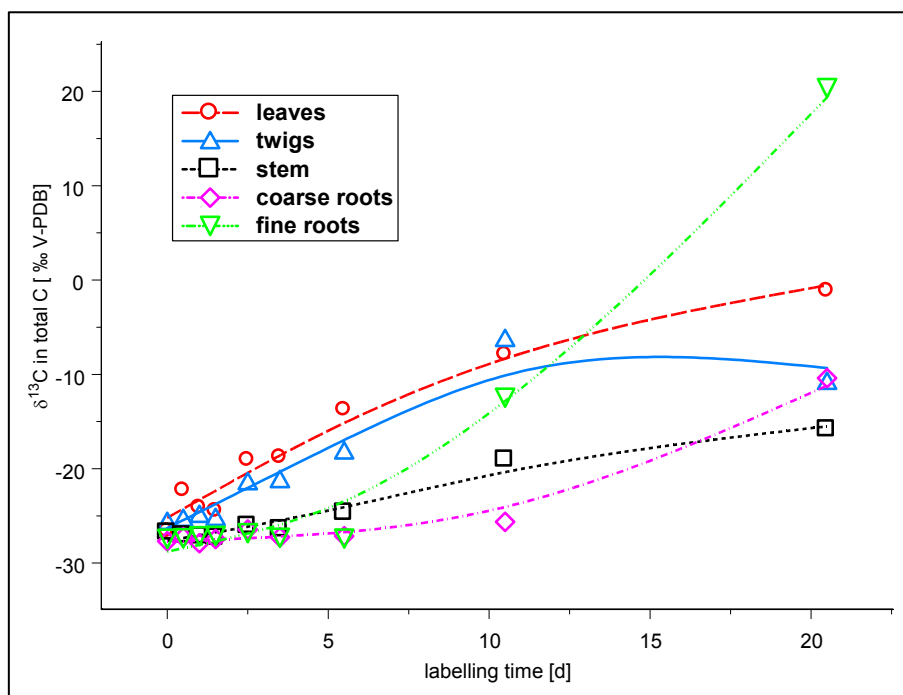


Fig. 9: ^{13}C incorporation in total carbon of beech plant parts [$\delta^{13}\text{C}$ in ‰ V-PDB] in a greenhouse pot experiment at different harvesting time points. Values are based on means ($n = 3$). Trends are visualized using smoothing splines. Standard deviations are presented in the Appendix, Tab. VIII-3)

1.2 Plant derived carbon in rhizosphere and bulk soil

1.2.1 Incorporation of plant derived carbon into dissolved organic carbon (DOC) and microbial biomass (C_{mic})

Microbial biomass carbon contents were higher compared to DOC contents in rhizosphere soil and bulk soil (310 to 400 mg C kg⁻¹ DS and 250 to 300 mg C kg⁻¹ DS, respectively) at all harvesting time points. Both C_{mic} and DOC showed higher abundances in rhizosphere soil compared to bulk soil (210 to 330 mg C kg⁻¹ DS and 200 to 250 mg C kg⁻¹ DS, respectively) in the course of the experiment (Fig. 10).

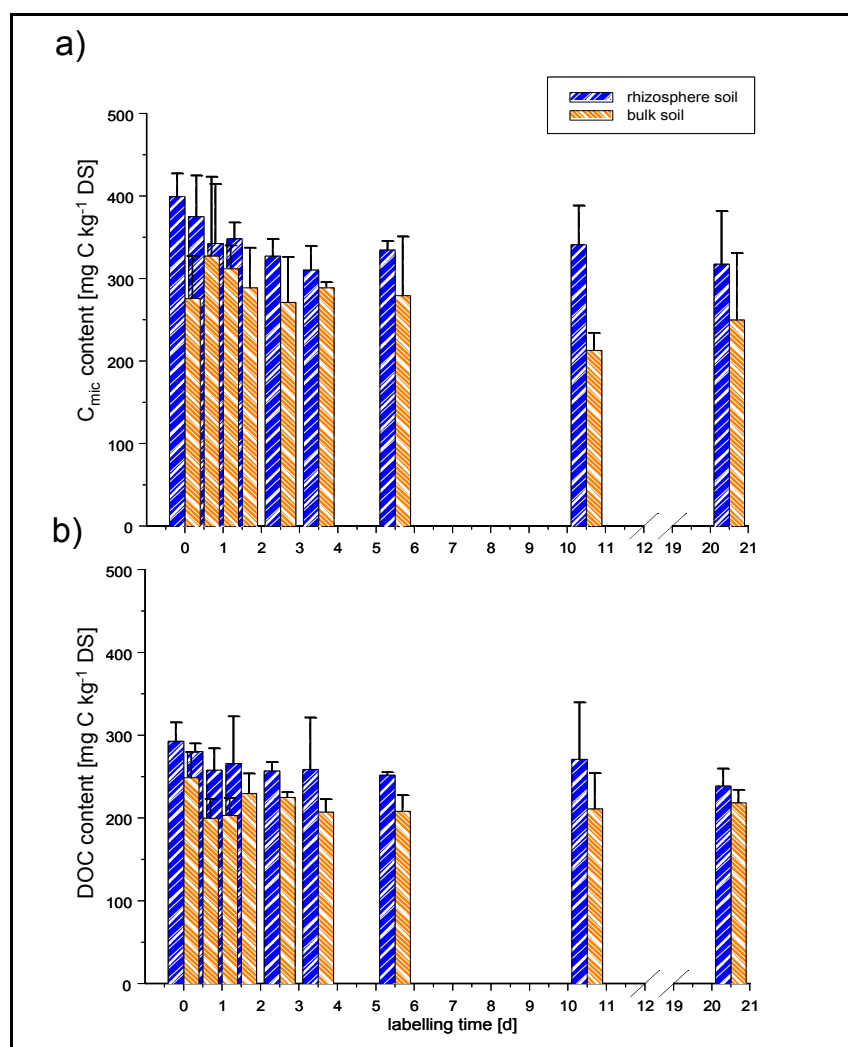


Fig. 10: Microbial biomass (C_{mic} , a) and dissolved organic carbon (DOC, b) contents in beech rhizosphere and bulk soil in the course of the greenhouse pot experiment. Values are based on mean values of triplicates with its standard deviations.

Figure 11 shows the carbon translocation below-ground: With respect to rhizosphere soil samples, ^{13}C -incorporation into the pools of organic carbon (DOC and C_{mic}) increased since labelling was initiated. The $\delta^{13}\text{C}$ values in rhizosphere C_{mic} (Fig. 11 a) showed first statistically significant ^{13}C -incorporation after 10 days of labelling ($p < 0.05$). DOC was also statistically significant enriched in ^{13}C after 10 days of labelling, to a lower amount compared to C_{mic} (Fig. 11, b).

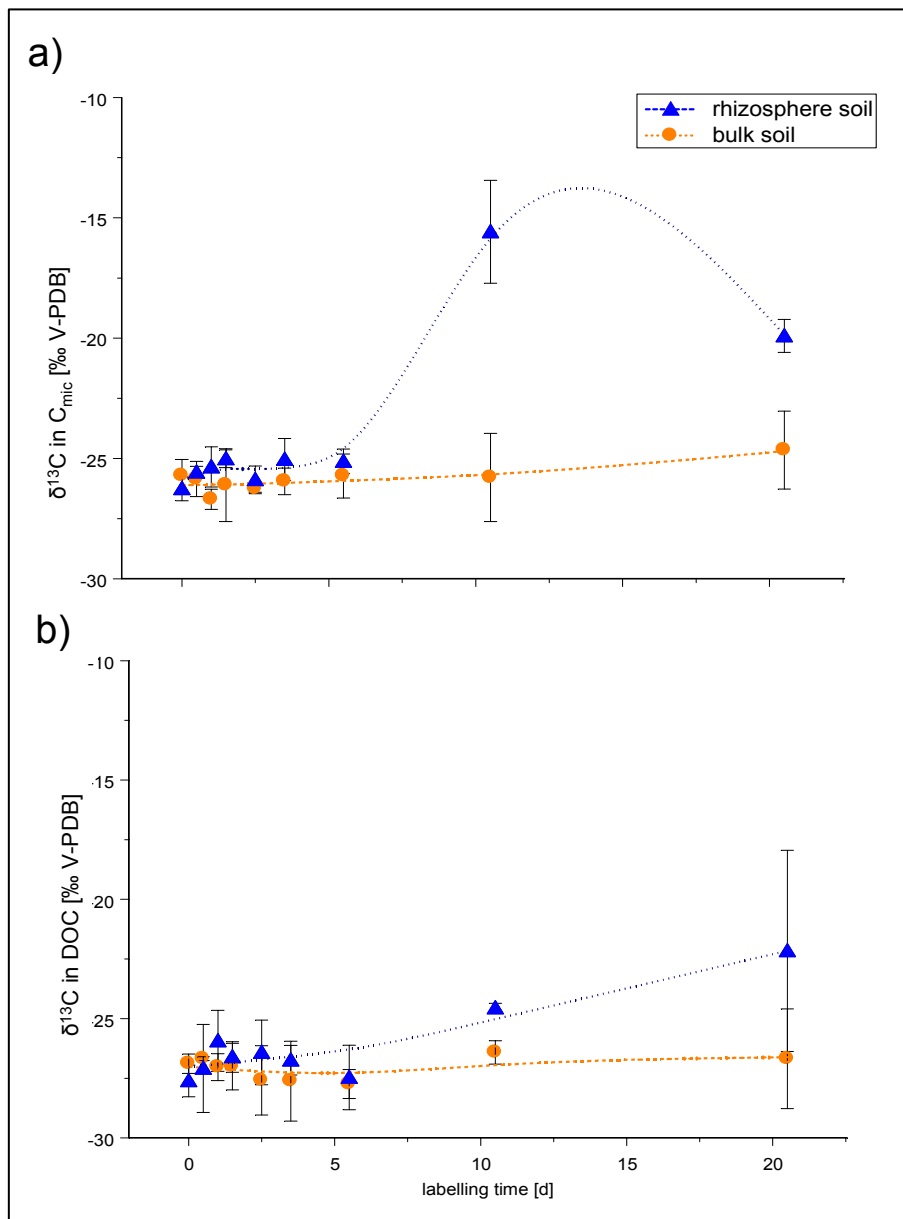


Fig. 11: ^{13}C incorporation [$\delta^{13}\text{C}$ in ‰ V-PDB] into microbial biomass (C_{mic} ; a) and dissolved organic carbon (DOC; b) in the course of the plant incubation experiment in pots. Visualisation was performed using a smoothing spline curve within mean values ($n = 3$) \pm standard deviations.

Neither DOC nor C_{mic} was statistically significantly affected by ^{13}C -labelling in bulk soil: Whereas DOC values remained comparable to the δ -values of total organic carbon in soil (see IV-1), C_{mic} -values in bulk soil were about 1‰ enriched compared to DOC in bulk soil and tended to increase from day 0 to the last harvesting date. Analyses of microbial biomass contents in unplanted soil at the beginning and the end of the experiment revealed unchanged abundances at the level of bulk soil and didn't show ^{13}C enrichment (Table 4). To reduce sample size for PLFA analysis, bulk soil samples were analysed only at the beginning, after 10 days and after 20 days of experimental duration.

Tab. 4: Microbial biomass C_{mic} [$mg\ C\ kg^{-1}\ DS$] and carbon isotopic signatures [$\delta^{13}C$ in ‰ V-PDB] in C_{mic} in unplanted soil at the beginning and at the end of the greenhouse pot experiment (mean \pm standard deviation; $n = 3$).

	labelling time [d]	
	0.0	20.5
C_{mic} [$mg\ C\ kg^{-1}\ DS$]	301.29	204.72
\pm	53.46	21.11
$\delta^{13}C_{mic}$ [‰ V-PDB]	-24.83	-23.19
\pm	0.93	0.70

1.2.2 PLFA profiles and $\delta^{13}C$ -signatures in PLFA biomarker

Phospholipid fatty acids (PLFA) fractions showed higher abundances in rhizosphere samples than in bulk soil samples; although statistical significance at $p < 0.05$ was not reached (Table 5). In both rhizosphere and bulk soil, total PLFA abundances increased at the latter harvesting time points, whereupon mono unsaturated (MUFA) and poly unsaturated (PUFA) fatty acids showed statistically significant higher values compared to the values at the beginning of the experiment. Total saturated fatty acids (SATFA) showed no increase throughout the experiment.

Tab. 5: Contents of SATFA, MUFA, PUFA and total PLFA [nmol g^{-1} DS] in rhizosphere and bulk soil at the beginning (day 0.0), in the middle (day 10.5) and at the end (day 20.5) of the greenhouse pot experiment. Values are based on mean of triplicates \pm standard deviation.

FA	[nmol g^{-1} DS]	labelling time [d]		
		0.0	10.5	20.5
SATFA	<i>rhiz</i>	109.48 \pm 27.41	149.04 \pm 22.06	110.86 \pm 15.72
	<i>bulk</i>	93.82 \pm 10.38	108.77 \pm 31.36	102.42 \pm 26.11
MUFA	<i>rhiz</i>	2.15 \pm 2.26	10.96 \pm 0.38	9.74 \pm 0.90
	<i>bulk</i>	3.37 \pm 0.80	7.37 \pm 3.44	7.45 \pm 1.80
PUFA	<i>rhiz</i>	2.64 \pm 1.78	15.29 \pm 12.42	6.45 \pm 2.69
	<i>bulk</i>	1.31 \pm 0.55	2.86 \pm 1.49	2.93 \pm 0.11
PLFA	<i>rhiz</i>	114.28 \pm 27.83	175.29 \pm 34.86	127.06 \pm 17.41
	<i>bulk</i>	98.50 \pm 10.61	119.00 \pm 34.82	112.80 \pm 27.57

The contribution of SATFA to total PLFA decreased continuously from 95% at the beginning to below 90% at the end of the experiment (Fig. 12). In contrast, MUFA and PUFA rised from approximately 2% to at least 5% at the latter harvesting time points. In bulk soil samples, the same distribution could be observed in SATFA and MUFA, whereas PUFA indicated lower contributions to total PLFA compared to rhizosphere soil (Tab. 5 and Appendix, Tab. VIII-5).

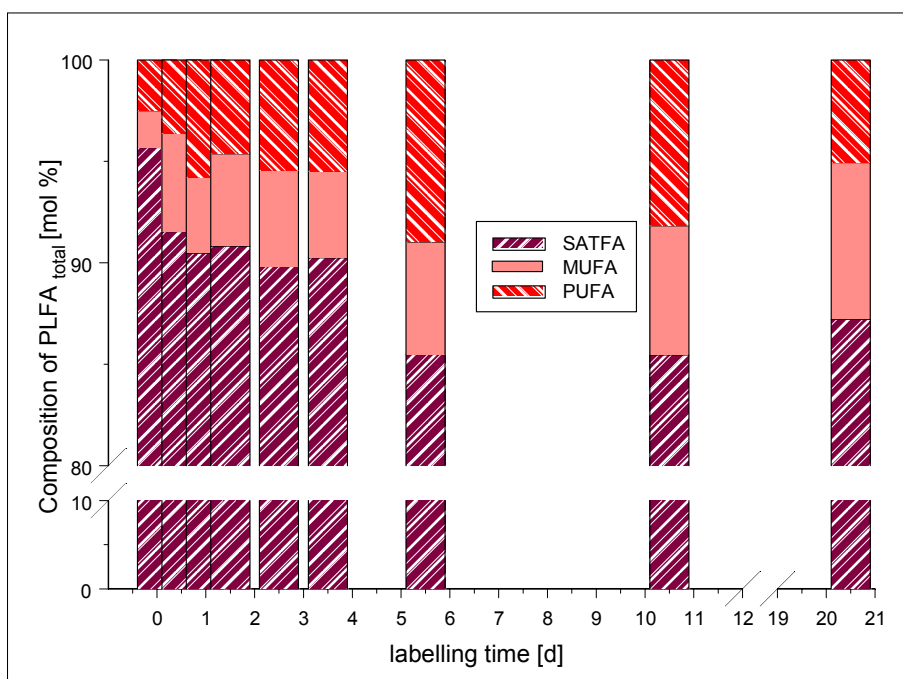


Fig. 12: Contribution of PLFA fractions SATFA, MUFA and PUFA [mol %] to total PLFA in rhizosphere soil at different harvesting time points of the greenhouse pot experiment. Values are based on mean of triplicates ($n = 3$).

In total a number of 40 PLFA have been separated. Individual fatty acids with respect to indicator values of different microbial groups in soil are presented in Table 6. SATFA i15:0 did not indicated any statistically significant changes in the course of the experiment, although some higher values were observed in rhizosphere soil. SATFA a16:0 showed no variation in bulk soil, but decreased statistically significant compared to day 0 in rhizosphere soil. MUFA 16:1 ω 9 and 18:1 ω 7, increased in the course of the experiment after 10.5 and 20.5 days statistically significant at $p < 0.05$ compared to day 0 in rhizosphere soil.

Tab. 6: Contribution of PLFA fractions (SATFA, MUFA, PUFA) and individual fatty acids [mol %] to total PLFA in beech rhizosphere soil and bulk soil of the greenhouse pot experiment. Representative fatty acids were chosen according to their indicator value for further interpretation. Values represent mean of triplicates \pm standard deviation. Asterisks (*) indicate statistical significance $p < 0.05$ between rhizosphere and bulk soil samples. Characters (a and b) represent statistical significant differences at $p < 0.05$ within the same soil fraction (rhizosphere soil and bulk soil, respectively) in the course of the experiment.

PLFA [mol %]	labelling time [d]					
	0.0		10.5		20.5	
	<i>rhiz</i>	<i>bulk</i>	<i>rhiz</i>	<i>bulk</i>	<i>rhiz</i>	<i>bulk</i>
SATFA	95.68 ^a	95.23 ^a	85.46 ^{b*}	91.50 ^b	87.22 ^b	90.64 ^b
\pm	0.82	0.70	4.41	0.50	1.49	1.33
MUFA	1.82 ^a	3.47 ^a	6.35 ^b	6.06 ^a	7.71 ^b	6.66 ^b
\pm	1.68	1.01	1.05	1.40	0.79	0.97
PUFA	2.51	1.30	8.18	2.44	5.06	2.70
\pm	1.82	0.40	5.46	1.05	2.02	0.64
i15:0	8.27	7.50	7.36	7.14	8.41	7.89
\pm	0.35	0.08	0.26	0.62	0.41	0.31
a16:0	19.34 ^{a*}	16.30	16.15 ^b	14.31	15.87 ^b	15.03
\pm	0.51	0.82	0.12	2.02	0.81	0.31
16:1 ω 9	0.06 ^a	0.14	0.16 ^b	0.12	0.20 ^b	0.14
\pm	0.06	0.03	0.01	0.03	0.03	0.04
18:1 ω 7	0.42 ^a	0.66 ^a	2.39 ^b	1.27 ^a	3.34 ^b	1.65 ^b
\pm	0.32	0.28	0.71	0.45	1.09	0.21
cy19:0	16.55	17.17	14.44	15.05	16.10	17.20
\pm	1.04	0.95	0.58	1.46	1.17	0.26
br10,19:0	1.07	1.05 ^a	0.98	0.90 ^a	0.68	0.71 ^b
\pm	0.17	0.14	0.33	0.15	0.06	0.09
20:4 ω 6,9,12,14	0.42 ^a	0.23	0.91 ^a	0.38	1.07 ^b	0.75
\pm	0.17	0.02	0.65	0.11	0.35	0.40
18:2 ω 6,9	1.94	1.08	6.29	1.95	3.72	1.95
\pm	1.36	0.39	3.94	0.80	1.48	0.24

SATFA cy19:0 indicated no statistically significant differences between rhizosphere and bulk soil, or between different harvesting time points. Generally, SATFA cy19:0 was present in rhizosphere soil as well as in bulk soil at very high amounts (14% to 17% of total PLFA). SATFA br10,19:0 was abundant with similar amounts in rhizosphere and bulk soil, but decreased throughout the experiment. In rhizosphere soil, PUFA 20:4 ω 6,9,12,15 and PUFA 18:2 ω 6,9 indicated higher values at the latter harvesting dates when compared to bulk soil, though an increase with time could be observed in both soil fractions. Similar results as described in Tab. 6 were observed for other fatty acids with similar indicator values (Appendix, Table VIII-6).

The incorporation of heavy ^{13}C in individual fatty acids is shown in Figure 13. Fatty acids in bulk soil were not statistically significantly enriched compared to day 0 within the experimental period (Fig. 13, a - h). The carbon isotopic signature of i15:0 (Fig. 13, a) indicated label incorporation already after 3.5 days ($p < 0.05$), whereas a16:0 (Fig. 13, b) showed a statistically significant ^{13}C incorporation at $p < 0.05$ compared to day 0 after 20.5 days of labelling. Additionally, a higher label incorporation ($p < 0.05$) was detected in 16:1 ω 9 and 18:1 ω 7, as well as in cy19:0 (Fig. 13, c, d, e) after 10.5 days of labelling, compared to day 0. A totally different ^{13}C incorporation pattern was observed in br10,19:0 (Fig. 13, f): Statistically significant higher $\delta^{13}\text{C}$ values were observed after 0.5 and 1 day of labelling only (similar results were detected in br10,17:0; Appendix, Tab. VIII-6). 20:4 ω 6,9,12,15 and 18:2 ω 6,9 (Fig. 13, g, h) indicated statistically significant ^{13}C incorporation after 20.5 days and after 10.5 days, respectively.

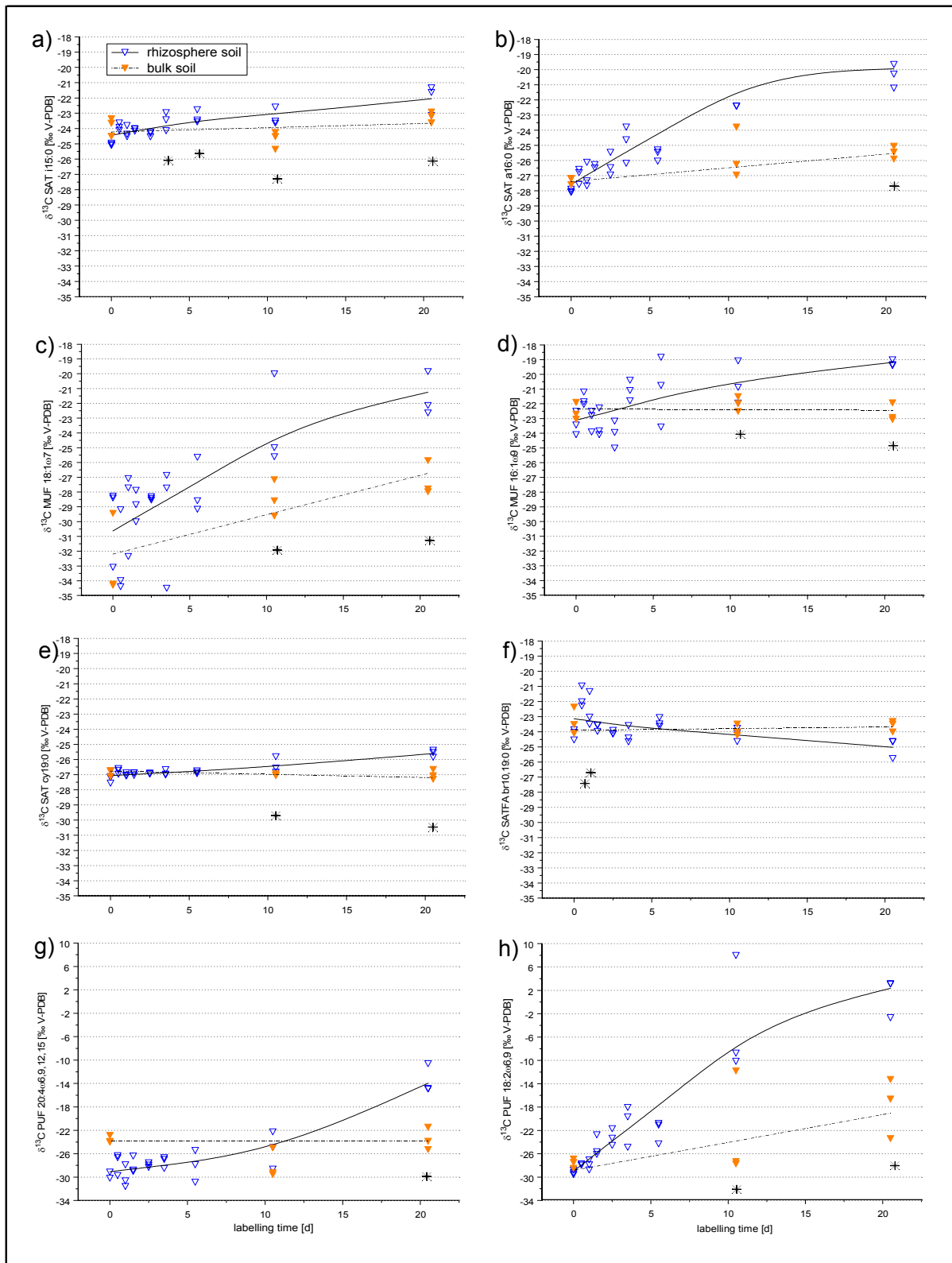


Fig. 13: Carbon isotopic signature [$\delta^{13}\text{C}$ in ‰ V-PDB] in individual beech rhizosphere and bulk soil PLFA at different time points throughout the greenhouse pot incubation experiment. Visualisation was performed using a smoothing spline curve within individual values ($n = 3$). Statistically significant differences ($p < 0.05$) compared to the control (day 0) are indicated by asterisks (*). To facilitate comparison, illustrations a) – f) are scaled from -35‰ to -18‰ V-PDB, due to high label incorporation, figures g) and h) are scaled from -34‰ to +10‰ V-PDB.

The maximum ^{13}C incorporation compared to day 0 ranged between 2‰ (cy19:0) and 30‰ (18:2 ω 6,9). PLFA in unplanted soil showed no ^{13}C enrichment at the end of the experiment (Appendix, Tab. VIII-7c). Related to the individual $\delta^{13}\text{C}$ content in the labelling atmosphere, the percentage of newly incorporated carbon into individual biomarker was calculated using a fractionation factor α_{comp} of the compound of interest towards the atmosphere.

$$\alpha_{\text{comp}} = [(\delta^{13}\text{C}_{\text{CO}_2} / 1000 + 1) / (\delta^{13}\text{C}_{\text{comp}} / 1000 + 1)] \quad (4)$$

For $\delta^{13}\text{C}_{\text{CO}_2}$ a mean value of -11‰ V-PDB was estimated and the calculated δ value (after equation 3) was applied for $\delta^{13}\text{C}_{\text{comp}}$. The newly incorporated carbon (C_{new}) proportion derives from the equations 5 and 6

$$\delta^{13}\text{C}_{\text{max}} = [(\delta^{13}\text{C}_{\text{alt}} / 1000 + 1) * \alpha_{\text{comp}} - 1] * 1000 \quad (5)$$

$$C_{\text{new}} = (\delta^{13}\text{C}_{\text{new}} - \delta^{13}\text{C}_{\text{comp}}) / (\delta^{13}\text{C}_{\text{max}} - \delta^{13}\text{C}_{\text{comp}}) * 100 \quad (6)$$

where $\delta^{13}\text{C}_{\text{max}}$ is calculated as the maximum label incorporation possible with respect to the individual α_{comp} and the δ value of the altered atmosphere ($\delta^{13}\text{C}_{\text{alt}}$), and $\delta^{13}\text{C}_{\text{new}}$ the δ value of the individual component measured under $\delta^{13}\text{C}_{\text{alt}}$, respectively.

Table 7 illustrates the plant derived carbon (in %) incorporated into individual PLFA after 10.5 and 20.5 days. In rhizosphere soil the percentage label incorporation into individual fatty acids was always higher than in bulk soil. At the end of the experiment, 20:4 ω 6,9,12,15 and 18:2 ω 6,9 showed the highest plant derived label incorporation among individual fatty acids, whereas 18:2 ω 6,9 contained already 30% of plant derived labelled carbon after 10.5 days. An increase of plant derived carbon incorporation was detected in bulk soil samples of PLFA 18:1 ω 7 and 18:2 ω 6,9, but this increase was lower compared to rhizosphere samples.

Tab. 7: Newly incorporated, plant derived carbon [%] into individual PLFA in beech rhizosphere soil and bulk soil of the greenhouse incubation pot experiment after 10.5 and 20.5 days of labelling. Values represent mean of triplicates \pm standard deviation.

total label (%)	rhizosphere soil		bulk soil	
	10.5	20.5	10.5	20.5
i15:0	2.10	3.66	-1.04	0.72
\pm	0.69	1.27	1.19	1.05
a16:0	9.30	9.37	1.97	2.28
\pm	4.46	1.09	1.90	0.30
br10,19:0	-0.02	-1.07	-0.69	-0.35
\pm	0.65	1.00	1.33	1.18
cy19:0	1.05	2.08	-0.16	-0.16
\pm	0.58	0.55	0.20	0.66
16:1ω9	3.20	5.00	0.64	-0.11
\pm	1.71	0.72	0.75	0.31
18:1ω7	7.45	10.27	4.93	6.62
\pm	6.54	2.27	3.63	4.28
18:2ω6,9	30.40	37.37	6.27	12.13
\pm	11.72	3.87	11.56	5.68
20:4ω6,9,12,14	5.16	19.90	-5.09	0.07
	4.39	2.62	2.23	1.71

2 Recovery of photosynthate ^{13}C in plant parts and rhizosphere organisms of beech (*Fagus sylvatica* L.) at two different growth stages in the open-top chamber experiment (B)

2.1 Carbon isotopic signature in above- and below-ground plant biomass of young beech trees

Leaves, twigs, fine roots and coarse roots from trees grown in the altered CO_2 -atmosphere were depleted statistically significant compared to trees grown in ambient atmosphere (Fig. 14), independent of the physiological stage. Stem parts showed a trend towards lower $\delta^{13}\text{C}$ ratios when grown in depleted atmosphere, but compared to ambient conditions statistical significance at $p < 0.05$ was not reached.

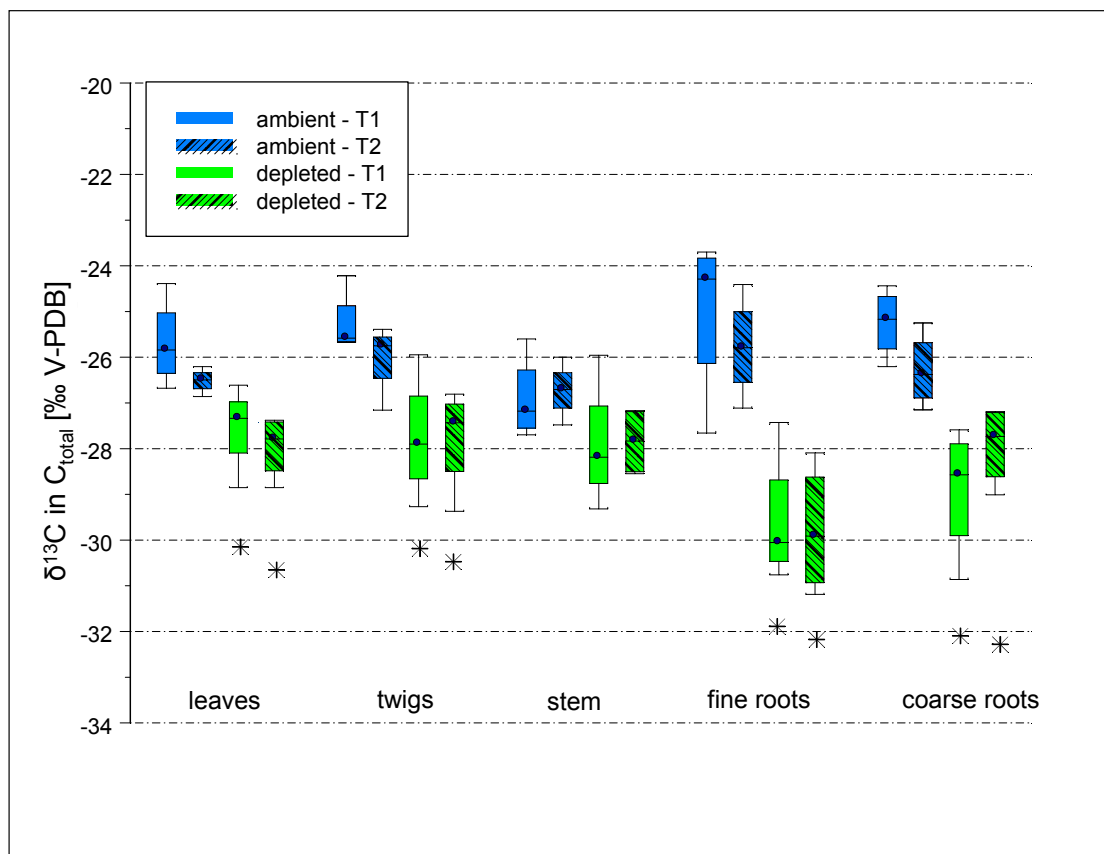


Fig. 14: Carbon isotopic signature in plant parts [$\delta^{13}\text{C}$ in C total ‰ V-PDB] of young beech trees grown in open-top chambers (OTC) for one vegetation period. T1 and T2 represent harvesting time points in the beginning and at the end of the vegetation period (physiological active and senescent stage, respectively). Box plot illustration including median (\bullet), whiskers represent upper and lower extreme values ($n = 4$). Statistically significant ($p < 0.05$) depletion compared to ambient treatments at the same time point are indicated by asterisks (*).

2.2 PLFA profile and carbon incorporation into PLFA biomarker of beech rhizosphere

Total PLFA abundances (Appendix, Tab. VIII-8) at the physiological active plant stage T1 were statistically significant higher in the rhizosphere (approximately 60 nmol g⁻¹ DS) than in bulk soil (around 20 nmol g⁻¹ DS). Rhizosphere soil samples indicated about 85% SATFA, 12% MUFA and around 3% PUFA (Tab. 8), whereas in bulk soil, SATFA contributed more to the total fatty acid abundance (90%) at the account of MUFA (only 5% to 8%).

Tab. 8: Contribution of SATFA, MUFA, PUFA and individual PLFA biomarker to total PLFA [mol%] in rhizosphere and bulk soil of beech trees grown in open-top chambers with ambient and depleted carbon isotopic CO₂ signature. Harvest was carried out at different physiological plant stages (active stage (T1) in mid-August and senescent stage (T2) in mid-October, respectively). Percentage values are calculated mean-based on absolute abundances in nmol g⁻¹ DS (n = 3). Characters (a and b) indicate statistical significance at p < 0.05 between rhizosphere and bulk soil at the individual plant stage.

PLFA [mol %]		T1				T2			
		ambient		depleted		ambient		depleted	
SATFA total	<i>rhiz</i>	85.00 ± 2.12	84.93 ± 6.34			65.50 ± 13.56	79.34 ± 14.76		
	<i>bulk</i>	89.48 ± 6.49	94.01 ± 10.37			84.06 ± 6.03	82.76 ± 1.34		
MUFA total	<i>rhiz</i>	12.69 ± 2.26	11.09 ± 7.83			18.67 ± 10.78	8.99 ± 5.89		
	<i>bulk</i>	8.42 ± 5.11	13.08 ± -			12.95 ± 3.97	13.31 ± 0.98		
PUFA total	<i>rhiz</i>	2.31 ± 0.50	3.97 ± 2.30			15.83 ± 10.68	11.66 ± 8.91		
	<i>bulk</i>	2.09 ± 1.38	4.16 ± -			2.99 ± 2.40	3.93 ± 0.36		
i15:0	<i>rhiz</i>	4.31 ± 0.40 ^b	3.99 ± 0.44 ^b			3.40 ± 0.79	3.01 ± 1.47 ^b		
	<i>bulk</i>	6.87 ± 0.30 ^a	6.92 ± 1.70 ^a			5.86 ± 1.11	7.01 ± 0.96 ^a		
a15:0	<i>rhiz</i>	2.72 ± 0.02 ^b	2.58 ± 0.54 ^b			2.86 ± 0.37 ^b	1.97 ± 0.89 ^b		
	<i>bulk</i>	4.42 ± 0.16 ^a	5.14 ± 1.40 ^a			4.32 ± 1.19 ^a	4.21 ± 0.27 ^a		
i16:0	<i>rhiz</i>	3.35 ± 0.23	3.30 ± 0.56 ^b			3.04 ± 0.13 ^b	2.53 ± 0.65 ^b		
	<i>bulk</i>	3.98 ± 0.46	5.32 ± 0.53 ^a			4.02 ± 0.23 ^a	4.17 ± 0.47 ^a		
br11,17:0	<i>rhiz</i>	4.35 ± 0.36	4.32 ± 1.00			3.88 ± 0.32	4.22 ± 1.21		
	<i>bulk</i>	5.02 ± 1.21	5.55 ± 0.95			5.15 ± 1.11	4.59 ± 0.37		
cy17:0	<i>rhiz</i>	2.64 ± 0.12 ^b	2.54 ± 0.82 ^b			2.00 ± 0.71	2.39 ± 0.50 ^b		
	<i>bulk</i>	3.98 ± 0.38 ^a	4.81 ± 0.41 ^a			3.25 ± 0.47	3.92 ± 0.44 ^a		
br10,19:0	<i>rhiz</i>	2.14 ± 0.13	2.17 ± 0.66			1.99 ± 0.08 ^a	2.03 ± 0.38		
	<i>bulk</i>	2.59 ± 0.27	3.19 ± 0.57			2.50 ± 0.34 ^b	2.63 ± 0.21		
18:1ω9	<i>rhiz</i>	4.05 ± 0.47	3.32 ± 2.25			5.99 ± 3.11	4.38 ± 0.18		
	<i>bulk</i>	2.74 ± 1.51	4.67 ± -			5.38 ± 1.19	4.74 ± 0.35		
18:2ω6,9	<i>rhiz</i>	2.31 ± 0.50 ^a	3.31 ± 1.63			15.60 ± 11.02	9.40 ± 6.96		
	<i>bulk</i>	0.74 ± 0.09 ^b	0.56 ± -			0.65 ± 0.11	0.50 ± 0.08		

Considering the advanced physiological senescent plant stage T2, total fatty acid abundance was lower in rhizosphere soil compared to T1 (around 50 nmol g⁻¹ DS) but no changes in bulk soil were observed. SATFA in the rhizosphere soil fraction decreased (80%) to the benefit of PUFA (5% to 9%) whereas MUFA accounted for 10% to 15% of total fatty acids. Although there was no change in the absolute PLFA abundance occurred in bulk soil, the contribution of PUFA (5%) and MUFA (13%) increased at the account of SATFA (82%). Individual fatty acids showed only few statistically significant differences between rhizosphere soil and bulk soil. Total PLFA abundances were calculated on the basis of 24 fatty acids which could be separated in this experiment (Appendix, Tab. VIII-8).

In the present experiment, the initiation was to recover the signature of CO₂-atmosphere, altered by the addition of CO₂ derived from fossil-fuel burning, in PLFA biomarker. PLFA indicating this signature are compiled in Table 8 and Figure 15. At the active physiological time point (T1), lower $\delta^{13}\text{C}$ values in individual fatty acids were observed in samples derived from labelled open-top chambers (Fig. 15, a). This depleted signature (in comparison with the ambient controls) was observed in rhizosphere as well as in bulk soil. In October, 18:2 ω 6,9 showed a statistically significant depleted $\delta^{13}\text{C}$ ratio ($p < 0.05$) in rhizosphere soil of samples from labelled atmosphere (Fig. 15, b) compared to samples from non-labelled atmosphere, while other fatty acids in the rhizosphere didn't indicate this result. PLFA in bulk soil samples derived from the altered CO₂ treatment tended to have lower $\delta^{13}\text{C}$ values compared to ambient treatments except PUFA 18:2 ω 6,9, which indicates no depletion in this soil fraction. Considering both harvesting dates T1 and T2, the most depleted carbon isotopic signature observed compared to ambient controls was detected in 18:2 ω 6,9 (around 3‰ to 5‰).

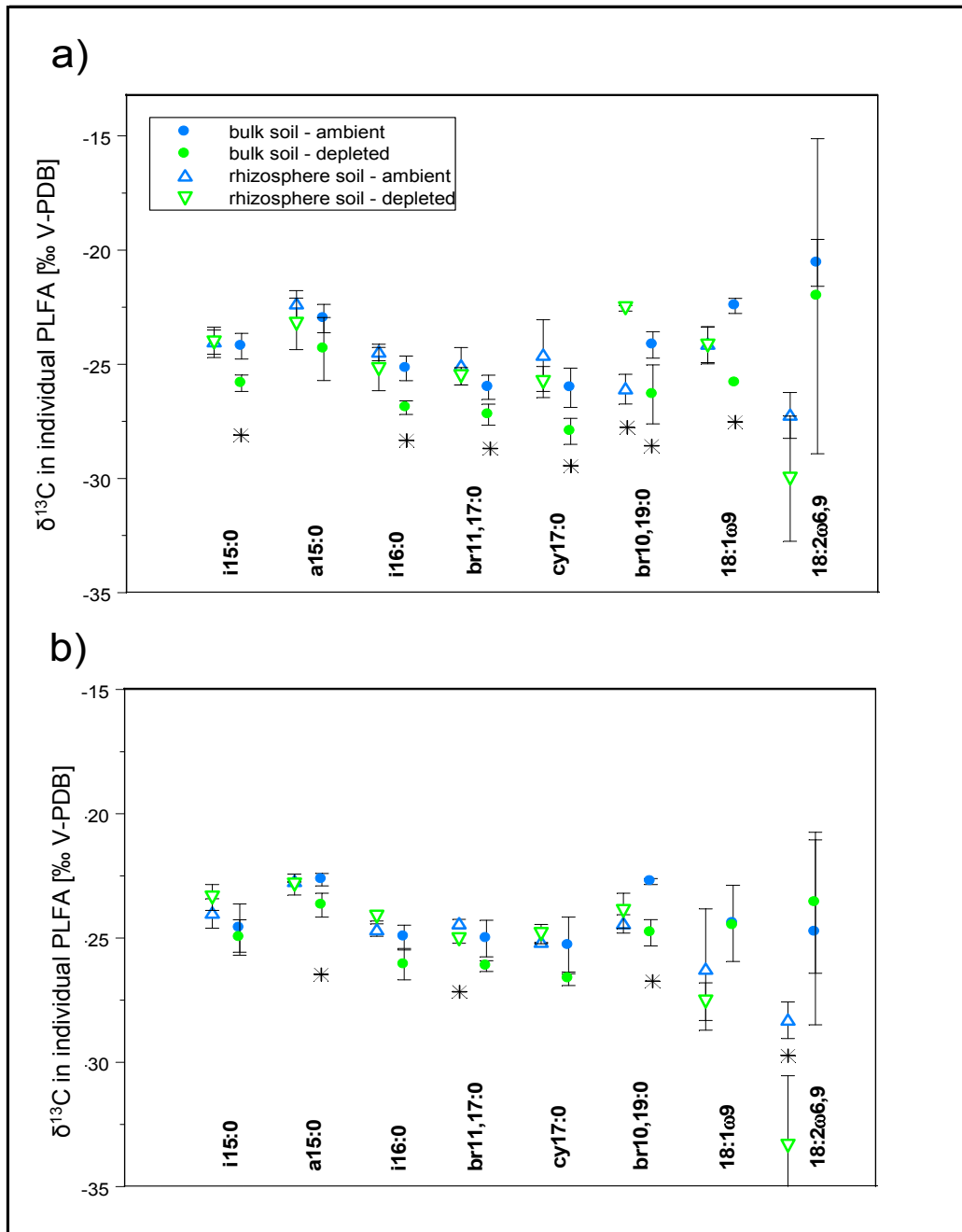


Fig. 15: Carbon isotopic signature [$\delta^{13}\text{C}$ in ‰ V-PDB] of individual PLFA of beech rhizosphere and bulk soil from the OTC experiment at the physiological active plant stage T1 (a) in mid-August and the senescent stage T2 (b) in mid-October, respectively. Values are based on mean of triplicates \pm standard deviation; asterisks (*) indicate statistical significance at $p < 0.05$ between labelled and ambient treated open-top chambers.

3 Rhizosphere microbial community structure in beech (*Fagus sylvatica* L.) and spruce (*Picea abies* (L.) Karst.) rhizosphere and its response to elevated ozone: The phytotron experiment (C)

3.1 Incorporation of plant derived carbon into DOC and C_{mic} of beech and spruce rhizosphere

Microbial biomass (C_{mic}) and DOC analyses from the first harvest time point in May were based on two harvested containers per treatment. In September, five replicates per treatment were harvested destructively (except of beech monocultures under $2 \times O_3$, where only four containers were available).

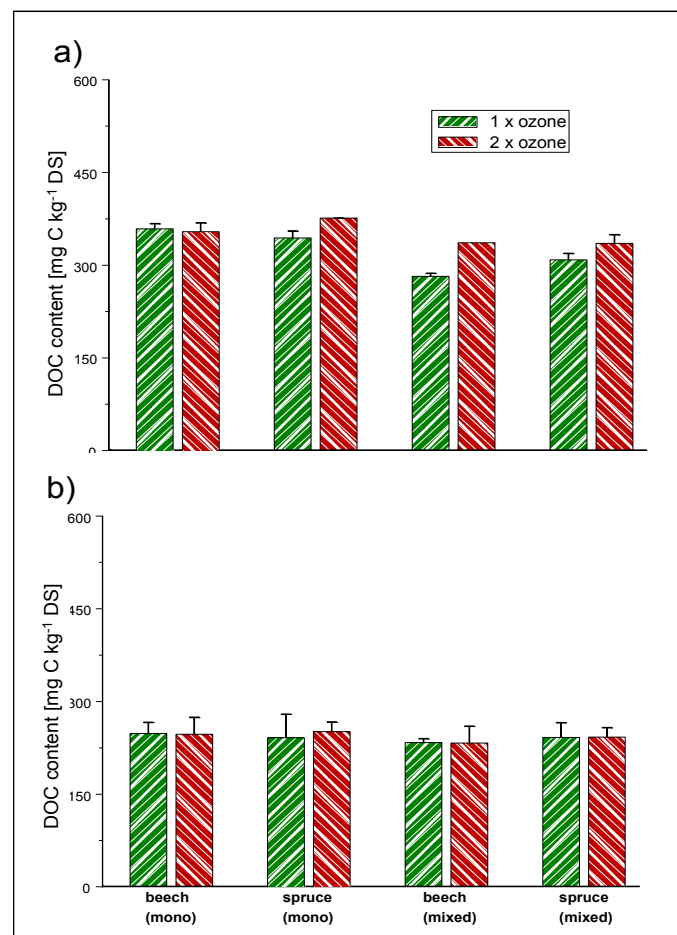


Fig. 16: DOC contents [mg C kg⁻¹ DS] in rhizosphere soil of beech and spruce trees in the phytotron experiment. Harvests were carried out in May (a) and at the end of the experiment in September (b). Values are based on means with standard deviation.

Analyses of DOC indicated no statistically significant differences between beech and spruce in May (Fig. 16, a) or in September (Fig. 16, b). Absolute abundances in September were lower in all treatments (around 250 mg C kg⁻¹ DS) compared to DOC contents in May (about 350 mg C kg⁻¹ DS). Between ozone treatments, no different DOC contents were observed in May or September, irrespective the experimental plant species and plantation type (mono/mixed).

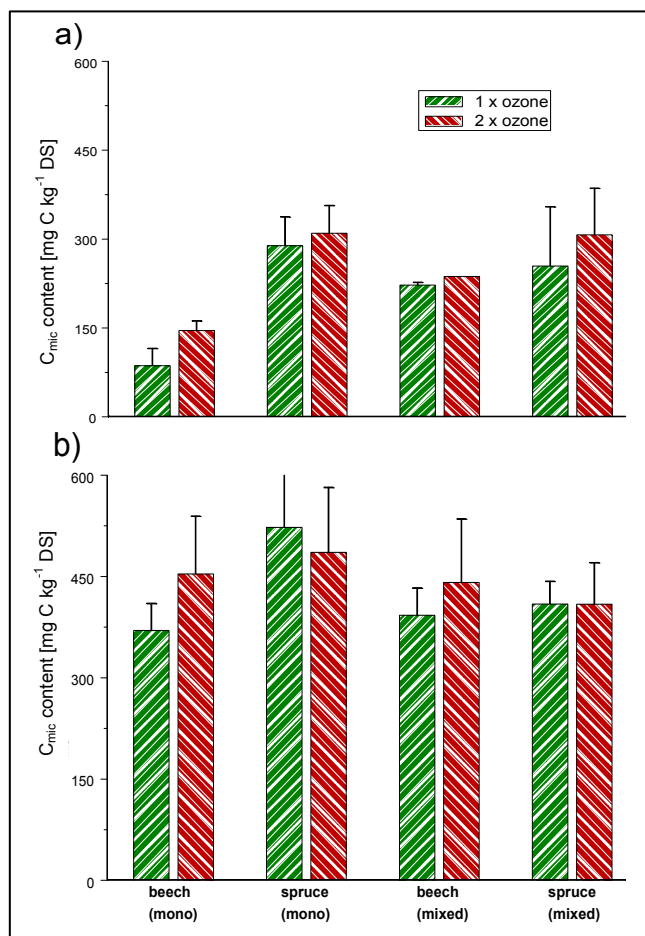


Fig. 17: Microbial biomass [mg C kg⁻¹ DS] in rhizosphere soil of beech and spruce trees of the phytotron experiment. Harvests were carried out in May (a) and at the end of the experiment in September (b). Values are based on means with standard deviation.

In May, at the beginning of the vegetation period (Fig. 17, a), C_{mic} in mono cultures was lower in beech rhizosphere samples (80 to 145 mg C kg⁻¹ DS) than in spruce (290 to 310 mg C kg⁻¹ DS). In mixed cultures, the same trends were observed, whereas higher values compared to mono beech samples were observed for mixed beech variants (220 to 235 mg C kg⁻¹ DS). In rhizosphere soil samples harvested in September (Fig. 17, b), higher C_{mic} contents in all treatments and plantations were detected compared to May. C_{mic} in beech mono cultures was

again lower (370 to 450 mg C kg⁻¹ DS) compared to spruce mono cultures (480 to 520 mg C kg⁻¹ DS). Beech and spruce rhizosphere soil samples obtained from mixed containers showed no difference with respect to C_{mic} (measured results varied between 390 and 440 mg C kg⁻¹ DS). No statistically significant differences between 1 x O₃ and 2 x O₃ treatments were observed in May or in September.

After containers were exposed to ¹³C enriched atmosphere in September, $\delta^{13}C$ signatures in DOC did not indicate any difference between rhizospheres of 1 x O₃ and 2 x O₃ treatments (Fig. 18, a). The isotopic carbon signature of DOC was around -26.5‰ V-PDB in all samples, comparable to the $\delta^{13}C$ signature in total soil organic carbon (see IV-1). In spruce mono cultures slightly enriched $\delta^{13}C$ values were detected compared to beech mono cultures. Microbial biomass in spruce mono cultures indicated statistically significant higher $\delta^{13}C$ values ($\delta^{13}C = -22‰$ V-PDB) than beech mono cultures ($\delta^{13}C = -25‰$ V-PDB; Fig. 18, b). This result was also observed in mixed cultures, but did not reach statistical significance at $p < 0.05$. C_{mic} in mixed beech cultures tended to have higher ¹³C-values compared to beech mono cultures, whereas spruce mixed cultures showed slightly depleted $\delta^{13}C$ values compared to spruce mono cultures. No difference was observed between ozone treatments in mono and mixed cultures irrespective of tree species planted in the container.

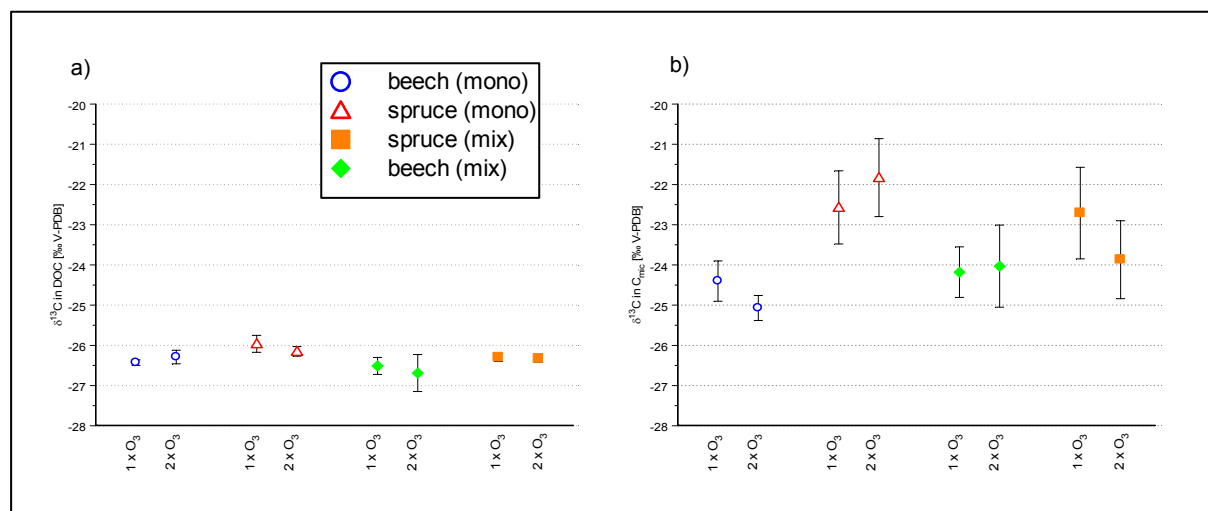


Fig. 18: Carbon isotopic signatures [$\delta^{13}C$ in ‰ V-PDB] in DOC (a) and C_{mic} (b) of beech and spruce rhizosphere soil from the phytotron experiment after five-day exposure to enriched ¹³C-atmosphere (approximately +130‰ V-PDB). Values are based on mean \pm standard deviation of $n = 4$.

3.2 PLFA profiles in beech and spruce rhizosphere from the phytotron experiment

3.2.1 PLFA profile at the beginning of the vegetation period (May)

PLFA analyses for the first harvest time point in May were performed on the same number of replicates as described for C_{mic} analyses. To reduce sample size for analyses of replicates harvested in September, only four containers per treatment of unique tree growth were taken. Therefore PLFA results illustrated for September are based on $n = 4$.

After bud break in May, lower abundances of total PLFA were observed in beech mono cultures (63 to 65 $\text{nmol g}^{-1}\text{DS}$) than in spruce mono cultures (100 to 110 $\text{nmol g}^{-1}\text{DS}$). This tendency was also observed by comparing beech and spruce within mixed cultures (Tab. 9). Generally, in mixed beech containers rhizosphere PLFA were more abundant compared to mono cultures (68 to 73 $\text{nmol g}^{-1}\text{DS}$), whereas abundances in spruce rhizosphere showed similar values in both variants. No difference was detected comparing 2 x O_3 treatments with its ambient 1 x O_3 counterparts. SATFA counted for about 90% of total PLFA in all treatments, whereas MUFA and PUFA contribute to total PLFA from 4% to 6% in all containers.

Tab. 9: Fractions of SATFA, MUFA, PUFA [$\text{nmol g}^{-1}\text{DS}$] and contribution to total PLFA [mol%] in rhizosphere soil of beech and spruce rhizosphere in May compared to September (phytotron experiment C). Values are based on mean \pm standard deviation according to the number of replicates at the individual harvesting time point.

			beech (mono)		spruce (mono)		beech (mixed)		spruce (mixed)	
			1 x ozone	2 x ozone	1 x ozone	2 x ozone	1 x ozone	2 x ozone	1 x ozone	2 x ozone
SATFA	mai	[$\text{nmol g}^{-1}\text{DS}$]	57.60 \pm 8.31	58.98 \pm 13.76	99.06 \pm 4.53	87.77 \pm 5.65	66.10 \pm 4.57	61.22 \pm 3.30	92.66 \pm 21.84	101.28 \pm 1.34
		[mol %]	90.64 \pm 0.91	89.83 \pm 4.95	88.96 \pm 1.26	87.70 \pm 0.78	89.95 \pm 0.16	89.64 \pm 0.14	89.52 \pm 2.48	92.35 \pm 2.85
	sept	[$\text{nmol g}^{-1}\text{DS}$]	50.00 \pm 29.59	72.36 \pm 25.60	72.07 \pm 26.19	100.20 \pm 13.56	64.28 \pm 14.84	80.68 \pm 5.18	86.21 \pm 5.31	93.86 \pm 13.57
		[mol %]	85.29 \pm 6.40	89.38 \pm 2.87	83.76 \pm 13.32	90.31 \pm 1.03	90.45 \pm 1.79	90.20 \pm 0.43	94.61 \pm 1.27	94.02 \pm 1.06
MUFA	mai	[$\text{nmol g}^{-1}\text{DS}$]	2.68 \pm 0.59	2.62 \pm 1.07	7.00 \pm 0.50	6.32 \pm 1.00	4.21 \pm 0.88	2.97 \pm 0.03	5.94 \pm 2.34	3.85 \pm 2.45
		[mol %]	4.20 \pm 0.30	4.23 \pm 2.41	6.29 \pm 0.64	6.29 \pm 0.56	5.79 \pm 1.60	4.35 \pm 0.18	6.13 \pm 3.55	3.49 \pm 2.18
	sept	[$\text{nmol g}^{-1}\text{DS}$]	2.63 \pm 0.34	3.65 \pm 0.41	2.71 \pm 1.44	3.85 \pm 1.31	3.06 \pm 0.70	4.73 \pm 1.01	2.54 \pm 0.79	3.44 \pm 0.70
		[mol %]	5.66 \pm 2.80	4.77 \pm 1.02	3.22 \pm 1.29	3.42 \pm 0.90	4.55 \pm 1.64	5.27 \pm 1.05	2.76 \pm 0.81	3.55 \pm 1.03
PUFA	mai	[$\text{nmol g}^{-1}\text{DS}$]	3.32 \pm 0.91	3.74 \pm 0.95	5.28 \pm 0.52	6.02 \pm 0.67	3.17 \pm 1.51	4.11 \pm 0.24	4.61 \pm 2.05	4.58 \pm 0.81
		[mol %]	5.17 \pm 0.62	5.94 \pm 2.54	4.75 \pm 0.62	6.01 \pm 0.23	4.27 \pm 1.76	6.00 \pm 0.04	4.35 \pm 1.07	4.17 \pm 0.67
	sept	[$\text{nmol g}^{-1}\text{DS}$]	4.35 \pm 0.98	4.38 \pm 0.21	8.76 \pm 5.82	6.81 \pm 0.78	3.55 \pm 0.92	4.04 \pm 0.88	3.01 \pm 0.53	2.43 \pm 0.37
		[mol %]	9.05 \pm 3.67	5.85 \pm 1.87	13.03 \pm 13.39	6.26 \pm 1.45	5.00 \pm 0.51	4.53 \pm 1.03	3.31 \pm 0.61	2.44 \pm 0.20
PLFA total	mai	[$\text{nmol g}^{-1}\text{DS}$]	63.60 \pm 9.81	65.34 \pm 11.73	111.33 \pm 3.51	100.10 \pm 7.33	73.48 \pm 5.21	68.30 \pm 3.56	103.21 \pm 21.55	109.71 \pm 1.93
		[mol %]	56.97 \pm 30.04	80.39 \pm 25.92	83.54 \pm 21.18	110.87 \pm 13.92	70.89 \pm 15.51	89.45 \pm 5.65	91.12 \pm 5.44	99.73 \pm 13.51
	sept	[$\text{nmol g}^{-1}\text{DS}$]								
		[mol %]								

Abundances of individual fatty acids ($\text{nmol g}^{-1}\text{DS}$) assessed in this experiment (Appendix, Tab. VIII-10) indicated no pronounced differences between ambient and twice ambient ozone treatments, but a similar fatty acid pattern was observed in any treatment. In mono cultures,

higher abundances of individual fatty acids were detected in spruce containers compared to beech ones, while mixed containers revealed similar values of fatty acids in beech and spruce rhizosphere. SATFA cy19:0 was the most abundant of all fatty acids, irrespective the experimental treatment and plant species.

3.2.2 PLFA profile at the end of the vegetation period (September)

In September, total PLFA abundances still were lower in beech containers compared to spruce containers (57 to 80 nmol g⁻¹ DS and 85 to 110 nmol g⁻¹ DS, respectively; Tab. 9). Grown in competition, the same trend could be observed. In mixed variants, fatty acid amounts in beech rhizosphere (70 to 90 nmol g⁻¹ DS) were higher compared to mono cultures. In contrast, in spruce rhizosphere, abundances were similar to spruce mono cultures (90 to 100 nmol g⁻¹ DS). With respect to elevated ozone treatments, all containers showed higher total PLFA values (although values between treatment differences did not reach statistical significance).

Mono cultures of beech and spruce indicated about 90% SATFA contribution to total PLFA in 2 x O₃ variants (Tab. 9), whereas only 85% SATFA were extracted from 1 x O₃ treated samples. MUFA were analysed in similar ranges (around 5%) in 1 x O₃ as well as 2 x O₃ treated samples of mono plantations. PUFA were observed to contribute more to total PLFA in 1 x O₃ variants (about 10%) compared to 2 x O₃ treatments (around 5%), when considering mono plantations. In mixed containers, total PLFA fractions revealed no differences between 1 x O₃ and 2 x O₃ treatments. SATFA tended to be higher in spruce rhizosphere (around 95%), whereas MUFA and PUFA indicated higher mole-percentages in beech rhizosphere (approximately 5% per fraction).

With respect to individual fatty acids, patterns observed at the beginning of the vegetation period remained unchanged (Appendix, Tab. VIII-10). Beech rhizosphere indicated lower PLFA abundances than spruce rhizosphere in mono cultures, while in mixed cultures similar amounts of fatty acids were detected. The majority of fatty acids were (not statistically significant) higher abundant in 2 x O₃ treatments. PUFA 18:2 ω 6,9 showed similar abundances in both ozone treatments. SATFA cy19:0 was still the most abundant fatty acid in all treatments at the end of the vegetation period.

In 2 x O₃ treatments, the absolute amount of MUFA was higher compared to 1 x O₃ variants (Tab. 10), but no increase was detected in the proportional contribution to total PLFA. In beech rhizosphere, higher values in 2 x O₃ treatments reached statistical significance at p < 0.05, whereas in spruce rhizosphere only trends could be observed.

Tab. 10: Total amounts of MUFA and individual mono unsaturated fatty acids detected in beech and spruce rhizosphere of the phytotron experiment at final harvest in September (means ± stdev; n = 4). Asterisks (*) indicate statistical significance at p < 0.05 between 1 x O₃ and 2 x O₃ treatments.

PLFA		beech (mono)		spruce (mono)		beech (mix)		spruce (mix)	
		1 x O ₃	2 x O ₃	1 x O ₃	2 x O ₃	1 x O ₃	2 x O ₃	1 x O ₃	2 x O ₃
MUFA	mol %	5.66 ± 2.80	4.77 ± 1.02	3.22 ± 1.29	3.42 ± 0.90	4.55 ± 1.64	5.27 ± 1.05	2.76 ± 0.81	3.55 ± 1.03
	nmol g ⁻¹ DS	2.63 ± 0.34 *	3.65 ± 0.41	2.71 ± 1.44	3.85 ± 1.31	3.06 ± 0.70	4.73 ± 1.01	2.54 ± 0.79	3.44 ± 0.70
15:1α6	mol %	0.22 ± 0.10	0.21 ± 0.05	0.16 ± 0.07	0.15 ± 0.05	0.19 ± 0.07	0.18 ± 0.04	0.12 ± 0.05	0.17 ± 0.04
	nmol g ⁻¹ DS	0.11 ± 0.01 *	0.16 ± 0.02	0.15 ± 0.06	0.17 ± 0.06	0.13 ± 0.04	0.16 ± 0.04	0.11 ± 0.05	0.16 ± 0.03
16:1α9	mol %	0.29 ± 0.16	0.30 ± 0.03	0.18 ± 0.08	0.21 ± 0.09	0.31 ± 0.15	0.32 ± 0.05	0.16 ± 0.02	0.18 ± 0.08
	nmol g ⁻¹ DS	0.13 ± 0.03 *	0.23 ± 0.06	0.17 ± 0.08	0.24 ± 0.10	0.21 ± 0.07	0.29 ± 0.06	0.15 ± 0.03	0.18 ± 0.05
16:1α7 cis	mol %	1.81 ± 0.90	1.47 ± 0.36	1.03 ± 0.54	1.11 ± 0.31	1.44 ± 0.51	1.58 ± 0.34	0.91 ± 0.28	1.12 ± 0.31
	nmol g ⁻¹ DS	0.84 ± 0.10 *	1.12 ± 0.08	0.97 ± 0.51	1.25 ± 0.47	0.97 ± 0.21 *	1.42 ± 0.33	0.83 ± 0.27	1.10 ± 0.22
16:1α7 trans	mol %	0.40 ± 0.19	0.36 ± 0.07	0.29 ± 0.12	0.29 ± 0.08	0.34 ± 0.12	0.40 ± 0.08	0.21 ± 0.07	0.28 ± 0.07
	nmol g ⁻¹ DS	0.19 ± 0.02 *	0.28 ± 0.04	0.23 ± 0.09	0.33 ± 0.11	0.23 ± 0.05 *	0.36 ± 0.08	0.19 ± 0.07	0.27 ± 0.04
16:1α5	mol %	1.68 ± 0.88	1.47 ± 0.30	1.11 ± 0.49	0.94 ± 0.25	1.28 ± 0.45	1.72 ± 0.43	0.75 ± 0.23	1.03 ± 0.33
	nmol g ⁻¹ DS	0.78 ± 0.14 *	1.13 ± 0.17	0.87 ± 0.30	1.06 ± 0.37	0.86 ± 0.18 *	1.54 ± 0.39	0.69 ± 0.22	1.00 ± 0.22
17:1α8 cis	mol %	0.30 ± 0.15	0.25 ± 0.07	0.16 ± 0.09	0.19 ± 0.06	0.23 ± 0.08	0.30 ± 0.09	0.14 ± 0.04	0.18 ± 0.05
	nmol g ⁻¹ DS	0.14 ± 0.02 *	0.19 ± 0.01	0.15 ± 0.08	0.22 ± 0.09	0.16 ± 0.03 *	0.27 ± 0.09	0.13 ± 0.04	0.18 ± 0.04
17:1α8 trans	mol %	0.96 ± 0.44	0.71 ± 0.16	0.66 ± 0.30	0.52 ± 0.13	0.76 ± 0.28	0.76 ± 0.07	0.47 ± 0.12	0.58 ± 0.17
	nmol g ⁻¹ DS	0.45 ± 0.05	0.55 ± 0.06	0.53 ± 0.24	0.59 ± 0.18	0.51 ± 0.12	0.68 ± 0.07	0.43 ± 0.12	0.57 ± 0.12

3.2.3 Incorporation of plant derived carbon into PLFA of beech and spruce rhizosphere

Neither a coherent incorporation of ¹³C into individual PLFA was observed, nor could any difference of statistical significance (p < 0.05) be detected between 1 x ozone and 2 x ozone treatments. However, the percentage amount of ¹³C detected in total SATFA, MUFA and PUFA indicate some trends described in the following section.

The calculation of percentage ¹³C in PLFA and individual fractions (atom %) was done after equation (7), where R_{PDB} is the ratio between heavy and light carbon isotopes (¹³C/¹²C = 0.0111802) of the international reference standard V-PDB (Vienna-Pee Dee Belemnite).

$$^{13}\text{C}_{\text{atm}} \% = [100 * R_{\text{PDB}} * (\delta^{13}\text{C}_{\text{PLFA}} / 1000 + 1)] / [1 + R_{\text{PDB}} * (\delta^{13}\text{C}_{\text{PLFA}} / 1000 + 1)] \quad (7)$$

SATFA indicated always (not statistically significantly) higher absolute values [in nmol g⁻¹ DS] in the rhizosphere of 2 x ozone treatments, whereas the proportion of heavy carbon

incorporated into total SATFA was observed to be higher in the rhizosphere of 1 x O₃ treated plants (Fig. 19, a). Indicating similar tendencies, mono unsaturated fatty acids (Fig. 19, b) showed higher abundances in 2 x O₃ replicates, whereas ¹³C was detected in higher percentages in 1 x O₃ treatments. ¹³C-PLFA distribution in PUFA was observed in higher amounts in 1 x O₃ variants, but high standard deviations occurred within most of the analysed replicates (Fig. 19, c). Total PUFA abundances in mixed and mono cultures of spruce showed higher values in 1 x O₃ treatments compared to 2 x O₃ treatments.

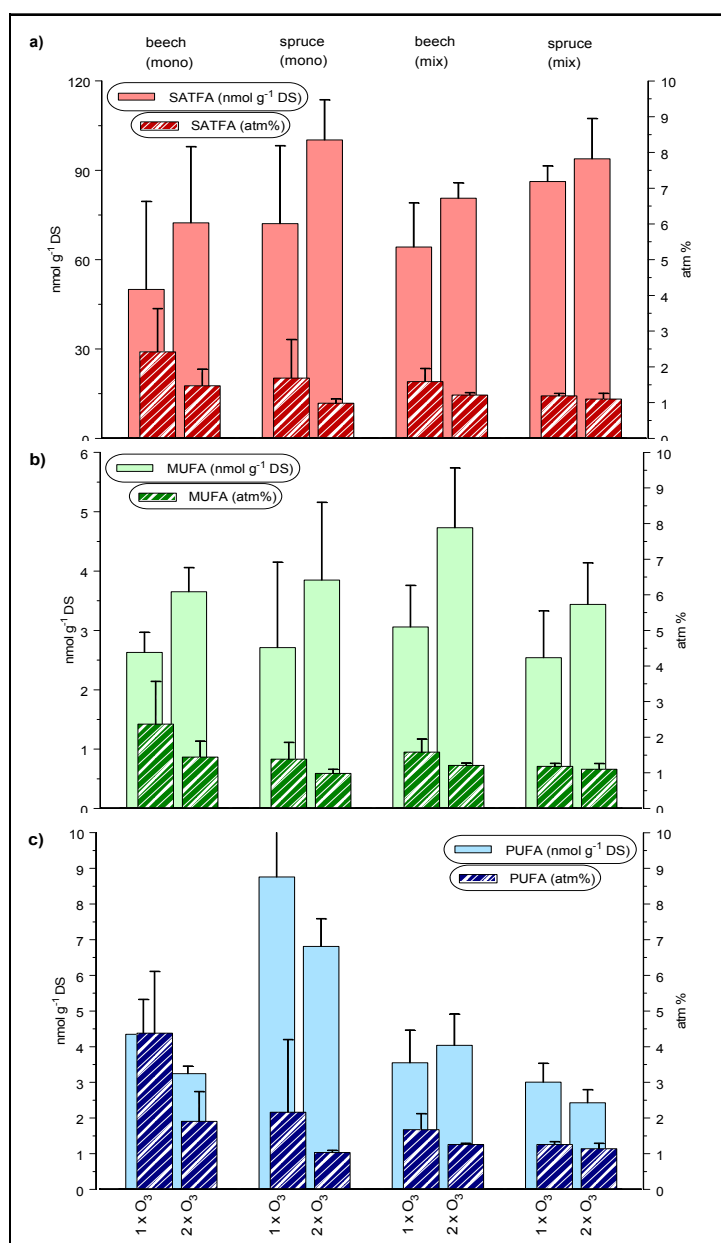


Fig. 19: Abundances [nmol g⁻¹ DS] of SATFA (a), MUFA (b) and PUFA (c) in comparison to the carbon isotopic signature [atom %] in beech and spruce rhizosphere soil of the phytotron experiment at the final harvesting time point in September. Results are based on means + standard deviation (n = 4).

4 Influence of long term elevated ozone exposure on rhizosphere microbial communities of mature beech trees (*Fagus sylvatica* L.) on the free-air lysimeter device (D)

4.1 Incorporation of plant derived carbon into DOC and C_{mic} in rhizosphere soil samples of mature beech trees

During the vegetation period from leaf expansion to September, rhizosphere of 4 beech trees was sampled monthly as described earlier. DOC contents indicated no differences within the vegetation period or between ozone treatments (Fig. 20). The carbon isotopic signature of DOC was not statistically significant different between 1 x O_3 and 2 x O_3 treatments. At the last harvesting time point at the end of August, statistically significant depleted $\delta^{13}C$ values ($p < 0.05$) compared to the beginning of the experiment were detected in both ozone treatments (differences around 1.5‰ V-PDB).

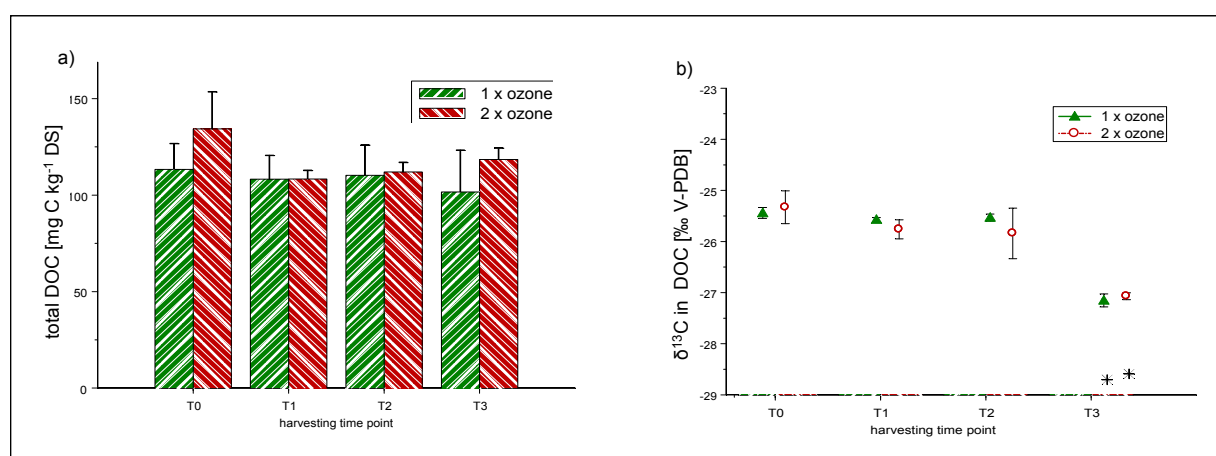


Fig. 20: DOC contents (a) [mg C kg⁻¹ DS] and carbon isotopic signature (b) in $\delta^{13}C$ ‰ V-PDB in the rhizosphere of beech trees from the lysimeter device under ambient (1 x) and twice ambient (2 x) ozone treatment at different harvesting time points (T) during the vegetation period. Values are based on mean values and standard deviations ($n = 4$).

Microbial biomass (C_{mic}) increased during the vegetation period (Fig. 21) from about 200 mg C kg⁻¹ DS at the beginning to 1200 mg C kg⁻¹ DS at the last harvesting time point (end of August), but no statistically significant difference was observed between 1 x O_3 and 2 x O_3 treatments. Within-treatment comparison revealed statistically significant depleted values in

the carbon isotopic signatures of C_{mic} (about 2‰ to 3‰) after two months of label exposure compared to harvesting timepoint T0 in both ozone treatments at $p < 0.05$.

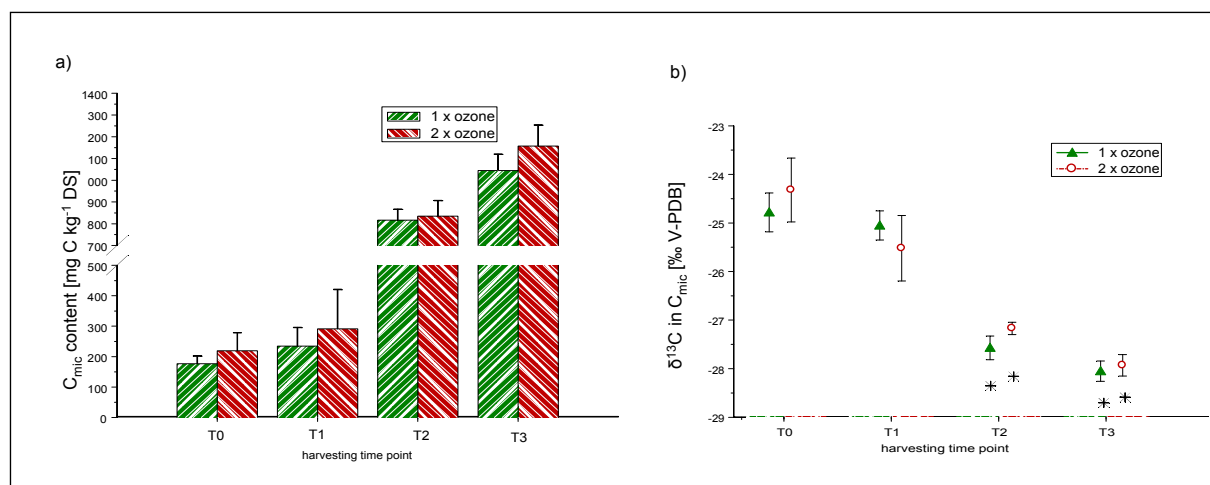


Fig. 21: C_{mic} contents (a) [mg C kg⁻¹ DS] and carbon isotopic signature (b) in $\delta^{13}C$ ‰ V-PDB in the rhizosphere of beech trees from the lysimeter device under ambient (1 x) and twice ambient (2 x) ozone treatment at different harvesting time points (T) during the vegetation period. Values are based on mean values and standard deviations (n = 4).

4.2 PLFA profiles in the rhizosphere of mature beech and carbon isotopic signatures therein

Total amounts of PLFA in the rhizosphere of mature beech trees did not reflect an increase during the vegetation period as observed in C_{mic} (Fig. 22, a). At the first two harvesting dates T0 and T1 both ozone treatments showed similar results (35 to 40 nmol g⁻¹ DS). At the harvesting time points T2 and T3 at the end of July and the end of August, respectively, 2 x O₃ treatments indicated higher PLFA abundances (about 55 nmol g⁻¹ DS) than observed in 1 x O₃ treatments (35 to 45 nmol g⁻¹ DS). Whereas PLFA values in 1 x O₃ variants did not change statistically significant compared to T0 within the vegetation period (although some higher abundances were detected at the last harvesting time point T3), an increase was observed in 2 x O₃ samples at the latter harvesting dates T2 (not statistically significant) and T3 ($p < 0.05$).

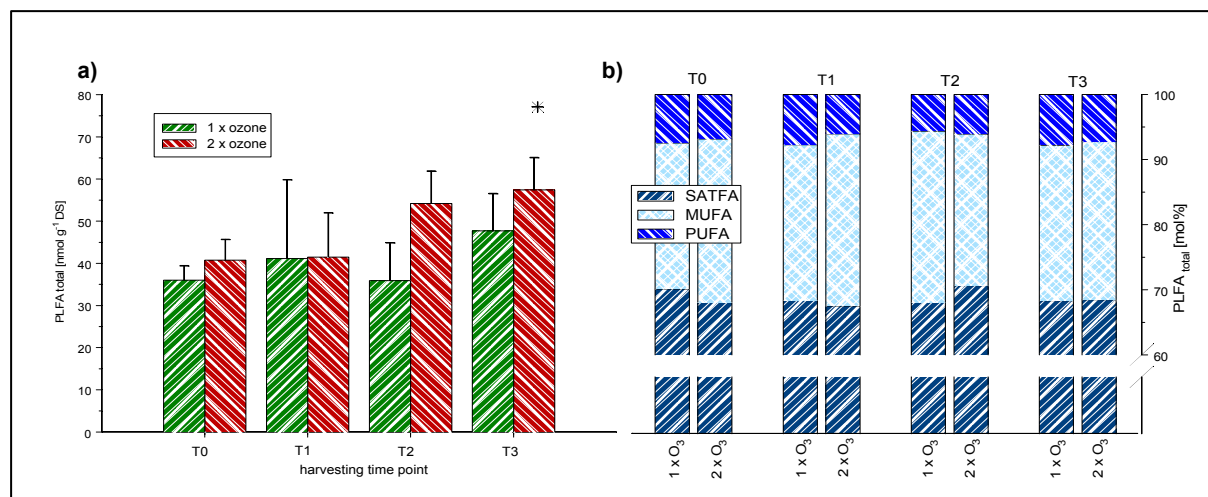


Fig. 22: (a) Total abundances of PLFA [nmol g⁻¹ DS] in the rhizosphere of mature beech trees under ambient (1 x) and twice ambient (2 x) ozone treatment on a lysimeter device. (b) Percentage contribution [mol%] of SATFA, MUFA and PUFA to total PLFA. Illustration based on means of n = 4. Standard deviations are indicated with error bars (a) and are given in the Appendix (b). Statistical significances at p < 0.05 compared to the beginning of the vegetation period T0 were illustrated by asterisks (*).

Within total fatty acids, around 70% of SATFA, 22% to 26% of MUFA and 6% to 8% of PUFA (Fig. 22, b) were detected. There was no pronounced difference between the two ozone treatments. During the vegetation period, the percentage distribution within total PLFA indicated no variation at p < 0.05.

Table 11 shows abundances of individual PLFA as well as the contribution [mol%] to total PLFA. SATFA cy19:0 indicated higher mole-percentages and abundances [nmol g⁻¹ DS] at the latter harvesting time points (T2 and T3) in 2 x O₃ treatments. Amounts and percentages of PUFA 18:3 and MUFA 16:1∞9 showed no difference between treatments or within the vegetation period. In other PLFA similar results were observed: Within the first month of experimental duration (T0 and T1), between June and July, rarely any change was observed in fatty acid abundances or the contribution to total PLFA. 1 x O₃ and 2 x O₃ treatments indicated similar results at these time points. At the latter harvesting dates T2 and T3, PLFA indicated higher abundances in 2 x O₃ treatments compared to the control harvested after leaf expansion (T0), whereas the percentage distribution of the same fatty acids did not change statistically significant. Individual PLFA did not increase in ambient ozone treatments in the course of the experiment.

Tab. 11: Total amounts of individual PLFA [nmol g^{-1} DS] and contribution [mol%] to total PLFA. Samples were obtained from beech rhizosphere soil of different ozone treatments on a lysimeter device. Values are based on means of $n = 4$ (\pm standard deviation). Characters (a and b) indicate statistical significances ($p < 0.05$) between ozone treatments. Asterisks (*) show statistically significant differences ($p < 0.05$) compared to T0.

PLFA		harvesting time point T							
		T0		T1		T2		T3	
		1 x O ₃	2 x O ₃	1 x O ₃	2 x O ₃	1 x O ₃	2 x O ₃	1 x O ₃	2 x O ₃
i15:0	mol%	6.94	6.38	6.12	6.22	6.48	7.25	6.97	6.98
	\pm	0.22	0.74	0.31	0.81	0.87	0.38	0.49	0.64
	nmol kg ⁻¹ DS	2.49	2.58	2.56	2.63	2.37 ^a	3.93 ^{*b}	3.35	4.03*
	\pm	0.17	0.16	1.26	0.88	0.80	0.57	0.80	0.77
a15:0	mol%	4.50	4.17	3.80	3.78	4.26	3.99	3.85	3.95
	\pm	0.18	0.28	0.25	0.39	0.27	0.36	0.15	0.17
	nmol kg ⁻¹ DS	1.62	1.69	1.53	1.59	1.53 ^a	2.15 ^b	1.84	2.27
	\pm	0.20	0.10	0.60	0.51	0.40	0.29	0.38	0.34
i16:0	mol%	3.14	2.98	2.88	2.72	2.58	2.85	2.90	2.81
	\pm	0.36	0.38	0.37	0.39	0.46	0.05	0.51	0.16
	nmol kg ⁻¹ DS	1.13	1.21	1.15	1.14	0.95 ^a	1.55 ^b	1.39	1.62
	\pm	0.13	0.19	0.41	0.35	0.38	0.24	0.42	0.28
cy19:0	mol%	14.29	17.72	17.77	17.63	15.36	22.35	14.65	18.94
	\pm	1.25	0.50	3.00	1.02	1.51	2.97	2.27	2.39
	nmol kg ⁻¹ DS	5.02 ^a	8.29 ^b	8.22	7.75	4.23 ^a	9.66 ^{*b}	6.96	8.69*
	\pm	0.70	0.93	4.22	1.67	2.04	0.29	2.07	1.45
br10,19:0	mol%	2.16	2.18	2.14	1.89	1.56	1.78	1.56	1.94
	\pm	0.16	0.30	0.32	0.23	0.30	0.21	0.28	0.06
	nmol kg ⁻¹ DS	0.76	1.02	0.99	0.83	0.43	0.77	0.74	0.89
	\pm	0.09	0.09	0.30	0.20	0.26	0.18	0.17	0.16
16:2 ω 6,9	mol%	5.15	5.21	3.70	3.46	4.10	5.16	5.75	3.95
	\pm	1.44	1.08	2.87	1.73	0.81	1.41	1.20	2.04
	nmol kg ⁻¹ DS	1.81	2.44	1.71	1.52	1.13	2.23	2.73	1.81
	\pm	0.71	0.60	0.54	1.08	0.65	1.06	0.26	1.50
18:3	mol%	0.68	1.03	0.45	0.32	0.62	0.46	0.57	0.33
	\pm	0.36	0.16	0.38	0.12	0.11	0.14	0.11	0.39
	nmol kg ⁻¹ DS	0.24	0.48	0.21	0.14	0.17	0.20	0.27	0.15
	\pm	0.16	0.11	0.05	0.07	0.01	0.09	0.00	0.24
16:1 ω 9	mol%	0.80	0.85	0.67	0.86	1.13	0.62	0.93	0.81
	\pm	0.08	0.09	0.14	0.08	0.17	0.13	0.09	0.14
	nmol kg ⁻¹ DS	0.28	0.40	0.31	0.38	0.31	0.27	0.44	0.37
	\pm	0.05	0.07	0.17	0.06	0.04	0.13	0.22	0.09

Analysing the carbon isotopic signature in individual PLFA, no differences at $p < 0.05$ were detected between 1 x O₃ and 2 x O₃ treatments at all harvesting time points. PLFA a15:0 and i16:0 (Fig. 23, a, c) indicated a statistically significant depleted $\delta^{13}\text{C}$ value compared to the beginning of the vegetation period ($p < 0.05$) in 2 x O₃ after two months (T2) and one month (T1) of labelling, respectively, but the differences only ranged within 0.5‰ and 1‰. Most other fatty acids, including i15:0, br10,19:0, cy19:0 or 16:1 ω 9 (Fig. 23; b, d, e, f) showed no statistically significant depleted $\delta^{13}\text{C}$ signature compared to the signature obtained before the initiation of labelling (T0). Often a high variation between the four individual samples was observed.

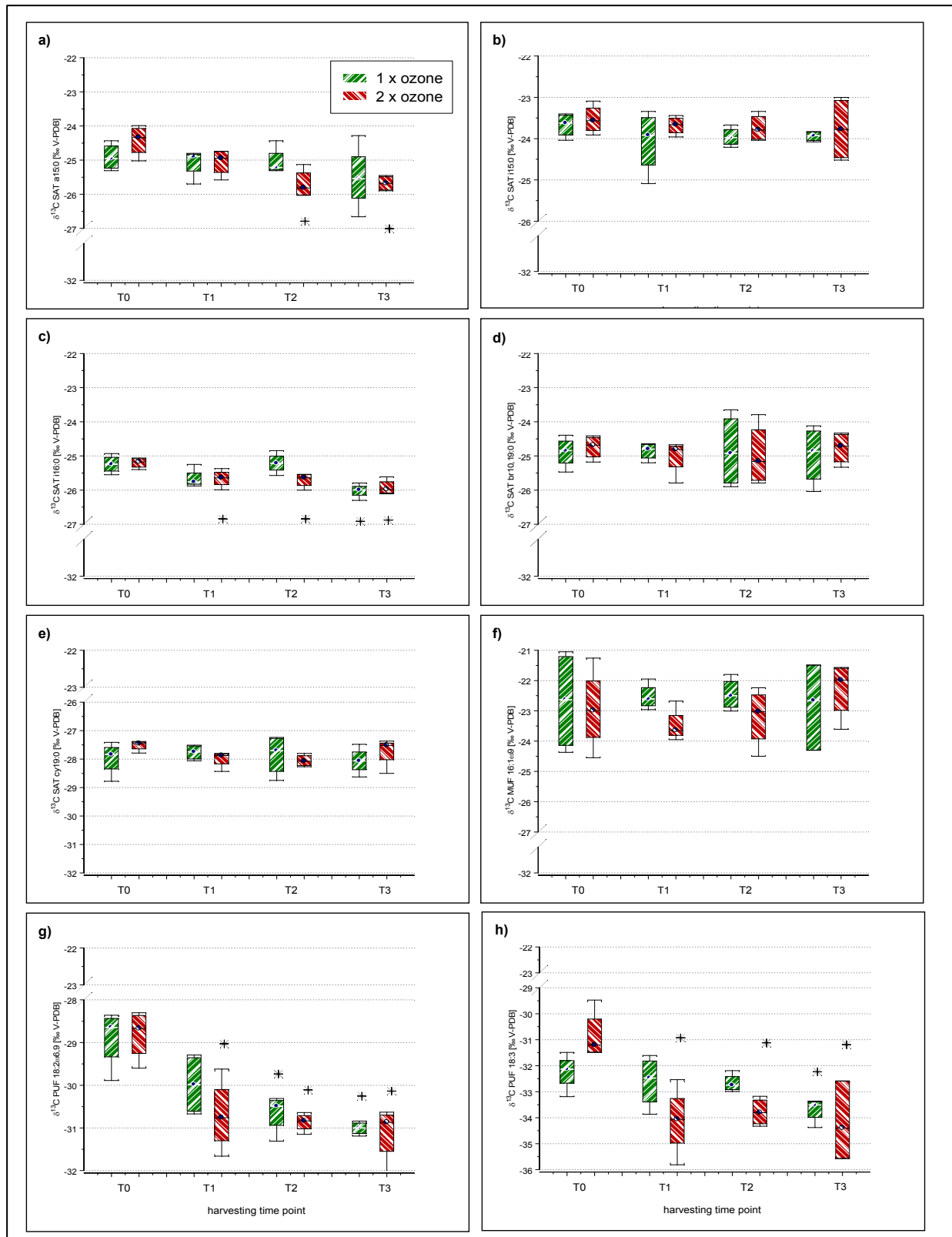


Fig. 23: Carbon isotopic signature [$\delta^{13}\text{C}$ in ‰ V-PDB] of individual PLFA in beech rhizosphere under ambient (1 x ozone) and twice ambient (2 x ozone) ozone treatments on a lysimeter device. Results are visualized in boxplots (n = 4) with median (•); whiskers represent upper and lower outliers. Statistical significances at $p < 0.05$ compared to the beginning of the vegetation period T0 are visualized by asterisks (*).

In PUFA 18:2 ω 6,9 (Fig. 23, g) $\delta^{13}\text{C}$ in 2 x O₃ treatments was statistically significant depleted ($p < 0.05$): about 2‰ V-PDB less compared to T0 after one month of labelling (T1). At T2 and T3 statistical significance at $p < 0.05$ was reached in both treatments compared to the beginning of the experiment. PUFA 18:3 (Fig. 23, h) also showed a depleted $\delta^{13}\text{C}$ signature after one month of labelling until the end of the experiment ($p < 0.05$) in 2 x O₃ treatments. Although high variations within the four individual plants of a treatment group were observed, 2 x O₃ treatments indicated a higher depletion (around 3‰) than 1 x O₃ variants (between 1‰ and 2‰). A statistically significant difference between 2 x O₃ and 1 x O₃ treatments was detected at harvesting time point T2.

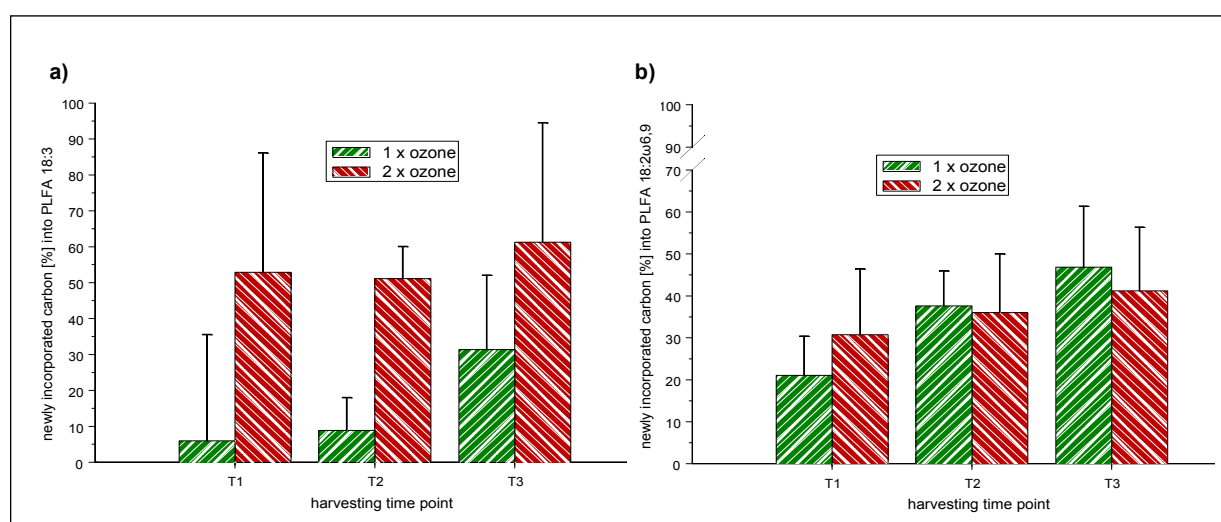


Fig. 24: Newly incorporated photosynthate carbon (%) into PLFA 18:3 (a) and PLFA 18:2 ω 6,9 (b) harvested from mature beech rhizosphere on a lysimeter device. Results are based on means and standard deviations ($n = 4$).

According to Fig. 23 (g, h), the most depleted $\delta^{13}\text{C}$ values were observed in poly unsaturated PLFA 18:2 ω 6,9 and 18:3. As described earlier, the amount of newly incorporated carbon into these PLFA was calculated against the labelling atmosphere as described above. PLFA 18:3 indicated around 50% of new carbon in 2 x O₃ treatments at every harvesting time point (Fig. 24, a), whereas in 1 x O₃ treatments between 10% and 30% of labelling carbon was incorporated. In 18:2 ω 6,9, no difference in incorporation of carbon was observed between treatments (Fig. 24 b), but an increasing amount of photosynthate derived carbon was incorporated into this PLFA within the vegetation period from 20% to 30% (T1) to nearly 50% at the end of the experiment (T3).

5 Synopses of results obtained from the four individual experiments (A – D)

Within the present study, four experiments were carried out using similar methodologies and techniques investigating carbon fluxes between plant and soil. Using chloroform fumigation extraction, water soluble carbon extraction and PLFA analysis, it was possible to confirm results obtained from greenhouse (A) and phytotrons (C) in experiments carried out in open-top chambers (B) and on a lysimeter device (D).

5.1 DOC and C_{mic} in combination with $\delta^{13}C$ analyses

The $\delta^{13}C$ signature in DOC indicated the contribution of plant derived carbon to DOC. Statistically significant incorporation of photosynthate carbon was only obtained after longer time periods compared to the initiation of labelling (experiments A, D). Recent assimilated carbohydrates, exudated into DOC were rapidly incorporated into C_{mic} (experiments A, C, D). When comparing ozone treatments, similar results from C_{mic} and DOC analyses were detected in younger (C) and mature beech trees (D). No pronounced difference in exudation or utilization of exudates in the pool of total microbial biomass was detected, and therefore no influence of ozone on total microbial biomass could be reported in younger or mature beech trees.

5.2 Total PLFA profiles in response to different environmental conditions

Overall, a total of 46 PLFA were extracted from soil samples harvested in the individual experiments A – D (Tab. 12). In experiments A and C, carried out under controlled conditions (phytotron and greenhouse, respectively) 40 PLFA have been detected, whereas under outdoor conditions, only 24 (experiment B, open-top chambers) and 29 (experiment D, lysimeters) PLFA were extracted from soil samples.

Tab. 12: Total numbers of PLFA detected in soil samples of the four individual experiments (A – D)

Experiment									
PLFA	A	B	C	D	PLFA	A	B	C	D
br12:0	✓		✓		br10,19:0	✓	✓	✓	✓
br13:0	✓				cy19:0	✓	✓	✓	✓
i14:0	✓	✓	✓	✓	br12,19:0			✓	
a14:0	✓		✓	✓	n20:0	✓	✓	✓	✓
i15:0	✓	✓	✓	✓	dic20:0	✓		✓	
a15:0	✓	✓	✓	✓	n22:0	✓	✓	✓	✓
n15:0	✓		✓	✓	dic22:0	✓		✓	
i16:0	✓	✓	✓	✓	n24:0	✓	✓	✓	✓
a16:0	✓	✓	✓	✓	15:1 ω 6	✓			
16:0 mix	✓				15:1 ω 8			✓	
i17:0	✓	✓	✓	✓	16:1 ω 5	✓	✓	✓	✓
a17:0	✓		✓	✓	16:1 ω 7 cis	✓	✓	✓	✓
n17:0	✓		✓		16:1 ω 7 trans	✓		✓	✓
br9,17:0		✓		✓	16:1 ω 9	✓		✓	✓
br10,17:0	✓	✓	✓		17:1 ω 8 cis	✓	✓	✓	✓
br11,17:0		✓	✓		17:1 ω 8 trans	✓		✓	✓
17:0 mix			✓		18:1 ω 7	✓	✓	✓	✓
cy17:0	✓	✓	✓	✓	18:1 ω 9	✓	✓	✓	✓
i18:0	✓	✓	✓	✓	17:2	✓			
n18:0			✓		18:2 ω 6,9	✓	✓	✓	✓
br10,18:0	✓	✓	✓		18:3	✓		✓	✓
cy18:0	✓	✓	✓	✓	20:4 ω 6,9,12,14	✓		✓	✓
dic18:0	✓		✓		20:5	✓			

The number of individual PLFA, as well as absolute abundances of total PLFA were always detected in higher abundances in experiments A and C compared to experiment B and D. Differences between on the one hand greenhouse and phytotron and on the other hand open-top chambers and lysimeters were also observed comparing the relative composition of total PLFA: In Figure 25, individual PLFA patterns are illustrated in subgroups according to the chemical character of fatty acids (see IV-6.7 for nomenclature of subgroups). The PLFA profile in rhizosphere soil (Fig. 25, A, a) obtained from the greenhouse experiment (A) indicated similar results as observed in the phytotron experiment (Fig. 25, C-1, c). Anteiso branched fatty acids showed slightly higher abundances (24%) than iso branched fatty acids (around 20%). In experiment C, beech and spruce rhizosphere comprised of 24% iso- and 20% anteiso-branched PLFA. Rhizosphere soil samples from the lysimeter experiment (Fig. 25, D, c) and the open-top chamber experiment (Fig. 25, B, a) comprised about 20% of iso- and anteiso fatty acids or even less. In both experiments, lower percentages of straight chained fatty acids (nor) were detected compared to A and C. Higher percentages of MUFA (16:1, 17:1, 18:1) were

detected in experiments under natural conditions (B, D). In all experiments, iso, anteiso (ant) and cyclopropyl (cyc) fatty acids were the most dominant groups in soil.

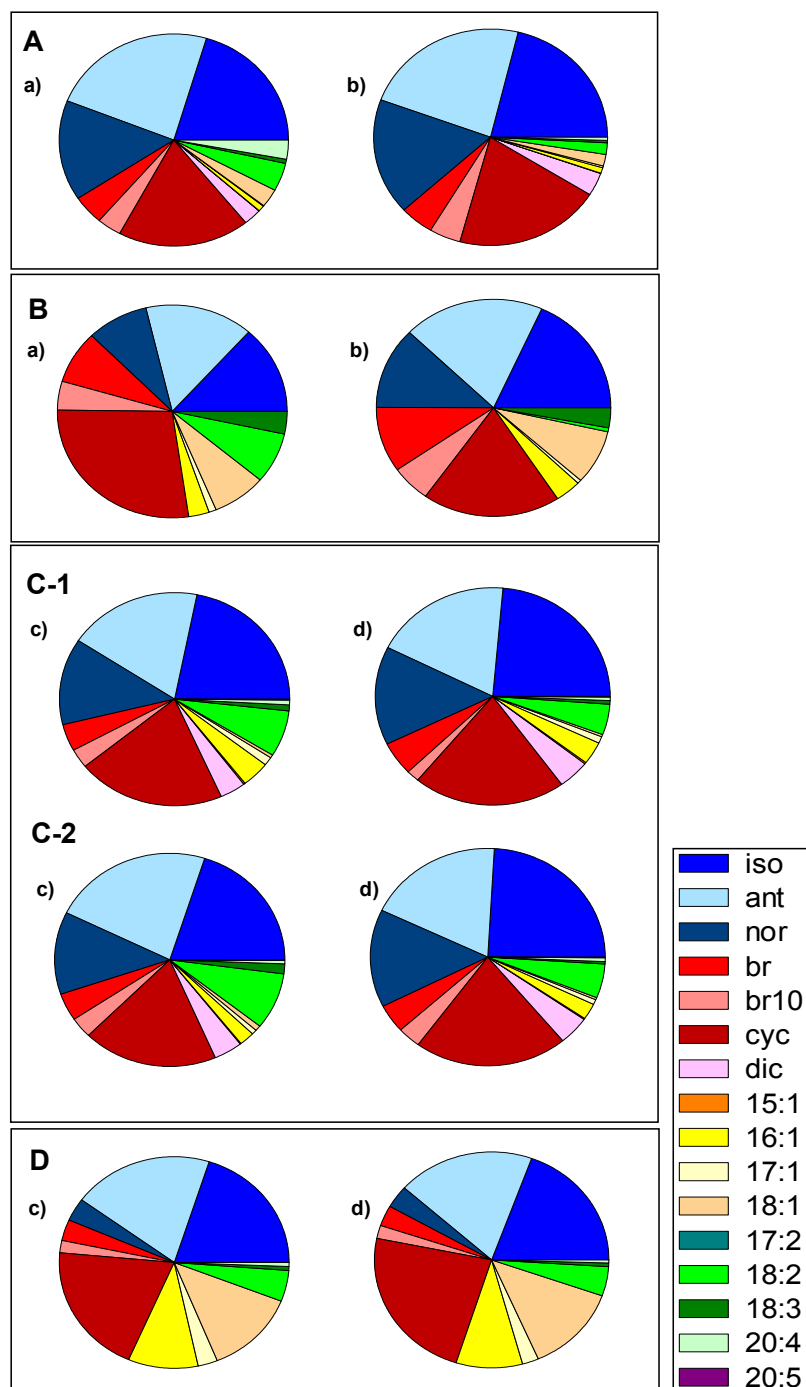


Fig. 25: Total PLFA pattern obtained in different experiments (A – D) illustrated in individual subgroups according to the chemical character of fatty acids. Capitals represent the individual experiment (A: greenhouse, B: open-top chambers, C-1: phytotron-beech, C-2: phytotron-spruce, D: lysimeters). Rhizosphere soil and bulk soil were illustrated in a) and b) Figures, respectively; ozone treatments were indicated by c) ($1 \times O_3$) and d) ($2 \times O_3$). All values are calculated as mean values throughout the individual experiments.

In experiment D, a totally different PLFA pattern was detected than in all other experiments (Fig. 25, D, c): MUFA (15:1, 16:1, 17:1, 18:1) were detected in higher percentages (around 25%) compared to experiments A, B and C, whereas straight chained fatty acids (nor) comprised only about 3%. In experiment D, experimental plants were older (10 years) than in the other experiments (2 – 3 years).

PLFA profiles in rhizosphere and bulk soil showed similar patterns in the greenhouse experiment (Fig., 25, A, a, b), but differed in the open-top experiment (Fig. 25, B, a, b). Cyclopropyl fatty acids in the open-top experiment indicated higher abundances in rhizosphere soil (around 28%) compared to bulk soil (20%), whereas iso- and anteiso fatty acids showed higher percentages in bulk soil.

Considering the distribution of PLFA obtained from 2 x O₃ treatments compared to 1 x O₃, no differences were observed (Fig. 25, C-1, C-2, D). Surprisingly, higher absolute values of individual PLFA were detected in 2 x O₃ treatments. In mature beech trees, slightly higher percentages of cyclopropyl fatty acids were detected in the rhizosphere (Fig. 25, D, b), probably as a response to altered growth conditions in the rhizosphere caused by ozone.

PLFA pattern of beech and spruce did not differ statistically significant within their percentage composition (Fig. 25, C-1, C-2), but spruce rhizosphere indicated higher absolute PLFA abundances than beech rhizosphere. When grown in intraspecific competition, beech trees probably invest in higher amounts of microbial biomass in the rhizosphere, whereas rarely any effect was observed in spruce. When comparing beech with spruce saplings with respect to elevated ozone treatments, MUFA were statistically significant higher in beech rhizosphere, whereas only trends were detected in spruce rhizosphere.

VI Discussion

1 Temporal dynamics of carbon distribution in a model plant-soil ecosystem exposed to continuous labelling atmosphere (A).

1.1 Carbon distribution within plant parts and soil

The results obtained from the pot experiment (A) contribute to clarify the carbon dynamics in plant-soil systems. The (labelled) carbon entering the plants by photosynthesis is used for leaf formation in the initial phase of growth, as reported by Dyckmans *et al.* (2002), but also transformed into sugars and amino acids for transportation and storage in different carbon sinks (twigs, stem). After a certain time lag, probably due to the length of the translocation pathway and anabolism of carbohydrates (Kozłowski *et al.*, 1991), photosynthates are recovered in high amounts in the root system, resulting in enhanced root growth (Ceulemans *et al.*, 1999). However, it should be taken into account that assimilated carbon is not only distributed between different plant parts and rhizosphere organisms, but a major part of recently fixed carbon is also lost via respiration (Damesin & Lelarge, 2003; Leake *et al.*, 2006).

From roots, large amounts of carbon are released into the soil in form of root exudates (5% to 21% of photosynthetically fixed carbon; Marschner, 1995). Carbon compounds released into the soil contribute to the pool of dissolved organic carbon (DOC). Therefore, higher amounts of DOC were detected in rhizosphere soil than in the surrounding bulk soil. Increasing ^{13}C values estimated in DOC of rhizosphere soil evidences the release of photosynthetically derived assimilates into the rhizosphere. DOC is postulated as a valuable C-source for microbial growth and productivity (Meyer *et al.*, 1987; Paterson, 2003). Further, an increase of exudation in the rhizosphere may be due to a higher presence of microbes (Meharg & Killham, 1991), increasing the sink strength by the consumption of exudates (Barber & Lynch, 1977). Higher ^{13}C contents in the microbial biomass fraction (C_{mic}) in rhizosphere soil result from the utilization of plant derived rhizodeposits, exuded into the pool of DOC. The higher $\delta^{13}\text{C}$ values observed in microbial biomass compared to $\delta^{13}\text{C}$ values of DOC are consistent with data reported by Potthoff *et al.* (2003) and Yevdokimov *et al.* (2006) and reflect very high utilization of rhizodeposits. It has been suggested that rhizodeposits are rapidly metabolized

by microorganisms, and thus the relatively small amounts of ^{13}C in DOC represent only a small fraction of the water soluble organic substances exuded by roots (Yevdokimov *et al.*, 2006; Marx *et al.*, 2007). Another reason for low amounts of ^{13}C detected in DOC is probably a rapid immobilization into the soil matrix, as reported by Marx *et al.* (2007). In bulk soil, where a minor microbial community pool and almost no incorporation of plant derived (labelled) carbon was observed in the pool of DOC, microbial communities profit less of rhizodeposits. Conclusively, these results confirm an enhanced activity of rhizosphere organisms and subsequently indicate a larger microbial biomass stock in the rhizosphere compared to bulk soil (Ceulemans *et al.*, 1999).

1.2 Differences between PLFA profiles of beech rhizosphere and bulk soil and incorporation of plant derived carbon into PLFA biomarker

The use of total PLFA abundances for estimating total microbial biomass in soil is well established in soil ecology (e.g. Frostegard & Bååth, 1996; Zelles, 1999; Esperschütz *et al.*, 2007) and was supported by close correlations of total PLFA with microbial biomass carbon (Gattinger *et al.*, 2004; Esperschütz *et al.*, 2007). In this study, results obtained from PLFA analyses confirm a higher microbial biomass in rhizosphere soil than in bulk soil, as discussed above. MUFA and PUFA contents increased throughout the experiment in rhizosphere and bulk soil, whereas SATFA abundances remained stable. With raising contents of MUFA and PUFA consequently the proportion of SATFA decreased statistically significant throughout the experiment. This indicates an increase of Gram-negative bacteria, fungi and eukaryotes rather than Gram-positive organisms (Zelles, 1999). An increase of Gram-negative organisms with increasing plant age was also observed by Steer & Harris (2000) in the rhizosphere of *Agrostis stolonifera*.

For further characterization of microbial communities, several indicator fatty acids commonly used in literature are presented in Table 6. MUFA (18:1 ω 7 and 16:1 ω 9), often used as biomarkers for Gram-negative bacteria (Zelles, 1997), showed an increasing abundance positive correlated with plant growth. An increasing ^{13}C content in these biomarkers also indicates a fast utilization of plant derived carbon. However, MUFA 16:1 ω 9 is also present in fungi as precursor in the fatty acid synthesis pathway of 18:2 ω 6,9, and therefore not only

indicates Gram-negative organisms. Indicators for Gram-positive organisms like i15:0 and a16:0 did not increase by time, mostly remained unchanged (i15:0) or even decreased in the case of a16:0. Since iso- and anteiso fatty acids were the PLFA most abundant in soil, a high percentage of Gram-positive organisms within microbial communities is suggested, according to Zelles (1997). Gram-negative bacteria may be stimulated by plant growth (Steer & Harris, 2000) and profit more from plant exudates than Gram-positive bacteria. Gram-negative and Gram-positive biomarker were inconsistent. Whereas some PLFA had about 10% of plant derived carbon incorporated, other PLFA comprised only 3% to 5% of labelled carbon. Since different strains of bacteria may synthesize different amounts of individual iso- and anteiso fatty acids, this indicates a diverse community composition within these groups of organisms (Zelles, 1997).

Since no statistically significant change within the amounts of cy19:0 was neither observed between bulk soil and rhizosphere soil, nor during the experimental period, these fatty acids may reflect a low activity of its contributing organisms within rhizosphere and bulk soil. Apart from PLFA br10:19,0, SATFA cy19:0 showed the lowest incorporation of plant derived carbon used within the experimental period. Similar results were observed by Butler and co-workers (2003) suggesting that cyclopropyl fatty acids not as major components of Gram-negative bacteria, as frequently described in literature (Leake *et al.*, 2001). Taken together, this indicates that cyclopropyl fatty acids were synthesized by very slow growing organisms of non Gram-negative origin, having low turnover rates. However, a higher incorporation of rhizodeposits in rather straight-chained or other branched-chained fatty acids than cyclopropyl fatty acids within an organism is possible.

SATFA br10:19,0, a PLFA detected mainly in actinomycetes (Lechevalier, 1977), showed a decrease in rhizosphere soil and bulk soil by increasing plant growth. Actinomycetes are known as oligotrophic organisms involved in the cycling of recalcitrant organic matter in soil (Paterson *et al.*, 2007). The composition of microbial communities in the rhizosphere can be altered by root exudates (Hodge & Millard, 1998). Since the composition of exudates varies in dependence on environmental and biological parameters, for example the stage of development (Baudoin *et al.*, 2003), a shift in the microbial community structure in the rhizosphere as a result of an altered exudate composition after bud break during shoot is conceivable. Characterizing actinomycetes on the basis of SATFA br10,19:0, the incorporation

of plant carbon was detected immediately after labelling. With progressive plant growth, a decrease in abundances as well as a decrease in label incorporation in this biomarker was observed. Actinomycetes therefore may lose ground to other microbial communities like ectomycorrhizal fungi, but were able to utilize rhizodeposits when present in the rhizosphere.

PLFA of non-bacterial origin like 20:4 ω 6,9,12,14 and 18:2 ω 6,9 also increased with plant age in rhizosphere soil, more than in bulk soil. PUFA 18:2 ω 6,9 is frequently used as a biomarker for fungi (Frostegard & Bååth, 1996), or in this case ectomycorrhizal fungi as usually observed in combination with beech roots. Through the growing season of trees, both roots and mycelia increase in biomass (Sung *et al.*, 1995). This is in accordance to a higher increase of 18:2 ω 6,9 due to mycorrhizal growth in rhizosphere soil compared to bulk soil. Since this fatty acid is known to be widespread among the eukaryotic kingdom (Zelles, 1997), one cannot completely exclude that it originates from plant roots or root tips, consequentially heightened in rhizosphere soil. Although harvest and sample preparation prior to extraction was accomplished with care, high fluctuation in 18:2 ω 6,9 obtained from rhizosphere soil after 10 days (Tab. 6) may result from such root material. MUFA 18:1 ω 9 was recently detected to be positively correlated with 18:2 ω 6,9 in forest soil (Högberg, 2006). In the present study, 18:1 ω 9 indicated similar trends as 18:2 ω 6,9 (Appendix, Tab. XIII-4, XIII-6). MUFA 18:1 ω 9 (oleic acid) and 16:1 ω 9 (palmitoleic acid) are both precursors in the fatty acid synthesis path way of 18:2 ω 6,9. Increasing abundances of these particular fatty acids with the growth of plants support an increasing mycorrhizal growth in the course of the experiment. In accordance with other studies (Arao, 1999; Butler *et al.*, 2003), 18:2 ω 6,9 was the most highly labelled PLFA. Since the use of this biomarker for ectomycorrhizal fungi was suggested earlier, this result indicates the highest activity utilizing rhizodeposits by mycorrhizal fungi. Fungal hyphae growing in symbiosis with the root system are consistently the first to profit from plant derived photosynthates. The $\delta^{13}\text{C}$ value of 18:2 ω 6,9 increased immediately after label initiation, indicating a fast transport and exudation of assimilated carbon into the rhizosphere. Within the experimental period of 21 days, the carbon derived from atmospherical labelling in 18:2 ω 6,9 was quantitatively around 30%.

Since 20:4 ω 6,9,12,14 was detected in high contents in micro-eukaryotes and prokaryotes (Lechevalier, 1977), a higher activity of these organisms is suggested in the rhizosphere compared to the bulk soil. PLFA 20:4 ω 6,9,12,15 also indicated higher incorporation of labelled

carbon with time: whereas at the beginning of the experiment within the first 10 days, no incorporation of photosynthate ^{13}C into this biomarker was observed, an increasing incorporation was observed after the 10th day of the experiment. According to their nature, micro-eukaryotes and probably protists graze on bacteria (Bonkowski *et al.*, 2000) and therefore incorporate the labelled carbon temporally shifted as secondary consumers. According to high percentages of labelled carbon (about 20% at the end of the experiment) detected in 20:4 ω 6,9,12,15, a high activity of micro-eukaryotes and protists in the rhizosphere of beech trees is postulated. The incorporation of plant derived carbon into 20:4 ω 6,9,12,15 was not known from other labelling experiments (Butler *et al.*, 2003; Lu *et al.*, 2004; Paterson *et al.*, 2007) where this biomarker obviously has not been detected in high amounts. Since these studies were carried out using annual plants (*Lolium multiflorum*, *Oryza sativa*, *Lolium perenne*), this may be due to a different microbial community structure in perennial plants, like beech. Since exudates' composition varies with plant species (Jones *et al.*, 2004), results from this study suggest that micro-eukaryotes may play a larger role in the rhizosphere of perennial plants, as it was observed in this experiment.

Conclusively, these results show the photosynthate-derived carbon distribution into plant parts and into the rhizosphere microbial biomass via rhizodepositon. A shift in microbial communities was suggested to be due to an altered exudate composition during plant growth. The amount of ^{13}C incorporated into individual PLFA indicates the use of plant derived carbon by microorganisms. As in other studies (Butler *et al.*, 2003; Lu *et al.*, 2004; Paterson *et al.*, 2007) assimilated carbon was not evenly distributed within PLFA, suggesting a different utilization of exudates within microbial communities. In this study the highest label incorporation was detected within poly unsaturated fatty acids. In this context, actinomycetes decrease with increasing plant growth while ectomycorrhizal fungi show enhanced growth. Different microbial communities indicate the utilization of plant derived carbon, whereas ectomycorrhizal fungi profit most of (labelled) plant derived carbohydrates. In bulk soil samples, no plant derived carbon was incorporated into PLFA biomarker in statistically significant amounts compared to the beginning of the experiment. Soil autotrophic CO_2 -fixation did not occur in this experiment, as concluded from results obtained from unplanted pots (Appendix, Tab. XIII-7).

2 Carbon distribution within the plant-soil system at two different physiological plant stages during a vegetation period (B)

2.1 Carbon incorporation into plant parts at different physiological plant stages of young beech trees

In accordance with other studies (Nogués *et al.*, 2006) and previous experiments (A) the obtained results illustrate the distribution and allocation of assimilated carbon within the plant. In leaves, photosynthetically fixed carbon is transformed into sugars and transported to different carbon sinks (twigs, fine roots and coarse roots) via phloem through the plant. Fine roots show the largest depletion compared to ambient treatments at both physiological plant stages, indicating a high accumulation of photosynthate-derived carbon. As fine roots and growing root hairs are sites of active growth and intensive exudation (Bertin *et al.*, 2003), these findings indicate a rather similar root growth activity and probably exudation into the rhizosphere at physiological active and senescence plant stages.

2.2 Incorporation of plant derived carbon into microbial communities at different physiological stages of plant growth

Carbon compounds, released from the roots in form of exudates are very important for microbial productivity in the rhizosphere (Paterson, 2003). Consequently, microbial communities in larger root distance profit less of rhizodeposits and therefore a minor microbial community pool is observed in such locations (Ceulemans *et al.*, 1999). The proportion of SATFA decreased with tree growth, whereas percentages of MUFA and PUFA increased. These findings support results obtained from the first experiment (A). Since SATFA are wide spread and mainly of Gram-positive origin (Zelles, 1997), this indicates a decline of bacterial population in rhizosphere soil to the benefit of Gram-negative bacteria and ectomycorrhizal fungi (indicated by MUFA and PUFA 18:2 ω 6,9, respectively). Seasonal shifts in the microbial community structure are reported in many other studies (Marschner *et al.*, 2002; Brant *et al.*, 2006) and mainly result from different exudate compositions (Aulakh *et al.*, 2001; Marschner *et al.*, 2005). In accordance with other studies (Sung *et al.*, 1995; Genet *et al.*,

2000; Nilsson *et al.*, 2007), higher abundances of fungi were detected in rhizosphere soil in autumn. High ectomycorrhizal fungi biomass is reported as a major carbon sink in late fall and winter, where carbohydrates are necessary for frutification (Sung *et al.*, 1995). Coherent with largely depleted $\delta^{13}\text{C}$ signatures in roots, the growth of ectomycorrhizal fungi covaries with tree root production and both are probably regulated by below-ground C allocation (Nilsson *et al.*, 2007). These findings were supported by a depleted $\delta^{13}\text{C}$ signature in PLFA 18:2 ω 6,9 and 18:1 ω 9, indicating a transport of photosynthetically fixed carbon into ectomycorrhizal fungi in the rhizosphere. However, it should be admitted that at least some parts of 18:2 ω 6,9 were probably of fine root origin, indicated by large variations within individual samples.

Between labelled and ambient open-top chambers, no statistically significant differences were detected in the abundances of PLFA biomarker. Out of it, a CO_2 concentration elevated at 75 ppm compared to the ambient CO_2 concentration had no influence on plant assimilation and rhizodepositon when given over a single vegetation period. In both rhizosphere and bulk soil, a trend of depleted $\delta^{13}\text{C}$ signature was observed in bacterial indicator fatty acids (i15:0, a15:0, i16:0, a16:0, cy17:0). Since known from other studies (Butler *et al.*, 2003) carbon compounds were cycled very fast through microbial communities. Another reason for bulk soil communities enriched in plant derived carbon is a rapid transport of carbohydrates in form of water soluble substances (Hütsch *et al.*, 2002) into root-free bulk soil by diffusion (Helal & Sauerbeck, 1984). According to long incubation periods between the harvesting time points (two months), it was not possible to investigate carbon dynamics between rhizosphere and bulk soil using this experimental setup. Whereas unexceptional higher absolute abundances of bacterial fatty acids were observed in the rhizosphere, the mole-percentages of these fatty acids were higher in bulk soil. Therefore a lower abundant, but structurally different microbial community in bulk soil compared to rhizosphere soil is suggested. However, not only rhizodeposits, but also structural differences between rhizosphere and bulk soil (Whalley *et al.*, 2005) can implicate differences in microbial communities within these soil fractions.

PLFA abundances at the two physiological plant stages did not differ statistically significant from each other (Appendix, Tab. XIII-8). However, abundances of individual bacterial communities decrease at the senescent plant stage in the rhizosphere, whereas no changes

were observed in bulk soil. Since ectomycorrhizal fungi in the rhizosphere incorporate higher amounts of carbon at this plant stage, less of rhizodeposits are available for bacterial communities. In consequence bacterial communities in rhizosphere that incorporated root exudates may change during plant development (Lynch & Whipps, 1990). In this study, decreases in the availability of rhizodeposits during the vegetation period resulted in a decrease of rhizodeposits utilizing microbial communities. In bulk soil there is a smaller stock of microbial communities present, probably due to a lack of stimulating root exudates (Marilley *et al.*, 1998).

Results from this experimental approach demonstrate the distribution of photosynthetically assimilated carbon within different plant parts and PLFA biomarker in the rhizosphere and bulk soil during different stages of plant development. The amounts of rhizodeposits available within these two soil compartments were suggested to provoke different microbial communities. Ectomycorrhizal fungi profit most of plant derived carbon in autumn, where the need for carbohydrates is high. Further it was possible to recover small differences in the carbon isotopic signature of labelling atmosphere in plant parts and microbial communities, providing a low cost labelling method for ambient-air experiments with unrequested CO₂-elevation.

3 Influence of elevated ozone on microbial communities in beech and spruce rhizosphere (C)

3.1 DOC and C_{mic} in beech and spruce rhizosphere and its response to elevated ozone exposure

Since rhizodeposition of plants vary in response to many factors, including plant age and stage of plant development (Baudoin *et al.*, 2003), it is assumed that also microbial communities are influenced by changes in plant development and hence rhizodeposition (Butler *et al.*, 2003). Different plant species often maintain different microbial communities within their rhizospheres (Myers *et al.*, 2001; Waldrop & Firestone, 2004), which at least may be a result of different quantity and quality of rhizodeposition (Jones *et al.*, 2004). Results from this experiment showed similar DOC contents in the rhizosphere of individual plants

irrespective of plantation (mono/mixed) and ozone treatment. This indicates no influence of elevated ozone on exudation of plant derived carbon into DOC. No photosynthate-carbon was detected in DOC fractions. This might be explained by too short exposure of plants to low enriched ^{13}C atmosphere along with a high utilization of photosynthate carbon by microorganisms and probably a stabilization of plant derived carbon in non-water extractable organic fractions (Fröberg *et al.*, 2006). However, ^{13}C was slightly enriched considering DOC of spruce mono cultures, which may indicate higher exudation of plant derived carbon compared to beech. This may result from a higher photosynthetic activity and higher amounts of CO_2 assimilated by spruce trees, since above-ground biomasses were higher in spruce trees compared to beeches, which is a species-specific phenomenon of saplings at this age (Pritsch *et al.*, 2005). Above-ground biomasses and activities were not part of this thesis and therefore no further experimental evidence is given for speculation on this topic.

C_{mic} indicated a higher abundance of total microbial biomass in spruce rhizosphere compared to beech rhizosphere when planted in mono cultures. According to experimental contributors, above-ground biomass was always higher in spruce compared to beech trees (Ritter, personal communication). Hence, higher amounts of carbon may be assimilated via photosynthesis and translocated below-ground. Supported by higher $\delta^{13}\text{C}$ values in C_{mic} of spruce rhizospheres compared to beech, this suggests distinct seasonal allocation patterns of perennial plants (according to Dickson, 1991) in accordance to a distinct physiological activity of beech and spruce throughout a vegetation period (In contrast to spruce trees, beech trees have to fulfil dormancy within the winter months). However, differences between microbial community structures of certain plant species are not surprising, since from recent studies it is already known, that plant species maintain different functional groups of microorganisms within their rhizosphere to maximize nutrient acquisition (Grayston *et al.*, 1998; Marschner *et al.*, 2005). Similar contents of DOC by different contents of C_{mic} between tree species indicate a different quality rather than a different quantity of rhizodeposition of deciduous trees and conifers, as reported by Priha *et al.* (1999). Since DOC and C_{mic} may vary statistically significant within a month, irrespective of external treatments (Yevdokimov, personal communication), these techniques should not be used when comparing results within a time period of several months. Nevertheless these techniques have proven suitable to compare treatments at one time point or within short time periods (Bailey *et al.*, 2002; Potthoff *et al.*, 2003; Marx *et al.*, 2007).

Using similar experimental conditions, competitive effects have been detected between the plant species beech and spruce (Liu *et al.*, 2004; Kozovits *et al.*, 2005). Kozovits *et al.* (2005) observed smaller crown volumes of beech displayed in mixed cultures compared to mono cultures, whereas spruce trees sequestered enhanced above-ground space in mixed cultures. In this thesis only below-ground microbial analyses were carried out: A higher presence of microbial biomass in beech rhizosphere as observed compared to non-competitive plants grown in mono cultures, whereas in spruce rhizospheres, similar or even lower contents of C_{mic} were detected compared to plants grown in mono cultures. This indicates different competitive strategies of beech and spruce. Beech trees probably invest in a higher maintenance of microbial biomass below-ground to increase the possibility of nutrient competition against spruce trees. On the other hand, spruce trees may invest in space sequestration above-ground. Coherently results from this study show that when grown in competition, incorporation of ^{13}C into C_{mic} increased in beech mixed cultures compared to mono cultures, whereas ^{13}C incorporation into C_{mic} decreased in spruce mixed cultures compared to mono cultures. However, it has to be mentioned, that according to the harvesting procedure in this experiment it was not always possible to clearly separate rhizosphere soil of beech and spruce in mixed containers. Therefore interpretation concerning intraspecific competition should be carried out with care.

Ozone stress is known to reduce carbon acquisition by plants and subsequent transportation of carbon to the roots (McCrary & Andersen, 2000). Effects of ozone on below-ground carbon processes are therefore indirect results of altered plant processes (Andersen & Rygiiewicz, 1991). Generally it is assumed that ozone may have a larger impact on processes below-ground than above-ground (Hofstra *et al.*, 1981), but numerous studies report inconsistent effects of ozone on assimilate translocation below-ground and subsequent changes in soil microbial community structure (McCrary & Andersen, 2000; Andersen, 2003; Matyssek & Sandermann, 2003; Dohrmann & Tebbe, 2005; Kasurinen *et al.*, 2005; Schloter *et al.*, 2005). In the present thesis, DOC and C_{mic} indicated rarely any differences when comparing ambient ($1 \times O_3$) and twice ambient ($2 \times O_3$) ozone treatments, neither at the beginning of the vegetation period, nor at the end. This was similar to a labelling study by Andersen & Rygiiewicz (1995) who observed no apparent change in root exudation as a result of ozone exposure. Interpreting these results, no influence of O_3 on the quantity of exudated carbohydrates and

hence no effect on rhizosphere microbial communities can be concluded. However, these results did not reflect those obtained from PLFA analyses (described in the following). Therefore using the more sensitive PLFA profiles to investigate ozone effects was suggested, since these techniques have proven suitable to investigate small changes within microbial community structures at different environmental conditions (e.g. Billings & Ziegler, 2005; Kasurinen *et al.*, 2005).

3.2 PLFA structure in rhizosphere soil of beech and spruce under different ozone regimes

Total PLFA abundances showed similar results compared to C_{mic} , indicating a higher microbial biomass in spruce rhizosphere than in beech rhizosphere. Competitive effects observed for C_{mic} could also be verified with PLFA analyses: On the one hand higher microbial biomass in beech rhizosphere of mixed cultures compared to beech rhizosphere of mono cultures, and on the other hand rather similar microbial biomass contents or even less in spruce rhizosphere of mixed cultures compared to mono cultures, indicate different competitive strategies as described above.

Considering responses to chronic ozone exposure at the beginning of the vegetation period, no pronounced differences within individual PLFA were observed between ozone treatments (Appendix, Tab. XIII-10). During the vegetation period, total PLFA abundances in rhizosphere of $2 \times O_3$ treated plants showed a higher increase when compared to $1 \times O_3$. This indicates a change of total microbial communities in the rhizosphere as a result of ozone exposure. SATFA and MUFA and individual fatty acids therein (Appendix, Tab. XIII-10) were (culture independent) more abundant in $2 \times O_3$ treatments, whereas ozone did not indicate an influence on PUFA contents (and hence ectomycorrhizal fungi). Therefore, a larger influence of elevated ozone concentrations on bacterial communities in the rhizosphere, rather than on eukaryotic and fungal populations is suggested. Since the percentage distribution within total PLFA indicated no difference between $1 \times O_3$ and $2 \times O_3$, a rather similar microbial community structure is suggested irrespective the ozone treatment. The percentage distribution of PLFA at the harvesting time point in September did not change statistically significant compared to the beginning of the vegetation period in May. However, individual fatty acids, especially

MUFA, increased in rhizosphere soil when plants were exposed to elevated ozone. This reflects the ability of O₃ to influence microbial community structure and individual organisms therein without altering total microbial biomass (as suggested by Andersen, 2003). PLFA patterns in rhizosphere soil of beech and spruce showed similar responses to elevated ozone exposure. Considering MUFA in beech rhizosphere, fatty acid abundances were detected in statistically significant higher amounts in 2 x O₃ compared to 1 x O₃ exposure. In spruce rhizospheres, similar trends were observed, but results did not reach statistical significance. MUFA are commonly used as indicator for Gram-negative bacteria (Zelles, 1997), hence these groups of bacteria responded indirectly to elevated ozone. Interpretation of these results suggests a higher sensitivity of beech trees to ozone stress. Recent studies (Braun *et al.*, 2004; Lu *et al.*, 2004) investigating ozone effects on beech and spruce trees reported altered concentrations of sugars and starch in fine roots of beech as a response to ozone exposure. Hence, rhizodeposition responds to ozone stress with a modified carbohydrate composition, which may attract Gram-negative populations in the rhizosphere. In comparison, spruce exposed to increasing ozone concentrations responded with higher starch concentrations in plant tissues more than in fine roots (Braun *et al.*, 2004), and therefore different composition of rhizodeposits may attract different microbial communities in the rhizosphere. Few studies have been carried out, indicating physiological stress conditions for bacteria by increasing amounts of MUFA as a consequence of changing environmental conditions (Guckert *et al.*, 1986; Ratledge & Wilkinson, 1989; Heipieper *et al.*, 1996). This finding is consistent with the results of this study, where higher absolute abundances of MUFA in 2 x O₃ treated samples were detected. Since no statistically significant results were detected in spruce samples compared to beech samples with respect to MUFA, generally these results reflect different strategies of beech and spruce trees to compete with increasing ozone concentrations.

Ozone does not influence soil compartments below the first few centimetres (Turner *et al.*, 1973; Blum & Tingey, 1977) and therefore an indirect ozone influence on microbial community structure via plants and rhizodeposition is rather obvious (Andersen, 2003). Since individual PLFA showed no coherent incorporation of plant derived ¹³C after the labelling period (probably due to inconsistent time lags between the end of the labelling period and harvest), ¹³C incorporation of individual PLFA was cumulated to illustrate ¹³C incorporation into total fractions of SATFA, MUFA and PUFA. Although higher absolute contents were detected as a

response to $2 \times O_3$, higher incorporation of plant derived carbon was observed in $1 \times O_3$ treatments. This indicates a stimulation of rhizosphere bacteria (SATFA, MUFA) via elevated O_3 concentrations, but this stimulation is not induced via increased carbohydrate exudation into the rhizosphere. Less incorporation of ^{13}C into rhizosphere PLFA suggests lower amounts of recently assimilated carbohydrates within exudates and hence a higher accumulation of photosynthate carbon may take place in plant parts. A reduced carbon transport to the roots resulting in a reduced rhizodeposition is already known from other studies (reviewed by Andersen, 2003) and probably due to a decreased carbon assimilation via photosynthesis. Van den Driessche (1991) reported a possible root growth via utilization of stored reserves when current photosynthate was absent. Hence other carbohydrates than from recent photosynthesis may be present also in root exudates and water extractable organic carbon (Bertin *et al.*, 2003). Therefore enhanced microbial community structure in rhizosphere soils of $2 \times O_3$ treatments was possibly due to different qualities of root exudates, rather than larger quantities. Evidences that carbohydrate composition of root exudates affect microbial community composition are known from other studies (Marschner *et al.*, 2002; Baudoin *et al.*, 2003). Microorganisms in soil are generally carbon limited (Zak *et al.*, 1994). Thus long term exposure to O_3 and hence a reduced carbohydrate transportation to the rhizosphere may shift the microbial community composition towards an increased decomposition of older soil organic matter (Andersen, 2003), which is coherent with lower ^{13}C signatures within the organisms.

Concluding the results obtained from this phytotron experiment, higher microbial biomasses were detected in rhizosphere soils of young spruce trees compared to young beeches. If grown in competition with spruce (as it naturally occurs commonly in Europe), beech trees indicated higher translocation of carbohydrates into below-ground microbial biomass compared to grown in interspecific competition. Elevated ozone influences growth conditions indirectly via exudate carbohydrate composition in the rhizosphere: Rhizosphere bacteria respond with increased decomposition of older organic matter or with a change in membrane structures to compete with such altered living conditions. Changes in the PLFA composition were therefore due to varying microbial communities or changes in the PLFA composition of cell membranes as a result of physiological adaption (Reichardt *et al.*, 1997). Microbial communities in the rhizosphere of beech trees respond more sensitive to chronic ozone exposure than in spruce.

The percentage distribution of individual fatty acids to total PLFA were not influenced statistically significant in 2 x O₃ treatments compared to 1 x O₃ treatments, indicating a stable microbial community structure present in the rhizosphere, able to compete with environmental changes caused by ozone. Taken together, results from this study obtained from C_{mic} and PLFA analyses are in accordance to Andersen (2003), who hypothesised an ozone influence on the microbial community structure in the rhizosphere of plants without altering total microbial biomass.

4 Influence of ozone on microbial community composition in the rhizosphere of mature beech trees during a vegetation period (D)

The following experiment was carried out on a Lysimeter device with the intention to confirm previous findings from greenhouse and phytotron experiments on mature plants. Mature trees and Two- to Three-year-old saplings used in the previous experiments differ in morphological and physiological characteristics (Kolb *et al.*, 1997; Kolb & Matyssek, 2001) and hence in their response to elevated O₃ (Ryan *et al.*, 1997; Bond, 2000). In the following, results obtained from rhizosphere soil of 10-year old beech trees were discussed with respect to chronic ozone stress, and with regard to comparability with younger plants.

4.1 DOC and C_{mic} in rhizospheres of mature beech trees during a vegetation period

DOC contents in rhizosphere soil of 10-year old beech trees were not statistically significant altered by elevated O₃ at any harvesting time point within the vegetation period when compared to ambient ozone exposure. No contribution of plant derived carbon to the pool of DOC was observed within the first months of the vegetation period (June to August), but a depleted carbon isotopic signature in DOC at the end of August indicates a contribution of plant exudates to water extractable organic carbon in soil compared to the beginning of the vegetation period. A major part of plant rhizodeposits is rapidly degraded by soil microorganisms, and therefore a minor part of (according to the labelling technique very low labelled) exudates remains within water extractable DOC (Yevdokimov *et al.*, 2006). Therefore the isotopic signature of this small part of plant rhizodeposits was not detectable according to

dilution in total DOC. Nevertheless, after 3 months of labelling, the carbon isotopic signature achieved by the addition of CO₂ derived from fossil-fuel burning may have accumulated in the pool of DOC, and hence was detected in this experiment in statistically significant amounts compared to the beginning of the experiment. Further a shift within rhizodeposition at the end of the vegetation period may be the reason of this high plant derived carbon input into DOC. Beech trees may change the carbohydrate composition within exudates at the end of a vegetation period, to maintain processes in the following period of dormancy during the winter months (Carbone *et al.*, 2007). Similar $\delta^{13}\text{C}$ signatures in the pool of DOC in both ozone treatments showed no decrease of carbohydrate allocation via rhizodeposition into DOC, which is again in accordance to previous findings (experiment C) and other studies (Andersen & Rygiewicz, 1995).

Microbial biomass (C_{mic}) increased during the vegetation period, but equally in 1 x O₃ and 2 x O₃ treatments. Hence no effect of ozone on total microbial biomass was detected. Investigating the utilization of plant derived carbon by total microbial biomass, results indicated high label incorporation after two months of labelling. This fits to the data stated above, indicating a rapid use of rhizodeposits by microorganisms. After one month of labelling plant derived carbon was not detectable within microbial biomass possibly due to the comparably low signature derived from “fossil-fuel” labelling.

4.2 PLFA profiles and incorporation of plant derived carbon into PLFA biomarker in mature beech rhizosphere during a vegetation period

Investigating total soil microbial biomass throughout the vegetation period, C_{mic} and PLFA techniques lead to different results. Here PLFA techniques were the more promising tool to compare microbial biomass in soil within longer timespans. Higher amounts of total PLFA were observed in 2 x O₃ treatments at the end of the vegetation period (T2 and T3) indicating an influence of ozone on microbial biomass in the rhizosphere. Since no effects of ozone on rhizodeposition and the incorporation of plant derived carbon into total microbial biomass carbon were detected, an indirect effect via the quality rather than the quantity of rhizodeposits is suggested. On the one hand, no change within the percentage distribution of total PLFA was observed, suggesting a rather stable microbial community in both, ambient

and twice ambient ozone treatments during the vegetation period. This is in accordance with previous findings (experiment C), where also a stable microbial community structure was detected in the rhizosphere of beech and spruce trees, irrespective of environmental changes. On the other hand, total PLFA abundances showed similar effects in $2 \times O_3$ treatments observed in the phytotron (experiment C) carried out with younger plants, confirming an ozone response of microbial communities in the rhizosphere.

Total PLFA distribution was different than observed in previous experiments with younger plants (A, B, C). Only about 70% of SATFA were detected within the fatty acid profile, whereas a large amount of MUFA was present (20% to 25%). This indicates an increase of Gram-negative bacteria in the rhizosphere of mature plants. These findings are also in accordance with other studies (Steer & Harris, 2000; Butler *et al.*, 2003), where increasing amounts of MUFA were observed with increasing plant growth. Therefore these fatty acids may act as sensitive responders to altered rhizosphere conditions, caused directly by the plant and rhizodeposits or indirectly via influencing plant growth (as observed in experiment C). Higher abundances of total PLFA at the end of the vegetation period by contributing similar percentages of individual groups of PLFA (SATFA, MUFA and PUFA) to total PLFA indicate an increase of microbial communities by stable microbial community composition.

Except MUFA 16:1 ω 9 and PUFA 18:3 ω 6,9,12,15, individual PLFA reflect similar trends observed within total PLFA. At the end of the vegetation period statistically significant increased abundances were detected as a response to elevated ozone compared to ambient ozone treatments and compared to the beginning of the vegetation period. PLFA 16:1 ω 9 and 18:3 ω 6,9,12,15 neither changed statistically significant during the vegetation period nor in response to ozone. Since different PLFA indicate distinct groups of microorganisms (Zelles, 1997), ozone stimulates different microbial communities in the rhizosphere of plants, as also observed in earlier studies (Andersen, 2001). As stated earlier, changes within a PLFA composition can also reflect changing lipid compositions in membranes as a response to physiological adaption (Wilkinson & Anderson, 2001). In this case, this is supported by higher amounts of cy19:0 in $2 \times O_3$ treatments, coherently with higher percentages within total PLFA. Cyclopropyl fatty acids may be synthesized in the stationary phase of bacteria, often as a response to physiological stress (Wang & Cronan, 1994), here represented by elevated ozone concentrations. An increasing formation of cyclopropyl fatty acids may additionally increase

membrane stability (Dufourc *et al.*, 1984), and hence increase the adaption to ozone altered conditions. Conclusively plants respond to elevated ozone by altering their microbial community structure but also rhizosphere organisms respond by altering the PLFA composition of their cell membranes.

Considering the carbon isotopic signature of individual PLFA biomarker, no coherent incorporation of plant derived carbon could be verified. This can be due to a very low utilization of rhizodeposits by individual groups of organisms (also according to experiment A and B). Although individual fatty acids of bacterial origin indicated a statistically significant depleted carbon signature at the end of the vegetation period (a15:0, i16:0), an interpretation of these results would be highly speculative due to very low differences and also high variations within replicates. However, within PUFA 18:2 ω 6,9 and 18:3 ω 6,9,12,15, both probably eukaryotic or fungal origin, a depleted carbon signature derived from fossil-fuel burning was detected already after one month of labelling. Incorporation of such “fossil-fuel” labelled, plant derived carbon showed no response to ozone. According to previous findings (experiment A, B) a high activity of fungal population degrading plant exudates may be present, since beech trees grow in close relationship with ectomycorrhizal fungi (Genet *et al.*, 2000). The result of similar label incorporation into PLFA coherently with increasing total abundances in 2 x O₃ treatments points into the direction of a response of microbial communities not directly via the incorporation of root exudates but rather indirectly by altering membrane lipid compositions in order to comp with altered living conditions.

Labelling in this experiment was difficult because of ambient-air conditions and environmental factors influencing the distribution of CO₂ derived from fossil-fuel burning within the experimental area. Since the carbon isotopic difference in the atmosphere throughout the experiment was not exactly stable, the percentage of labelled carbon assimilated within the experimental period was calculated compared to the non-labelled control at the beginning of the experiment. PLFA 18:3 ω 6,9,12,15 showed consequently higher incorporation of labelled carbon in 2 x O₃ treatments compared to 1 x O₃. This indicates a high stimulation of eukaryots or probably fungi in response to ozone. Within three months, around 50% of carbon was incorporated into this PLFA under 2 x O₃. Contrasting, no coherent response of 18:2 ω 6,9 was observed, suggesting that these two PLFA have different origins. Since both PLFA were reported to be rather of eukaryotic or fungal origin (Zelles, 1999), and

18:2 ω 6,9 was used frequently as indicator for fungi (e.g Baath & Anderson, 2003; Butler *et al.*, 2003; Lu *et al.*, 2004; Nilsson *et al.*, 2007), 18:3 ω 6,9,12,15 probably originates from small root caps or root debris, also present in the rhizosphere (Nguyen, 2003; Marschner *et al.*, 2005; Gregory, 2006). The amounts of such compounds released from roots may vary in response to different abiotic and biotic factors influencing root development (Dakora & Phillips, 2002), here in response to ozone. Since such compounds released into the rhizosphere are probably not easily degradable by microorganisms, the so altered quality of rhizodeposition indirectly influences microbial communities as they are forced to degrade other organic compounds in the rhizosphere (Andersen, 2003). Nevertheless, this is more of speculative origin, but may point in a direction for necessary further studies investigating mechanisms how ozone alters the soil microbial community structure. Another possibility might be an origin of 18:3 ω 6,9,12,15 from fine roots, and hence accumulation of sugars and other carbohydrates within such plant organs as a response to ozone (Braun *et al.*, 2004; Liu *et al.*, 2004). Out of it, DOC contains less plant derived carbohydrates and rhizosphere microbial community structure changes as a result again due to a shift in the food supply.

Concluding results from this experiment, no different utilization of rhizodeposits was detected in organisms in response to elevated ozone exposure. Nevertheless, higher absolute abundances of PLFA in 2 x O₃ treatments indicated a response to elevated ozone without changing total microbial biomass, which is postulated as a stable microbial community structure in the course of the experiment. An increase in individual PLFA can be due to stimulation of individual microbial communities, or rather changes within the membrane lipid composition as a response of physiological adaption to ozone-altered growth conditions in the rhizosphere. Bacteria did not indicate a use of rhizodeposits in this experiment due to low carbon isotopic differences between the ambient and the labelling atmosphere. However, again ectomycorrhizal fungi, which were highly involved in degrading plant exudates in greenhouse and open-top chamber experiments (A, B), showed high incorporation of plant derived carbon. Elevated chronic ozone exposure further increased ¹³C incorporation of probably root derived PLFA in the rhizosphere leading to a change in the quality of exudation.

5 Conclusion

Using stable isotope techniques, it was possible to trace carbon fluxes from beech and spruce trees into the soil and soil microbial biomass. Microbial communities actively utilized rhizodeposits derived from recently fixed CO₂ within short time periods and showed distinct utilization patterns of such plant derived carbohydrates in the rhizosphere. A fast utilization of rhizodeposits was observed by different groups of bacteria. However, the fastest utilization was detected in the group of ectomycorrhizal fungi, grown in close partnership to the trees. A time-lagged incorporation of labelled carbon in PLFA, characteristic for micro-eukaryotes or probably protists indicated the flow of the plant derived carbon into microbial food webs. The results also indicate that microbial communities in the rhizosphere are more actively involved in utilizing plant rhizodeposits than microbial communities in bulk soil. Incorporation of plant derived carbon into bulk soil communities was detected but might have occurred due to transport of water soluble carbohydrates from rhizosphere soil into bulk soil, or an indirect incorporation via secondary consumers indicating a microbial food web utilizing plant derived carbon in soil. Using several experimental setups it was further possible to confirm results obtained from the greenhouse (A) in outdoor experiments (B) as well as for mature plants (D).

Since the same soil was used in all experiments, a rather similar microbial community structure in all experiments was influenced by different kinds of environmental conditions: Different responses to environmental conditions of beech and spruce saplings (C), young and mature beech trees (B, D), but also different responses within plants of different developmental stages (B) were observed. Higher numbers and abundances of extracted PLFA in experiments carried out under controlled conditions were demonstrated, probably due to better conditions for microorganisms in soil. Plants in greenhouse (A) and phytotron experiments (C) received fertilizer and were irrigated when necessary. Therefore growth conditions in the rhizosphere were probably more attractive to rhizosphere organisms than compared to experiments (B) and (D), where no additional irrigation and fertilization was performed. In contrast to (A) and (C), plants exposed to natural environmental conditions had to compete with changes in the environment (e.g. rain, drought, high temperatures) that influenced indirectly the microbial community structure within the rhizosphere in a different

way than observed under controlled conditions. In general, microbial communities in the rhizosphere were influenced by plant species, plant age, plant development or climate conditions.

As frequently postulated, a response of microbial communities in the rhizosphere to chronic ozone stress was observed. Elevated ozone exposure over long time periods influenced individual microbial communities or caused physiological changes within microbial communities as a response of adaption to altered growth conditions in the rhizosphere. Since a direct influence of ozone on rhizosphere microbial communities was thought to be rather low, results from this study suggest an indirect influence via changes in the carbohydrate composition within plants and rhizodeposition. In $2 \times O_3$ variants, higher amounts of PLFA occurred due to changes in the microbial community structure or probably changes within the membrane lipid composition. Further, increased PLFA abundances observed in response to elevated ozone were evidenced not to be stimulated via recent assimilates (C, D). However, similar PLFA distribution in different ozone treatments indicate a stable microbial community, in the rhizosphere of plants, able to face environmental stresses like elevated ozone without altering the total and active microbial community structure.

VII References

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VIII Appendix

1 Abbreviations

a.m.	forenoon, <i>ante meridiem</i>
ANOVA	analysis of variance
ant, a	anteiso branched
br	branched chain
C	carbon (element)
C _{mic}	microbial biomass carbon
CO ₂	carbon dioxide
CuO	copper oxide
cyc, cy	cyclopropyl
dic	dicarboxylic
DNA	desoxyribonucleinacid
DOC	dissolved organic carbon
DS	dry substance
e.g.	for example, <i>exempli gratia</i>
EA	elemental analyzer
EL-PLFA	ester linked phospholipid fatty acid(s)
FAME	fatty acid methyl ester
GC	gas chromatograph
H ₂ O	water (deionized)
He	helium
IRMS	isotope ratio mass spectrometer
iso, i	iso branched
mRNA	messenger ribonucleic acid
MS	mass spectrometer
MUFA	mono unsaturated fatty acid(s)
N ₂	nitrogen
NEL-PLFA	non ester linked phospholipid fatty acid(s)
nor	straight chain
O ₂	oxygen
O ₃	ozone
p.m.	afternoon, <i>post meridiem</i>
PCR	polymerase chain reaction
PLFA	phospholipid fatty acid(s)
PLOH	hydroxy substituted phospholipid fatty acid(s)
ppm	parts per million
PUFA	poly unsaturated fatty acid(s)
qPCR	quantitative polimerase chain reaction
SATFA	saturated fatty acid(s)
T1, T2, ...	harvesting time point 1, 2, ...
v / v	volume per volume
V-PDB	Vienna-Pee Dee Belemnite
w / v	weight per volume

2 Chemicals and fertilizer composition

Tab. VIII-1: Chemicals and gases used in laboratory analyses and experiments

acetic acid (p. a.)	CH ₃ COOH	Merck, Darmstadt, Germany
acetone (for residue analysis)	C ₃ H ₆ O	Sigma-Aldrich, Seelze, Germany
acetonitrile (for HPLC)	CH ₃ CN	Sigma-Aldrich, Seelze, Germany
sodium peroxodisulfate (p. a.)	Na ₂ O ₈ S ₂	Fluka, Buchs, Switzerland
calcium chloride (p. a.)	CaCl ₂	Merck, Darmstadt, Germany
celite 545	particle size 0.02 - 0.1 mm	Merck, Darmstadt, Germany
chloroform (for HPLC)	CHCl ₃	Merck, Darmstadt, Germany
chloroform (p. a.)	CHCl ₃	Merck, Darmstadt, Germany
Chromabond Sorbenz NH ₂	for glass columns	Machery-Nagel, Düren, Germany
Chromabond filter elements	for glass columns	Machery-Nagel, Düren, Germany
dichloromethane (for residue analysis)	CH ₂ Cl ₂	Sigma-Aldrich, Seelze, Germany
diethyl ether (p. a.)	C ₂ H ₅ O ₆	Merck, Darmstadt, Germany
dimethyl disulfide	(CH ₃ S) ₂	Fluka, Buchs, Switzerland
distilled water	H ₂ O _{dest}	Elix Millipore, Billerica MA, USA
hexane (for residue analysis)	C ₆ H ₁₄	Sigma-Aldrich, Seelze, Germany
iodine (p. a.)	I ₂	Merck, Darmstadt, Germany
isooctane (p. a.)	C ₈ H ₁₈	Merck, Darmstadt, Germany
potassium sulfate (p. a.)	K ₂ SO ₄	Merck, Darmstadt, Germany
methanol (for residue analysis)	CH ₃ OH	Sigma-Aldrich, Seelze, Germany
ortho-phosphoric acid, 85% (p. a.)	H ₃ PO ₄	Merck, Darmstadt, Germany
potassium hydroxide (p. a.)	KOH	Merck, Darmstadt, Germany
SCX-column (0.5 g / 3 mL)	Bond Elut	Varian GmbH, Darmstadt, Germany
SI-column (2 g / 12 mL)	Mega Bond Elut	Varian GmbH, Darmstadt, Germany
silver nitrate (p. a.)	AgNO ₃	Merck, Darmstadt, Germany
sodalime	pellets with indicator	Merck, Darmstadt, Germany
sodium sulfate (anhydrous for synthesis)	Na ₂ SO ₄	Merck, Darmstadt, Germany
toluene (scintillation grade)	C ₇ H ₈	Merck, Darmstadt, Germany
myristic acid methyl ester	C ₁₄ H ₂₈ O ₂	Sigma, St. Louis, USA
nonadecanoic acid methyl ester	C ₂₀ H ₄₀ O ₂	Sigma, St. Louis, USA
¹³ CO ₂ (experiment C)	¹³ C/ ¹² C = 99,9 atm%	Sigma-Aldrich, Seelze, Germany
¹³ CO ₂ (experiment A)	¹³ C/ ¹² C = 1.3 atm%	Messer AG, Lenzburg, Switzerland
CO ₂ fossil fuel (experiment B)	δ ¹³ C = -40‰ V-PDB	Air Liquide, Krefeld, Germany
CO ₂ fossil fuel (experiment D)	δ ¹³ C = -47‰ V-PDB	Air Liquide, Krefeld, Germany
CO ₂ reference	δ ¹³ C = -3.8‰ V-PDB	Air Liquide, Krefeld, Germany
helium 5.0	purity, % ≥ 99.999	Linde, Munich, Germany
nitrogen 5.0	purity, % ≥ 99.999	Linde, Munich, Germany

Tab. VIII-2: Fertilizer composition for experiment A and B in greenhouse and phytotrons.

Macronutrients	Molarity
KNO ₃	14.5 mM
MgSO ₄ ·7H ₂ O	1 mM
KH ₂ PO ₄	1.3 mM
Na ₂ HPO ₄	0.4 mM
CaCl ₂ ·2H ₂ O	600 µM
FeSO ₄ -EDTA	100 µM
Micronutrients	Molarity
Al ₂ (SO ₄) ₃ ·18H ₂ O	2 nM
KJ	2 nM
KBr	2 nM
SnCl ₂ ·2H ₂ O	2 nM
LiCl	2 nM
MnCl ₂ ·4H ₂ O	2 µM
H ₃ BO ₃	10 µM
ZnSO ₄ ·7H ₂ O	1 µM
CuSO ₄ ·5H ₂ O	1 µM
NiSO ₄ ·6H ₂ O	2 nM
Co(NO ₃) ₂ ·6H ₂ O	2 nM
(NH ₄) ₆ Mo ₇ O ₂₄	10 nM

3 Supplementary data

3.1 Temporal dynamics of photosynthate ¹³C distribution in young beech trees (*Fagus sylvatica* L.): The model plant-soil ecosystem under continuous labelling atmosphere (A)

Tab. VIII-3: Total carbon contents [%] and carbon isotopic signatures of plant parts in the course of the greenhouse continuous labelling experiment in pots (mean of n = 3 ± standard deviation). Asterisks (*) represent statistically significant differences (p < 0.05) compared to the beginning of labelling.

		labelling time [d]								
		0.0	0.5	1.0	1.5	2.5	3.5	5.5	10.5	20.5
leaves	C _{total} [%]	48.14	49.14	49.18	49.39	48.12	48.28	47.52	49.31	48.25
	±	0.14	0.69	0.64	0.29	1.05	0.32	1.69	0.37	0.65
	C _{total} [‰ V-PDB]	-26.63	-22.32	-24.14	-24.48	-19.09	-18.79*	-13.76*	-7.91*	-1.15*
	±	0.87	0.31	0.82	1.18	0.52	1.23	1.05	2.06	9.12
twigs	C _{total} [%]	46.09	49.59	48.10	48.26	46.52	47.67	46.01	48.90	49.02*
	±	1.34	3.71	0.17	0.46	1.55	1.08	1.45	0.32	0.84
	C _{total} [‰ V-PDB]	-25.64	-25.30	-24.87	-25.20	-21.42	-21.19	-18.17	-6.24*	10.79*
	±	0.82	1.10	0.88	0.92	0.21	1.25	1.07	6.27	7.78
stem	C _{total} [%]	45.88	47.84	49.36	49.59	47.36	49.49	49.15	50.44	49.98
	±	0.71	1.38	1.93	1.71	1.68	0.77	1.30	2.44	0.62
	C _{total} [‰ V-PDB]	-26.79	-27.08	-27.20	-27.31	-26.08	-26.42	-24.66	-19.06*	-15.84*
	±	0.26	0.08	0.06	0.17	0.77	0.25	1.22	1.47	3.68
coarse roots	C _{total} [%]	43.30	46.91	49.87	47.11	45.07	46.54	49.09	46.22	47.24
	±	1.71	1.20	0.68	1.38	4.16	0.99	4.32	1.70	1.57
	C _{total} [‰ V-PDB]	-27.68	-27.25	-27.90	-27.45	-26.44	-27.26	-27.15	-25.63	-10.39*
	±	0.57	0.51	0.35	0.30	0.82	0.37	1.00	0.50	15.26
fine roots	C _{total} [%]	22.41	23.69	31.46	31.23	30.62	30.52	36.14	32.73	32.66
	±	1.57	5.98	10.96	5.87	8.82	6.23	6.95	9.56	3.54
	C _{total} [‰ V-PDB]	-27.42	-27.38	-27.14	-27.13	-26.83	-27.32	-27.41	-12.48	20.34*
	±	0.22	0.50	0.48	0.29	0.62	0.61	0.62	16.81	18.94

Tab. VIII-4: PLFA abundances [nmol g⁻¹ DS] in rhizosphere soil (a) and bulk soil (b) at different harvesting time points in the course of the greenhouse continuous labelling experiment (mean ± standard deviation, n = 3). Asterisks (*) represent statistically significant differences (p < 0.05) compared to the beginning of labelling.

a)

FA [nmol g ⁻¹ DS]	labelling time [d]								
	0.0	0.5	1.0	1.5	2.5	3.5	5.5	10.5	20.5
br12:0	0.26	-	0.20	0.17	0.22	0.41	0.38	0.56	0.46
±	0.12	-	0.11	0.10	0.09	0.37	0.05	0.08	0.20
i14:0	0.44	0.17	0.28	0.34	0.32	0.37	0.38	0.59	0.49
±	0.01	0.03	0.12	0.09	0.16	0.06	0.09	0.12	0.06
a14:0	2.29	1.52	2.20	2.29	2.08	2.31	2.28	3.52	2.80
±	0.92	0.36	0.70	0.31	0.85	0.19	0.32	0.54	0.36
i15:0	9.50	6.57	8.96	8.88	8.39	8.26	8.02	12.37	10.67
±	2.59	1.27	2.09	0.65	3.09	2.60	1.52	2.35	1.30
a15:0	4.42	3.05	4.35	4.18	4.19	4.25	4.15	5.66	4.61
±	1.14	0.67	0.91	0.35	0.67	0.33	0.72	0.95	0.50
n15:0	0.81	0.52	0.66	0.77	0.81	0.79	0.71	1.13	0.84
±	0.28	0.10	0.08	0.09	0.25	0.17	0.24	0.14	0.05
i16:0	6.61	4.94	5.58	6.29	6.77	5.95	4.91	8.08	5.68
±	1.90	0.90	0.84	0.78	1.96	1.54	2.03	0.97	0.50
br10,17:0	0.99	0.72	1.12	-	-	2.72	-	2.97	3.21
±	-	-	0.22	-	-	-	-	1.97	3.08
a16:0	22.16	18.25	22.47	21.69	19.70	19.09	18.36	27.25	20.07
±	5.69	2.86	2.86	1.06	4.40	5.37	2.06	4.54	1.68
i17:0	9.08	7.93	9.09	9.91	9.92	8.50	8.03	11.98	8.04
±	2.23	1.12	0.95	0.73	2.57	2.75	1.69	1.14	0.84
br11,17:0	1.55	1.35	1.61	1.61	1.51	1.26	1.31	1.94	1.44
±	0.39	0.15	0.16	0.15	0.42	0.41	0.19	0.23	0.13
a17:0	1.89	1.31	1.91	1.81	1.78	1.48	1.33	2.47	1.94
±	0.41	0.15	0.22	0.06	0.52	0.51	0.27	0.52	0.26
br17:0 (mixpeak)	3.62	2.81	3.39	3.68	4.02	3.53	3.08	4.28	3.02
±	0.81	0.28	0.40	0.28	0.25	0.35	0.90	0.20	0.20
n17:0	0.74	0.49	0.67	0.73	0.71	0.52	0.54	0.84	0.66
±	0.15	0.04	0.08	0.04	0.08	0.12	0.01	0.03	0.12
br10,18:0	1.88	1.53	1.76	2.26	2.33	1.82	1.62	2.58	1.46
±	0.48	0.13	0.25	0.22	0.53	0.61	0.54	0.10	0.11
i18:0	0.94	0.79	0.96	0.99	0.94	0.85	0.78	1.18	0.98
±	0.23	0.11	0.07	0.05	0.23	0.27	0.13	0.13	0.12
n18:0	4.46	3.39	4.50	4.61	4.11	4.34	3.49	5.59	4.38
±	1.23	0.28	0.29	0.28	0.79	0.33	0.38	0.09	0.50
cy17:0	3.48	2.71	3.51	3.74	3.42	2.96	2.89	4.29	3.24
±	0.67	0.25	0.48	0.16	0.83	1.07	0.46	0.41	0.26
cy18:0	0.46	0.37	0.45	0.52	0.54	0.33	0.31	0.42	0.44
±	0.11	0.07	0.09	0.12	0.12	0.13	0.04	0.07	0.07
br10,19:0	1.21	0.81	1.08	1.37	1.40	1.07	0.89	1.59	0.86
±	0.30	0.03	0.22	0.09	0.34	0.40	0.28	0.20	0.04
br12,19:0	0.51	-	0.45	0.48	0.39	0.36	-	0.48	-
±	0.01	-	0.03	0.07	0.04	0.03	-	0.08	-
cy19:0	18.73	17.75	20.81	20.10	18.73	16.73	16.95	24.76	20.36
±	3.62	2.38	1.18	1.37	5.17	5.81	2.82	2.95	1.81
n20:0	3.77	3.09	4.38	4.28	3.72	3.46	2.86	4.54	3.67
±	1.14	0.49	0.07	0.38	0.58	0.43	0.39	0.45	0.45
n22:0	6.07	4.87	7.34	7.16	6.28	5.60	4.68	7.35	5.73
±	1.67	0.81	0.30	0.61	0.74	0.58	0.65	0.96	0.89
n24:0	3.32	2.54	3.69	4.41	3.85	3.46	2.38	3.46	2.59
±	0.88	0.70	0.30	0.38	0.36	0.22	0.36	0.83	0.20
dic18:0	-	0.23	0.22	-	-	0.40	-	0.57	0.84
±	-	-	0.04	-	-	-	-	0.26	0.71
dic20:0	0.68	0.39	0.87	0.44	0.38	0.68	-	1.65	1.57
±	0.32	0.33	0.34	0.06	-	0.63	-	0.42	1.23
dic22:0	0.91	0.64	1.49	1.16	0.47	10.32	0.21	1.74	2.18
±	0.47	0.23	0.69	1.01	0.31	16.74	0.02	0.24	1.77
SATFA total	109.48	88.11	113.32	113.74	106.64	108.48	90.56	149.04	110.86
±	27.41	11.23	10.51	7.59	23.82	11.30	11.88	22.06	15.72
15:1ω8	0.03	0.05	0.06	0.05	0.08	0.06	0.07	0.12	0.10
±	0.03	0.01	0.01	0.02	0.02	-	0.01	0.04	0.02
16:1ω5	0.29	0.46	0.45	0.49	0.56	0.54	0.61	1.21*	1.24*
±	0.35	0.10	0.15	0.18	0.26	0.23	0.22	0.25	0.14
16:1ω9	0.07	0.11	0.10	0.12	0.12	0.11	0.14	0.28*	0.26*
±	0.08	0.03	0.04	0.05	0.04	0.04	0.04	0.06	0.02
16:1ω7 cis	0.31	0.62	0.65	0.76	0.73	0.67	0.76	1.75*	1.62*
±	0.31	0.14	0.15	0.22	0.26	0.24	0.18	0.50	0.23
16:1ω7 trans	0.06	0.13	0.09	0.15	0.17	0.12	0.16	0.31*	0.23*
±	0.06	0.04	0.03	0.05	0.07	0.06	0.07	0.04	0.01
17:1ω8 cis	0.02	0.08	0.07	0.09*	0.10*	0.08	0.09	0.19*	0.17*
±	0.02	0.02	0.00	0.04	0.03	0.03	0.03	0.03	0.03
17:1ω8 trans	0.06	0.18	0.17	0.20*	0.21*	0.20	0.21*	0.46*	0.46*
±	0.07	0.05	0.03	0.05	0.07	0.07	0.05	0.09	0.03
18:1ω9	0.81	1.97	1.87	2.39	2.41	2.12	2.40	4.53	4.13
±	0.91	0.50	0.54	0.71	0.54	0.87	0.38	0.67	-
18:1ω7	0.49	1.11	1.20	1.43	1.31	1.36	1.46	3.70*	4.28*
±	0.43	0.29	0.22	0.34	0.28	0.57	0.12	1.81	1.64
MUFA total	2.15	4.71	4.61	5.69	5.65	5.22	5.89	10.96	9.74
±	2.26	1.08	1.17	1.63	1.59	2.08	1.10	6.38	6.90
18:2ω6,9	2.07	2.99	5.82	4.54	5.05	5.47	8.41	10.35*	4.71
±	1.39	2.19	1.88	2.39	0.94	3.88	4.80	6.85	1.87
20:4ω6,9,12,14	0.42	0.25	0.38	0.43	0.56	0.58	0.51	1.73*	1.39
±	0.03	0.13	0.06	0.20	0.17	0.30	0.09	1.03	0.59
18:3	0.29	0.43	0.99	0.84	0.63	0.89	1.02	1.44*	0.53*
±	0.17	0.39	0.31	0.58	0.16	0.75	0.74	1.51	0.03
PUFA total	2.64	3.66	7.19	5.82	6.24	6.93	9.95	15.29	6.45
±	1.78	2.71	2.24	3.16	1.10	4.89	5.56	12.42	2.69

b)

FA [nmol g ⁻¹ DS]	labelling time [d]		
	0.0	10.5	20.5
br12:0	0.12	0.54*	0.42*
±	0.11	0.16	0.10
i14:0	0.27	0.38	0.40
±	0.03	0.09	0.09
a14:0	2.08	2.45	2.31
±	0.35	0.49	0.37
i15:0	7.38	8.43	8.87
±	0.71	2.25	1.99
a15:0	3.63	3.85	4.00
±	0.48	1.14	0.72
n15:0	0.63	0.73	0.62
±	0.07	0.21	0.21
i16:0	5.40	5.66	4.75
±	1.07	1.89	1.84
br10,17:0	0.55	2.15	2.95
±	0.50	1.65	0.47
a16:0	16.03	16.93	16.89
±	1.45	5.06	3.84
i17:0	7.86	8.17	7.64
±	1.15	2.67	2.52
br11,17:0	1.44	1.42	1.45
±	0.19	0.39	0.32
a17:0	1.65	1.72	1.72
±	0.22	0.54	0.49
br17:0 (mixpeak)	3.20	3.24	2.83
±	0.52	0.98	0.84
n17:0	0.58	0.63	0.55
±	0.05	0.12	0.11
br10,18:0	1.72	1.80	1.41
±	0.37	0.78	0.62
i18:0	0.83	0.82	0.82
±	0.08	0.41	0.45
n18:0	3.84	3.93	3.86
±	0.25	0.97	0.49
cy17:0	2.88	3.06	3.06
±	0.20	0.92	0.93
cy18:0	0.44	0.54	0.51
±	0.04	0.13	0.08
br10,19:0	1.04	1.07	0.81
±	0.24	0.36	0.28
br12,19:0	0.26	0.30	0.39
±	0.23	0.26	0.02
cy19:0	16.86	17.72	19.40
±	1.32	4.59	4.78
n20:0	3.93	3.92	3.80
±	0.49	1.07	0.82
n22:0	6.26	6.21	5.92
±	0.77	1.55	1.57
n24:0	3.17	3.12	2.84
±	0.22	1.08	0.37
dic18:0	0.09	0.38	0.71
±	0.08	0.49	0.46
dic20:0	0.65	1.22	2.00
±	0.38	0.80	1.05
dic22:0	1.02	1.88	2.49
±	0.38	1.15	0.50
SATFA total	93.82	108.77	102.42
±	10.38	31.36	26.11
15:1ω8	0.06	0.06	0.05
±	0.03	0.01	0.01
16:1ω5	0.48	0.58*	0.85*
±	0.17	0.06	0.17
16:1ω9	0.14	0.14	0.16
±	0.04	0.02	0.05
16:1ω7 cis	0.48	0.66	0.85*
±	0.09	0.07	0.22
16:1ω7 trans	0.13	0.15	0.16
±	0.05	0.03	0.05
17:1ω8 cis	0.02	0.10	0.12*
±	0.03	0.04	0.04
17:1ω8 trans	0.16	0.21	0.34
±	0.03	0.04	0.10
18:1ω9	1.26	2.08	3.10*
±	0.41	0.22	0.79
18:1ω7	0.63	1.48	1.84*
±	0.23	0.66	0.44
MUFA total	3.37	7.37	7.45
±	0.80	3.44	1.80
18:2ω6,9	1.09	2.27	2.16
±	0.51	1.13	0.30
20:4ω6,9,12,14	0.22	0.44	0.77*
±	0.04	0.11	0.19
18:3	-	0.44	-
±	-	-	-
PUFA total	1.31	2.86	2.93
±	0.55	1.49	0.11

Tab. VIII-5: Contribution of individual PLFA [mol%] to total PLFA in rhizosphere soil (a) and bulk soil (b) at different harvesting time points in the course of the greenhouse continuous labelling experiment (mean \pm standard deviation, n = 3). Asterisks (*) represent statistically significant differences ($p < 0.05$) compared to the beginning of labelling.

a)

FA [mol %]	labelling time [d]								
	0.0	0.5	1.0	1.5	2.5	3.5	5.5	10.5	20.5
br12:0	0.20	-	0.15	0.13	0.16	0.36	0.37	0.34	0.38
±	0.10	-	0.08	0.07	0.08	0.35	0.09	0.02	0.19
i14:0	0.33	0.18	0.22	0.27	0.26	0.31	0.36	0.35	0.39
±	0.00	0.04	0.08	0.06	0.10	0.05	0.02	0.01	0.06
a14:0	1.94	1.58	1.74	1.82	1.70	1.93	2.15	2.10	2.21
±	0.38	0.26	0.47	0.18	0.42	0.12	0.07	0.04	0.28
i15:0	8.27	6.78	7.12	7.09	6.89	6.79	7.52	7.36	8.41
±	0.35	0.44	1.39	0.40	1.33	1.66	0.14	0.26	0.41
a15:0	3.86	3.14	3.46	3.34	3.57	3.55	3.95	3.40	3.63
±	0.14	0.25	0.58	0.18	0.22	0.21	0.84	0.03	0.11
n15:0	0.69	0.54	0.52	0.62	0.67	0.65	0.65	0.68	0.67
±	0.09	0.04	0.04	0.06	0.10	0.07	0.12	0.05	0.07
i16:0	5.74	5.11	4.44	5.01	5.64	4.89	4.53	4.59	4.49
±	0.36	0.28	0.39	0.32	0.50	0.77	1.34	0.13	0.26
br10,17:0	0.78	0.90	0.89	-	-	2.45	-	1.93	2.26
±	-	-	0.09	-	-	-	-	0.99	1.99
a16:0	19.34	18.90	17.92	17.35	16.59	15.66	17.37	16.15	15.87
±	0.51	0.21	1.30	1.03	0.45	2.49	1.08	0.12	0.81
i17:0	7.95	8.23	7.25	7.91	8.31	6.97	7.53	7.06	6.35
±	0.31	0.31	0.28	0.20	0.44	1.64	0.68	0.58	0.23
br11,17:0	1.36	1.41	1.28	1.29	1.26	1.04	1.23	1.15	1.14
±	0.03	0.06	0.05	0.06	0.10	0.26	0.03	0.07	0.08
a17:0	1.67	1.36	1.53	1.45	1.48	1.22	1.24	1.49	1.53
±	0.15	0.09	0.10	0.09	0.13	0.37	0.04	0.07	0.12
br17:0 (mixpeak)	3.19	2.92	2.71	2.94	3.52	2.95	2.92	2.45	2.39
±	0.17	0.15	0.21	0.05	0.90	0.28	0.94	0.33	0.17
n17:0	0.65	0.51	0.54	0.59	0.61	0.43	0.51	0.49	0.53
±	0.04	0.05	0.07	0.04	0.08	0.07	0.08	0.12	0.12
br10,18:0	1.65	1.59	1.41	1.80	1.97	1.49	1.51	1.50	1.15
±	0.09	0.12	0.14	0.10	0.10	0.39	0.35	0.38	0.07
i18:0	0.82	0.82	0.77	0.79	0.79	0.70	0.74	0.69	0.77
±	0.00	0.02	0.01	0.01	0.03	0.15	0.04	0.04	0.01
n18:0	3.88	3.54	3.60	3.68	3.48	3.65	3.32	3.23	3.47
±	0.16	0.26	0.28	0.14	0.08	0.57	0.51	0.59	0.44
cy17:0	3.07	2.82	2.80	2.99	2.87	2.42	2.73	2.52	2.56
±	0.19	0.20	0.22	0.08	0.10	0.69	0.26	0.20	0.16
cy18:0	0.40	0.38	0.36	0.41	0.45	0.27	0.29	0.23	0.35
±	0.01	0.02	0.08	0.07	0.02	0.08	0.04	0.08	0.10
br10,19:0	1.07	0.85	0.86	1.10	1.18	0.88	0.83	0.98	0.68
±	0.17	0.12	0.14	0.07	0.07	0.31	0.18	0.33	0.06
br12,19:0	0.39	-	0.36	0.38	0.33	0.29	-	0.25	-
±	0.02	-	0.01	0.03	0.04	0.03	-	0.02	-
cy19:0	16.55	18.44	16.66	16.08	15.64	13.72	16.01	14.44	16.10
±	1.04	0.82	0.84	1.12	1.14	3.74	2.05	0.58	1.17
n20:0	3.26	3.20	3.51	3.42	3.18	2.89	2.74	2.78	2.89
±	0.24	0.21	0.19	0.14	0.34	0.34	0.60	0.49	0.14
n22:0	5.28	5.06	5.87	5.71	5.40	4.66	4.48	4.61	4.50
±	0.26	0.54	0.17	0.16	0.85	0.40	0.99	1.05	0.21
n24:0	2.91	2.62	2.96	3.52	3.33	2.78	2.27	2.29	2.05
±	0.24	0.49	0.30	0.10	0.63	0.29	0.45	0.80	0.16
dic18:0	-	0.29	0.17	-	-	0.36	-	0.34	0.59
±	-	-	0.01	-	-	-	-	0.13	0.45
dic20:0	0.63	0.45	0.69	0.34	0.42	0.59	-	0.99	1.16
±	0.11	0.45	0.27	0.05	-	0.59	-	0.11	0.77
dic22:0	0.83	0.70	1.21	0.89	0.46	9.27	0.20	1.08	1.62
±	0.40	0.37	0.63	0.74	0.40	15.14	0.03	0.14	1.09
SATFA total	95.68	91.54	90.48	90.82	89.82	90.25	85.48	85.46	87.22
±	0.82	2.54	2.50	1.19	1.07	4.31	3.26	4.41	1.49
15:1 ω 8	0.03	0.05	0.05	0.04	0.06	0.05	0.06	0.06	0.08
±	0.02	0.01	0.01	0.02	0.01	-	0.00	0.02	0.02
16:1 ω 5	0.24	0.48	0.37	0.39	0.46	0.44	0.56	0.73*	0.98*
±	0.26	0.05	0.15	0.13	0.14	0.18	0.11	0.02	0.06
16:1 ω 9	0.06	0.12	0.08	0.10	0.10	0.09	0.13	0.16*	0.20*
±	0.06	0.02	0.03	0.04	0.01	0.03	0.03	0.01	0.03
16:1 ω 7 cis	0.26	0.64	0.52	0.61	0.60	0.55	0.72	1.09*	1.28*
±	0.23	0.06	0.14	0.17	0.10	0.20	0.15	0.11	0.20
16:1 ω 7 trans	0.05	0.13	0.07	0.12	0.14	0.10	0.15	0.18*	0.18*
±	0.05	0.02	0.03	0.04	0.03	0.05	0.06	0.01	0.02
17:1 ω 8 cis	0.02	0.09	0.06	0.07*	0.08*	0.07	0.08	0.11*	0.13*
±	0.02	0.01	0.00	0.03	0.02	0.02	0.02	0.00	0.01
17:1 ω 8 trans	0.05	0.19	0.14	0.16*	0.17*	0.16	0.20*	0.28*	0.36*
±	0.05	0.02	0.03	0.03	0.03	0.05	0.02	0.00	0.04
18:1 ω 9	0.68	2.02	1.51	1.91	2.04	1.73	2.27	2.69	3.43
±	0.68	0.26	0.52	0.54	0.16	0.55	0.27	-	-
18:1 ω 7	0.42	1.14	0.97	1.15	1.10	1.11	1.39	2.39*	3.34*
±	0.32	0.19	0.23	0.29	0.04	0.42	0.19	0.71	1.09
MUFA total	1.82	4.84	3.73	4.55	4.73	4.27	5.55	6.35	7.71
±	1.68	0.48	1.14	1.26	0.49	1.48	0.74	1.05	0.79
18:2 ω 6,9	1.94	2.96	4.69	3.61	4.41	4.32	7.57	6.29*	3.72
±	1.36	1.90	1.70	1.84	1.24	2.49	2.92	3.94	1.48
20:4 ω 6,9,12,14	0.42	0.25	0.31	0.34	0.47	0.47	0.49	0.91*	1.07
±	0.17	0.10	0.06	0.15	0.06	0.22	0.11	0.65	0.35
18:3	0.29	0.42	0.80	0.67	0.57	0.69	0.91	0.97	0.41
±	0.22	0.35	0.26	0.45	0.25	0.49	0.50	0.88	0.05
PUFA total	2.51	3.62	5.79	4.63	5.45	5.48	8.98	8.18	5.06
±	1.82	2.34	2.02	2.43	1.46	3.14	3.36	5.46	2.02

b)

FA [mol %]	labelling time [d]		
	0.0	10.5	20.5
br12:0	0.20	0.48*	0.39*
±	0.03	0.17	0.15
i14:0	0.28	0.32	0.36
±	0.01	0.03	0.04
a14:0	2.10	2.10	2.08
±	0.16	0.23	0.23
i15:0	7.50	7.14	7.89
±	0.08	0.62	0.31
a15:0	3.68	3.24	3.59
±	0.17	0.31	0.29
n15:0	0.65	0.62	0.54
±	0.08	0.10	0.09
i16:0	5.46	4.75	4.09
±	0.68	0.77	0.72
br10,17:0	0.82	2.41	2.29
±	0.07	2.46	0.21
a16:0	16.30	14.31	15.03
±	0.82	2.02	0.31
i17:0	7.96	6.84	6.67
±	0.32	0.90	0.68
br11,17:0	1.46	1.20	1.30
±	0.05	0.12	0.08
a17:0	1.67	1.50	1.51
±	0.05	0.21	0.08
br17:0 (mixpeak)	3.23	2.72	2.49
±	0.21	0.29	0.15
n17:0	0.59	0.54	0.50
±	0.03	0.07	0.11
br10,18:0	1.73	1.47	1.20
±	0.20	0.36	0.28
i18:0	0.84	0.65	0.68
±	0.02	0.20	0.27
n18:0	3.91	3.35	3.51
±	0.18	0.38	0.59
cy17:0	2.93	2.57	2.68
±	0.16	0.21	0.19
cy18:0	0.45	0.46	0.46
±	0.05	0.10	0.05
br10,19:0	1.05	0.90	0.71
±	0.14	0.15	0.09
br12,19:0	0.39	0.32	0.36
±	0.00	0.00	0.08
cy19:0	17.17	15.05	17.20
±	0.95	1.46	0.26
n20:0	3.99	3.32	3.39
±	0.16	0.38	0.16
n22:0	6.36	5.29	5.24
±	0.26	0.59	0.22
n24:0	3.24	2.64	2.60
±	0.30	0.58	0.52
dic18:0	0.13	0.66	0.58
±	0.01	0.73	0.30
dic20:0	0.65	1.23	1.68
±	0.35	1.17	0.60
dic22:0	1.02	1.62	2.39
±	0.32	0.85	1.15
SATFA total	95.23	91.50	90.64
±	0.70	0.50	1.33
15:1 ω 8	0.06	0.06	0.05
±	0.02	0.02	0.03
16:1 ω 5	0.49	0.51*	0.77*
±	0.18	0.13	0.18
16:1 ω 9	0.14	0.12	0.14
±	0.03	0.03	0.04
16:1 ω 7 cis	0.48	0.58	0.77*
±	0.08	0.13	0.15
16:1 ω 7 trans	0.13	0.13	0.15
±	0.04	0.02	0.03
17:1 ω 8 cis	0.06	0.09	0.10*
±	-	0.03	0.02
17:1 ω 8 trans	0.16	0.18	0.30
±	0.03	0.03	0.05
18:1 ω 9	1.31	1.82	2.76*
±	0.51	0.40	0.35
18:1 ω 7	0.66	1.27	1.65*
±	0.28	0.45	0.21
MUFA total	3.47	6.06	6.66
±	1.01	1.40	0.97
18:2 ω 6,9	1.08	1.95	1.95
±	0.39	0.80	0.24
20:4 ω 6,9,12,14	0.23	0.38	0.75*
±	0.02	0.11	0.40
18:3	-	0.34	-
±	-	-	-
PUFA total	1.30	2.44	2.70
±	0.40	1.05	0.64

Tab. VIII-6: Carbon isotopic signature [$\delta^{13}\text{C}$ in ‰ V-PDB] in individual PLFA in rhizosphere soil (a) and bulk soil (b) in the course of the greenhouse continuous labelling experiment (mean \pm standard deviation, n = 3). Asterisks (*) represent statistically significant differences (p < 0.05) compared to the beginning of labelling.

	a)										b)			
	$\delta^{13}\text{C}$ [‰ V-PDB]	labelling time [d]									$\delta^{13}\text{C}$ [‰ V-PDB]	labelling time [d]		
	0.0	0.5	1.0	1.5	2.5	3.5	5.5	10.5	20.5		0.0	10.5	20.5	
br12:0	-31.24	-	-30.60	-32.53	-31.22	-29.13	-29.50	-31.40	-29.48	br12:0	-20.21	-31.59	-29.40	
\pm	0.70	-	0.00	2.45	1.77	0.85	0.71	1.18	0.71	\pm	17.52	0.38	0.63	
i14:0	-25.53	-24.05	-25.97	-26.16	-26.47	-24.48	-25.19	-24.94	-23.13	i14:0	-26.43	-27.42	-24.92	
\pm	0.70	0.78	3.18	0.35	0.27	0.74	1.49	1.08	0.90	\pm	1.76	1.39	1.24	
a14:0	-31.58	-30.34	-31.12	-30.80	-30.98	-30.60	-29.75	-29.57	-27.77*	a14:0	-31.97	-30.92*	-29.72*	
\pm	0.88	0.90	0.90	0.32	1.01	0.38	0.57	1.56	0.21	\pm	0.64	0.32	0.18	
i15:0	-25.04	-23.89	-24.24	-24.07	-24.36	-23.51*	-23.26*	-23.26*	-22.04*	i15:0	-23.84	-24.72	-23.25	
\pm	0.07	0.24	0.38	0.09	0.16	0.59	0.43	0.57	0.97	\pm	0.60	0.57	0.36	
a15:0	-24.09	-23.26	-23.90	-24.51	-24.16	-22.90	-23.54	-23.18	-21.48*	a15:0	-23.96	-24.09	-22.91	
\pm	0.28	1.16	1.29	0.22	0.24	0.51	1.12	0.89	0.89	\pm	0.74	0.44	0.89	
n15:0	-28.16	-27.26	-26.24	-28.75	-28.32	-28.61	-28.28	-26.80	-25.86	n15:0	-27.42	-28.42	-28.93	
\pm	1.68	2.12	0.99	0.41	1.73	0.54	0.55	2.13	0.93	\pm	1.57	0.34	0.86	
i16:0	-25.99	-25.55	-25.64	-25.80	-25.66	-24.98	-26.16	-24.22	-24.05*	i16:0	-25.61	-25.32	-25.17	
\pm	0.45	1.20	0.93	0.06	0.76	0.43	1.05	0.73	0.52	\pm	0.60	0.60	1.12	
br10,17:0	-27.12	-24.09	-29.59	-	-	-27.73	-	-27.74	-26.13	br10,17:0	-17.60	-27.81	-28.64	
\pm	-	-	2.65	-	-	-	-	2.68	2.50	\pm	15.25	3.40	1.63	
a16:0	-28.02	-26.99	-27.05	-26.35	-26.30	-24.87	-25.60	-20.18*	-20.39*	a16:0	-27.33	-25.67	-25.47	
\pm	0.11	0.53	0.82	0.13	0.76	1.22	0.39	3.85	0.79	\pm	0.23	1.66	0.43	
i17:0	-25.68	-24.66	-25.26	-25.49	-25.45	-25.26	-25.54	-24.84	-24.70	i17:0	-25.14	-25.29	-25.35	
\pm	0.38	0.65	0.82	0.11	0.17	0.33	0.31	0.59	0.49	\pm	0.17	0.49	0.49	
br11,17:0	-24.33	-23.23	-24.43	-25.15	-25.45	-24.12	-24.05	-25.07	-24.05	br11,17:0	-24.47	-24.91	-24.18	
\pm	0.52	0.63	0.66	0.57	0.35	0.31	0.37	0.32	0.27	\pm	0.43	0.36	0.41	
a17:0	-23.34	-21.49	-22.26	-23.07	-23.24	-21.92	-22.39	-23.06	-22.34	a17:0	-22.91	-23.27	-23.36	
\pm	0.79	1.19	1.44	0.40	0.25	0.61	0.53	0.33	0.79	\pm	0.26	0.34	0.78	
br17:0 (mixpeak)	-25.68	-24.43	-24.94	-25.63	-25.73	-25.50	-25.30	-25.21	-24.92	br17:0 (mixpeak)	-25.44	-25.54	-25.31	
\pm	0.17	0.51	0.89	0.06	0.53	0.19	0.24	0.31	0.86	\pm	0.16	0.31	0.60	
n17:0	-26.92	-26.91	-27.06	-26.94	-27.41	-28.80	-28.14	-25.07	-25.13	n17:0	-27.36	-26.36	-28.42	
\pm	0.61	0.10	0.58	0.51	0.62	1.52	2.02	0.72	1.71	\pm	0.79	0.14	0.88	
br10,18:0	-25.42	-23.71	-25.00	-25.69	-25.70	-25.80	-25.45	-25.32	-25.40	br10,18:0	-25.47	-25.46	-25.23	
\pm	0.44	0.88	0.84	0.06	0.17	0.10	0.75	0.17	0.38	\pm	0.71	0.10	0.43	
i18:0	-25.29	-23.60	-24.79	-25.13	-25.19	-24.71	-25.04	-24.77	-23.65	i18:0	-24.89	-26.17	-23.89	
\pm	1.01	0.84	0.48	0.45	0.88	0.87	1.16	0.25	0.37	\pm	1.20	1.22	0.77	
n18:0	-25.91	-24.33	-25.11	-25.31	-25.30	-25.17	-24.19	-22.09*	-20.41*	n18:0	-25.21	-24.68	-24.15*	
\pm	0.11	0.37	0.98	0.16	0.53	0.88	1.53	1.34	0.51	\pm	0.22	0.51	0.44	
cy17:0	-25.53	-24.50	-25.22	-25.20	-25.17	-25.37	-25.16	-23.89*	-23.34*	cy17:0	-25.06	-24.95	-25.36	
\pm	0.60	0.56	0.52	0.18	0.08	0.48	0.55	0.40	0.76	\pm	0.35	0.45	0.26	
cy18:0	-24.70	-22.66	-23.44	-24.80	-25.02	-25.80	-25.21	-28.76	-26.64	cy18:0	-25.05	-25.77	-24.64	
\pm	1.51	1.31	1.07	0.64	0.93	2.37	1.78	3.76	1.34	\pm	1.07	0.58	1.27	
br10,19:0	-24.15	-21.76	-22.63	-23.70	-24.06	-24.22	-23.39	-24.16	-25.03	br10,19:0	-23.33	-23.91	-23.61	
\pm	0.35	0.70	1.14	0.23	0.13	0.56	0.30	0.45	0.64	\pm	0.88	0.38	0.36	
br12,19:0	-24.19	-	-25.93	-25.56	-26.14	-27.41	-	-25.29	-	br12,19:0	-16.94	-18.53	-25.15	
\pm	0.60	-	0.16	0.81	0.43	1.14	-	1.25	-	\pm	14.67	16.05	2.21	
cy19:0	-27.29	-26.76	-27.00	-26.94	-26.93	-26.89	-26.85	-26.41*	-25.59*	cy19:0	-26.87	-27.01	-27.00	
\pm	0.24	0.19	0.12	0.10	0.03	0.19	0.09	0.53	0.23	\pm	0.21	0.06	0.33	
n20:0	-27.57	-26.02*	-27.03	-27.95	-28.02	-27.47	-26.78	-27.62	-26.27*	n20:0	-27.61	-28.47	-27.10	
\pm	0.34	0.19	1.03	0.07	0.38	0.24	0.54	0.34	0.87	\pm	0.43	0.22	0.09	
n22:0	-28.72	-26.56*	-28.09	-28.99	-29.19	-28.51	-27.54	-28.42	-27.56	n22:0	-29.02	-29.28	-27.80*	
\pm	0.23	0.30	1.49	0.14	0.18	0.21	0.41	1.07	1.07	\pm	0.16	0.23	0.37	
n24:0	-28.79	-25.81*	-27.39	-29.15	-29.10	-28.41	-27.12	-28.35	-25.74*	n24:0	-27.84	-27.63	-27.37	
\pm	0.53	0.30	1.27	0.22	0.24	0.52	0.29	1.48	1.27	\pm	1.64	1.54	0.66	
dic18:0	-	-26.73	-32.67	-	-	-30.35	-	-31.37	-27.89	dic18:0	-20.12	-21.52	-29.70	
\pm	-	-	0.71	-	-	-	-	0.29	3.25	\pm	17.42	18.64	0.91	
dic20:0	-29.60	-23.76	-28.82	-29.24	-30.82	-28.56	-	-29.49	-27.96	dic20:0	-29.57	-29.57	-28.02	
\pm	2.05	2.35	3.58	0.01	-	0.34	-	0.80	0.72	\pm	1.60	1.41	0.80	
dic22:0	-24.33	-27.16	-29.13	-29.65	-30.95	-27.16	-27.94	-29.34	-27.25	dic22:0	-30.02	-29.64	-29.68	
\pm	9.07	0.81	1.95	0.90	1.35	1.42	3.43	0.34	0.89	\pm	0.55	0.66	1.09	
15:1ω8	-24.09	-23.03	-22.34	-23.70	-24.40	-25.15	-22.46	-24.70	-25.43	15:1ω8	-21.59	-24.65	-23.15	
\pm	2.42	0.98	2.98	0.96	0.04	0.00	0.73	0.41	1.19	\pm	1.76	1.00	2.78	
16:1ω5	-22.36	-20.69	-20.65	-22.18	-22.00	-20.53	-20.70	-21.52*	-21.35*	16:1ω5	-18.91	-20.53*	-20.78*	
\pm	1.18	0.39	0.50	0.74	0.67	0.62	0.17	0.24	0.11	\pm	0.77	0.47	0.28	
16:1ω9	-23.35	-21.70	-23.08	-23.40	-24.05	-21.09	-21.06	-20.64*	-19.25*	16:1ω9	-22.55	-22.00	-22.64	
\pm	0.79	0.44	0.74	0.97	0.42	0.70	2.38	1.45	0.21	\pm	0.59	0.51	0.62	
16:1ω7 cis	-26.69	-25.38	-25.10	-25.54	-25.80	-24.95	-24.18	-22.15*	-21.18*	16:1ω7 cis	-23.72	-25.35	-25.94	
\pm	1.65	0.36	0.37	0.51	0.52	0.90	0.82	2.46	1.39	\pm	0.51	0.46	1.17	
16:1ω7 trans	-26.46	-27.26	-27.35	-27.14	-27.72	-31.99	-26.36	-26.94	-25.91	16:1ω7 trans	-27.32	-27.16	-26.24	
\pm	1.19	1.11	1.55	0.67	0.37	8.67	1.11	0.42	0.37	\pm	2.06	0.83	0.61	
17:1ω8 cis	-28.28	-27.66	-25.78	-29.01	-27.57	-27.06	-25.74	-25.91	-27.14	17:1ω8 cis	-8.55	-26.69	-28.68	
\pm	1.27	1.24	0.76	0.54	2.11	3.87	2.38	1.19	0.22	\pm	14.81	1.39	2.14	
17:1ω8 trans	-36.27	-29.18	-29.74	-28.82	-30.45	-29.70	-31.86	-32.97	-31.07	17:1ω8 trans	-30.47	-33.44	-29.20	
\pm	3.33	0.99	2.21	1.24	2.05	1.57	1.86	0.99	1.84	\pm	1.85	2.36	0.58	
18:1ω9	-25.19	-24.34	-22.40	-24.25	-24.26	-23.02	-23.33	-22.69	-21.35	18:1ω9	-24.78	-22.67	-23.52	
\pm	1.59	0.77	0.30	1.35	1.14	1.04	0.84	1.53	0.00	\pm	0.40	2.08	1.67	
18:1ω7	-29.93	-33.53	-29.06	-28.92	-28.43	-29.71	-27.80	-23.54*	-21.55*	18:1ω7	-32.66	-28.46	-27.22	
\pm	2.74	2.89	2.88	1.07	0.12	4.18	1.88	3.07	1.49	\pm	2.79	1.23	1.16	
18:2ω6,9	-29.22	-27.83	-27.91	-24.83	-23.20	-20.87	-22.06	-3.65*	1.17*	18:2ω6,9	-27.64	-22.29	-17.77	
\pm	0.40	0.12	0.87	1.83	1.43	3.57	1.95	10.10	3.34	\pm	0.82	9.08	5.16	
20:4ω6,9,12,14	-29.66	-27.59	-30.04	-28.07	-27.94	-27.40	-28.07	-25.29	-13.48*	20:4ω6,9,12,14	-23.60	-27.92	-23.55	
\pm	0.74	1.87	1.90	1.46	0.39	0.99	2.72	3.20	2.48	\pm	0.64	2.54	1.93	
18:3	-31.94	-32.16	-33.95	-29.79	-28.46	-25.44	-26.12	3.50*	13.41*	18:3	-	-16.98	-	
\pm	2.76	2.99	0.72	0.47	2.31	5.74	3.34	5.76	4.91	\pm	-	-	-	

Tab. VIII-7: Abundances of individual PLFA [nmol g⁻¹ DS, a], contribution to total PLFA [mol%, b] and carbon isotopic signature [$\delta^{13}\text{C}$ in ‰ V-PDB, c] in unplanted soil at the beginning and at the end of the experiment (mean \pm standard deviation, n = 3).

a)			b)			c)		
FA [nmol g ⁻¹ DS]	labelling time [d]		FA [mol %]	labelling time [d]		$\delta^{13}\text{C}$ [‰ V-PDB]	labelling time [d]	
	0.0	20.5		0.0	20.5		0.0	20.5
br12:0	0.29	0.38	br12:0	0.28	0.34	br12:0	-28.19	-31.72
±	-	0.07	±	-	0.02	±	-	0.01
i14:0	0.27	0.35	i14:0	0.26	0.32	i14:0	-23.22	-27.46
±	0.13	0.01	±	0.11	0.06	±	0.51	1.97
a14:0	1.43	2.02	a14:0	1.55	2.03	a14:0	-28.88	-32.25
±	0.90	0.45	±	0.68	0.08	±	0.60	0.44
i15:0	6.30	7.29	i15:0	7.06	7.34	i15:0	-22.52	-24.47
±	2.69	1.38	±	1.46	0.19	±	0.15	0.36
a15:0	2.66	3.35	a15:0	2.95	3.33	a15:0	-22.76	-24.46
±	1.33	0.90	±	0.84	0.20	±	0.99	0.46
n15:0	0.49	0.54	n15:0	0.56	0.55	n15:0	-25.59	-28.88
±	0.16	0.12	±	0.08	0.08	±	1.26	0.57
i16:0	4.86	4.30	i16:0	5.62	4.30	i16:0	-25.34	-26.13
±	1.22	1.00	±	0.35	0.11	±	1.37	0.16
br10,17:0	0.57	1.75	br10,17:0	0.89	1.79	br10,17:0	-31.71	-27.68
±	-	1.23	±	-	1.23	±	-	3.27
a16:0	14.57	14.10	a16:0	16.74	14.20	a16:0	-26.88	-27.32
±	3.85	2.70	±	0.78	0.34	±	1.04	0.15
i17:0	7.45	6.89	i17:0	8.55	6.87	i17:0	-25.35	-25.96
±	2.00	1.76	±	0.53	0.29	±	0.26	0.32
br11,17:0	1.43	1.27	br11,17:0	1.66	1.27	br11,17:0	-23.54	-24.98
±	0.30	0.33	±	0.06	0.05	±	0.44	0.28
a17:0	1.39	1.55	a17:0	1.59	1.55	a17:0	-22.95	-23.48
±	0.39	0.40	±	0.13	0.08	±	0.05	0.12
br17:0 (mixpeak)	2.77	2.84	br17:0 (mixpeak)	3.20	2.84	br17:0 (mixpeak)	-24.94	-25.83
±	0.67	0.69	±	0.13	0.08	±	0.09	0.07
n17:0	0.44	0.62	n17:0	0.51	0.62	n17:0	-27.04	-27.29
±	0.09	0.12	±	0.04	0.02	±	0.84	0.77
br10,18:0	1.58	1.56	br10,18:0	1.82	1.52	br10,18:0	-24.78	-25.92
±	0.35	0.60	±	0.04	0.31	±	0.24	0.21
i18:0	0.83	0.77	i18:0	0.96	0.75	i18:0	-24.05	-25.46
±	0.18	0.36	±	0.04	0.26	±	0.31	1.12
n18:0	3.17	3.63	n18:0	3.68	3.66	n18:0	-24.61	-25.12
±	0.69	0.67	±	0.22	0.18	±	0.51	0.21
cy17:0	2.58	2.85	cy17:0	2.96	2.84	cy17:0	-24.89	-25.32
±	0.66	0.73	±	0.15	0.12	±	0.36	0.11
cy18:0	0.37	0.59	cy18:0	0.43	0.59	cy18:0	-24.87	-24.87
±	0.05	0.15	±	0.05	0.03	±	1.11	0.98
br10,19:0	0.88	1.02	br10,19:0	1.03	1.02	br10,19:0	-22.82	-24.36
±	0.16	0.29	±	0.08	0.08	±	0.45	0.80
br12,19:0	-	-	br12,19:0	-	-	br12,19:0	-	-
±	-	-	±	-	-	±	-	-
cy19:0	16.35	17.88	cy19:0	18.97	18.07	cy19:0	-26.86	-26.95
±	3.52	3.20	±	1.30	1.26	±	0.16	0.10
n20:0	3.14	3.88	n20:0	3.64	3.86	n20:0	-26.79	-27.27
±	0.68	1.08	±	0.19	0.32	±	0.40	0.36
n22:0	4.92	6.10	n22:0	5.70	6.07	n22:0	-27.12	-28.75
±	1.17	1.76	±	0.45	0.53	±	0.40	0.16
n24:0	2.71	2.98	n24:0	3.09	2.97	n24:0	-26.71	-29.17
±	0.88	0.86	±	0.33	0.35	±	0.90	0.54
dic18:0	0.16	0.62	dic18:0	0.25	0.64	dic18:0	-27.28	-30.33
±	-	0.37	±	-	0.38	±	-	2.28
dic20:0	0.73	1.62	dic20:0	0.93	1.64	dic20:0	-27.97	-30.52
±	0.06	0.49	±	0.39	0.46	±	0.74	1.07
dic22:0	0.81	1.60	dic22:0	1.00	1.64	dic22:0	-29.51	-30.35
±	0.45	0.13	±	0.66	0.25	±	2.49	1.20
SATFA total	82.13	92.09	SATFA total	94.53	92.42	15:1 ω 8	-22.59	-24.74
±	20.97	19.79	±	1.65	0.71	±	1.58	-
15:1 ω 8	0.06	0.07	15:1 ω 8	0.07	0.06	16:1 ω 5	-19.34	-20.54
±	0.02	-	±	0.02	-	±	0.84	0.93
16:1 ω 5	0.51	0.72	16:1 ω 5	0.59	0.72	16:1 ω 9	-22.03	-23.07
±	0.15	0.18	±	0.09	0.04	±	1.31	0.64
16:1 ω 9	0.13	0.20	16:1 ω 9	0.15	0.23	16:1 ω 7 cis	-24.18	-25.82
±	0.04	0.09	±	0.05	0.14	±	0.98	0.18
16:1 ω 7 cis	0.54	0.52	16:1 ω 7 cis	0.64	0.49	16:1 ω 7 trans	-27.05	-27.77
±	0.05	0.36	±	0.12	0.24	±	1.06	0.81
16:1 ω 7 trans	0.13	0.15	16:1 ω 7 trans	0.16	0.14	17:1 ω 8 cis	-27.44	-27.57
±	0.03	0.06	±	0.04	0.03	±	-	1.92
17:1 ω 8 cis	0.08	0.11	17:1 ω 8 cis	0.09	0.11	17:1 ω 8 trans	-29.91	-29.23
±	-	0.03	±	-	0.00	±	0.27	2.24
17:1 ω 8 trans	0.19	0.29	17:1 ω 8 trans	0.23	0.29	18:1 ω 9	-24.69	-25.33
±	0.01	0.06	±	0.05	0.02	±	2.07	0.49
18:1 ω 9	1.37	2.24	18:1 ω 9	1.70	2.22	18:1 ω 7	-32.52	-27.73
±	0.47	0.88	±	0.84	0.48	±	3.60	0.65
18:1 ω 7	0.72	1.50	18:1 ω 7	0.93	1.52	18:2 ω 6,9	-26.98	-26.44
±	0.42	0.46	±	0.66	0.43	±	0.63	0.36
MUFA total	3.68	5.68	MUFA total	1.65	0.71	20:4 ω 6,9,12,14	-24.03	-25.22
±	0.64	1.85	±	1.88	1.38	±	-	1.11
18:2 ω 6,9	0.75	1.37	18:2 ω 6,9	0.83	1.41	18:3	-31.24	-
±	0.48	0.28	±	0.46	0.35	±	-	-
20:4 ω 6,9,12,14	0.22	0.49	20:4 ω 6,9,12,14	0.24	0.50	PUFA total	0.88	1.86
±	-	0.05	±	-	0.06	±	0.67	0.30
18:3	0.16	-	18:3	0.18	-			
±	-	-	±	-	-			
PUFA total	0.88	1.86	PUFA total	0.96	1.91			
±	0.67	0.30	±	0.69	0.40			

3.2 Recovery of photosynthate ^{13}C in plant parts and rhizosphere organisms of beech (*Fagus sylvatica* L.) at two different growth stages in the open-top chamber experiment (B)

Tab. VIII-8: PLFA abundances [$\text{nmol g}^{-1}\text{ DS}$] of individual PLFA in rhizosphere and bulk soil (mean \pm standard deviation, $n = 3$) of young beech trees in open-top chambers harvested at two different time points (T1 = physiological active, mid-June and T2 = senescent, mid-October) in the vegetation period. Letters (a, b) indicate statistically significant differences ($p < 0.05$) between rhizosphere and bulk soil.

FA [$\text{nmol g}^{-1}\text{ DS}$]		T1		T2	
		ambient	depleted	ambient	depleted
i14:0	rhiz	0.40 \pm 0.06 ^a	0.60 \pm 0.13 ^a	0.37 \pm 0.04 ^a	- \pm -
	bulk	0.09 \pm 0.02 ^b	0.09 \pm - ^b	0.14 \pm - ^b	0.10 \pm 0.02
i15:0	rhiz	2.70 \pm 0.61 ^a	2.51 \pm 0.81 ^a	2.84 \pm 0.28 ^a	1.39 \pm 0.73
	bulk	1.54 \pm 0.14 ^b	1.33 \pm 0.42 ^b	1.30 \pm 0.61 ^b	1.64 \pm 0.46
a15:0	rhiz	1.69 \pm 0.23 ^a	1.62 \pm 0.53 ^a	2.53 \pm 1.13	0.91 \pm 0.44
	bulk	0.99 \pm 0.11 ^b	0.99 \pm 0.34 ^b	0.99 \pm 0.60	0.98 \pm 0.21
i16:0	rhiz	2.08 \pm 0.28 ^a	2.02 \pm 0.38 ^a	2.62 \pm 0.75 ^a	1.16 \pm 0.35
	bulk	0.89 \pm 0.03 ^b	1.01 \pm 0.15 ^b	0.86 \pm 0.23 ^b	0.97 \pm 0.24
a16:0	rhiz	7.64 \pm 0.62 ^a	8.45 \pm 0.45 ^a	8.71 \pm 8.14	6.34 \pm 0.90 ^a
	bulk	3.23 \pm 0.36 ^b	3.12 \pm 0.44 ^b	3.63 \pm 1.82	3.45 \pm 0.35 ^b
i17:0	rhiz	1.38 \pm 0.15 ^a	1.25 \pm 0.21 ^a	1.35 \pm 0.02 ^a	0.91 \pm 0.36 ^a
	bulk	0.68 \pm 0.05 ^b	0.55 \pm 0.12 ^b	0.42 \pm 0.02 ^b	0.48 \pm 0.06 ^b
br9,17:0	rhiz	2.54 \pm 0.42 ^a	2.38 \pm 0.56 ^a	2.85 \pm 0.01 ^a	1.68 \pm 0.43
	bulk	1.23 \pm 0.13 ^b	1.08 \pm 0.13 ^b	0.93 \pm 0.10 ^b	1.15 \pm 0.18
br10,17:0	rhiz	0.93 \pm 0.17 ^a	1.07 \pm 0.24 ^a	1.01 \pm 0.16 ^a	0.63 \pm 0.23 ^a
	bulk	0.46 \pm 0.04 ^b	0.32 \pm 0.08 ^b	0.29 \pm 0.03 ^b	0.32 \pm 0.05 ^b
br11,17:0	rhiz	2.70 \pm 0.30 ^a	2.62 \pm 0.48 ^a	3.32 \pm 0.82 ^a	1.92 \pm 0.62 ^a
	bulk	1.11 \pm 0.16 ^b	1.05 \pm 0.18 ^b	1.06 \pm 0.08 ^b	1.06 \pm 0.15 ^b
cy17:0	rhiz	1.65 \pm 0.26 ^a	1.51 \pm 0.26 ^a	1.64 \pm 0.05 ^a	1.09 \pm 0.27
	bulk	0.89 \pm 0.13 ^b	0.92 \pm 0.16 ^b	0.70 \pm 0.25 ^b	0.90 \pm 0.15
i18:0	rhiz	2.50 \pm 0.21 ^a	3.10 \pm 0.80 ^a	2.23 \pm 1.50	2.17 \pm 0.18 ^a
	bulk	1.10 \pm 0.17 ^b	0.88 \pm 0.09 ^b	1.27 \pm 0.57	0.94 \pm 0.01 ^b
cy18:0	rhiz	9.51 \pm 1.74 ^a	9.17 \pm 2.52 ^a	6.42 \pm 4.13 ^a	6.09 \pm 2.03 ^a
	bulk	0.17 \pm 0.06 ^b	0.10 \pm 0.05 ^b	0.05 \pm 0.02 ^b	0.08 \pm 0.05 ^b
br10,18:0	rhiz	0.60 \pm 0.11 ^a	0.70 \pm 0.01 ^a	0.77 \pm 0.16 ^a	- \pm -
	bulk	0.27 \pm 0.02 ^b	0.29 \pm 0.03 ^b	0.28 \pm 0.06 ^b	0.31 \pm 0.07
br10,19:0	rhiz	1.33 \pm 0.13 ^a	1.32 \pm 0.38 ^a	1.71 \pm 0.49 ^a	0.96 \pm 0.18 ^a
	bulk	0.58 \pm 0.07 ^b	0.61 \pm 0.12 ^b	0.54 \pm 0.17 ^b	0.61 \pm 0.13 ^b
cy19:0	rhiz	9.51 \pm 1.74 ^a	9.17 \pm 2.52 ^a	6.42 \pm 4.13	6.09 \pm 2.03 ^a
	bulk	4.02 \pm 0.67 ^b	3.40 \pm 0.70 ^b	2.68 \pm 0.30	3.02 \pm 0.23 ^b
n20:0	rhiz	1.34 \pm 0.07 ^a	1.31 \pm 0.33 ^a	1.41 \pm 0.20 ^a	1.24 \pm 0.08 ^a
	bulk	0.53 \pm 0.02 ^b	0.55 \pm 0.05 ^b	0.54 \pm 0.02 ^b	0.57 \pm 0.01 ^b
n22:0	rhiz	2.83 \pm 0.26 ^a	1.91 \pm 0.23 ^a	2.22 \pm 1.23	2.44 \pm 0.39 ^a
	bulk	1.01 \pm 0.15 ^b	0.83 \pm 0.04 ^b	1.07 \pm 0.11	1.16 \pm 0.04 ^b
n24:0	rhiz	1.63 \pm 0.16 ^a	1.80 \pm 0.55 ^a	1.73 \pm 0.04 ^a	1.37 \pm 0.27
	bulk	1.23 \pm 0.18 ^b	0.80 \pm 0.11 ^b	1.22 \pm 0.36 ^b	1.39 \pm 0.34
SATFA total	rhiz	52.84 \pm 6.96^a	52.07 \pm 8.09^a	42.08 \pm 31.69	36.07 \pm 8.03^a
	bulk	19.98 \pm 1.47^b	17.86 \pm 2.24^b	17.87 \pm 4.31	19.10 \pm 2.58^b
16:1 ω 5	rhiz	0.55 \pm 0.10 ^a	0.70 \pm 0.21 ^a	0.57 \pm 0.26 ^a	0.50 \pm 0.22 ^a
	bulk	0.18 \pm 0.01 ^b	0.11 \pm - ^b	0.14 \pm 0.02 ^b	0.12 \pm 0.03 ^b
16:1 ω 7	rhiz	1.37 \pm 0.33 ^a	1.37 \pm 1.03 ^a	1.53 \pm 0.78	0.67 \pm 0.48
	bulk	0.37 \pm 0.24 ^b	0.71 \pm - ^b	0.75 \pm 0.62	0.80 \pm 0.19
17:1 ω 8	rhiz	0.67 \pm 0.16 ^a	0.93 \pm 0.34 ^a	0.62 \pm 0.28 ^a	0.37 \pm 0.06 ^a
	bulk	0.16 \pm 0.03 ^b	0.11 \pm - ^b	0.12 \pm 0.03 ^b	0.11 \pm 0.03 ^b
18:1 ω 9	rhiz	2.51 \pm 0.26 ^a	2.24 \pm 1.83 ^a	2.78 \pm 1.62	1.95 \pm 0.07 ^a
	bulk	0.63 \pm 0.36 ^b	0.92 \pm - ^b	1.21 \pm 0.65	1.10 \pm 0.25 ^b
18:1 ω 7	rhiz	2.77 \pm 0.71 ^a	2.80 \pm 2.28 ^a	2.70 \pm 1.26	1.31 \pm 1.02
	bulk	0.72 \pm 0.45 ^b	0.87 \pm - ^b	0.76 \pm 0.59	0.97 \pm 0.20
MUFA total	rhiz	7.87 \pm 1.55^a	7.50 \pm 6.14^a	8.21 \pm 4.14	4.03 \pm 2.63
	bulk	1.95 \pm 1.24^b	0.91 \pm 1.57^b	2.98 \pm 1.90	3.10 \pm 0.69
18:2 ω 6,9	rhiz	1.46 \pm 0.51 ^a	2.02 \pm 0.91 ^a	2.48 \pm 1.01	4.19 \pm 3.05 ^a
	bulk	0.49 \pm 0.08 ^b	1.15 \pm 0.25 ^b	0.94 \pm 0.67	1.08 \pm 0.24 ^b
PUFA total	rhiz	1.46 \pm 0.51^a	2.02 \pm 0.91^a	2.48 \pm 1.01	4.19 \pm 3.05^a
	bulk	0.49 \pm 0.08^b	1.15 \pm 0.25^b	0.94 \pm 0.67	1.08 \pm 0.24^b
PLFA	rhiz	62.17 \pm 9.02^a	61.59 \pm 15.14^a	52.76 \pm 36.84	44.28 \pm 13.71^a
	bulk	22.42 \pm 2.79^b	19.92 \pm 4.06^b	21.78 \pm 6.87	23.28 \pm 3.51^b

Tab. VIII-9: Carbon isotopic signature [$\delta^{13}\text{C}$ in ‰ V-PDB] of individual PLFA in rhizosphere and bulk soil (mean \pm standard deviation, $n=3$) of young beech trees grown in open-top chambers at two different time points (T1 = physiological active, mid-June and T2 = senescent, mid-October) in the vegetation period. Asterisks (*) represent statistically significant differences ($p < 0.05$) between labelled and ambient treatments.

FA $\delta^{13}\text{C}$		T1				T2			
[‰ V-PDB]		ambient		depleted		ambient		depleted	
i14:0	<i>rhiz</i>	-27.62	\pm 0.03	-27.91	\pm 1.22	-26.39	\pm 0.04	-	\pm -
	<i>bulk</i>	-26.55	\pm 0.49	-25.84	\pm -	-27.41	\pm -	-26.14	\pm 0.40
i15:0	<i>rhiz</i>	-24.03	\pm 0.53	-24.04	\pm 0.66	-24.01	\pm 0.59	-23.37	\pm 0.52
	<i>bulk</i>	-24.21	\pm 0.56	* -25.83	\pm 0.36	-24.60	\pm 0.97	-24.98	\pm 0.71
a15:0	<i>rhiz</i>	-22.37	\pm 0.60	-23.23	\pm 1.13	-22.74	\pm 0.01	-22.85	\pm 0.42
	<i>bulk</i>	-23.00	\pm 0.62	-24.33	\pm 1.38	-22.65	\pm 0.25	* -23.68	\pm 0.48
i16:0	<i>rhiz</i>	-24.48	\pm 0.36	-25.21	\pm 0.95	-24.68	\pm 0.25	-24.14	\pm 0.18
	<i>bulk</i>	-25.18	\pm 0.54	* -26.90	\pm 0.30	-24.95	\pm 0.47	-26.08	\pm 0.60
a16:0	<i>rhiz</i>	-26.12	\pm 0.20	-27.33	\pm 0.79	-25.72	\pm 1.73	-27.76	\pm 1.90
	<i>bulk</i>	-11.30	\pm 0.83	* 3.83	\pm 7.35	-19.33	\pm 3.60	-12.41	\pm 2.81
i17:0	<i>rhiz</i>	-23.72	\pm 0.33	-24.17	\pm 0.93	-22.97	\pm 0.19	-23.49	\pm 0.49
	<i>bulk</i>	-25.16	\pm 1.71	* -33.05	\pm 0.63	-26.58	\pm 1.60	-27.49	\pm 0.53
br9,17:0	<i>rhiz</i>	-25.34	\pm 0.45	-25.81	\pm 0.36	-25.04	\pm 0.57	-25.27	\pm 0.61
	<i>bulk</i>	-24.92	\pm 1.06	* -27.36	\pm 0.41	-25.81	\pm 0.38	-26.08	\pm 0.09
br10,17:0	<i>rhiz</i>	-23.48	\pm 0.28	-23.18	\pm 0.81	-22.66	\pm 0.41	-22.70	\pm 1.92
	<i>bulk</i>	-23.56	\pm 1.59	* -30.99	\pm 2.59	-24.61	\pm 1.08	-24.70	\pm 0.58
br11,17:0	<i>rhiz</i>	-25.09	\pm 0.82	-25.52	\pm 0.38	-24.44	\pm 0.19	* -25.05	\pm 0.16
	<i>bulk</i>	-26.01	\pm 0.53	* -27.21	\pm 0.46	-25.02	\pm 0.74	-26.13	\pm 0.22
cy17:0	<i>rhiz</i>	-24.62	\pm 1.57	-25.78	\pm 0.68	-25.19	\pm 0.01	-24.84	\pm 0.39
	<i>bulk</i>	-26.03	\pm 0.86	* -27.94	\pm 0.57	-25.30	\pm 1.14	-26.64	\pm 0.27
i18:0	<i>rhiz</i>	-24.80	\pm 0.82	-25.90	\pm 0.48	-25.31	\pm 0.57	-25.16	\pm 0.16
	<i>bulk</i>	-19.06	\pm 1.16	* -8.46	\pm 5.28	-22.56	\pm 1.29	* -18.56	\pm 0.89
cy18:0	<i>rhiz</i>	-29.01	\pm 2.06	-27.69	\pm 0.33	-28.88	\pm 1.90	-28.87	\pm 2.40
	<i>bulk</i>	-25.97	\pm 1.36	* -31.63	\pm 2.30	-26.87	\pm 2.65	-28.29	\pm 3.13
br10,18:0	<i>rhiz</i>	-24.51	\pm 1.41	-25.81	\pm 0.84	-25.10	\pm 0.88	-	\pm -
	<i>bulk</i>	-25.79	\pm 0.91	-27.37	\pm 0.51	-24.44	\pm 1.12	* -26.49	\pm 0.46
br10,19:0	<i>rhiz</i>	-24.09	\pm 0.65	* -22.55	\pm 0.12	-24.43	\pm 0.37	-23.91	\pm 0.71
	<i>bulk</i>	-24.15	\pm 0.58	-26.32	\pm 1.29	-22.73	\pm 0.12	* -24.79	\pm 0.53
cy19:0	<i>rhiz</i>	-29.04	\pm 2.06	-27.72	\pm 0.33	-28.90	\pm 1.89	-28.89	\pm 2.39
	<i>bulk</i>	-26.94	\pm 0.43	-27.45	\pm 0.19	-27.37	\pm 0.52	-27.44	\pm 0.25
n20:0	<i>rhiz</i>	-28.10	\pm 0.32	-28.59	\pm 0.55	-27.81	\pm 0.76	-26.98	\pm 0.59
	<i>bulk</i>	-20.97	\pm 1.42	-11.53	\pm 4.58	-25.12	\pm 1.27	* -22.79	\pm 0.04
n22:0	<i>rhiz</i>	-29.10	\pm 0.51	-29.16	\pm 0.41	-28.39	\pm 1.45	-29.47	\pm 0.09
	<i>bulk</i>	-27.88	\pm 0.90	* -25.21	\pm 1.07	-28.56	\pm 0.32	* -29.38	\pm 0.37
n24:0	<i>rhiz</i>	-29.34	\pm 0.60	* -31.00	\pm 0.81	-29.02	\pm 0.29	-29.80	\pm 0.69
	<i>bulk</i>	-29.04	\pm 0.08	* -25.74	\pm 1.30	-29.70	\pm 0.18	-30.13	\pm 0.78
16:1 ω 5	<i>rhiz</i>	-18.05	\pm 1.98	-18.52	\pm 3.31	-21.21	\pm 4.64	-19.88	\pm 2.06
	<i>bulk</i>	-20.69	\pm 0.31	-21.45	\pm -	-21.33	\pm 1.74	-22.17	\pm -
16:1 ω 7	<i>rhiz</i>	-26.46	\pm 0.75	-24.39	\pm 2.78	-26.05	\pm 1.43	-27.72	\pm 1.04
	<i>bulk</i>	-25.03	\pm 0.77	-28.01	\pm -	-27.07	\pm 1.76	-27.91	\pm -
17:1 ω 8	<i>rhiz</i>	-23.52	\pm 1.30	-23.91	\pm 0.13	-22.78	\pm 3.34	-20.75	\pm 1.11
	<i>bulk</i>	-27.09	\pm 0.50	-25.52	\pm -	-28.12	\pm 0.94	-28.05	\pm -
18:1 ω 9	<i>rhiz</i>	-24.14	\pm 0.79	-24.18	\pm 0.80	-26.27	\pm 2.44	-27.56	\pm 0.76
	<i>bulk</i>	-22.44	\pm 0.33	* -25.82	\pm -	-24.41	\pm 1.53	-24.50	\pm -
18:1 ω 7	<i>rhiz</i>	-28.11	\pm 0.98	-27.47	\pm 3.99	-29.05	\pm 1.16	-25.79	\pm 5.80
	<i>bulk</i>	-28.79	\pm 0.38	-29.91	\pm -	-30.49	\pm 1.80	-28.02	\pm -
18:2 ω 6,9	<i>rhiz</i>	-27.24	\pm 1.00	-30.01	\pm 2.74	-28.31	\pm 0.74	* -33.36	\pm 2.82
	<i>bulk</i>	-20.56	\pm 1.03	-22.02	\pm 6.90	-24.77	\pm 3.72	-23.58	\pm 2.84

3.3 Rhizosphere microbial community structure in beech (*Fagus sylvatica* L.) and spruce (*Picea abies* (L.) Karst.) rhizosphere and its response to elevated ozone: The phytotron experiment (C)

Tab. VIII-10 a-d: PLFA abundances [nmol g⁻¹ DS] and contribution [%] to total PLFA in beech and spruce rhizosphere in the phytotron experiment in May (n=2) and September (n=4) (mean ± standard deviation).

a)

PLFA	beech (mono)		spruce (mono)		beech (mix)		spruce (mix)		unplanted		
	1 x O ₃	2 x O ₃	1 x O ₃	2 x O ₃	1 x O ₃	2 x O ₃	1 x O ₃	2 x O ₃	1 x O ₃	2 x O ₃	
SATFA	mai	90.64 ± 0.91	89.83 ± 4.95	88.96 ± 1.26	87.70 ± 0.78	89.95 ± 0.16	89.64 ± 0.14	89.52 ± 2.48	92.35 ± 2.85	90.59 ± 3.01	89.97 ± 5.59
	sept	57.60 ± 8.31	58.98 ± 13.76	99.06 ± 4.53	87.77 ± 5.65	66.10 ± 4.57	61.22 ± 3.30	92.66 ± 21.84	101.28 ± 1.34	79.10 ± 14.64	76.19 ± 23.28
MUFA	mai	4.20 ± 0.30	4.23 ± 2.41	6.29 ± 0.64	6.29 ± 0.56	5.79 ± 1.60	4.35 ± 0.18	6.13 ± 3.55	3.49 ± 2.18	4.84 ± 1.57	5.34 ± 3.68
	sept	2.68 ± 0.59	2.62 ± 1.07	7.00 ± 0.88	6.32 ± 1.00	4.21 ± 0.88	2.97 ± 0.03	5.94 ± 2.34	3.85 ± 2.45	4.06 ± 0.54	4.33 ± 2.04
PUFA	mai	5.17 ± 0.62	5.94 ± 2.54	4.75 ± 0.62	6.01 ± 0.23	4.27 ± 1.76	6.00 ± 0.04	4.35 ± 1.07	4.17 ± 0.67	4.57 ± 2.21	4.69 ± 2.22
	sept	9.05 ± 3.67	5.85 ± 1.87	13.03 ± 13.39	6.02 ± 0.67	3.17 ± 1.51	4.11 ± 0.24	4.61 ± 2.05	4.58 ± 0.81	3.46 ± 0.63	3.70 ± 1.43
br12:0	mai	0.40 ± -	0.38 ± -	0.29 ± 0.29	- ± -	- ± -	- ± -	0.14 ± -	- ± -	0.25 ± 0.13	0.35 ± 0.15
	sept	0.25 ± 0.05	0.28 ± -	0.33 ± 0.33	- ± -	- ± -	- ± -	0.16 ± -	- ± -	- ± -	- ± -
br13:0	mai	0.39 ± 0.03	0.35 ± -	0.25 ± 0.08	0.18 ± -	0.64 ± -	0.52 ± -	0.13 ± 0.05	0.34 ± -	0.23 ± 0.10	0.33 ± 0.21
	sept	0.25 ± 0.02	0.26 ± -	0.28 ± 0.10	0.17 ± -	0.49 ± -	0.37 ± -	0.14 ± 0.08	0.38 ± -	0.17 ± -	0.24 ± -
al4:0	mai	1.48 ± 0.09	1.36 ± 0.51	1.72 ± 0.12	1.10 ± 0.30	1.04 ± 0.03	0.98 ± 0.18	1.37 ± 0.23	1.10 ± 0.06	1.35 ± 0.26	1.28 ± 0.37
	sept	0.95 ± 0.21	0.92 ± 0.49	1.92 ± 0.20	1.10 ± 0.22	0.76 ± 0.03	0.67 ± 0.16	1.44 ± 0.54	1.21 ± 0.09	1.19 ± 0.29	1.13 ± 0.58
l14:0	mai	0.34 ± 0.15	0.81 ± 0.02	0.55 ± 0.39	0.50 ± 0.09	0.36 ± 0.31	0.57 ± 0.50	0.20 ± 0.08	0.26 ± 0.10	0.34 ± 0.14	0.39 ± 0.22
	sept	0.73 ± 0.44	0.94 ± 0.36	1.16 ± 0.18	1.27 ± 0.18	0.86 ± 0.23	1.29 ± 0.20	1.01 ± 0.21	1.11 ± 0.30	1.33 ± 0.31	1.49 ± 0.44
a15:0	mai	0.34 ± 0.03	0.39 ± -	0.30 ± 0.09	0.21 ± -	0.16 ± 0.05	0.20 ± -	0.25 ± 0.11	0.22 ± 0.11	0.22 ± 0.08	0.22 ± 0.10
	sept	0.22 ± 0.05	0.29 ± -	0.34 ± 0.11	0.20 ± -	0.12 ± 0.04	0.14 ± -	0.27 ± 0.16	0.24 ± -	0.20 ± 0.08	0.19 ± 0.10
h15:0	mai	4.27 ± 1.00	4.58 ± 0.81	3.63 ± 0.13	3.49 ± 0.56	3.73 ± 0.13	4.18 ± 0.28	3.62 ± 0.04	3.80 ± 0.12	3.21 ± 0.62	3.20 ± 0.34
	sept	2.67 ± 0.22	2.95 ± 0.01	4.05 ± 0.27	3.51 ± 0.82	2.74 ± 0.10	2.85 ± 0.04	3.74 ± 0.82	4.17 ± 0.06	2.93 ± 0.52	2.75 ± 1.06
n15:0	mai	7.84 ± 0.64	8.10 ± 1.89	8.13 ± 1.05	6.30 ± 1.21	7.40 ± 0.13	7.19 ± 1.30	7.92 ± 0.68	7.93 ± 1.29	7.52 ± 1.28	7.02 ± 0.82
	sept	5.02 ± 1.17	5.41 ± 2.18	9.08 ± 1.45	6.26 ± 0.75	5.44 ± 0.29	4.89 ± 0.63	8.25 ± 2.40	8.69 ± 1.26	6.75 ± 1.40	6.06 ± 2.23
	mai	3.86 ± 2.49	5.58 ± 1.89	6.49 ± 0.76	7.94 ± 2.15	4.99 ± 1.39	6.81 ± 1.73	6.51 ± 1.22	6.84 ± 1.25	6.51 ± 2.39	7.59 ± 2.16
	sept	0.94 ± 0.37	0.89 ± 0.33	0.82 ± 0.18	0.92 ± 0.26	0.84 ± 0.16	0.87 ± 0.17	0.72 ± 0.04	0.91 ± 0.25	0.64 ± 0.13	0.64 ± 0.08
	mai	0.58 ± 0.14	0.56 ± 0.11	0.91 ± 0.18	0.93 ± 0.33	0.63 ± 0.16	0.60 ± 0.15	0.75 ± 0.20	1.00 ± 0.30	0.59 ± 0.13	0.55 ± 0.17
	sept	1.00 ± 0.26	0.89 ± 0.29	0.90 ± 0.29	1.08 ± 0.08	1.20 ± 0.27	1.10 ± 0.17	1.12 ± 0.20	1.16 ± 0.22	0.97 ± 0.17	0.90 ± 0.23
		0.59 ± 0.36	0.76 ± 0.43	0.84 ± 0.25	1.19 ± 0.08	0.83 ± 0.16	0.98 ± 0.19	1.02 ± 0.18	1.16 ± 0.29	0.98 ± 0.22	0.92 ± 0.30

b)

PLEA	beech (mono)				spruce (mono)				beech (mix)				spruce (mix)				unplanted					
	1 x O ₃		2 x O ₃		1 x O ₃		2 x O ₃		1 x O ₃		2 x O ₃		1 x O ₃		2 x O ₃		1 x O ₃		2 x O ₃			
	mai	sept	mai	sept	mai	sept	mai	sept	mai	sept	mai	sept	mai	sept	mai	sept	mai	sept	mai	sept		
ai16:0	mai	14.73 ± 0.19	15.78 ± 0.24	13.21 ± 2.40	12.46 ± 0.35	13.48 ± 0.25	14.74 ± 1.21	13.01 ± 0.32	14.20 ± 0.58	13.06 ± 1.66	12.59 ± 1.59	mai	14.73 ± 0.19	15.78 ± 0.24	13.21 ± 2.40	12.46 ± 0.35	13.48 ± 0.25	14.74 ± 1.21	13.01 ± 0.32	14.20 ± 0.58	13.06 ± 1.66	12.59 ± 1.59
	sept	9.36 ± 1.32	10.30 ± 1.69	14.75 ± 3.14	12.49 ± 1.27	9.90 ± 0.52	10.05 ± 0.30	13.47 ± 3.13	15.57 ± 0.37	11.54 ± 3.35	10.81 ± 3.95	sept	9.36 ± 1.32	10.30 ± 1.69	14.75 ± 3.14	12.49 ± 1.27	9.90 ± 0.52	10.05 ± 0.30	13.47 ± 3.13	15.57 ± 0.37	11.54 ± 3.35	10.81 ± 3.95
ii16:0	mai	13.16 ± 1.32	13.45 ± 0.54	19.38 ± 12.43	13.23 ± 0.42	13.92 ± 0.88	13.41 ± 0.60	13.85 ± 0.37	12.68 ± 0.36	12.78 ± 2.89	13.34 ± 0.46	mai	13.16 ± 1.32	13.45 ± 0.54	19.38 ± 12.43	13.23 ± 0.42	13.92 ± 0.88	13.41 ± 0.60	13.85 ± 0.37	12.68 ± 0.36	12.78 ± 2.89	13.34 ± 0.46
	sept	7.80 ± 4.78	10.72 ± 3.04	14.23 ± 3.74	14.71 ± 2.32	9.84 ± 2.03	11.98 ± 0.76	12.62 ± 0.76	12.64 ± 1.65	12.59 ± 3.54	13.77 ± 2.85	sept	7.80 ± 4.78	10.72 ± 3.04	14.23 ± 3.74	14.71 ± 2.32	9.84 ± 2.03	11.98 ± 0.76	12.62 ± 0.76	12.64 ± 1.65	12.59 ± 3.54	13.77 ± 2.85
ii16:0	mai	4.73 ± 0.19	5.33 ± 0.35	5.03 ± 0.70	4.42 ± 0.46	4.74 ± 0.15	5.03 ± 0.13	4.56 ± 0.14	5.16 ± 0.32	4.39 ± 0.58	4.38 ± 0.69	mai	4.73 ± 0.19	5.33 ± 0.35	5.03 ± 0.70	4.42 ± 0.46	4.74 ± 0.15	5.03 ± 0.13	4.56 ± 0.14	5.16 ± 0.32	4.39 ± 0.58	4.38 ± 0.69
	sept	3.02 ± 0.59	3.46 ± 0.40	4.41 ± 0.95	4.41 ± 0.14	3.48 ± 0.13	3.44 ± 0.09	4.72 ± 1.13	5.66 ± 0.25	3.93 ± 0.86	3.73 ± 1.47	sept	3.02 ± 0.59	3.46 ± 0.40	4.41 ± 0.95	4.41 ± 0.14	3.48 ± 0.13	3.44 ± 0.09	4.72 ± 1.13	5.66 ± 0.25	3.93 ± 0.86	3.73 ± 1.47
16:0 mix	mai	4.17 ± 0.48	4.16 ± 0.13	4.33 ± 0.10	4.55 ± 0.15	4.44 ± 0.44	4.68 ± 0.89	4.47 ± 0.39	4.58 ± 0.27	4.15 ± 1.11	4.54 ± 0.52	mai	4.17 ± 0.48	4.16 ± 0.13	4.33 ± 0.10	4.55 ± 0.15	4.44 ± 0.44	4.68 ± 0.89	4.47 ± 0.39	4.58 ± 0.27	4.15 ± 1.11	4.54 ± 0.52
	sept	2.48 ± 1.53	3.34 ± 1.09	4.07 ± 0.18	5.05 ± 0.70	3.15 ± 0.72	4.17 ± 0.65	4.07 ± 0.40	4.57 ± 0.67	4.08 ± 1.23	4.74 ± 1.29	sept	2.48 ± 1.53	3.34 ± 1.09	4.07 ± 0.18	5.05 ± 0.70	3.15 ± 0.72	4.17 ± 0.65	4.07 ± 0.40	4.57 ± 0.67	4.08 ± 1.23	4.74 ± 1.29
ai17:0	mai	3.52 ± 0.73	3.65 ± 0.63	3.43 ± 0.05	3.47 ± 0.05	3.97 ± 0.05	3.83 ± 0.18	3.54 ± 0.15	3.49 ± 0.10	2.95 ± 0.71	3.09 ± 0.65	mai	3.52 ± 0.73	3.65 ± 0.63	3.43 ± 0.05	3.47 ± 0.05	3.97 ± 0.05	3.83 ± 0.18	3.54 ± 0.15	3.49 ± 0.10	2.95 ± 0.71	3.09 ± 0.65
	sept	2.21 ± 0.12	2.35 ± 0.01	3.82 ± 0.06	3.48 ± 0.21	2.92 ± 0.24	2.61 ± 0.01	3.67 ± 0.91	3.84 ± 0.18	2.72 ± 0.55	2.61 ± 0.82	sept	2.21 ± 0.12	2.35 ± 0.01	3.82 ± 0.06	3.48 ± 0.21	2.92 ± 0.24	2.61 ± 0.01	3.67 ± 0.91	3.84 ± 0.18	2.72 ± 0.55	2.61 ± 0.82
ii17:0	mai	3.40 ± 0.38	3.77 ± 0.03	3.71 ± 0.06	3.49 ± 0.20	3.94 ± 0.26	3.60 ± 0.27	4.05 ± 0.15	3.92 ± 0.25	3.41 ± 1.01	3.87 ± 0.21	mai	3.40 ± 0.38	3.77 ± 0.03	3.71 ± 0.06	3.49 ± 0.20	3.94 ± 0.26	3.60 ± 0.27	4.05 ± 0.15	3.92 ± 0.25	3.41 ± 1.01	3.87 ± 0.21
	sept	2.02 ± 1.25	3.04 ± 1.00	3.49 ± 0.16	3.89 ± 0.71	2.80 ± 0.67	3.23 ± 0.35	3.68 ± 0.13	3.93 ± 0.72	3.41 ± 0.96	3.96 ± 0.56	sept	2.02 ± 1.25	3.04 ± 1.00	3.49 ± 0.16	3.89 ± 0.71	2.80 ± 0.67	3.23 ± 0.35	3.68 ± 0.13	3.93 ± 0.72	3.41 ± 0.96	3.96 ± 0.56
ai17:0	mai	2.18 ± 0.64	2.65 ± 1.09	1.92 ± 0.02	2.10 ± 0.18	2.50 ± 0.06	2.46 ± 0.11	2.20 ± 0.10	2.15 ± 0.05	1.74 ± 0.42	1.82 ± 0.41	mai	2.18 ± 0.64	2.65 ± 1.09	1.92 ± 0.02	2.10 ± 0.18	2.50 ± 0.06	2.46 ± 0.11	2.20 ± 0.10	2.15 ± 0.05	1.74 ± 0.42	1.82 ± 0.41
	sept	1.36 ± 0.19	1.67 ± 0.40	2.14 ± 0.04	2.11 ± 0.33	1.84 ± 0.18	1.68 ± 0.01	2.28 ± 0.58	2.36 ± 0.10	1.60 ± 0.37	1.54 ± 0.41	sept	1.36 ± 0.19	1.67 ± 0.40	2.14 ± 0.04	2.11 ± 0.33	1.84 ± 0.18	1.68 ± 0.01	2.28 ± 0.58	2.36 ± 0.10	1.60 ± 0.37	1.54 ± 0.41
ii17:0	mai	2.44 ± 0.23	2.61 ± 0.03	3.08 ± 1.32	2.26 ± 0.13	2.75 ± 0.31	2.39 ± 0.17	2.71 ± 0.14	2.63 ± 0.13	2.25 ± 0.41	2.43 ± 0.12	mai	2.44 ± 0.23	2.61 ± 0.03	3.08 ± 1.32	2.26 ± 0.13	2.75 ± 0.31	2.39 ± 0.17	2.71 ± 0.14	2.63 ± 0.13	2.25 ± 0.41	2.43 ± 0.12
	sept	1.44 ± 0.85	2.09 ± 0.67	2.37 ± 0.22	2.52 ± 0.45	1.95 ± 0.47	2.14 ± 0.19	2.47 ± 0.14	2.62 ± 0.37	2.18 ± 0.56	2.49 ± 0.44	sept	1.44 ± 0.85	2.09 ± 0.67	2.37 ± 0.22	2.52 ± 0.45	1.95 ± 0.47	2.14 ± 0.19	2.47 ± 0.14	2.62 ± 0.37	2.18 ± 0.56	2.49 ± 0.44
ii17:0	mai	6.89 ± 0.46	8.10 ± 0.69	7.44 ± 1.60	8.16 ± 1.55	8.35 ± 0.90	8.08 ± 0.84	7.94 ± 0.75	8.48 ± 0.14	6.88 ± 1.23	7.14 ± 1.22	mai	6.89 ± 0.46	8.10 ± 0.69	7.44 ± 1.60	8.16 ± 1.55	8.35 ± 0.90	8.08 ± 0.84	7.94 ± 0.75	8.48 ± 0.14	6.88 ± 1.23	7.14 ± 1.22
	sept	4.41 ± 0.97	5.25 ± 0.49	8.32 ± 2.04	8.23 ± 2.15	6.16 ± 1.10	5.51 ± 0.29	8.28 ± 2.49	9.31 ± 0.01	6.22 ± 1.63	6.04 ± 2.14	sept	4.41 ± 0.97	5.25 ± 0.49	8.32 ± 2.04	8.23 ± 2.15	6.16 ± 1.10	5.51 ± 0.29	8.28 ± 2.49	9.31 ± 0.01	6.22 ± 1.63	6.04 ± 2.14
cy17:0	mai	8.15 ± 0.36	9.13 ± 0.28	8.79 ± 1.16	9.22 ± 0.31	8.38 ± 0.92	8.08 ± 0.77	9.25 ± 0.59	10.14 ± 0.24	7.93 ± 1.73	9.19 ± 0.79	mai	8.15 ± 0.36	9.13 ± 0.28	8.79 ± 1.16	9.22 ± 0.31	8.38 ± 0.92	8.08 ± 0.77	9.25 ± 0.59	10.14 ± 0.24	7.93 ± 1.73	9.19 ± 0.79
	sept	4.65 ± 2.45	7.39 ± 2.61	8.28 ± 1.34	10.24 ± 1.49	6.00 ± 1.71	7.22 ± 0.69	8.42 ± 0.63	10.10 ± 1.24	7.75 ± 1.97	9.48 ± 2.14	sept	4.65 ± 2.45	7.39 ± 2.61	8.28 ± 1.34	10.24 ± 1.49	6.00 ± 1.71	7.22 ± 0.69	8.42 ± 0.63	10.10 ± 1.24	7.75 ± 1.97	9.48 ± 2.14
ni17:0	mai	0.52 ± -	0.52 ± -	0.62 ± 0.34	0.53 ± 0.47	0.85 ± 0.35	0.49 ± 0.39	0.89 ± 0.46	0.56 ± 0.46	0.73 ± 0.40	0.52 ± 0.28	mai	0.52 ± -	0.52 ± -	0.62 ± 0.34	0.53 ± 0.47	0.85 ± 0.35	0.49 ± 0.39	0.89 ± 0.46	0.56 ± 0.46	0.73 ± 0.40	0.52 ± 0.28
	sept	0.37 ± -	0.38 ± -	0.69 ± 0.35	0.52 ± 0.43	0.64 ± 0.30	0.34 ± 0.28	0.97 ± 0.66	0.62 ± 0.52	0.69 ± 0.35	0.41 ± 0.19	sept	0.37 ± -	0.38 ± -	0.69 ± 0.35	0.52 ± 0.43	0.64 ± 0.30	0.34 ± 0.28	0.97 ± 0.66	0.62 ± 0.52	0.69 ± 0.35	0.41 ± 0.19
br10-17:0	mai	0.64 ± 0.39	0.89 ± 0.28	1.01 ± 0.08	0.80 ± 0.18	0.82 ± 0.39	0.78 ± 0.41	1.05 ± 0.08	1.06 ± 0.11	0.90 ± 0.30	1.03 ± 0.07	mai	0.64 ± 0.39	0.89 ± 0.28	1.01 ± 0.08	0.80 ± 0.18	0.82 ± 0.39	0.78 ± 0.41	1.05 ± 0.08	1.06 ± 0.11	0.90 ± 0.30	1.03 ± 0.07
	sept	0.49 ± 0.40	0.75 ± 0.40	0.95 ± 0.11	0.91 ± 0.32	0.61 ± 0.34	0.70 ± 0.38	0.96 ± 0.13	1.07 ± 0.20	0.92 ± 0.25	1.06 ± 0.19	sept	0.49 ± 0.40	0.75 ± 0.40	0.95 ± 0.11	0.91 ± 0.32	0.61 ± 0.34	0.70 ± 0.38	0.96 ± 0.13	1.07 ± 0.20	0.92 ± 0.25	1.06 ± 0.19
br10-18:0	mai	2.92 ± 0.44	2.25 ± 1.59	3.18 ± 0.11	1.88 ± 1.64	3.08 ± 0.40	3.38 ± 0.32	3.90 ± 0.96	3.04 ± 0.18	2.93 ± 0.62	2.63 ± 0.37	mai	2.92 ± 0.44	2.25 ± 1.59	3.18 ± 0.11	1.88 ± 1.64	3.08 ± 0.40	3.38 ± 0.32	3.90 ± 0.96	3.04 ± 0.18	2.93 ± 0.62	2.63 ± 0.37
	sept	1.88 ± 0.57	1.56 ± 1.30	3.55 ± 0.01	1.83 ± 1.51	2.26 ± 0.13	2.30 ± 0.10	4.13 ± 1.83	3.33 ± 0.14	2.68 ± 0.63	2.24 ± 0.81	sept	1.88 ± 0.57	1.56 ± 1.30	3.55 ± 0.01	1.83 ± 1.51	2.26 ± 0.13	2.30 ± 0.10	4.13 ± 1.83	3.33 ± 0.14	2.68 ± 0.63	2.24 ± 0.81
br10-18:0	mai	2.99 ± 0.14	4.07 ± 0.47	4.22 ± 1.25	3.68 ± 0.78	3.58 ± 0.80	3.28 ± 0.58	3.47 ± 0.58	3.27 ± 1.11	3.32 ± 0.67	3.39 ± 0.72	mai	2.99 ± 0.14	4.07 ± 0.47	4.22 ± 1.25	3.68 ± 0.78	3.58 ± 0.80	3.28 ± 0.58	3.47 ± 0.58	3.27 ± 1.11	3.32 ± 0.67	3.39 ± 0.72
	sept	1.71 ± 0.94	3.35 ± 1.43	3.38 ± 0.85	4.14 ± 1.39	2.61 ± 1.05	2.92 ± 0.41	3.18 ± 0.65	3.30 ± 1.30	3.40 ± 0.72	3.55 ± 1.10	sept	1.71 ± 0.94	3.35 ± 1.43	3.38 ± 0.85	4.14 ± 1.39	2.61 ± 1.05	2.92 ± 0.41	3.18 ± 0.65	3.30 ± 1.30	3.40 ± 0.72	3.55 ± 1.10
ii18:0	mai	0.79 ± 0.03	0.89 ± 0.28	0.86 ± 0.01	0.91 ± 0.05	0.85 ± 0.03	0.85 ± 0.04	0.80 ± 0.05	0.87 ± 0.11	0.66 ± 0.16	0.73 ± 0.18	mai	0.79 ± 0.03	0.89 ± 0.28	0.86 ± 0.01	0.91 ± 0.05	0.85 ± 0.03	0.85 ± 0.04	0.80 ± 0.05	0.87 ± 0.11	0.66 ± 0.16	0.73 ± 0.18
	sept	0.50 ± 0.06	0.57 ± 0.08	0.96 ± 0.02	0.91 ± 0.01	0.63 ± 0.06	0.58 ± 0.06	0.83 ± 0.12	0.96 ± 0.13	0.60 ± 0.14	0.61 ± 0.23	sept	0.50 ± 0.06	0.57 ± 0.08	0.96 ± 0.02	0.91 ± 0.01	0.63 ± 0.06	0.58 ± 0.06	0.83 ± 0.12	0.96 ± 0.13	0.60 ± 0.14	0.61 ± 0.23
ii18:0	mai	0.80 ± 0.11	0.88 ± 0.04	1.08 ± 0.36	0.96 ± 0.01	0.98 ± 0.12	1.04 ± 0.12	1.01 ± 0.10	1.05 ± 0.10	0.89 ± 0.09	0.99 ± 0.12	mai	0.80 ± 0.11	0.88 ± 0.04	1.08 ± 0.36	0.96 ± 0.01	0.98 ± 0.12	1.04 ± 0.12	1.01 ± 0.10	1.05 ± 0.10	0.89 ± 0.09	0.99 ± 0.12
	sept	0.48 ± 0.29	0.71 ± 0.24	0.85 ± 0.04	1.07 ± 0.13	0.70 ± 0.17	0.93 ± 0.12	0.92 ± 0.10	1.05 ± 0.18	0.89 ± 0.13	1.03 ± 0.23	sept	0.48 ± 0.29	0.71 ± 0.24	0.85 ± 0.04	1.07 ± 0.13	0.70 ± 0.17	0.93 ± 0.12	0.92 ± 0.10	1.05 ± 0.18	0.89 ± 0.13	1.03 ± 0.23
ii18:0	mai	1.21 ± 0.39	2.45 ± 1.47	1.38 ± 0.18	1.91 ± 0.52	1.32 ± 0.06	1.24 ± 0.03	1.11 ± 0.43	1.27 ± 0.03	1.12 ± 0.13	1.27 ± 0.32	mai	1.21 ± 0.39	2.45 ± 1.47	1.38 ± 0.18	1.91 ± 0.52	1.32 ± 0.06	1.24 ± 0.03	1.11 ± 0.43	1.27 ± 0.03	1.12 ± 0.13	1.27 ± 0.32
	sept	0.79 ± 0.37	1.52 ± 0.67	1.54 ± 0.25	1.94 ± 0.66	0.97 ± 0.02	0.85 ± 0.06	1.10 ± 0.21	1.39 ± 0.06	0.99 ± 0.12	1.05 ± 0.44	sept	0.79 ± 0.37	1.52 ± 0.67	1.54 ± 0.25	1.94 ± 0.66	0.97 ± 0.02	0.85 ± 0.06	1.10 ± 0.21	1.39 ± 0.06	0.99 ±	

C)

PLFA	beech (mono)				spruce (mono)				beech (mix)				spruce (mix)				unplanted				
	1 x O ₃		2 x O ₃		1 x O ₃		2 x O ₃		1 x O ₃		2 x O ₃		1 x O ₃		2 x O ₃		1 x O ₃	2 x O ₃			
	mol %	nmol g ⁻¹ DS	mol %	nmol g ⁻¹ DS	mol %	nmol g ⁻¹ DS	mol %	nmol g ⁻¹ DS	mol %	nmol g ⁻¹ DS	mol %	nmol g ⁻¹ DS	mol %	nmol g ⁻¹ DS	mol %	nmol g ⁻¹ DS	mol %	nmol g ⁻¹ DS			
cyl180	mai	1.00 ± 0.11	0.88 ± 0.19	1.20 ± 0.63	0.98 ± 0.19	0.88 ± 0.04	0.97 ± 0.03	0.86 ± 0.11	0.98 ± 0.01	1.05 ± 0.32	0.91 ± 0.22	mai	1.05 ± 0.32	0.98 ± 0.01	1.05 ± 0.32	0.91 ± 0.22	mai	1.05 ± 0.32	0.98 ± 0.01	1.05 ± 0.32	0.91 ± 0.22
	sept	0.63 ± 0.03	0.57 ± 0.02	1.33 ± 0.66	0.98 ± 0.12	0.65 ± 0.04	0.66 ± 0.06	0.88 ± 0.07	0.88 ± 0.07	1.08 ± 0.01	0.98 ± 0.38	0.76 ± 0.23	sept	0.88 ± 0.07	1.08 ± 0.01	0.88 ± 0.07	0.76 ± 0.23	sept	0.88 ± 0.07	1.08 ± 0.01	0.88 ± 0.07
dic180	mai	1.00 ± 0.19	1.36 ± 0.86	1.59 ± 1.06	0.96 ± 0.12	0.88 ± 0.29	0.82 ± 0.04	0.82 ± 0.04	1.62 ± 0.93	1.00 ± 0.30	0.91 ± 0.27	mai	1.62 ± 0.93	1.00 ± 0.30	1.62 ± 0.93	0.91 ± 0.27	mai	1.62 ± 0.93	1.00 ± 0.30	1.62 ± 0.93	0.91 ± 0.27
	sept	0.55 ± 0.46	1.23 ± 1.14	1.46 ± 1.01	1.07 ± 0.22	0.65 ± 0.32	0.73 ± 0.03	0.73 ± 0.03	1.50 ± 0.94	1.00 ± 0.35	0.93 ± 0.26	sept	1.50 ± 0.94	1.00 ± 0.35	1.50 ± 0.94	0.93 ± 0.26	sept	1.50 ± 0.94	1.00 ± 0.35	1.50 ± 0.94	0.93 ± 0.26
cyl190	mai	1.31 ± 0.11	1.21 ± 0.52	1.12 ± 0.26	1.45 ± 0.31	1.03 ± 0.04	0.97 ± 0.30	1.18 ± 0.01	1.20 ± 0.18	1.61 ± 0.59	1.73 ± 0.38	mai	1.18 ± 0.01	1.20 ± 0.18	1.18 ± 0.01	1.20 ± 0.18	mai	1.61 ± 0.59	1.20 ± 0.18	1.61 ± 0.59	1.73 ± 0.38
	sept	0.84 ± 0.20	0.76 ± 0.20	1.25 ± 0.25	1.47 ± 0.42	0.76 ± 0.08	0.67 ± 0.24	0.67 ± 0.24	1.22 ± 0.25	1.31 ± 0.17	1.44 ± 0.56	sept	0.84 ± 0.20	0.76 ± 0.20	1.22 ± 0.25	1.31 ± 0.17	sept	1.22 ± 0.25	1.31 ± 0.17	1.22 ± 0.25	1.44 ± 0.56
br10-19:0	mai	0.94 ± 0.11	1.13 ± 0.17	1.15 ± 0.06	1.13 ± 0.05	0.84 ± 0.44	1.04 ± 0.31	1.05 ± 0.33	1.22 ± 0.23	1.23 ± 0.23	1.27 ± 0.17	mai	1.05 ± 0.33	1.22 ± 0.23	1.05 ± 0.33	1.22 ± 0.23	mai	1.22 ± 0.23	1.23 ± 0.23	1.22 ± 0.23	1.27 ± 0.17
	sept	0.56 ± 0.34	0.94 ± 0.45	1.08 ± 0.03	1.25 ± 0.14	0.60 ± 0.33	0.95 ± 0.33	0.95 ± 0.33	0.97 ± 0.34	1.23 ± 0.34	1.31 ± 0.33	sept	0.60 ± 0.33	0.95 ± 0.33	0.97 ± 0.34	1.23 ± 0.34	sept	0.97 ± 0.34	1.23 ± 0.34	0.97 ± 0.34	1.31 ± 0.33
dic200	mai	18.16 ± 1.47	18.79 ± -	17.59 ± 0.03	17.46 ± 0.35	18.55 ± 0.59	18.88 ± 0.64	18.50 ± 0.45	19.05 ± 0.63	17.93 ± 3.49	16.59 ± 2.96	mai	18.55 ± 0.59	18.88 ± 0.64	18.50 ± 0.45	19.05 ± 0.63	mai	17.93 ± 3.49	17.93 ± 3.49	17.93 ± 3.49	16.59 ± 2.96
	sept	11.48 ± 0.85	13.83 ± -	19.59 ± 0.58	17.47 ± 0.93	13.65 ± 1.39	12.91 ± 1.11	13.65 ± 1.39	19.15 ± 4.45	20.90 ± 0.32	14.01 ± 3.86	sept	13.65 ± 1.39	12.91 ± 1.11	19.15 ± 4.45	20.90 ± 0.32	sept	16.27 ± 2.47	16.27 ± 2.47	16.27 ± 2.47	14.01 ± 3.86
n200	mai	18.81 ± 1.37	18.25 ± 0.66	19.04 ± 0.72	18.97 ± 0.65	20.26 ± 1.15	17.90 ± 0.64	20.64 ± 1.01	19.22 ± 0.89	19.85 ± 1.53	18.58 ± 0.53	mai	17.90 ± 0.64	18.97 ± 0.65	20.64 ± 1.01	19.22 ± 0.89	mai	19.85 ± 1.53	19.85 ± 1.53	19.85 ± 1.53	18.58 ± 0.53
	sept	10.84 ± 6.13	14.76 ± 5.25	17.92 ± 1.30	20.97 ± 1.97	14.33 ± 3.00	16.02 ± 1.25	14.33 ± 3.00	18.78 ± 0.87	19.13 ± 2.37	19.12 ± 3.63	sept	14.33 ± 3.00	20.97 ± 1.97	18.78 ± 0.87	19.13 ± 2.37	sept	19.90 ± 1.77	19.90 ± 1.77	19.90 ± 1.77	19.12 ± 3.63
dic220	mai	1.44 ± 0.03	1.50 ± 0.26	1.05 ± 0.01	1.13 ± 0.09	1.27 ± 0.03	1.25 ± 0.01	1.13 ± 0.14	1.09 ± 0.08	0.93 ± 0.13	1.04 ± 0.12	mai	1.05 ± 0.01	1.13 ± 0.09	1.27 ± 0.03	1.25 ± 0.01	mai	0.93 ± 0.13	0.93 ± 0.13	0.93 ± 0.13	1.04 ± 0.12
	sept	0.92 ± 0.12	0.97 ± 0.01	1.18 ± 0.05	1.13 ± 0.01	0.93 ± 0.04	0.86 ± 0.05	0.93 ± 0.04	1.15 ± 0.10	1.20 ± 0.11	0.86 ± 0.21	sept	1.18 ± 0.05	1.13 ± 0.01	1.15 ± 0.10	1.20 ± 0.11	sept	0.82 ± 0.12	0.82 ± 0.12	0.82 ± 0.12	0.86 ± 0.21
n220	mai	0.95 ± 0.17	0.85 ± 0.06	1.06 ± 0.16	0.96 ± 0.07	0.98 ± 0.05	0.98 ± 0.14	1.22 ± 0.04	1.45 ± 0.67	1.04 ± 0.16	0.98 ± 0.17	mai	0.96 ± 0.07	0.96 ± 0.07	1.22 ± 0.04	1.45 ± 0.67	mai	1.04 ± 0.16	1.04 ± 0.16	1.04 ± 0.16	0.98 ± 0.17
	sept	0.57 ± 0.37	0.57 ± 0.16	0.99 ± 0.10	1.06 ± 0.06	0.70 ± 0.17	0.88 ± 0.14	0.70 ± 0.17	1.08 ± 0.03	1.46 ± 0.74	0.99 ± 0.13	sept	0.99 ± 0.10	1.06 ± 0.06	1.08 ± 0.03	1.46 ± 0.74	sept	1.04 ± 0.15	1.04 ± 0.15	1.04 ± 0.15	0.99 ± 0.13
n240	mai	1.85 ± 0.27	2.43 ± 1.19	1.80 ± 0.56	2.48 ± 0.41	1.87 ± 0.02	1.47 ± 0.19	2.02 ± 0.07	2.00 ± 0.41	2.61 ± 1.03	2.90 ± 0.46	mai	1.80 ± 0.56	2.48 ± 0.41	2.02 ± 0.07	2.00 ± 0.41	mai	2.61 ± 1.03	2.61 ± 1.03	2.61 ± 1.03	2.90 ± 0.46
	sept	1.17 ± 0.01	1.52 ± 0.49	2.00 ± 0.57	2.48 ± 0.59	1.37 ± 0.08	1.01 ± 0.18	1.37 ± 0.08	2.08 ± 0.37	2.19 ± 0.41	2.46 ± 1.05	sept	2.00 ± 0.57	2.48 ± 0.59	2.08 ± 0.37	2.19 ± 0.41	sept	2.02 ± 0.43	2.02 ± 0.43	2.02 ± 0.43	2.46 ± 1.05
15:1α6	mai	1.55 ± 0.18	1.92 ± 0.32	1.88 ± 0.18	1.88 ± 0.15	1.48 ± 0.64	1.80 ± 0.44	1.80 ± 0.50	2.18 ± 0.30	1.87 ± 0.61	2.16 ± 0.31	mai	1.88 ± 0.18	1.88 ± 0.15	1.48 ± 0.64	1.80 ± 0.44	mai	2.18 ± 0.30	2.18 ± 0.30	2.18 ± 0.30	2.16 ± 0.31
	sept	0.92 ± 0.54	1.60 ± 0.78	1.77 ± 0.11	2.07 ± 0.12	1.06 ± 0.52	1.63 ± 0.48	1.06 ± 0.52	1.65 ± 0.51	2.18 ± 0.48	2.26 ± 0.66	sept	1.77 ± 0.11	2.07 ± 0.12	1.65 ± 0.51	2.18 ± 0.48	sept	1.88 ± 0.62	1.88 ± 0.62	1.88 ± 0.62	2.26 ± 0.66
15:1α6	mai	2.27 ± 0.36	2.72 ± 0.68	2.27 ± 0.54	2.63 ± 0.18	2.59 ± 0.25	2.00 ± 0.10	2.55 ± 0.11	2.47 ± 0.17	3.07 ± 0.73	3.49 ± 0.66	mai	2.27 ± 0.54	2.63 ± 0.18	2.59 ± 0.25	2.00 ± 0.10	mai	3.07 ± 0.73	3.07 ± 0.73	3.07 ± 0.73	3.49 ± 0.66
	sept	1.46 ± 0.45	1.74 ± 0.13	2.52 ± 0.52	2.63 ± 0.01	1.90 ± 0.05	1.37 ± 0.14	1.90 ± 0.05	2.62 ± 0.44	2.71 ± 0.14	2.90 ± 0.94	sept	2.52 ± 0.52	2.63 ± 0.01	1.90 ± 0.05	1.37 ± 0.14	sept	2.48 ± 0.41	2.48 ± 0.41	2.48 ± 0.41	2.90 ± 0.94
15:1α6	mai	2.16 ± 0.57	1.97 ± 0.25	2.04 ± 0.32	2.49 ± 0.30	1.99 ± 0.32	2.23 ± 0.54	2.62 ± 0.54	2.92 ± 0.31	2.68 ± 0.47	2.54 ± 0.36	mai	2.04 ± 0.32	2.49 ± 0.30	1.99 ± 0.32	2.23 ± 0.54	mai	2.68 ± 0.47	2.68 ± 0.47	2.68 ± 0.47	2.54 ± 0.36
	sept	1.32 ± 0.89	1.61 ± 0.62	1.92 ± 0.31	2.73 ± 0.05	1.44 ± 0.51	2.02 ± 0.64	1.44 ± 0.51	2.38 ± 0.51	2.89 ± 0.30	2.59 ± 0.52	sept	1.92 ± 0.31	2.73 ± 0.05	1.44 ± 0.51	2.02 ± 0.64	sept	2.67 ± 0.57	2.67 ± 0.57	2.67 ± 0.57	2.59 ± 0.52
15:1α6	mai	1.30 ± 0.02	1.85 ± 0.88	1.25 ± 0.39	1.80 ± 0.15	1.17 ± 0.01	1.54 ± 0.93	1.23 ± 0.00	1.82 ± 0.57	1.94 ± 1.04	2.02 ± 0.41	mai	1.25 ± 0.39	1.80 ± 0.15	1.17 ± 0.01	1.54 ± 0.93	mai	2.02 ± 0.41	2.02 ± 0.41	2.02 ± 0.41	2.02 ± 0.41
	sept	0.83 ± 0.14	1.16 ± 0.36	1.39 ± 0.39	1.81 ± 0.28	0.86 ± 0.07	1.07 ± 0.69	0.86 ± 0.07	1.27 ± 0.27	2.00 ± 0.66	1.72 ± 0.73	sept	1.39 ± 0.39	1.81 ± 0.28	0.86 ± 0.07	1.07 ± 0.69	sept	1.43 ± 0.20	1.43 ± 0.20	1.43 ± 0.20	1.72 ± 0.73
15:1α6	mai	1.06 ± 0.24	1.19 ± 0.21	1.53 ± 0.50	1.17 ± 0.07	1.09 ± 0.44	1.59 ± 0.56	1.18 ± 0.27	1.40 ± 0.16	1.32 ± 0.40	1.59 ± 0.55	mai	1.53 ± 0.50	1.17 ± 0.07	1.09 ± 0.44	1.59 ± 0.56	mai	1.32 ± 0.40	1.32 ± 0.40	1.32 ± 0.40	1.59 ± 0.55
	sept	0.62 ± 0.38	0.99 ± 0.49	1.45 ± 0.52	1.29 ± 0.11	0.79 ± 0.44	1.41 ± 0.47	0.79 ± 0.44	1.08 ± 0.27	1.40 ± 0.28	1.67 ± 0.80	sept	1.45 ± 0.52	1.29 ± 0.11	0.79 ± 0.44	1.41 ± 0.47	sept	1.33 ± 0.31	1.33 ± 0.31	1.33 ± 0.31	1.67 ± 0.80
15:1α6	mai	3.43 ± 0.36	4.28 ± 1.65	3.42 ± 1.14	4.22 ± 0.14	3.71 ± 0.34	3.00 ± 0.18	3.65 ± 0.48	3.90 ± 0.38	4.97 ± 1.72	5.29 ± 1.26	mai	3.42 ± 1.14	4.22 ± 0.14	3.71 ± 0.34	3.00 ± 0.18	mai	4.97 ± 1.72	4.97 ± 1.72	4.97 ± 1.72	5.29 ± 1.26
	sept	2.20 ± 0.57	2.70 ± 0.58	3.79 ± 1.15	4.23 ± 0.45	2.72 ± 0.06	2.05 ± 0.23	2.72 ± 0.06	3.72 ± 0.29	4.27 ± 0.34	4.44 ± 1.81	sept	3.79 ± 1.15	4.23 ± 0.45	2.72 ± 0.06	2.05 ± 0.23	sept	3.89 ± 0.51	3.89 ± 0.51	3.89 ± 0.51	4.44 ± 1.81
15:1α6	mai	3.10 ± 0.28	3.19 ± 0.34	3.21 ± 0.17	3.22 ± 0.14	3.13 ± 0.47	3.30 ± 0.52	3.34 ± 0.21	3.55 ± 0.35	3.65 ± 0.48	3.72 ± 0.32	mai	3.21 ± 0.17	3.22 ± 0.14	3.13 ± 0.47	3.30 ± 0.52	mai	3.65 ± 0.48	3.65 ± 0.48	3.65 ± 0.48	3.72 ± 0.32
	sept	1.83 ± 1.10	2.62 ± 1.12	3.02 ± 0.20	3.56 ± 0.30	2.24 ± 0.67	2.97 ± 0.62	2.24 ± 0.67	3.04 ± 0.19	3.57 ± 0.79	3.85 ± 0.85	sept	3.02 ± 0.20	3.56 ± 0.30	2.24 ± 0.67	2.97 ± 0.62	sept	3.62 ± 0.51	3.62 ± 0.51	3.62 ± 0.51	3.85 ± 0.85
15:1α6	mai	4.14 ± 0.11	5.39 ± 2.04	4.44 ± 1.12	5.08 ± 0.46	3.57 ± 0.76	3.24 ± 0.59	3.85 ± 0.38	4.07 ± 0.75	5.88 ± 1.68	5.80 ± 1.13	mai	4.44 ± 1.12	5.08 ± 0.46	3.57 ± 0.76	3.24 ± 0.59	mai	5.88 ± 1.68	5.88 ± 1.68	5.88 ± 1.68	5.80 ± 1.13
	sept	2.64 ± 0.47	3.41 ± 0.70	4.93 ± 1.10	5.11 ± 0.83	2.61 ± 0.37	2.23 ± 0.52	2.61 ± 0.37	3.93 ± 0.44	4.46 ± 0.74	4.84 ± 1.91	sept	4.93 ± 1.10	5.11 ± 0.83	2.61 ± 0.37	2.23 ± 0.52	sept	4.72 ± 1.01	4.72 ± 1.01	4.72 ± 1.01	4.84 ± 1.91
15:1α6	mai	3.66 ± 0.52	4.17 ± 0.14	3.92 ± 0.34	3.81 ± 0.37	3.20 ± 1.40	3.68 ± 0.97	3.72 ± 0.93	3.98 ± 0.84	3.60 ± 1.34	4.30 ± 0.39	mai	3.92 ± 0.34	3.81 ± 0.37	3.20 ± 1.40	3.68 ± 0.97	mai	3.60 ± 1.34	3.60 ± 1.34	3.60 ± 1.34	4.30 ± 0.39
	sept	2.11 ± 1.28	3.37 ± 1.20	3.68 ± 0.30	4.25 ± 0.90	2.27 ± 1.09	3.32 ± 1.07	2.27 ± 1.09	3.42 ± 0.98	4.01 ± 1.25	4.41 ± 0.89	sept	3.68 ± 0.30	4.25 ± 0.90	2.27 ± 1.09	3.32 ± 1.07	sept	3.62 ± -	3.62 ± -	3.62 ± -	4.41 ± 0.89
15:1α6	mai	0.23 ± 0.02	0.20 ± 0.09	0.37 ± 0.09	0.32 ±																

d)

PLFA	beech (mono)						spruce (mono)						beech (mix)						spruce (mix)						unplanted					
	1 x O ₃		2 x O ₃		1 x O ₃		2 x O ₃		1 x O ₃		2 x O ₃		1 x O ₃		2 x O ₃		1 x O ₃		2 x O ₃		1 x O ₃		2 x O ₃		1 x O ₃		2 x O ₃			
	med %	nmol g ⁻¹ DS	med %	nmol g ⁻¹ DS	med %	nmol g ⁻¹ DS	med %	nmol g ⁻¹ DS	med %	nmol g ⁻¹ DS	med %	nmol g ⁻¹ DS	med %	nmol g ⁻¹ DS	med %	nmol g ⁻¹ DS	med %	nmol g ⁻¹ DS	med %	nmol g ⁻¹ DS	med %	nmol g ⁻¹ DS	med %	nmol g ⁻¹ DS	med %	nmol g ⁻¹ DS	med %	nmol g ⁻¹ DS		
16:1c9	mai	0.26 ± 0.04	0.17 ± 0.05	0.24 ± 0.15	0.15 ± 0.07	0.38 ± 0.05	0.40 ± 0.09	0.24 ± 0.05	0.21 ± 0.01	0.27 ± 0.15	0.23 ± 0.11	0.27 ± 0.11	0.23 ± 0.11	0.27 ± 0.15	0.26 ± 0.10	0.23 ± 0.11	0.27 ± 0.11	0.23 ± 0.11	0.27 ± 0.15	0.26 ± 0.10	0.23 ± 0.11	0.27 ± 0.15	0.23 ± 0.11	0.27 ± 0.15	0.23 ± 0.11	0.27 ± 0.15	0.23 ± 0.11	0.27 ± 0.15	0.23 ± 0.11	0.27 ± 0.15
	sept	0.17 ± 0.05	0.29 ± 0.16	0.30 ± 0.03	0.13 ± 0.03	0.17 ± 0.08	0.23 ± 0.10	0.41 ± 0.12	0.18 ± 0.02	0.31 ± 0.15	0.16 ± 0.02	0.18 ± 0.08	0.18 ± 0.08	0.16 ± 0.02	0.32 ± 0.05	0.18 ± 0.08	0.18 ± 0.08	0.16 ± 0.02	0.32 ± 0.05	0.18 ± 0.08	0.18 ± 0.08	0.16 ± 0.02	0.32 ± 0.05	0.18 ± 0.08	0.18 ± 0.08	0.16 ± 0.02	0.32 ± 0.05	0.18 ± 0.08	0.18 ± 0.08	0.16 ± 0.02
16:1c7 cis	mai	1.66 ± 0.08	1.06 ± 0.21	1.52 ± 0.78	0.95 ± 0.33	2.51 ± 0.27	2.33 ± 0.18	2.30 ± 0.68	1.73 ± 0.13	2.46 ± 1.45	1.94 ± -	2.46 ± 1.45	1.94 ± -	2.30 ± 0.68	1.73 ± 0.13	2.46 ± 1.45	1.94 ± -	2.30 ± 0.68	1.73 ± 0.13	2.46 ± 1.45	1.94 ± -	2.30 ± 0.68	1.73 ± 0.13	2.46 ± 1.45	1.94 ± -	2.30 ± 0.68	1.73 ± 0.13	2.46 ± 1.45	1.94 ± -	2.30 ± 0.68
	sept	1.81 ± 0.90	0.84 ± 0.10	1.47 ± 0.36	1.12 ± 0.08	1.03 ± 0.54	1.11 ± 0.31	2.79 ± 0.35	1.67 ± 0.38	1.48 ± 0.03	2.39 ± 0.97	2.16 ± 1.03	1.12 ± 0.31	1.48 ± 0.03	1.58 ± 0.34	1.44 ± 0.51	1.42 ± 0.33	1.48 ± 0.03	1.58 ± 0.34	1.44 ± 0.51	1.42 ± 0.33	1.48 ± 0.03	1.58 ± 0.34	1.44 ± 0.51	1.42 ± 0.33	1.48 ± 0.03	1.58 ± 0.34	1.44 ± 0.51	1.42 ± 0.33	1.48 ± 0.03
16:1c7 trans	mai	0.30 ± 0.04	0.19 ± 0.06	0.27 ± 0.15	0.17 ± 0.06	0.43 ± 0.05	0.47 ± 0.02	0.38 ± 0.07	0.30 ± 0.01	0.41 ± 0.22	0.35 ± 0.00	0.41 ± 0.22	0.35 ± 0.00	0.38 ± 0.07	0.30 ± 0.01	0.41 ± 0.22	0.35 ± 0.00	0.38 ± 0.07	0.30 ± 0.01	0.41 ± 0.22	0.35 ± 0.00	0.38 ± 0.07	0.30 ± 0.01	0.41 ± 0.22	0.35 ± 0.00	0.38 ± 0.07	0.30 ± 0.01	0.41 ± 0.22	0.35 ± 0.00	0.38 ± 0.07
	sept	0.40 ± 0.19	0.19 ± 0.02	0.36 ± 0.07	0.28 ± 0.04	0.28 ± 0.09	0.33 ± 0.11	0.48 ± 0.04	0.28 ± 0.04	0.34 ± 0.12	0.21 ± 0.07	0.40 ± 0.08	0.21 ± 0.07	0.34 ± 0.12	0.21 ± 0.07	0.40 ± 0.08	0.21 ± 0.07	0.34 ± 0.12	0.21 ± 0.07	0.40 ± 0.08	0.21 ± 0.07	0.34 ± 0.12	0.21 ± 0.07	0.40 ± 0.08	0.21 ± 0.07	0.34 ± 0.12	0.21 ± 0.07	0.40 ± 0.08	0.21 ± 0.07	0.34 ± 0.12
16:1c5	mai	0.91 ± 0.04	0.58 ± 0.11	1.08 ± 0.73	0.66 ± 0.35	1.37 ± 0.07	1.53 ± 0.21	1.30 ± 0.39	0.92 ± 0.03	1.37 ± 0.86	1.12 ± -	1.37 ± 0.86	1.12 ± -	1.30 ± 0.39	0.92 ± 0.03	1.37 ± 0.86	1.12 ± -	1.30 ± 0.39	0.92 ± 0.03	1.37 ± 0.86	1.12 ± -	1.30 ± 0.39	0.92 ± 0.03	1.37 ± 0.86	1.12 ± -	1.30 ± 0.39	0.92 ± 0.03	1.37 ± 0.86	1.12 ± -	1.30 ± 0.39
	sept	1.68 ± 0.88	0.78 ± 0.14	1.47 ± 0.30	1.13 ± 0.17	1.11 ± 0.49	0.94 ± 0.25	1.54 ± 0.32	0.95 ± 0.22	1.28 ± 0.45	1.72 ± 0.43	1.28 ± 0.45	1.72 ± 0.43	0.95 ± 0.22	1.28 ± 0.45	1.72 ± 0.43	1.28 ± 0.45	1.72 ± 0.43	1.28 ± 0.45	1.72 ± 0.43	1.28 ± 0.45	1.72 ± 0.43	1.28 ± 0.45	1.72 ± 0.43	1.28 ± 0.45	1.72 ± 0.43	1.28 ± 0.45	1.72 ± 0.43	1.28 ± 0.45	1.72 ± 0.43
17:1c8 cis	mai	0.09 ± 0.13	0.13 ± -	0.17 ± 0.08	0.11 ± 0.04	0.25 ± 0.02	0.31 ± 0.02	0.24 ± 0.05	0.21 ± 0.00	0.26 ± 0.13	0.23 ± 0.02	0.26 ± 0.13	0.23 ± 0.02	0.24 ± 0.05	0.21 ± 0.00	0.26 ± 0.13	0.23 ± 0.02	0.24 ± 0.05	0.21 ± 0.00	0.26 ± 0.13	0.23 ± 0.02	0.24 ± 0.05	0.21 ± 0.00	0.26 ± 0.13	0.23 ± 0.02	0.24 ± 0.05	0.21 ± 0.00	0.26 ± 0.13	0.23 ± 0.02	0.24 ± 0.05
	sept	0.30 ± 0.15	0.14 ± 0.02	0.25 ± 0.07	0.19 ± 0.01	0.16 ± 0.09	0.22 ± 0.09	0.19 ± 0.06	0.23 ± 0.08	0.16 ± 0.03	0.27 ± 0.09	0.18 ± 0.04	0.16 ± 0.03	0.23 ± 0.08	0.16 ± 0.03	0.27 ± 0.09	0.18 ± 0.04	0.16 ± 0.03	0.27 ± 0.09	0.18 ± 0.04	0.16 ± 0.03	0.27 ± 0.09	0.18 ± 0.04	0.16 ± 0.03	0.27 ± 0.09	0.18 ± 0.04	0.16 ± 0.03	0.27 ± 0.09	0.18 ± 0.04	0.16 ± 0.03
17:1c8 trans	mai	0.76 ± 0.05	0.48 ± 0.04	0.77 ± 0.43	0.48 ± 0.19	0.98 ± 0.10	0.94 ± 0.04	1.02 ± 0.26	0.78 ± 0.04	1.01 ± 0.55	0.86 ± 0.11	1.01 ± 0.55	0.86 ± 0.11	0.78 ± 0.04	1.01 ± 0.55	0.86 ± 0.11	1.01 ± 0.55	0.86 ± 0.11	1.01 ± 0.55	0.86 ± 0.11	1.01 ± 0.55	0.86 ± 0.11	1.01 ± 0.55	0.86 ± 0.11	1.01 ± 0.55	0.86 ± 0.11	1.01 ± 0.55	0.86 ± 0.11	1.01 ± 0.55	0.86 ± 0.11
	sept	0.96 ± 0.44	0.45 ± 0.05	0.71 ± 0.16	0.55 ± 0.06	0.66 ± 0.30	0.52 ± 0.13	0.95 ± 0.11	0.74 ± 0.14	0.76 ± 0.28	0.47 ± 0.12	0.76 ± 0.28	0.47 ± 0.12	0.74 ± 0.14	0.76 ± 0.28	0.47 ± 0.12	0.76 ± 0.28	0.47 ± 0.12	0.76 ± 0.28	0.47 ± 0.12	0.76 ± 0.28	0.47 ± 0.12	0.76 ± 0.28	0.47 ± 0.12	0.76 ± 0.28	0.47 ± 0.12	0.76 ± 0.28	0.47 ± 0.12	0.76 ± 0.28	0.47 ± 0.12
18:2c6,9	mai	3.86 ± 0.57	2.49 ± 0.74	4.49 ± 1.93	2.82 ± 0.74	3.50 ± 0.45	4.39 ± 0.11	3.16 ± 1.29	4.51 ± 0.13	3.18 ± 0.77	2.94 ± 0.48	3.18 ± 0.77	2.94 ± 0.48	3.16 ± 1.29	4.51 ± 0.13	3.18 ± 0.77	2.94 ± 0.48	3.18 ± 0.77	2.94 ± 0.48	3.18 ± 0.77	2.94 ± 0.48	3.18 ± 0.77	2.94 ± 0.48	3.18 ± 0.77	2.94 ± 0.48	3.18 ± 0.77	2.94 ± 0.48	3.18 ± 0.77	2.94 ± 0.48	3.18 ± 0.77
	sept	6.88 ± 2.82	3.30 ± 0.79	4.44 ± 1.59	3.30 ± 0.30	9.75 ± 9.51	6.64 ± 4.09	4.96 ± 1.14	3.72 ± 0.37	3.47 ± 0.69	1.82 ± 0.17	3.47 ± 0.69	1.82 ± 0.17	4.96 ± 1.14	3.72 ± 0.37	3.47 ± 0.69	1.82 ± 0.17	3.47 ± 0.69	1.82 ± 0.17	3.47 ± 0.69	1.82 ± 0.17	3.47 ± 0.69	1.82 ± 0.17	3.47 ± 0.69	1.82 ± 0.17	3.47 ± 0.69	1.82 ± 0.17	3.47 ± 0.69	1.82 ± 0.17	3.47 ± 0.69
18:3	mai	0.52 ± 0.03	0.33 ± 0.07	0.53 ± 0.19	0.34 ± 0.06	0.32 ± 0.05	0.51 ± 0.10	0.32 ± 0.13	0.57 ± 0.05	0.35 ± 0.13	0.36 ± 0.15	0.35 ± 0.13	0.36 ± 0.15	0.32 ± 0.13	0.57 ± 0.05	0.35 ± 0.13	0.36 ± 0.15	0.35 ± 0.13	0.36 ± 0.15	0.35 ± 0.13	0.36 ± 0.15	0.35 ± 0.13	0.36 ± 0.15	0.35 ± 0.13	0.36 ± 0.15	0.35 ± 0.13	0.36 ± 0.15	0.35 ± 0.13	0.36 ± 0.15	0.35 ± 0.13
	sept	0.89 ± 0.45	0.44 ± 0.22	0.53 ± 0.32	0.37 ± 0.17	1.72 ± 2.74	1.00 ± 1.36	0.35 ± 0.02	0.36 ± 0.08	0.34 ± 0.15	0.15 ± 0.04	0.36 ± 0.08	0.34 ± 0.15	0.35 ± 0.02	0.36 ± 0.08	0.34 ± 0.15	0.15 ± 0.04	0.36 ± 0.08	0.34 ± 0.15	0.15 ± 0.04	0.36 ± 0.08	0.34 ± 0.15	0.15 ± 0.04	0.36 ± 0.08	0.34 ± 0.15	0.15 ± 0.04	0.36 ± 0.08	0.34 ± 0.15	0.15 ± 0.04	0.36 ± 0.08
20:4c6,9,12,15	mai	0.46 ± 0.00	0.29 ± 0.04	0.50 ± 0.23	0.32 ± 0.09	0.47 ± 0.05	0.53 ± 0.01	0.44 ± 0.17	0.50 ± 0.07	0.46 ± 0.09	0.41 ± 0.02	0.46 ± 0.09	0.41 ± 0.02	0.44 ± 0.17	0.50 ± 0.07	0.46 ± 0.09	0.41 ± 0.02	0.46 ± 0.09	0.41 ± 0.02	0.46 ± 0.09	0.41 ± 0.02	0.46 ± 0.09	0.41 ± 0.02	0.46 ± 0.09	0.41 ± 0.02	0.46 ± 0.09	0.41 ± 0.02	0.46 ± 0.09	0.41 ± 0.02	0.46 ± 0.09
	sept	0.71 ± 0.33	0.34 ± 0.08	0.50 ± 0.05	0.40 ± 0.14	0.57 ± 0.09	0.59 ± 0.16	0.50 ± 0.09	0.41 ± 0.11	0.28 ± 0.04	0.22 ± 0.03	0.28 ± 0.04	0.22 ± 0.03	0.50 ± 0.09	0.41 ± 0.11	0.28 ± 0.04	0.22 ± 0.03	0.50 ± 0.09	0.41 ± 0.11	0.28 ± 0.04	0.22 ± 0.03	0.50 ± 0.09	0.41 ± 0.11	0.28 ± 0.04	0.22 ± 0.03	0.50 ± 0.09	0.41 ± 0.11	0.28 ± 0.04	0.22 ± 0.03	0.50 ± 0.09
20:5	mai	- ± -	- ± -	- ± -	- ± -	0.08 ± 0.00	0.10 ± 0.01	0.09 ± -	0.08 ± -	0.07 ± -	0.08 ± 0.01	0.09 ± 0.01	0.08 ± -	0.09 ± 0.01	0.08 ± -	0.07 ± -	0.08 ± 0.01	0.09 ± 0.01	0.08 ± -	0.07 ± -	0.08 ± 0.01	0.09 ± 0.01	0.08 ± -	0.07 ± -	0.08 ± 0.01	0.09 ± 0.01	0.08 ± -	0.07 ± -	0.08 ± 0.01	0.09 ± 0.01
	sept	0.15 ± 0.10	0.08 ± 0.00	0.11 ± -	0.12 ± -	0.11 ± 0.01	0.10 ± 0.01	0.11 ± 0.02	0.09 ± 0.01	0.11 ± 0.02	0.02 ± -	0.09 ± 0.01	0.02 ± -	0.11 ± 0.02	0.09 ± 0.01	0.11 ± 0.02	0.02 ± -	0.09 ± 0.01	0.11 ± 0.02	0.02 ± -	0.09 ± 0.01	0.11 ± 0.02	0.02 ± -	0.09 ± 0.01	0.11 ± 0.02	0.02 ± -	0.09 ± 0.01	0.11 ± 0.02	0.02 ± -	0.09 ± 0.01
17:2	mai	0.33 ± 0.02	0.21 ± 0.04	0.41 ± 0.18	0.26 ± 0.07	0.38 ± 0.07	0.47 ± 0.01	0.30 ± 0.10	0.37 ± 0.01	0.33 ± 0.04	0.38 ± 0.03	0.33 ± 0.04	0.38 ± 0.03	0.30 ± 0.10	0.37 ± 0.01	0.33 ± 0.04	0.38 ± 0.03	0.30 ± 0.10	0.37 ± 0.01	0.33 ± 0.04	0.38 ± 0.03	0.30 ± 0.10	0.37 ± 0.01	0.33 ± 0.04	0.38 ± 0.03	0.30 ± 0.10	0.37 ± 0.01	0.33 ± 0.04	0.38 ± 0.03	0.30 ± 0.10
	sept	0.46 ± 0.24	0.21 ± 0.00	0.33 ± 0.06	0.27 ± 0.10	0.34 ± 0.08	0.37 ± 0.05	0.48 ± 0.05	0.26 ± 0.09	0.34 ± 0.03	0.25 ± 0.02	0.48 ± 0.05	0.26 ± 0.09	0.34 ± 0.03	0.25 ± 0.02	0.48 ± 0.05	0.26 ± 0.09	0.34 ± 0.03	0.25 ± 0.02	0.48 ± 0.05	0.26 ± 0.09	0.34 ± 0.03	0.25 ± 0.02	0.48 ± 0.05	0.26 ± 0.09	0.34 ± 0.03	0.25 ± 0.02	0.48 ± 0.05	0.26 ± 0.09	0.34 ± 0.03

Tab. VIII-11: Carbon isotopic signature of SATFA, MUFA, PUFA and individual PLFA [atom%] in September (n=4) in beech and spruce rhizosphere of the phytotron experiment (mean \pm standard deviation).

	beech		spruce		beech (mixed)		spruce (mixed)		unplanted	
	1 x ozone	2 x ozone	1 x ozone	2 x ozone	1 x ozone	2 x ozone	1 x ozone	2 x ozone	1 x ozone	2 x ozone
SATFA	2.4157 \pm 1.2133	1.4654 \pm 0.4708	1.6865 \pm 0.0818	0.9841 \pm 0.1181	1.5883 \pm 0.3694	1.2101 \pm 0.0709	1.1893 \pm 0.0728	1.0992 \pm 0.1644	2.6173 \pm 4.2267	1.0852 \pm 0.1913
MUFA	2.3681 \pm 1.2042	1.4424 \pm 0.4604	1.3841 \pm 0.4740	0.9840 \pm 0.1199	1.5837 \pm 0.3660	1.2073 \pm 0.0727	1.1825 \pm 0.0669	1.1002 \pm 0.1627	3.9519 \pm 5.6607	1.0833 \pm 0.1895
PUFA	3.2474 \pm 1.7334	1.9084 \pm 0.8370	2.1684 \pm 2.0351	1.0312 \pm 0.6857	1.6760 \pm 0.4480	1.2569 \pm 0.0365	1.2579 \pm 0.0845	1.1392 \pm 0.1683	4.4628 \pm 6.0549	1.2113 \pm 0.2883
br12:0	- \pm -	- \pm -	1.0775 \pm 0.0029	1.0781 \pm -	1.0797 \pm 0.0015	1.0762 \pm 0.0006	1.0785 \pm 0.0035	1.0786 \pm 0.0014	1.0838 \pm 0.0099	1.0786 \pm 0.0016
br13:0	1.0843 \pm 0.0045	1.0822 \pm 0.0040	1.0778 \pm 0.0026	1.0776 \pm 0.0014	1.0752 \pm 0.0004	1.0787 \pm 0.0011	1.0783 \pm 0.0019	1.0785 \pm 0.0015	1.0803 \pm 0.0035	1.0789 \pm 0.0012
al14:0	1.0806 \pm 0.0063	1.0789 \pm 0.0052	1.0834 \pm 0.0193	1.0744 \pm 0.0022	1.0785 \pm 0.0011	1.0744 \pm 0.0005	1.0746 \pm 0.0008	1.0728 \pm 0.0007	1.0778 \pm 0.0076	1.0742 \pm 0.0023
il14:0	1.0793 \pm 0.0009	1.0797 \pm 0.0003	1.0786 \pm 0.0003	1.0786 \pm 0.0008	1.0790 \pm 0.0007	1.0792 \pm 0.0011	1.0783 \pm 0.0014	1.0774 \pm 0.0004	1.0791 \pm 0.0008	1.0788 \pm 0.0015
al15:0	1.0800 \pm 0.0006	1.0798 \pm 0.0008	1.0755 \pm 0.0078	1.0791 \pm 0.0002	1.0790 \pm 0.0017	1.0800 \pm 0.0015	1.0803 \pm 0.0011	1.0811 \pm 0.0007	1.0795 \pm 0.0013	1.0797 \pm 0.0012
il15:0	1.0794 \pm 0.0005	1.0795 \pm 0.0013	1.0788 \pm 0.0006	1.0793 \pm 0.0020	1.0790 \pm 0.0009	1.0790 \pm 0.0006	1.0781 \pm 0.0011	1.0775 \pm 0.0012	1.0786 \pm 0.0011	1.0792 \pm 0.0013
n15:0	1.0834 \pm 0.0039	1.0825 \pm 0.0028	1.0790 \pm 0.0010	1.0792 \pm 0.0002	1.0799 \pm 0.0021	1.0805 \pm 0.0016	1.0819 \pm 0.0015	1.0824 \pm 0.0009	1.0823 \pm 0.0063	1.0809 \pm 0.0020
al16:0	1.2102 \pm 0.1659	1.1745 \pm 0.0825	1.3416 \pm 0.5292	1.0922 \pm 0.2866	1.0925 \pm 0.0237	1.0874 \pm 0.0121	1.0935 \pm 0.0077	1.0882 \pm 0.0042	1.1686 \pm 0.1753	1.1008 \pm 0.0301
il16:0	1.0778 \pm 0.0004	1.0785 \pm 0.0006	1.0776 \pm 0.0010	1.0777 \pm 0.0004	1.0779 \pm 0.0006	1.0777 \pm 0.0004	1.0778 \pm 0.0004	1.0775 \pm 0.0005	1.0775 \pm 0.0008	1.0780 \pm 0.0010
16:0 mix	1.0932 \pm 0.0170	1.0869 \pm 0.0080	1.0783 \pm 0.0010	1.0794 \pm 0.0020	1.0809 \pm 0.0035	1.0802 \pm 0.0016	1.0810 \pm 0.0012	1.0807 \pm 0.0003	1.0868 \pm 0.0076	1.0810 \pm 0.0030
al7:0	1.1006 \pm 0.0243	1.0912 \pm 0.0112	1.1330 \pm 0.1089	1.0806 \pm 0.0023	1.0821 \pm 0.0056	1.0811 \pm 0.0027	1.0826 \pm 0.0018	1.0826 \pm 0.0003	1.0925 \pm 0.0243	1.0827 \pm 0.0047
il7:0	1.0992 \pm 0.0248	1.0903 \pm 0.0118	1.0771 \pm 0.0004	1.0787 \pm 0.0028	1.0801 \pm 0.0040	1.0790 \pm 0.0020	1.0799 \pm 0.0009	1.0795 \pm 0.0002	1.0894 \pm 0.0217	1.0805 \pm 0.0038
cy17:0	1.1119 \pm 0.0623	1.1069 \pm 0.0239	1.0778 \pm 0.0028	1.0826 \pm 0.0083	1.0871 \pm 0.0091	1.0853 \pm 0.0078	1.0831 \pm 0.0032	1.0823 \pm 0.0006	1.1056 \pm 0.0468	1.0839 \pm 0.0071
n17:0	1.0804 \pm 0.0036	1.0800 \pm 0.0022	1.0763 \pm 0.0037	1.0791 \pm 0.0016	1.0790 \pm 0.0007	1.0789 \pm 0.0010	1.0786 \pm 0.0004	1.0787 \pm 0.0007	1.0812 \pm 0.0091	1.0790 \pm 0.0009
br10-17:0	1.0730 \pm 0.0013	1.0740 \pm 0.0004	1.0690 \pm 0.0089	1.0732 \pm 0.0005	1.0744 \pm 0.0027	1.0748 \pm 0.0020	1.0761 \pm 0.0007	1.0772 \pm 0.0014	1.0744 \pm 0.0019	1.0753 \pm 0.0019
br10-18:0	1.0883 \pm 0.0159	- \pm -	1.0805 \pm 0.0035	1.0788 \pm 0.0008	1.0792 \pm 0.0018	1.0803 \pm 0.0026	1.0785 \pm 0.0009	1.0781 \pm 0.0007	1.0785 \pm 0.0017	1.0796 \pm 0.0017
il18:0	1.1512 \pm 0.0839	1.1312 \pm 0.0482	1.0791 \pm 0.0004	1.0880 \pm 0.0152	1.0892 \pm 0.0126	1.0853 \pm 0.0050	1.0885 \pm 0.0050	1.0851 \pm 0.0023	1.1325 \pm 0.1022	1.0896 \pm 0.0144
cy18:0	1.0933 \pm 0.0212	1.0851 \pm 0.0122	1.0800 \pm 0.0021	1.0807 \pm 0.0007	1.0848 \pm 0.0052	1.0813 \pm 0.0006	1.0820 \pm 0.0014	1.0820 \pm 0.0027	1.1325 \pm 0.1022	1.0812 \pm 0.0022
dic18:0	1.0747 \pm 0.0015	1.0752 \pm 0.0014	1.0731 \pm 0.0005	1.0739 \pm 0.0009	1.0740 \pm 0.0015	1.0746 \pm 0.0015	1.0738 \pm 0.0007	1.0748 \pm 0.0007	1.0750 \pm 0.0034	1.0741 \pm 0.0010
cy19:0	1.0756 \pm 0.0008	1.0762 \pm 0.0004	1.0759 \pm 0.0005	1.0764 \pm 0.0002	1.0759 \pm 0.0005	1.0766 \pm 0.0007	1.0766 \pm 0.0007	1.0768 \pm 0.0002	1.0758 \pm 0.0008	1.0765 \pm 0.0006
br10-19:0	1.1121 \pm 0.0378	1.1109 \pm 0.0024	1.0884 \pm 0.0150	1.0817 \pm 0.0037	1.0834 \pm 0.0055	1.0820 \pm 0.0025	1.0827 \pm 0.0011	1.0820 \pm 0.0005	1.0995 \pm 0.0410	1.0838 \pm 0.0054
dic20:0	1.0735 \pm 0.0006	1.0740 \pm 0.0001	1.0734 \pm 0.0006	1.0737 \pm 0.0007	1.0743 \pm 0.0009	1.0754 \pm 0.0012	1.0738 \pm 0.0006	1.0746 \pm 0.0013	1.0739 \pm 0.0011	1.0741 \pm 0.0010
n20:0	1.1123 \pm 0.0403	1.1074 \pm 0.0272	1.0769 \pm 0.0005	1.0823 \pm 0.0087	1.0843 \pm 0.0083	1.0810 \pm 0.0035	1.0824 \pm 0.0023	1.0809 \pm 0.0007	1.1012 \pm 0.0427	1.0848 \pm 0.0099
dic22:0	1.0742 \pm 0.0004	1.0748 \pm 0.0002	1.0737 \pm 0.0007	1.0735 \pm 0.0007	1.0740 \pm 0.0010	1.0755 \pm 0.0010	1.0742 \pm 0.0007	1.0745 \pm 0.0010	1.0744 \pm 0.0014	1.0741 \pm 0.0010
n22:0	1.0832 \pm 0.0094	1.0817 \pm 0.0064	1.0748 \pm 0.0002	1.0761 \pm 0.0023	1.0770 \pm 0.0019	1.0767 \pm 0.0014	1.0764 \pm 0.0007	1.0764 \pm 0.0001	1.0809 \pm 0.0110	1.0770 \pm 0.0023
n24:0	1.0791 \pm 0.0071	1.0775 \pm 0.0039	1.0735 \pm 0.0004	1.0744 \pm 0.0014	1.0755 \pm 0.0014	1.0750 \pm 0.0008	1.0750 \pm 0.0005	1.0753 \pm 0.0001	1.0761 \pm 0.0063	1.0749 \pm 0.0017
15:1w6	1.0756 \pm 0.0020	1.0763 \pm 0.0019	1.0764 \pm 0.0022	1.0758 \pm 0.0015	1.0773 \pm 0.0023	1.0759 \pm 0.0022	1.0742 \pm 0.0004	1.0751 \pm 0.0012	1.0765 \pm 0.0015	1.0761 \pm 0.0016
16:1w9	1.0854 \pm 0.0081	1.0840 \pm 0.0024	1.0802 \pm 0.0011	1.0799 \pm 0.0039	1.0793 \pm 0.0008	1.0800 \pm 0.0017	1.0794 \pm 0.0010	1.0808 \pm 0.0005	1.0814 \pm 0.0024	1.0807 \pm 0.0023
16:1w7 cis	1.0847 \pm 0.0087	1.0832 \pm 0.0037	1.0795 \pm 0.0008	1.0795 \pm 0.0028	1.0792 \pm 0.0008	1.0792 \pm 0.0012	1.0795 \pm 0.0015	1.0790 \pm 0.0004	1.0831 \pm 0.0073	1.0795 \pm 0.0015
16:1w7 trans	1.0744 \pm 0.0014	1.0756 \pm 0.0008	1.0750 \pm 0.0012	1.0744 \pm 0.0006	1.0751 \pm 0.0016	1.0759 \pm 0.0014	1.0748 \pm 0.0012	1.0751 \pm 0.0007	1.0759 \pm 0.0011	1.0762 \pm 0.0009
16:1w5	1.0835 \pm 0.0027	1.0841 \pm 0.0007	1.0861 \pm 0.0018	1.0833 \pm 0.0007	1.0830 \pm 0.0013	1.0842 \pm 0.0010	1.0831 \pm 0.0011	1.0834 \pm 0.0009	1.0845 \pm 0.0025	1.0838 \pm 0.0007
17:1w8 cis	1.0809 \pm 0.0056	1.0799 \pm 0.0024	1.0767 \pm 0.0022	1.0772 \pm 0.0015	1.0779 \pm 0.0008	1.0773 \pm 0.0013	1.0776 \pm 0.0010	1.0771 \pm 0.0012	1.0783 \pm 0.0026	1.0776 \pm 0.0014
17:1w8 trans	1.0744 \pm 0.0016	1.0749 \pm 0.0018	1.0766 \pm 0.0025	1.0747 \pm 0.0005	1.0742 \pm 0.0013	1.0752 \pm 0.0010	1.0758 \pm 0.0023	1.0748 \pm 0.0007	1.0759 \pm 0.0028	1.0752 \pm 0.0008
18:2w6,9	1.6226 \pm 0.6379	1.4691 \pm 0.3452	1.6262 \pm 0.9911	1.1528 \pm 0.1244	1.1494 \pm 0.1018	1.1322 \pm 0.0613	1.1607 \pm 0.0506	1.1370 \pm 0.0213	1.4514 \pm 0.6793	1.2457 \pm 0.2068
18:3	1.1694 \pm 0.1096	1.1484 \pm 0.0694	1.1547 \pm 0.1639	1.0896 \pm 0.0286	1.0895 \pm 0.0226	1.0927 \pm 0.0141	1.0918 \pm 0.0170	1.0845 \pm 0.0091	1.1514 \pm 0.1400	1.1135 \pm 0.0522
20:4w6,9,12,15	1.0798 \pm 0.0034	1.0793 \pm 0.0017	1.0775 \pm 0.0022	1.0758 \pm 0.0040	1.0773 \pm 0.0005	1.0768 \pm 0.0005	1.0771 \pm 0.0025	1.0760 \pm 0.0029	1.0794 \pm 0.0022	1.0781 \pm 0.0052
20:5	1.0722 \pm 0.0080	1.0744 \pm -	1.0748 \pm 0.0019	1.0727 \pm 0.0001	1.0756 \pm 0.0036	1.0718 \pm 0.0006	- \pm -	1.0917 \pm -	1.0746 \pm 0.0047	1.0751 \pm 0.0018
17:2	1.0802 \pm 0.0002	1.0793 \pm 0.0016	1.0801 \pm 0.0019	1.0787 \pm 0.0020	1.0785 \pm 0.0003	1.0793 \pm 0.0010	1.0789 \pm 0.0012	1.0782 \pm 0.0009	1.0791 \pm 0.0017	1.0787 \pm 0.0013

3.4 Influence of long term elevated ozone exposure on rhizosphere microbial communities of mature beech trees (*Fagus sylvatica* L.) on the free-air lysimeter device (D)

Tab. VIII-12: PLFA abundances [nmol g⁻¹ DS] in beech rhizosphere of ambient and elevated ozone treatments on a lysimeter device, monthly (m) during the vegetation period (n=4; means ± standard deviations). Asterisks (*) represent statistically significant differences (p < 0.05) compared to the beginning of labelling. Letters (a, b) indicate statistically significant differences (p < 0.05) between different ozone treatments.

PLFA conc [nmol g ⁻¹ DS]	labelling time [m]							
	0		1		2		3	
	1 x O ₃	2 x O ₃	1 x O ₃	2 x O ₃	1 x O ₃	2 x O ₃	1 x O ₃	2 x O ₃
i14:0	0.10	0.12	0.07	0.09	0.05	0.14	0.12	0.14*
±	0.07	0.02	0.08	0.06	0.06	0.03	0.08	0.09
a14:0	0.34	0.37	0.32	0.32	0.25 ^a	0.46 ^b	0.41	0.53
±	0.05	0.07	0.16	0.11	0.07	0.07	0.11	0.13
i15:0	2.49	2.58	2.56	2.63	2.37 ^a	3.93 ^{a,b}	3.35	4.03*
±	0.17	0.16	1.26	0.88	0.80	0.57	0.80	0.77
a15:0	1.62	1.69	1.53	1.59	1.53 ^a	2.15 ^b	1.84	2.27
±	0.20	0.10	0.60	0.51	0.40	0.29	0.38	0.34
n15:0	0.16	0.17	0.17	0.13	0.20	0.35*	0.25	0.27*
±	0.12	0.11	0.12	0.08	0.14	0.06	0.14	0.19
i16:0	1.13	1.21	1.15	1.14	0.95 ^a	1.55 ^b	1.39	1.62
±	0.13	0.19	0.41	0.35	0.38	0.24	0.42	0.28
a16:0	4.53	4.88	4.95	4.91	4.37 ^a	6.55 ^b	5.88	6.90
±	0.78	0.35	1.89	1.65	1.24	0.95	0.96	1.19
i17:0	2.40	2.58	2.62	2.46	2.30 ^a	3.37 ^b	2.91	3.58
±	0.27	0.35	1.09	0.73	0.53	0.42	0.76	0.56
a17:0	0.89	0.90	1.01	0.95	0.81 ^a	1.33 ^b	1.01	1.43*
±	0.18	0.17	0.38	0.31	0.20	0.18	0.36	0.23
cy17:0	1.35	1.38	1.35	1.43	1.30 ^a	1.92 ^{a,b}	1.92	2.01*
±	0.22	0.12	0.52	0.41	0.33	0.20	0.34	0.26
br9,17:0	1.46	1.11	1.46	1.39	1.10 ^a	1.72 ^b	1.49	1.81*
±	0.24	0.32	0.57	0.45	0.38	0.23	0.24	0.38
i18:0	0.96	1.10	1.07	1.10	0.96 ^a	1.51 ^b	1.18	1.36
±	0.12	0.22	0.39	0.27	0.16	0.33	0.15	0.23
cy18:0	0.21 ^a	0.35 ^b	-	0.34	0.21 ^a	0.38 ^b	0.31	0.34
±	0.08	0.07	-	0.07	0.10	0.09	0.10	0.24
cy19:0	5.02 ^a	8.29 ^b	8.22	7.75	4.23 ^a	9.66 ^{a,b}	6.96	8.69*
±	0.70	0.93	4.22	1.67	2.04	0.29	2.07	1.45
br10,19:0	0.76	1.02	0.99	0.83	0.43	0.77	0.74	0.89
±	0.09	0.09	0.30	0.20	0.26	0.18	0.17	0.16
i20:0	0.24	0.39	0.35	0.55	0.29	0.52	0.64	0.49*
±	0.04	0.06	0.29	0.13	0.07	0.14	0.15	0.14
n22:0	0.65	0.71	0.79	1.05	0.64 ^a	0.94 ^{a,b}	0.89	0.90*
±	0.04	0.10	0.25	0.22	0.07	0.04	0.17	0.12
n24:0	0.35	0.41	0.41	0.55	0.38 ^a	0.51 ^{a,b}	0.45	0.43*
±	0.03	0.05	0.15	0.10	0.01	0.02	0.08	0.09
SATFA total	25.26	27.63	28.15	28.21	24.58	37.99	32.69	39.31
±	2.87	2.16	12.57	7.94	6.85	3.02	7.06	5.52
18:2ω6,9	1.81	2.44	1.71	1.52	1.13	2.23	2.73	1.81
±	0.71	0.60	0.54	1.08	0.65	1.06	0.26	1.50
18:3	0.24	0.48	0.21	0.14	0.17	0.20	0.27	0.15
±	0.16	0.11	0.05	0.07	0.01	0.09	0.00	0.24
20:4ω6,9,12,15	0.27	0.28	0.16	0.19	0.00	0.15	0.34	0.24
±	0.04	0.03	0.05	0.04	0.07	0.08	0.04	0.06
PUFA total	2.73	2.82	2.78	2.52	2.06	3.34	3.65	4.25
±	0.86	0.68	0.61	1.19	0.69	1.23	0.28	1.74
17:1ω8 cis	0.30	0.29	0.34	0.30	0.21	0.23	0.44	0.34*
±	0.03	0.05	0.12	0.06	0.04	0.11	0.22	0.13
17:1ω8 trans	0.64	0.76	0.78	0.76	0.64	0.57	0.86	0.84
±	0.08	0.11	0.38	0.09	0.07	0.30	0.09	0.08
16:1ω9	0.28	0.40	0.31	0.38	0.31	0.27	0.44	0.37
±	0.05	0.07	0.17	0.06	0.04	0.13	0.22	0.09
16:1ω7 trans	0.10	0.07	0.12	0.09	0.05	0.15	0.12	0.16
±	0.01	0.08	0.05	0.06	0.06	0.05	0.09	0.04
16:1ω7 cis	1.49	1.51	1.84	1.83	1.64	2.31	2.07	2.36
±	0.23	0.56	0.91	0.32	0.40	0.86	1.21	0.35
16:1ω5	1.49	1.51	1.84	1.83	1.64	2.31	1.69	2.36
±	0.23	0.56	0.91	0.32	0.40	0.86	1.21	0.35
18:1ω9	2.32	2.31	2.47	2.21	1.76	2.57	2.50	3.89
±	0.87	0.52	0.96	0.39	0.37	0.76	0.40	2.58
18:1ω7	1.96	3.71	2.55	3.44	2.97	3.75	3.56	3.35
±	1.48	0.63	2.93	0.59	0.35	0.99	0.62	1.98
MUFA total	8.01	10.33	10.22	10.75	9.29	12.87	11.37	13.86
±	0.98	2.48	6.21	1.81	1.65	3.94	3.03	1.69
PLFA total	35.99	40.78	41.15	41.47	35.93	54.19	47.70	57.42
±	3.44	4.92	18.72	10.52	8.96	7.71	8.87	7.70

Tab. VIII-13: Contribution of individual PLFA [mol%] to total PLFA in beech rhizosphere (n=4) of ambient and elevated ozone treatments on a lysimeter device, monthly (m) during the vegetation period (means \pm standard deviations).

PLFA conc [mol %]	labelling time [m]							
	0		1		2		3	
	1 x O ₃	2 x O ₃	1 x O ₃	2 x O ₃	1 x O ₃	2 x O ₃	1 x O ₃	2 x O ₃
i14:0	0.36	0.30	0.24	0.25	0.27	0.26	0.30	0.30
±	0.04	0.03	0.03	0.03	0.05	0.04	0.05	0.02
a14:0	0.93	0.91	0.77	0.75	0.70	0.85	0.85	0.91
±	0.13	0.21	0.09	0.12	0.09	0.08	0.10	0.12
i15:0	6.94	6.38	6.12	6.22	6.48	7.25	6.97	6.98
±	0.22	0.74	0.31	0.81	0.87	0.38	0.49	0.64
a15:0	4.50	4.17	3.80	3.78	4.26	3.99	3.85	3.95
±	0.18	0.28	0.25	0.39	0.27	0.36	0.15	0.17
n15:0	0.44	0.41	0.37	0.28	0.67		0.49	0.65
±	0.31	0.22	0.18	0.14	0.02	0.05	0.23	0.02
i16:0	3.14	2.98	2.88	2.72	2.58	2.85	2.90	2.81
±	0.36	0.38	0.37	0.39	0.46	0.05	0.51	0.16
a16:0	12.53	12.04	12.31	11.60	12.11	12.09	12.37	11.97
±	1.08	1.11	0.91	1.31	0.59	0.20	1.06	0.59
i17:0	6.68	6.34	6.42	5.88	6.43	6.27	6.06	6.22
±	0.43	0.67	0.49	0.29	0.36	0.76	0.85	0.34
a17:0	2.46	2.20	2.53	2.27	2.31	2.45	2.08	2.49
±	0.30	0.27	0.31	0.22	0.64	0.19	0.43	0.21
cy17:0	3.61	3.31	3.78	3.62	3.74	3.60	3.98	3.55
±	0.40	0.23	0.40	0.26	0.14	0.28	0.34	0.10
br9,17:0	3.41	2.39	3.98	3.27	2.54	3.72	2.76	3.05
±	0.42	1.05	0.95	0.28	0.70	0.44	0.40	0.44
i18:0	2.50	2.33	2.51	2.68	3.01	2.87	2.61	2.24
±	0.14	0.70	0.27	0.09	0.26	0.56	0.19	0.13
cy18:0	0.57	0.96	-	0.75	0.58	0.81	0.51	0.87
±	0.17	0.10	-	0.09	0.24	0.19	0.16	0.15
cy19:0	14.29	17.72	17.77	17.63	15.36	22.35	14.65	18.94
±	1.25	0.50	3.00	1.02	1.51	2.97	2.27	2.39
br10,19:0	2.16	2.18	2.14	1.89	1.56	1.78	1.56	1.94
±	0.16	0.30	0.32	0.23	0.30	0.21	0.28	0.06
i20:0	0.68	0.83	0.76	1.25	1.05	1.20	1.35	1.07
±	0.07	0.11	0.25	0.22	0.07	0.29	0.20	0.18
n22:0	1.85	1.52	1.71	2.39	2.32	2.17	1.87	1.96
±	0.23	0.29	0.36	0.29	0.30	0.31	0.08	0.23
n24:0	1.00	0.88	0.89	1.25	1.38	1.18	0.95	0.94
±	0.14	0.13	0.29	0.15	0.24	0.17	0.04	0.12
SATFA total	70.12	68.07	68.38	67.51	68.06	70.64	68.31	68.48
±	2.48	4.22	4.80	3.82	2.88	5.05	5.25	3.20
18:2ω6,9	5.15	5.21	3.70	3.46	4.10	5.16	5.75	3.95
±	1.44	1.08	2.87	1.73	0.81	1.41	1.20	2.04
18:3	0.68	1.03	0.45	0.32	0.62	0.46	0.57	0.33
±	0.36	0.16	0.38	0.12	0.11	0.14	0.11	0.39
20:4ω6,9,12,15	0.77	0.60	0.35	0.43	-	0.35	0.72	0.52
±	0.10	0.03	0.11	0.07	-	0.11	0.07	0.04
PUFA total	7.49	6.86	7.74	6.05	5.65	6.09	7.81	7.24
±	1.75	1.09	3.35	1.89	0.74	1.64	1.37	2.38
17:1ω8 cis	0.85	0.62	0.74	0.68	0.76	0.53	0.93	0.74
±	0.07	0.06	0.08	0.12	0.06	0.11	0.34	0.17
17:1ω8 trans	1.82	1.62	1.69	1.73	2.32	1.32	1.81	1.83
±	0.12	0.10	0.19	0.28	0.33	0.42	0.16	0.20
16:1ω9	0.80	0.85	0.67	0.86	1.13	0.62	0.93	0.81
±	0.08	0.09	0.14	0.08	0.17	0.13	0.09	0.14
16:1ω7 trans	0.28	0.29	0.29	0.25	0.23	0.28	0.33	0.29
±	0.00	0.08	0.04	0.04	0.02	0.05	0.06	0.03
16:1ω7 cis	4.11	3.63	4.53	4.50	4.60	4.14	4.32	4.14
±	0.29	1.02	1.23	0.56	0.71	1.17	0.82	0.64
16:1ω5	4.11	3.63	4.53	4.50	4.60	4.14	3.51	4.14
±	0.29	1.02	1.23	0.56	0.71	1.17	2.38	0.64
18:1ω9	6.38	5.61	6.46	5.42	4.94	4.67	5.26	6.66
±	2.04	0.61	2.67	0.54	0.36	0.81	0.19	4.01
18:1ω7	5.80	9.06	6.19	8.47	8.52	6.81	7.51	5.99
±	4.39	0.45	4.74	1.09	1.50	0.99	0.84	3.56
MUFA total	22.41	25.07	23.89	26.43	26.29	23.28	23.89	24.28
±	3.44	3.26	5.81	2.90	3.28	4.55	4.90	2.46

Tab. VIII-14: Carbon isotopic signature [$\delta^{13}\text{C}$ in ‰ V-PDB] in PLFA of beech rhizosphere (n=4) of ambient and elevated ozone treatments on a Lysimeter device, monthly (m) during the vegetation period (means \pm standard deviations). Asterisks (*) represent statistically significant differences ($p < 0.05$) compared to the beginning of labelling. Letters (a, b) indicate statistically significant differences ($p < 0.05$) between the two different ozone treatments.

PLFA $\delta^{13}\text{C}$ [‰ V-PDB]	labelling time [m]							
	0		1		2		3	
	1 x O ₃	2 x O ₃	1 x O ₃	2 x O ₃	1 x O ₃	2 x O ₃	1 x O ₃	2 x O ₃
i14:0	-23.87	-23.08	-23.28	-24.55	-24.21	-24.12	-25.07	-23.72
\pm	1.60	1.51	0.65	0.52	1.31	0.41	1.13	0.28
a14:0	-25.45	-25.36	-25.79	-25.90	-26.46 ^a	-25.27 ^b	-25.84	-25.38
\pm	0.42	0.50	0.28	0.42	0.69	0.16	0.69	0.31
i15:0	-23.67	-23.53	-24.07	-23.68	-23.96	-23.74	-23.94	-23.77
\pm	0.30	0.35	0.77	0.23	0.23	0.33	0.12	0.80
a15:0	-24.91	-24.42	-25.07	-25.05	-25.04	-25.70*	-25.51	-25.68*
\pm	0.40	0.46	0.42	0.40	0.41	0.42	0.97	0.23
n15:0	-31.28	-27.08	-27.19	-31.57	-26.96	-27.43	-27.51	-27.65
\pm	4.96	1.80	2.84	4.84	0.37	1.49	0.78	1.04
i16:0	-25.24	-25.20	-25.67	-25.66*	-25.21 ^b	-25.71* ^a	-26.02*	-25.92*
\pm	0.26	0.16	0.28	0.26	0.30	0.22	0.21	0.23
a16:0	-24.09	-23.51	-22.49*	-24.03	-25.32	-25.73	-25.91*	-25.59
\pm	0.62	2.33	1.22	0.73	0.81	0.25	0.40	0.68
i17:0	-25.60 ^a	-24.90 ^b	-24.86	-25.35	-25.51	-25.30	-25.94	-25.26
\pm	0.22	0.52	0.58	0.30	0.82	0.51	0.38	0.53
a17:0	-27.74	-27.58	-27.82	-27.73	-28.54	-28.08	-29.00	-27.16
\pm	0.58	0.92	0.46	0.32	0.91	0.47	2.38	1.03
cy17:0	-27.11	-26.65	-27.24	-27.30*	-27.06	-27.33*	-27.14	-27.26*
\pm	0.55	0.48	0.50	0.24	0.39	0.21	0.59	0.25
br9,17:0	-27.05	-27.90	-27.47	-27.36	-27.75	-27.68	-26.97	-27.11
\pm	0.34	1.66	0.90	0.38	0.51	1.01	0.40	1.39
i18:0	-24.82	-24.79	-23.69	-24.52	-25.12	-25.56	-25.50	-25.54
\pm	0.51	1.39	1.01	0.24	0.98	0.80	0.52	0.41
cy18:0	-31.03	-28.09	-28.04	-29.31	-31.50	-30.30	-29.17	-29.14
\pm	4.58	1.04	0.36	1.50	2.57	1.88	3.97	1.83
cy19:0	-27.97	-27.52	-27.77	-28.00	-27.85	-28.06	-28.06	-27.73
\pm	0.58	0.19	0.27	0.29	0.72	0.21	0.47	0.52
br10,19:0	-24.89	-24.74	-24.86	-25.02	-24.85	-24.98	-24.97	-24.77
\pm	0.45	0.35	0.26	0.52	1.11	0.93	0.87	0.48
i20:0	-27.79	-27.14	-26.49	-27.42	-28.88	-29.71*	-29.51	-29.46
\pm	0.46	1.33	1.93	1.41	0.35	0.85	1.41	0.65
n22:0	-30.73	-30.19	-30.08	-30.55	-30.89	-30.79	-31.06	-30.66
\pm	0.85	0.53	0.60	0.27	0.37	0.42	0.33	0.31
n24:0	-30.49	-30.81	-31.28*	-31.64*	-32.09 ^a	-31.34 ^b	-31.78	-31.29
\pm	0.63	0.62	1.24	0.35	0.39	0.34	0.66	0.10
18:2ω6,9	-28.89	-28.81	-29.98*	-30.70*	-30.65*	-30.87*	-31.01*	-31.13*
\pm	0.69	0.59	0.73	0.85	0.45	0.22	0.15	0.68
18:3	-32.24	-30.84	-32.61	-34.12*	-32.67 ^b	-33.78* ^a	-33.69*	-34.19*
\pm	0.70	0.95	1.00	1.34	0.35	0.54	0.47	1.50
20:4ω6,9,12,15	-27.56 ^a	-26.94 ^b	-26.95 ^b	-28.38* ^a	-27.14	-27.70	-27.99	-27.70
\pm	0.20	0.25	0.22	0.56	-	0.60	0.73	0.64
17:1ω8 cis	-27.11	-26.83	-26.99	-27.53	-27.25	-26.59	-26.87	-26.32
\pm	1.15	0.38	0.82	0.40	0.82	0.75	0.97	1.10
17:1ω8 trans	-24.94	-25.84	-26.10	-25.83	-25.52 ^a	-26.44 ^b	-25.85	-25.08
\pm	1.21	0.64	1.27	0.64	0.46	0.31	0.56	0.67
16:1ω9	-22.67	-22.95	-22.53 ^a	-23.48 ^b	-22.46	-23.20	-22.82	-22.29
\pm	1.70	1.36	0.43	0.55	0.54	0.98	1.41	0.95
16:1ω7 trans	-25.57	-25.36	-24.76	-25.31	-22.94*	-24.18	-25.07 ^a	-23.31 ^b
\pm	0.00	0.91	0.86	1.57	0.47	0.61	0.33	0.10
16:1ω7 cis	-24.89 ^a	-23.48 ^b	-24.32	-24.10	-23.71	-24.27	-24.78	-24.59
\pm	0.40	0.40	0.91	0.65	1.42	0.77	0.85	1.41
16:1ω5	-24.74 ^a	-23.68 ^b	-24.67	-25.48	-26.19	-26.50	-27.04	-28.15*
\pm	0.31	0.58	0.48	1.13	1.87	1.17	1.11	3.97
18:1ω9	-21.80	-19.78	-20.32	-20.18	-19.80	-19.34	-20.35	-21.11
\pm	5.07	1.26	5.70	1.82	0.40	1.80	0.70	3.38
18:1ω7	-30.12	-29.50	-28.21	-29.55	-28.63	-30.35	-30.04	-32.13*
\pm	0.91	0.59	1.87	0.42	0.68	1.35	0.88	2.29

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