University of Zurich[UZH]

Interactions between the C- and the N-Cycle in plant-soil systems

Effects of elevated CO_2 on three Swiss Crop Species regarding the interaction between the C- and the N-Cycle

GEO 511 Master's Thesis

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28. January 2019
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Acknowledgements

First, I would like to thank my supervisor Samuel Abiven for guiding me well through this master thesis and making time to support my learning process. Moreover, I would like to thank Nadia Huber for helping me with the initial soil sampling and introducing me to the MICE facility. Many thanks also go to Thomas Keller and Tatjana Kraut, who introduced me to the laboratory and gave me helpful inputs during my laboratory work. Furthermore, I would like to thank UFA Samen for providing the seeds for the MICE experiment. Last but not least, I also thank Nathanaël Perraudin for the helpful inputs and the mental support.

Abstract

In order to keep Earth system in a relatively stable state, climate change as well as N pollution should be mitigated (Steffen et al., 2015). Studies have shown that soil organic matter (SOM) plays an important role in both of these environmental challenges (Weil & Brady, 2017). However, there are still important knowledge gaps that have to be filled in order to find effective mitigation strategies. Some of them are finding the factors driving or inhibiting SOM priming and NO_3^- leaching as well as defining the quantity of rhizodeposition (RD) and understanding its possible impacts on SOM priming.

In order to better understand the factors stabilizing and destabilizing SOM, this work aimed at quantifying RD and analyzing its impact on SOM priming. Furthermore, the effects of N and CO_2 fertilization on above ground biomass (AGB), below ground biomass (BGB), NO_3^- leaching, RD and on SOM priming were analyzed. Moreover, the work tested a possible influence of different species with different root architectures on the results. Therefore, the Swiss Crop species oat and barley, which develop a branched root system, and rape, which shows a taproot structure, were selected. Moreover, this is one of the few studies testing the microbial N mining hypothesis. To do so, a 48-day experiment in the MICE (Multi Isotope Labeling in a Controlled Environment) facility was conducted under controlled conditions and ^{13}C isotopes were used to trace C dynamics.

This work showed that AGB and BGB react differently to CO_2 and N fertilization. While the AGB increased in either fertilization treatment, they had, except for one exception, no effect on the BGB. This shows well that the knowledge of the AGB cannot be transferred to the BGB. Moreover, RD accounted on average for 60% of the total root-derived C, which is higher than previously reported by most studies. Additionally, N fertilization led to a higher RD in the soil depth 0-12 cm, which indicates a possible N mining strategy of the plants. Surprisingly, RD was not correlated to the amount of positive priming, that was observed in all samples. Therefore, this study suggests that not only the quantity but also the quality of RD might influence PE. However, this hypothesis needs further testing.

Furthermore, the three different plant species did not influence SOM priming. By contrast, they showed different N take up capacities. However, the N-take-up was neither linked to the quantity of BGB, nor to the root architecture, but to the rooting depth. Barley was the specie with the deepest roots and the highest N content. However, as the root growth was restricted in this experiment, field studies with no restricted root growth are needed to further test this hypothesis. Additionally, it was interesting that even though the plant species took up different amounts of N, the NO_3^- leaching was not influenced by the different plant species.

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Abbreviations

AGB	Above ground biomass
ANOVA	Analysis of variance (in this work two-way ANOVA)
BGB	Below ground biomass
C	Carbon
CO_2	Carbon dioxide
^{13}C	Stable carbon isotope with atomic mass 13
RD	Rhizodeposition
max	Maximum value
MICE	Multi-isotope labelling under controlled environment
min	Minimum value
N	Nitrogen
NO_3^-	Nitrate
n.s.	not significant
PE	Priming effect
ppm	parts per million
RD	Rhizodeposition
R:S ratio	Root:Shoot ratio
SOM	Soil organic matter
*	Significance level of 5% ($P<0.05$)
**	Significance level of 1% ($P<0.01$)
***	Significance level of 0.1% ($P<0.001$)

1 Introduction

The relatively stable state of Earth system, as experienced during the 11'700-year-long Holocene epoch, is increasingly threatened by humankind. As this state of Earth system is the only one that we know for certain, that can support contemporary human societies, increasing effort is made to counteract recent developments. In this context, the planetary boundaries were formulated (Fig. 1). These are based on a scientific analysis, which estimated the risk that human perturbations will destabilize Earth system at the planetary scale (Steffen et al., 2015).

This work focuses on two of the nine planetary boundaries: Climate change and Nitrogen (N) as part of Biogeochemical flows and how they might be interconnected in the plant-soil system. Climate change is categorized in the zone of uncertainty, which means it is an increasing risk to destabilize the Earth system. N as a part of biogeochemical flows is even beyond the zone of uncertainty. Steffen et al. (2015) estimate that N is at high risk to destabilize Earth system (Fig. 1). The following subchapters explain how these two boundaries are connected to the plant-soil system.

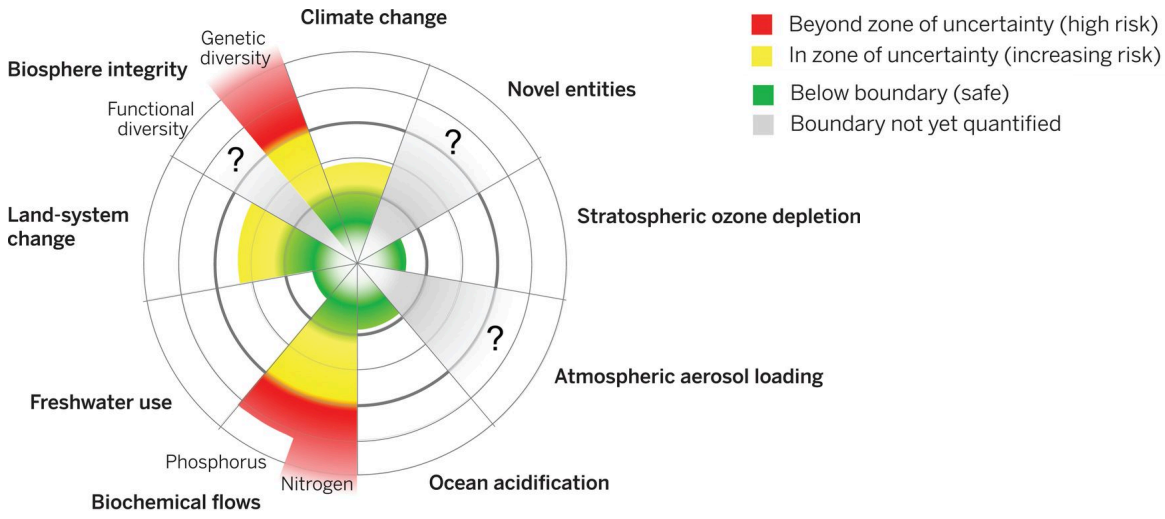


Figure 1: Current status of the planetary boundaries (Steffen et al., 2015).

1.1 Climate Change

Due to a high atmospheric CO_2 and other greenhouse gas concentrations, there has already been several observed changes in the global earth system (Steffen et al., 2015). For example, researchers detected an increase in the intensity, frequency, and duration of heat waves (IPCC, 2012). Furthermore, the number of heavy rainfall events in many regions of the world is increasing and changes in atmospheric circulation patterns lead to an increase of droughts in some regions of the world (IPCC, 2012). Due to these and other changes, climate change carries an increasing risk to destabilize the Earth system (Steffen et al., 2015). Therefore, researchers in different fields are searching for ways to mitigate climate change.

As soil store more carbon (C) than found in the plant biomass and the Earth's atmosphere together (D. S. Schimel, 1995), researchers have paid increased attention to soil processes as a strategy to mitigate climate change. One proposed solution is to reduce atmospheric CO_2 levels through increased plant photosynthesis and to stock the fixed C in soils. This strategy is also referred to as C sequestration (Keith Paustian et al., 2016). However, it should be mentioned that soils have only a finite capacity to sequester C. Therefore, the increase of soil C to mitigate climate change does not reduce the necessity of other kinds of climate actions (Weil & Brady, 2017). Nevertheless, the potential of agricultural soil to mitigate climate change is still important. Minasny et al. (2017) report that if C stocks are increased by 0.4% in the upper meter of soil in global agroecosystems, they could sequester 2-3 Gt C per year, which would offset global anthropogenic greenhouse gas emissions by 20-35%. Moreover, agricultural soil is not only linked to the C cycle and thus climate change, they also play an important role in the planetary boundary concerning Nitrogen (N).

1.2 Biogeochemical Flows: Nitrogen

The invention of the Haber-Bosch process to produce industrially reduced-N fertilizer has brought important benefits to humankind. It is estimated that at least two billion people would not be alive today without the anthropogenic production of mineral N fertilizers (Smil, 2004).

However, the profound changes human activities have brought to the N cycle through the production of reduced-N fertilizers, the fixation of Nitrogen gas by cultivated legumes and through the combustion of fossil fuels, have also caused major problems. The annual N fixation through anthropogenic activities has surpassed the N fixation through natural processes (Fowler et al., 2013). Problematically, much of the anthropogenic N is lost to air, water, and land, where it causes environmental and human health issues. The major ones are eutrophication of fresh and marine waters, which depletes the oxygen content in the water

ultimately resulting in disastrous effects on the aquatic life (Smith et al., 1999; Vitousek et al., 1997), and the production of nitrous oxide. This molecule is not only a 300-fold stronger greenhouse gas than CO_2, but it also destroys the ozone layer actively (IPCC, 2014; Ravishankara et al., 2009). Therefore, N flows are at high risk to destabilize Earth system.

However, Figure 2 shows that N flows have a strong regional operating scale (Steffen et al., 2015). Zones at high risk to destabilize Earth system are mostly located in some parts of the US, Europe, India and China. Steffen et al. (2015) explain that the main contributor to these high-risk zones are a few agricultural regions of very high N application rates through fertilization. However, in some parts of the world food production is still N-deficient. Thus, it is important to better understand the N dynamics in the plant-soil system in order to maximize the benefits of anthropogenic N, while minimizing its unwanted consequences such as eutrophication through N leaching (Galloway et al., 2008).

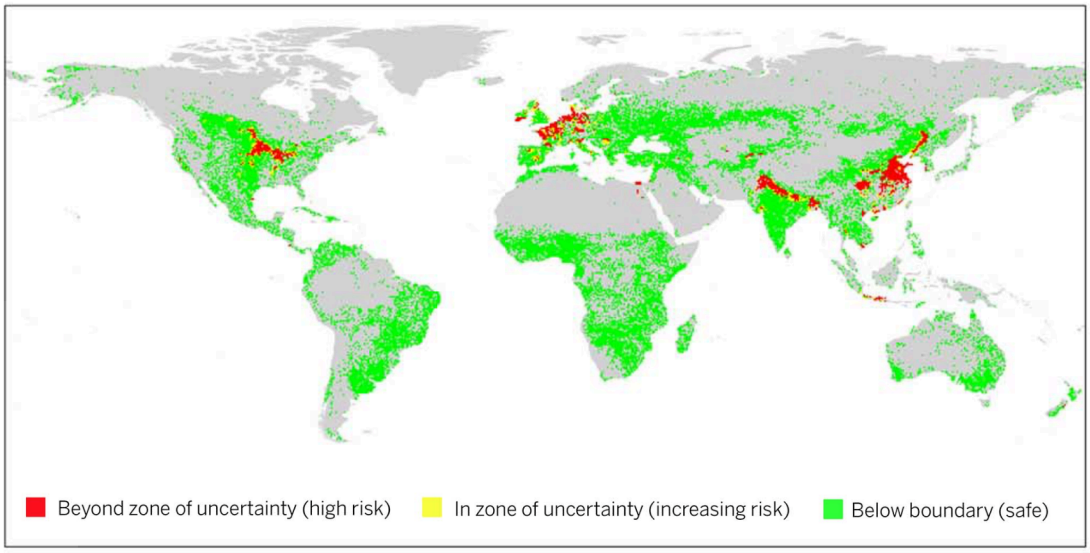


Figure 2: The distribution and the current status of biogeochemical flows of N (Steffen et al., 2015).

1.3 The Plant-Soil System

The previous subchapters highlighted the important role of soil in the C and the N cycle. This chapter and its following subchapters focus more specifically on the plant-soil system and its processes influencing the C and the N cycle and their interactions.

The primary source of C in ecosystems is atmospheric CO_2 fixed in plants by photosynthesis and added to the soil mainly as above- and below ground biomass (Warembourg & Paul, 1977). Eventually, microbes incorporate the biomass into the soil C stock, the so-called soil organic matter (SOM). SOM refers to the organic fraction of the soil that includes plant, animal and microbial residues in various stages of decomposition. Furthermore, biomass of

soil microorganisms and substances produced by plant roots and other soil organisms are also part of SOM. Therefore, SOM is a complex mixture of substances that exist in association with other soil components (Weil & Brady, 2017).

An increase of SOM is not only of interest to fix additional CO_2 from the atmosphere and thereby mitigating climate change, it is also beneficial for the soil quality. SOM provides, for example, the water-holding capacity, is largely responsible for the aggregate formation and stabilization and SOM is also a reservoir of plant nutrients such as N (Weil & Brady, 2017). For all these reasons, it is of interest to increase SOM through additional C inputs and reduce its C losses. Figure 3 shows an overview over the main C sources of SOM and the main losses of C from SOM. However, many processes leading to SOM decomposition or stabilization are still poorly understood (*see chapters 1.2.1 and 1.2.2*).

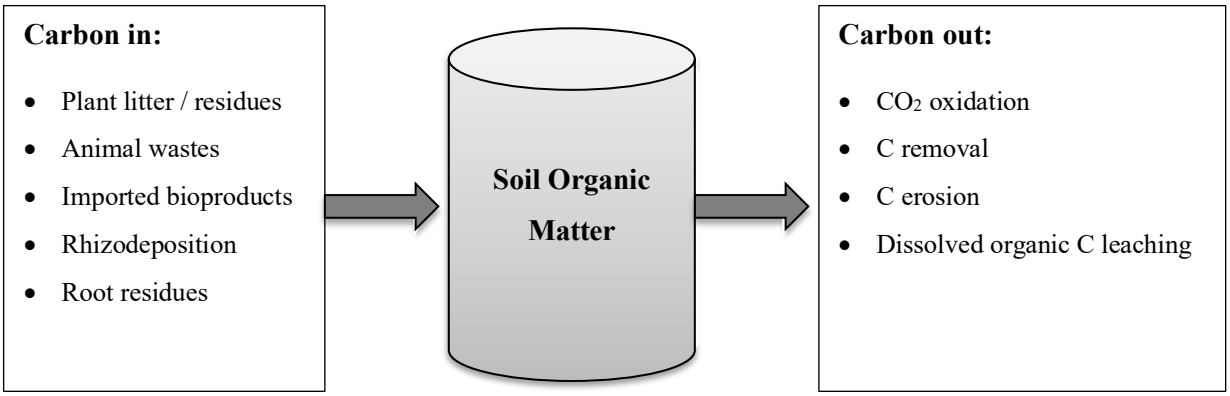


Figure 3: Overview of the main sources and losses of C in SOM (modified figure from Weil & Brady, 2017)

As a first step to understand SOM dynamics, it is important to get reliable estimates of the proportion of the net primary productivity (NPP), which eventually gets returned to the soil as SOM (Bolinder et al., 2006; Paustian et al., 1997). As N availability plays an important role in determining the long-term evolution of plants, litter, and SOM pools within land ecosystems (Chapin et al., 1986; Vitousek & Howarth, 1991), it is crucial to take the N cycle and its interactions with the C cycle into account.

N_2 is the most abundant molecule in the Earth's atmosphere (78%). However, this form of N is only utilizable by N-fixing organisms. Plant roots take up principally mineral N in the form of nitrate (NO_3^-) and ammonium (NH_4^+) ions (Weil & Brady, 2017). By contrast, most of the soil N (95-99%) is stored in large organic molecules as part of SOM. Even though in this organic form N is unavailable for plants, it is also protected from loss. Soil microbes can then break down the large N-containing organic molecules, and eventually the N gets released as NH_4^+. Subsequently, certain soil bacteria and archaea oxidize NH_4^+ to nitrites (NO_2^-) and later to NO_3^-. This enzymatic process, which is generally rapid under aerobic conditions, is called nitrification (Weil & Brady, 2017). Nevertheless, plant available N is low in most soils. While

NH_4^+ gets fixated in clays and SOM, NO_3^- is not absorbed by the negatively charged colloids in the soil. Thus, it moves freely with drainage water and is readily leached from the soil. Therefore, the greatest losses of N from agroecosystems are leached nitrates, causing not only a loss of this valuable nutrient but also serious water-quality problems (Weil & Brady, 2017).

Therefore, research efforts are made to find solutions to reduce NO_3^- leaching, while keeping the crop yields high. Studies suggested that the rate, depth and distribution of root growth may play an important role in the N uptake and thus reducing the need for N fertilizers in agroecosystems (Strebel et al., 1989; Thorup-Kristensen, 2001; Vos et al., 1998). Nevertheless, the relation between root parameters, such as root architecture and root biomass, and NO_3^- leaching is still not fully understood (Dunbabin et al., 2003).

This highlights well the importance of analyzing below ground biomass. However, well-developed rooting systems do not only have the potential to take up nutrients more efficiently and thus tackle the problem of NO_3^- leaching, they are also crucial for SOM dynamics. Studies have shown that root-derived C is more persistent in soil than the above ground residues (Rasse et al., 2005). It is estimated that 30-90% of the total organic C in agroecosystems is root-derived (Kätterer et al., 2011). Therefore, increasing below ground C inputs to soil is also an effective strategy to increase SOM. Hence, the promotion of crop roots has been proposed as a strategy to mitigate climate change, improve soil quality and to reduce NO_3^- leaching (Kell, 2012; Keith Paustian et al., 2016).

Nevertheless, below ground C inputs to soil is still one of the most poorly understood attributes of terrestrial ecosystems (Laurenroth, 2000). In order to improve the quality of agricultural soil and mitigate climate change, this knowledge gap is important to be filled. So far, studies have shown that root architecture and biomass of crops respond to different site conditions (Rich & Watt, 2013). Also, the below ground biomass (BGB) of different species have been reported to react differently to certain conditions (Ontl et al., 2013; Thorup-Kristensen et al., 2009). However, it is important to keep in mind that root-derived C does not only consist of root biomass, which is in this work referred to as below ground biomass (BGB). The other important component of root-derived C is rhizodeposition (Kuzyakov & Domanski, 2000).

1.3.1 Rhizodeposition

Rhizodeposition (RD) refers to the process of living roots releasing organic compounds into the soil (Jones et al., 2009; Kuzyakov & Domanski, 2000). These so-called rhizodeposits are highly bioavailable and enter the soil through a wide range of processes. Jones et al. (2009) summarized, as shown in Figure 4, that roots release C to soil through (1) losses of root cap and border cell, (2) loss of insoluble mucilage, (3) loss of soluble root exudates, (4) loss of volatile organic C, (5) loss of C to symbionts like mycorrhizas and (6) loss of C due to death and lysis of root epidermal and cortical cells. However, in this study, as in most experimental studies, the different types of RD will not be distinguished. Precisely, the term RD in this work refers to the net rhizodeposition, which is the part of rhizodeposits that remain in soil after immediate microbial mineralization (Johanna Pausch & Kuzyakov, 2017).

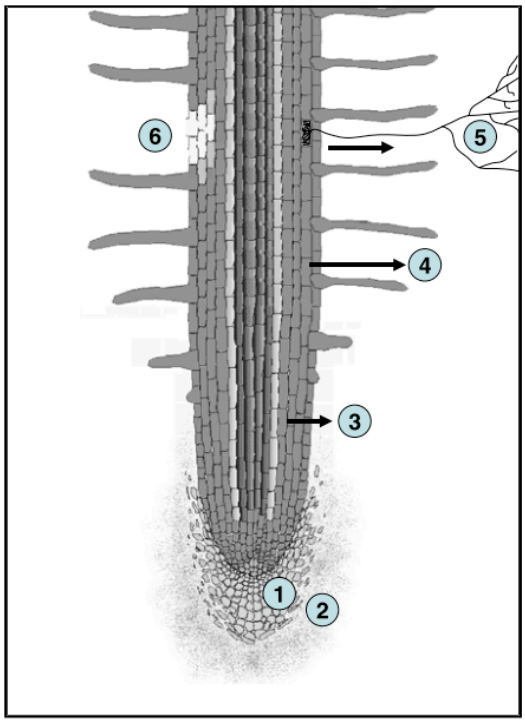


Figure 4: Schematic representation of a growing root showing the six major sites of RD (Jones et al., 2009)

RD is of great importance. It plays not only a crucial role in C turnover and C sequestration (Kögel-Knabner, 2002), roots actually regulate a wide range of ecological soil functions through RD. Pausch & Kuzyakov (2017) explain that RD has been reported among other things to regulate water fluxes (Moradi et al., 2012), the formation of aggregates (Six et al., 2004), structure microbial communities (Paterson et al., 2007) and to influence the microbial activity (Kuzyakov & Blagodatskaya, 2015).

However, even though RD plays a role in many crucial soil processes it still remains the most hidden part of the C cycle (Johanna Pausch & Kuzyakov, 2017). This is partially due to the difficulty to measure RD and is also due to the fact that RD is influenced by many factors. McNear (2013) reports that the amount and composition of the released rhizodeposits are influenced by the plant type, climatic conditions, insect herbivory, nutrient deficiency or toxicity, and the chemical, physical and biological properties of the surrounding soil. Nevertheless, the mechanism influencing RD are still poorly understood. Furthermore, there is a lack of a proper quantification of RD. Also Dijkstra et al. (2013) state that it is critical that future research focuses on better quantifying the different C fluxes in the rhizosphere. Additionally, the complexity of RD is further highlighted by its opposing effects on SOM.

1.3.2 Priming Effects

The previous subchapter mentioned that RD can have opposing effects on SOM. These so-called priming effects (PE) in the rhizosphere refer to changes in the decomposition of native SOM caused by the addition of new substrates like for example rhizodeposits (Kuzyakov, 2002). Through the addition these substrates, SOM decomposition can either be enhanced, in which case the term 'positive priming' is used. Or the added substrates can also slow down SOM decomposition, which is referred to as 'negative priming' (Fig. 5).

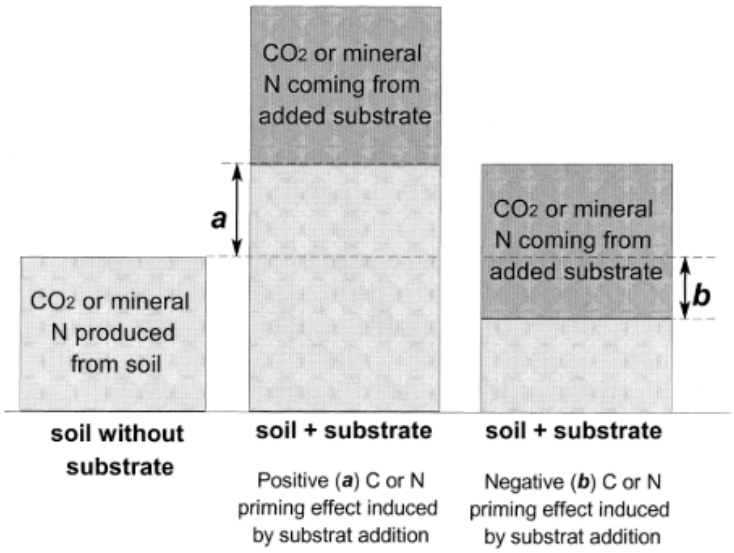


Figure 5: Schematization of the priming effects; (a) positive priming: acceleration of SOM decomposition, (b) negative priming: retardation of SOM decomposition (Kuzyakov et al., 2000)

PE play a crucial role in soil C dynamics (Dijkstra et al., 2013). In contrast to previous understandings, recent studies have reported that PE can also affect old soil C pools and have long-lasting effects on C stock in the soil (Dijkstra & Cheng, 2007; Fontaine et al., 2007).

However, even though PE have frequently been reported, the factors influencing its magnitude and the direction of priming are still poorly understood (Kuzyakov et al., 2000). RD is a process that can be associated with either positive and negative PE. The latter can be explained by the fact that rhizodeposits have been reported to increase the formation of aggregates (Six et al., 2004). Hence, it is possible that C in SOM is physically protected from microbial mineralization through the aggregates, which could lead to a negative PE. However, this needs further research. By contrast, the positive priming through RD can be explained with the nutrient demand of microbes. As RD is an important energy source for microbes, they decompose, in consequence, native SOM to meet their nutrient demand (Averill & Finzi, 2011; Blagodatskaya & Kuzyakov, 2008; Schimel & Weintraub, 2003). The reasons for these

opposing PE induced by RD have also been linked to nutrient availability for plant uptake (Dijkstra et al., 2013).

1.3.3 Soil Nutrient Availability and Priming

Several hypotheses have been proposed to explain the relationship between the soil nutrient availability and different PE (Fig. 6). All three hypotheses propose a strong interaction between the C and the N Cycle. The preferential substrate utilization hypothesis states that in soil of high nutrient availability microbes may start utilizing labile root exudates for their C requirement instead of decomposing SOM (Blagodatskaya et al., 2007; Guenet et al., 2010). Hence, soil of high nutrient availability are, according to this hypothesis, expected to induce a negative PE (Cheng, 1999).

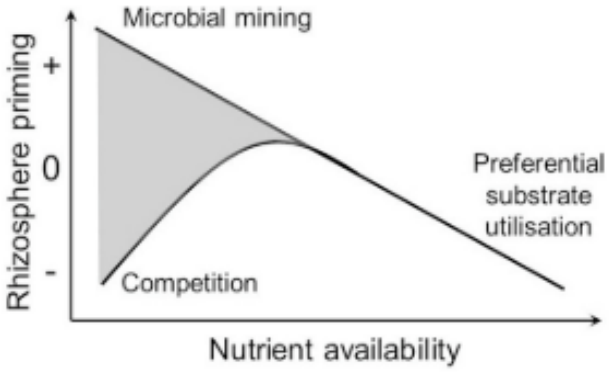


Figure 6: Hypothetical relationship between soil nutrient availability and PE (Dijkstra et al., 2013)

By contrast, in a soil with low nutrient availability, two opposing hypotheses have been proposed (Dijkstra et al., 2013). The competition hypothesis links negative PE to low nutrient availability (Cheng, 1999). Due to the fact that plants and microbes compete for the same nutrients. Therefore, the hypothesis suspects that plants take up nutrients from the soil, leaving fewer nutrients for the microbes, which may reduce microbial decomposition (Dijkstra et al., 2010; Pausch et al., 2013). In contrast, the microbial mining hypothesis expects a positive PE in soil of low nutrient availability (Craine et al., 2007; Fontaine et al., 2011). The explanation behind it is that microbes use the RD inputs for the production of extracellular enzymes. These enzymes can then release nutrients locked in SOM, which microbes take up to meet their nutrient requirement (Asmar et al., 1994; Brzostek et al., 2013). Hence, the plants might eventually get increased access to mineral N, as the turnover of microbes is faster compared to roots (Frank & Groffman, 2009; Kuzyakov & Xu, 2013). However, even though some studies have reported that RD increased N availability to plants by 6-100% (Chapin et al., 1988; Griffiths & Robinson, 1992; Herman et al., 2006; Phillips & Fahey, 2008), there is still a need to better understand when and why RD in low nutrient soil lead to a positive and when and why to a negative PE (Dijkstra et al., 2013).

1.4 Related Work

The previous subchapters highlighted some important knowledge gaps, which should be in the focus of future research in order to be able to reduce the risk of the two planetary boundaries 'climate change' and 'biogeochemical flows: N' to destabilize Earth system. This subchapter aims at highlighting some research that has already been conducted in this field. Recent research investigated increasingly in analyzing below ground parameters such as root biomass, root architecture and rhizodeposition and in finding factors which influence these parameters. This allows a better understanding of the C dynamics in the terrestrial C cycle.

For example, a fellow student conducted an experiment under comparable conditions and with similar methods to this work, in order to ensure comparability (Huber, 2018). However, the focus was on other factors that might be of importance for below ground C dynamics. Huber (2018) aimed at analyzing the effects of different atmospheric CO_2 levels, different soil bulk density and different soil clay concentrations on root-derived C of barley. The author reported that while the atmospheric CO_2 concentrations did not influence root-derived C, BGB was significantly lower when grown in a high soil bulk density.

Furthermore, Zhu et al. (2014) quantified the PE of soybeans and sunflowers in prairie and farm soil. Additionally, they investigated in the factors driving PE. Therefore, the authors conducted an 88-day greenhouse experiment and sampled at two phenological stages (vegetative and mature stage). On the one hand, they confirmed that living roots significantly increase soil C mineralization by 27-245% through a rise of microbial biomass C. Interestingly, the positive PE was neither influenced by the soil type nor by the phenological stages. By contrast, they did observe a greater PE in sunflowers than in soybeans. This result supports a possible interaction between the C and the N cycle, as soybean nodules can fix atmospheric N, which in consequence reduces the N demand in the rhizosphere. Also Dijkstra et al. (2009) focused on the possible interaction between PE and N mineralization. The authors report that at day 105 of the greenhouse experiment, gross N mineralization was positively correlated to PE. Therefore, they concluded that N availability is not only influenced by soil properties, but also by root-soil interactions. By contrast, Hirte et al. (2018), who conducted a field study with maize and wheat, concluded that fertilization has only a little potential to influence root-derived C inputs to deep soil and that the crop choice is actually more important than fertilization intensity regarding C sequestration (Hirte et al., 2018). This shows well that the factors that influence RD and PE are still not fully understood.

2 Objectives

Some of the important knowledge gaps that have been identified in the chapter 1 and its subchapters are the factors driving or inhibiting SOM priming and NO_3^- leaching as well as the quantity of RD and its possible impacts on PE. Therefore, this thesis aims at quantifying RD and analyzing its impact on SOM priming. A further aim is to test the effects of N and CO_2 fertilization on AGB, BGB, RD and PE and check if the effects are the same at different soil depths and in three different Swiss crop species (oat, rape and barley) with different root architectures (taproot vs. branched roots).

Moreover, this thesis aims at analyzing possible interactions between the C and the N cycle. Therefore, a goal is to test if there is an interaction between N fertilization, RD and SOM priming, as predicted by the N mining hypothesis (*see chapter 1.3.3*). Additionally, this work analyzes if higher atmospheric CO_2 or N fertilization changes NO_3^- leaching and if certain rooting systems lead to higher NO_3^- leaching than others. This is likely to give valuable insights into the plant processes influencing NO_3^- leaching today and in a possible future with higher atmospheric CO_2 levels.

2.1 Hypotheses

According to the objectives of this master thesis, the following four hypotheses were formulated:

N mining hypothesis

With no added N fertilizer, the plant rhizodeposition will increase in order to get the plants access to organic N.

Biomass hypothesis

More N fertilizer will lead to a higher (above ground) biomass in an elevated CO_2 environment.

Leaching hypothesis

In a higher CO_2 environment, less NO_3^- is leached.

Plant species hypothesis

Branched rooting systems take up N more efficiently than taproot systems.

3 Material and Methods

In this chapter, the materials used in this experiment and the species selection process will be described. Furthermore, all methods applied during the experiment as well as for the data analysis will be explained.

3.1 Plant Species

The plant species were selected among recommended Swiss crop species (Courvoisier et al., 2017). As during the experiment, the plants did not experience a cold period, only summer crops were considered. Furthermore, studies have shown that morphological traits of the roots influence the plant's ability to acquire water and nutrients (Hirte et al., 2018; Saengwilai et al., 2014). Therefore, plant species with different rooting systems were selected in order to analyze the influence of different rooting systems on the outcome. The crop species barley (lat. *Hordeum vulgare),* rape (lat. *Brassica napus L.*) and oat (lat. *Avena sativa*) fulfill this requirement. Oat and barley develop similar branched root systems (Figure 7). They consist of three to six primary roots growing from the seed, which develop first, second and third order lateral branches. Furthermore, once tillering starts, they develop secondary roots, which also form lateral roots with abundant root hairs (Lucas et al., 2000). By contrast, rape has a taproot from which laterals branch. However, the three plant species were reported to develop roots that reach similar soil depths (Lucas et al., 2000).

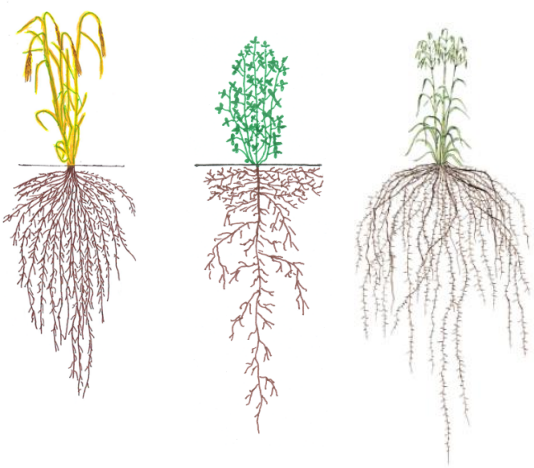


Figure 7: Rooting systems of barley, rape and oat species (CDFA, 2018; Sears, 2018)

Furthermore, rape was selected because it is the most important oilseed of Switzerland and its production has been increasing the last ten years. Besides, rape is the third most important oil crop worldwide, behind soybean and palm oil (Bouchet et al., 2016). Moreover, barley is also an important crop in the Swiss agriculture. With 46.7% it represents the highest share of the

Swiss feed grain production. By contrast, oat production is with 2.9% of the Swiss feed grain production quantitatively less important within Switzerland (landwirtschaft.ch, 2019).

Finally, the plant varieties with the shortest plant height were selected due to the limited space in the experiment chambers. These criteria led to the selection of *Sydney Sommergerste* (barley), *Campino Sommerraps* (rape) and *Zorro Sommerhafer* (oat).

Sydney Sommergerste was described as a very short crop with medium to high stability and a high yield potential. This barley variety shows an early to medium harvest maturity and is very resistant against diseases (Courvoisier et al., 2017).

Campino Sommerraps is a short rape variety with an early to medium harvest maturity and a high yield potential (UFA Samen, 2018).

Zorro Sommerhafer was described as medium to short oat variety with a medium yield potential. This crop shows a medium to late harvest maturity and a medium stability (Courvoisier et al., 2017).

3.2 Soil Type

In order to assure comparability with the thesis of N. Huber, the same soil as her low clay soil was used (Huber, 2018). The soil was sampled on the 8$^{th\ of}$ March 2018 in Dinhard ZH (47.552588, 8.746421 - Fig. 8) on an agricultural field that was covered with grass at the sampling time. Only the upper 15 cm of the topsoil were taken. The sampled soil had a clay content of 11% and contained 1.97% of total organic C.

Liquid manure was applied to the field two weeks prior to the sampling date (8. March 2018). However, there was some rainfall between the manure application and the sampling date.

Before the start of the experiment, roots were removed from the soil by hand and the soil humidity was increased to about 20%. Furthermore, the Nitrate (NO_3^-) content of the soil was measured and showed a low value of 18 mg NO_3^-/liter.

Figure 8: Location of the sample site in Dinhard (map.geo.admin.ch)

3.3 MICE (Multi-Isotope labeling in a Controlled Environment)

The experiment was conducted in the Multi-Isotope labeling in a Controlled Environment (MICE) facility. This is a facility developed to study holistically the interaction of plants and soils under controlled environmental conditions. The MICE facility consists of two climate chambers. In each chamber the following atmospheric and soil parameters can independently be controlled : light, CO_2 concentration, air temperature, atmospheric humidity, soil temperature and moisture. MICE can be used to label organic matter continuously with stable isotopes (e.g. ^{13}C, ^{18}O, ^{15}N, ^{2}H). These isotopes can then be traced within the whole system, from the plants into the soil. This is extremely helpful to improve the understanding of plant-soil interactions in the C cycle and its changes through climate change. The advantage of using a continuous labeling technique is the increasing signal strength of the stable isotopes with time. Furthermore, the pools (e.g. leaves, roots, soil) are labeled homogeneously (Studer et al., 2017). In this experiment, the only stable isotope traced was ^{13}C. The C isotope enabled a distinction between the C, that already existed in the soil before the experiment, and the new soil C added by plants. The isotopes were injected continuously into the atmosphere as 10 atom % $^{13}CO_2$. Hence, the plants assimilated the labeled CO_2 through photosynthesis. Such a high $^{13}CO_2$ concentration applied continuously provides valuable information about the RD, which was often neglected in previous studies.

3.3.1 Experimental Design

In each climate chamber of MICE the three different plant species (oat, rape and barley) were planted. Of each plant species, there were five replicates which received no fertilization during the experiment and five replicates which were fertilized during the experiment. Furthermore, there were five replicates of control soil in each chamber. This results in a total of 70 tubes, which were arranged as a multi-factorial design (Fig. 9).

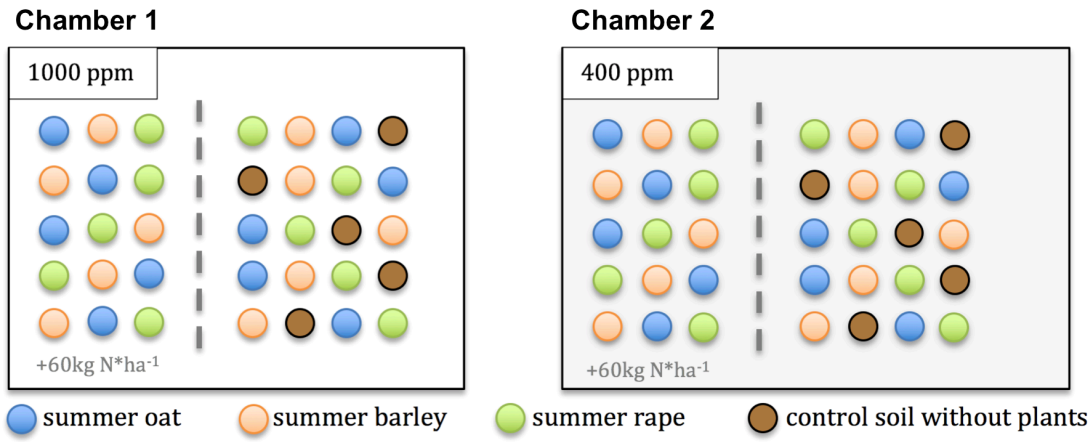


Figure 9: Experimental design in the MICE facility

The tubes (height: 0.35 m; diameter: 0.058 m) were filled with the sampled soil to reach a dry bulk density of 0.9 g/cm^3. This rather low bulk density was chosen to assure the comparability with the Master Thesis of Nadia Huber (Huber, 2018).

Chamber 1 was set to contain on average 1000 ppm CO_2 in the atmosphere, while chamber 2 was set at 400 ppm CO_2. Therefore, chamber 2 represents the actual concentration of CO_2 in today's atmosphere. By contrast, chamber 1 is a simulation of possible future atmospheric CO_2 concentrations. For example, the A1FI Emission Scenario of the IPCC (Intergovernmental Panel on Climate Change) estimates 1000 ppm CO_2 in the atmosphere by the end of this century. The A1FI scenario assumes a rapid economic growth, a global population that reaches 9 billion in 2050 and then gradually declines. The scenario is based on a future with a quick spread of new and efficient technologies and a convergent world, in which income and the way of life converge between regions (IPCC, 2001).

3.3.2 Growing Conditions

The atmospheric temperature during the experiment was in both chambers the same. During the day it was 24°C and during the night 19°C. The daytime, created by plasma light engines, lasted 14 hours a day. Besides, the atmospheric humidity was similar in both chambers with a variation between 15 and 20%. The plants were watered three times a week with a drip irrigation system (Fig. 11). Each sample received a total amount of 1657.5 ml of water (variation of +/- 10% due to the irrigation system) during the growing period (Table 1).

Table 1: Chamber conditions in MICE during the experiment

Parameter	**Chamber 1**	**Chamber 2**
CO_2 concentration	1000 ppm	400 ppm
Temperature (day)	24°C	24°C
Temperature (night)	19°C	19°C
Daytime duration	14h	14h
Atmospheric humidity	15-20%	15-20%
Total irrigation per tube	1657.5 ml (± 10%)	1657.5 ml (± 10%)

The total length of the plant growth period was 48 days. However, the first week the chambers were left open while the plants germinated without any isotope labeling. Hence, the seeds, which did not germinate, could be replaced by seeds that germinated under the same conditions. In total, seven seeds were replaced (3 in chamber 1, 4 in chamber 2). As a result,

there was only one oat plant in chamber 1 that did not grow. The labeling period lasted, therefore, 41 days. Table 2 gives an overview over the most important steps taken during the experiment.

Table 2: Schedule of the experiment.

Day	Date	Description
-	~ 22.02.2018	Application of liquid manure to the soil
-	08.03.2018	Soil sampling in Dinhard ZH
1	12.04.2018	Sowing in open chambers, no isotope labeling
8	19.04.2018	Replacement of seeds that did not germinate, closing chamber, start isotope labeling
27	09.05.2018	Fertilizer application (+60kg N /ha) to half of the plant samples
48	30.05.2018	End of experiment – opening of the chambers

3.4 Fertilizer

At day 27 of the running experiment, the chambers were opened to add fertilizer to half of the plant samples (Fig. 10). The plants were fertilized with 43 mg ammonium nitrate (NH_4NO_3) diluted in 50 ml of water, which represents 60 kg N / ha. The plants, which were not treated with fertilizer, were irrigated with 50 ml of water to ensure the same water conditions. There was no fertilizer applied at the beginning of the experiment, as the measured NO_3^- leaching was high (*see chapter 4.6.3*).

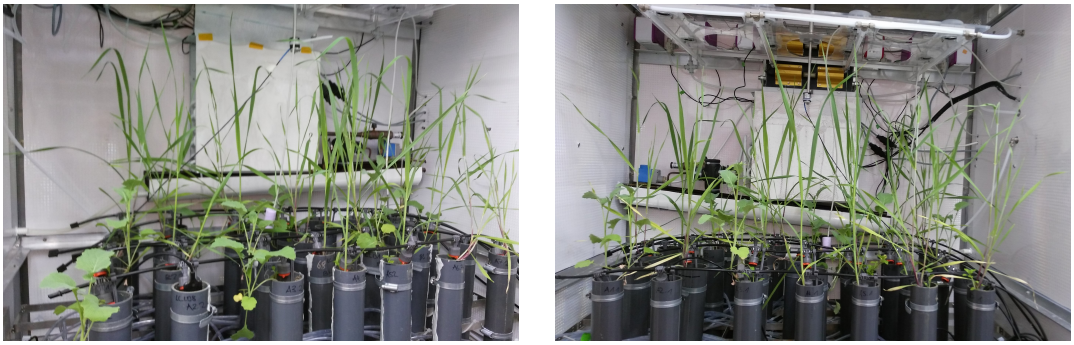


Figure 10: Plant state during N fertilizer application (day 27)

3.4.1 Leaching System

Each tube contained three holes at the bottom through which the irrigated water could percolate. The leached water was then collected in a small container from which a transparent tube went to the front of the chamber (Fig. 11). A small window of each chamber was opened, two to three times a week, to extract the collected water through the transparent tubes

with a syringe. The quantity of the leached water per tube was immediately measured and the NO_3^- content determined with a Nitrate Ion Meter (Model: HORIBA LAQUAtwin 3200456569 Model B-743 Compact Nitrate Ion Meter).

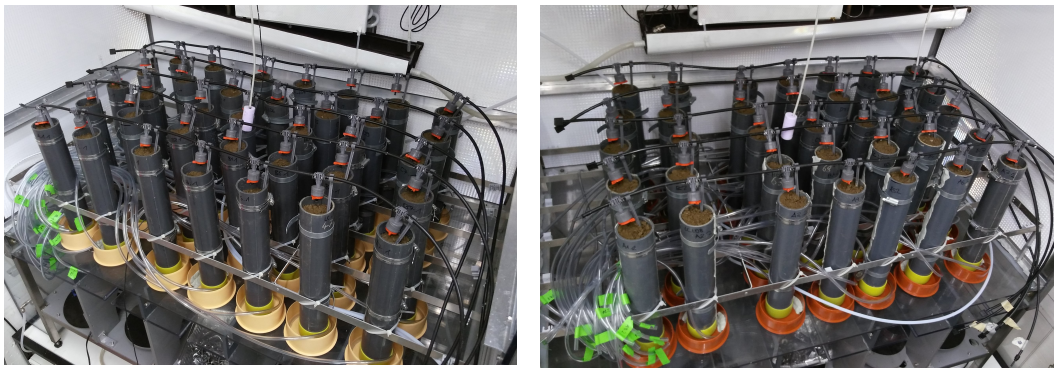


Figure 11: Leaching and irrigation systems in chamber 1 and 2 at the beginning of the experiment.

3.5 Laboratory Analysis

After the end of the experiment, the chambers were opened, the number of tillers per sample were counted and the chlorophyll content was quantified. In the oat and barley samples anthers of cereals were visible. Rape was flowering and seed fill began in some samples (Fig. 12).

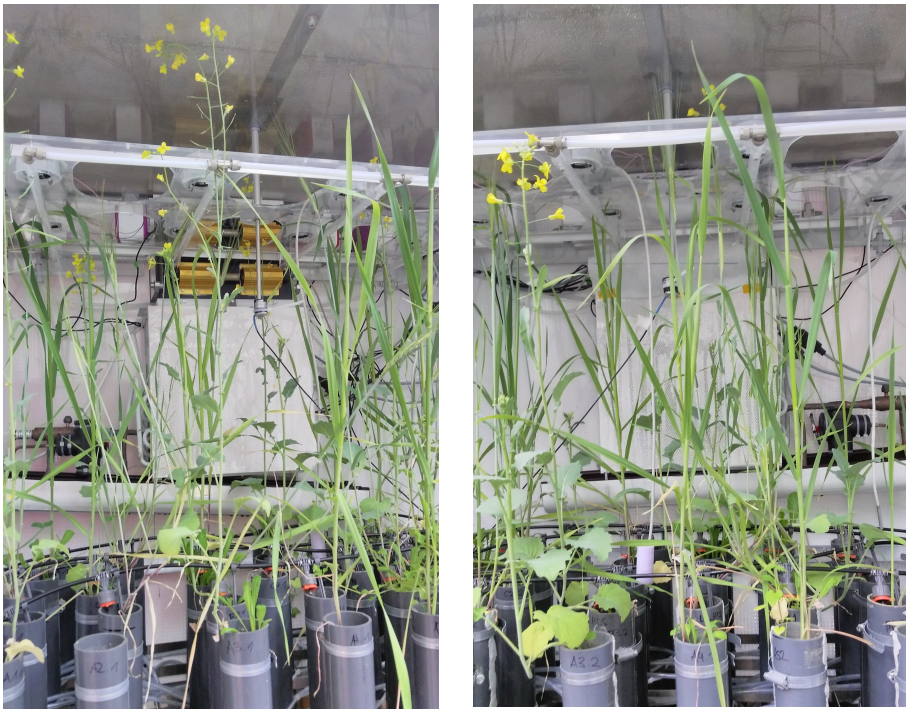


Figure 12: Plant state in chamber 1 and 2 at the end of the experiment.

3.5.1 Quantification of the Chlorophyll Content

The chlorophyll content in the leaves was measured with a chlorophyll meter at two different heights. The chlorophyll was measured three times on the lowest leaf of the plant and three times on the second-lowest leaf. The average of these six values was taken as a value of the chlorophyll content of the lower leaves. The same procedure was done for the highest and the second-highest leaves to determine the average chlorophyll content of the upper leaves.

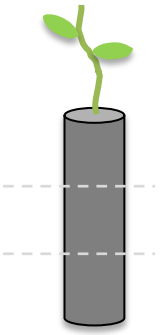
3.5.2 Biomass Quantification (above and below ground)

After the quantification of the chlorophyll content in the leaves, the above ground biomass was cut, separated between weeds, leaves and stems of the experimental plants and, if existing, the fruits of the experimental plant. The biomass was then weighted before and after they were dried in the oven at 40°C.

The tubes with the below ground biomass and the soil were cooled in a refrigerator at 4°C until further use. As the soil humidity was still very high, especially in the lower third of the tube, the soil was let to air dry one to two days at room temperature. This facilitated the root-picking. Next, the soil in the tubes was separated into three depths (Table 3).

Table 3: Soil depth definition

	cm below the soil surface	**∅ soil depth [m]**
Depth 1	0-12 cm	0.06
Depth 2	12 – 23.5 cm	0.18
Depth 3	23.5 – 35 cm	0.29



The depth of the upper third was measured in order to define the bulk density per depth. The visible roots were then hand-picked by these three depths, washed with tap water and then dried in the oven at 40°C. The dry below ground biomass was then weighted. This will later be referred to as BGB. Rhizodeposition, by contrast, indicates the rest of the root-derived C, which was detected with the stable isotope ^{13}C.

3.5.3 Root-derived C Quantification (^{13}C)

The remaining soil, without visible roots, was dried in the oven at 40°C separated by depth. Once the soil, the roots and the above ground biomass were dried, they were shaken by hand for homogenization and milled to fine powder. In order to analyze the C concentration and the

$\delta^{13}C$ signature of the samples, a Cavity Ring Down Spectroscopy (CRDS) analyzer was used (G2121-I CM-CRDS, Picarro Inc., USA).

As preparation, subsamples of 10-17 mg of the soil and 1.5-3.5 mg of the roots and above ground biomass were put into tin capsules. Furthermore, tin capsules with standards were prepared. The soil standard was Chernozem (total C content: 2.01%; $\delta^{13}C$ signature: -28.6‰) and the plant standard was Miscanthus (total C content: 47.5%; $\delta^{13}C$ signature: -14.8‰).

Furthermore, the C content in the control soil ($C_{control}$) was measured with the same method as the other samples. This control soil was not placed into the MICE, but was stored at about 15°C with no light. After the experiment, the control soil was dried in the oven like the other samples. The control soil had an average C content of 1.97% with a $\delta^{13}C$ signal of -28.77‰.

3.5.4 Quantification of the N Content

To quantify the N content in the samples, the milled subsamples were filled into tin capsules. For the above- and below ground biomass 0.4 – 1.3 mg and for the soil samples 3 – 5 mg were used. Theses subsamples were then analyzed in an element analyzer (EA IsoLink™ IRMS System).

3.6 Calculations

The following subchapters explain how the rhizodeposition and the priming effect were calculated.

3.6.1 Rhizodeposition

As a first step to calculate rhizodeposition (RD), the $\delta^{13}C$ signal of the soil samples, the soil control and the root samples was transformed from ‰ to atom fraction as follows:

$$x(^{13}C) = \frac{1}{1 + \frac{1}{\left(\frac{\delta^{13}C}{1000} + 1\right) * R_{V-PDB}}}$$

$R_{V\text{-}PDB}$ stands for the isotopic ratio of the heavy to the light carbon isotope of the international standard Vienna Pee Dee Belemnite (V_{PDB}, $^{13}C/^{12}C = 0.0111802$).

The average ^{13}C signal of the control soil [atom fraction] was then subtracted from the ^{13}C signal of the soil and root samples [atom fraction] to get the excess ^{13}C signal in the soil and in the roots.

Once the ^{13}C excess soil and roots was calculated, the RD was calculated as follows:

$$RD[\frac{g\ C}{kg\ dry\ soil}] = \frac{^{13}C\ excess\ soil\ [atom\ fraction]}{^{13}C\ excess\ roots\ [atom\ fraction]} \times C_{new}[\%] \times 10$$

C_{new} stands for the measured C content [%] in the soil samples after the MICE experiment.

3.6.2 Priming Effect

The priming effect (PE) was calculated as the difference in the bulk soil C between the planted soil samples after the MICE experiment and the control soil samples, which were not placed into the MICE facility. This representation of PE as a cumulative deviation from the control SOC over the period of the experiment differs from the classical PE presentation, which is based on changes of CO_2 efflux (Friedli, 2017). Calculating the PE in the bulk soil, which is possible due to the continuous ^{13}C labeling method, brings the advantage that the PE amplitude can be compared to the bulk C content of the soil.

With the RD, the priming effect (PE) can be calculated. The absolute PE was calculated as follows:

$$PE[\frac{g\ C}{kg\ dry\ soil}] = \left(Total\ C_{new}[\frac{g\ C}{kg\ dry\ soil}] - RD[\frac{g\ C}{kg\ dry\ soil}]\right) - Total\ C_{control}[\frac{g\ C}{kg\ dry\ soil}]$$

Total C_{new} stands for the measured C content [g C / kg dry soil] in the soil samples after the MICE experiment. By contrast, total $C_{control}$ refers to the averaged C content [g C / kg dry soil] in the control sample, which were not placed in the MICE. As the PE is indicated as g C per kg of dry soil, it is estimated that the bulk density remained relatively constant at around 0.9 g per cm^3 during the experiment.

The relative PE was then calculated as follows:

$$PE[\%_{C\ control}] = \frac{PE\ [\frac{g\ C}{kg\ dry\ soil}]}{Total\ C_{control}[\frac{g\ C}{kg\ dry\ soil}]} \times 100$$

3.7 Statistical Analysis

For the statistical analysis RStudio, version 1.1.453, was used with the addition of the package ‘agricolae’, from which the post-hoc test was used. Furthermore, some plots were created with the Pivot Tables function of Excel, version 14.7.7.

As a first step, the datasets were visually checked for unrealistic outliers with a dot plot in RStudio. Big outliers were remeasured to exclude technical errors. However, all remeasurements were in the same range as the initial measurement taking into account the higher variability in the soil samples.

As a next step, the effects of the different treatments on various soil and plant parameters were tested with a two-way analysis of variance (ANOVA) in RStudio. The different treatments were plant species (barley vs. oat vs. rape), atmospheric CO_2 level (1000 ppm vs. 400 ppm), fertilizer treatment (60 kg N/ ha at day 27 vs. no fertilizer addition) and for some parameters soil depth (0-12 cm, 12-23.5 cm, 23.5-35 cm). The second soil depth (12-23.5 cm) was not always analyzed due to time constraints.

The significance levels of the ANOVA are indicated in the following chapter in brackets next to the treatments. ‘(*)’ stands for a significance level of 5%, ‘(**)’ for 1% and ‘(***)’ for 0.01%. Not significant results are indicated as ‘n.s.’.

4 Results

The results of the MICE experiment will be shown in the following subchapters. The discussion of the results will then follow in chapter 5.

4.1 Above Ground Biomass (AGB)

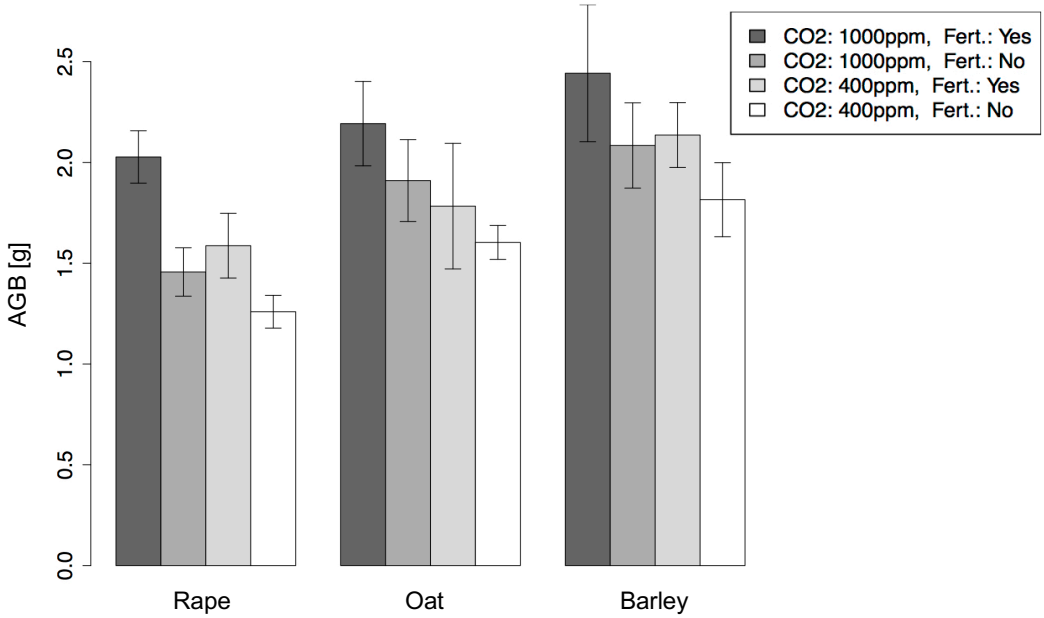


Figure 13: Mean and standard error of the AGB of the different treatments.

Table 4 and Figure 13 show that the total above ground biomass (AGB) was significantly higher in oat and barley compared to rape. Rape showed a mean of 1.58 g dry AGB, ranging from 1.04 g to 2.36 g. However, oat had a mean AGB of 1.87 g, ranging from 0.68 g to 2.61 g. Barley produced the most AGB with a mean of 2.12 g, ranging from 1.26 g to 3.29 g.

Furthermore, the CO_2 level in the atmosphere had a strong effect on the AGB. Samples grown in 400 ppm CO_2 had a mean of 1.70 g AGB (min: 0.68 g; max: 2.49 g), while the ones grown in 1000 ppm CO_2 had a mean of 2.02 g AGB (min: 1.16 g; max: 3.29 g. This results accounts for an increase of 18.8% dry AGB.

The strongest effect, however, had the fertilizer treatment (+20.8%). Fertilized samples had a mean AGB of 2.03 g, ranging from 0.68 g to 3.29 g. In contrast, not fertilized samples had a mean AGB of 1.68 g (min: 1.04 g; max: 2.61 g).

Figure 13 further shows that the samples, which were N and CO_2 fertilized, developed clearly the highest amount of AGB. Moreover, N limitation can strongly reduce the positive effect of an elevated CO_2 atmosphere on the AGB growth.

Table 4: Mean and standard deviation of the AGB and results of ANOVA and post-hoc test.

	CO_2 level (**)		Fertilizer (**)		Plant species (**)		
	1000ppm	400ppm	Yes	No	Rape	Oat	Barley
∅ AGB [g]	2.02	1.70	2.03	1.68	1.58	1.87	2.12
Standard Deviation	(±0.53)	(±0.46)	(±0.55)	(±0.42)	(±0.39)	(±0.49)	(±0.53)
Post-hoc test	*a*	*b*	*a*	*b*	*b*	*a*	*a*

4.2 Below Ground Biomass (BGB)

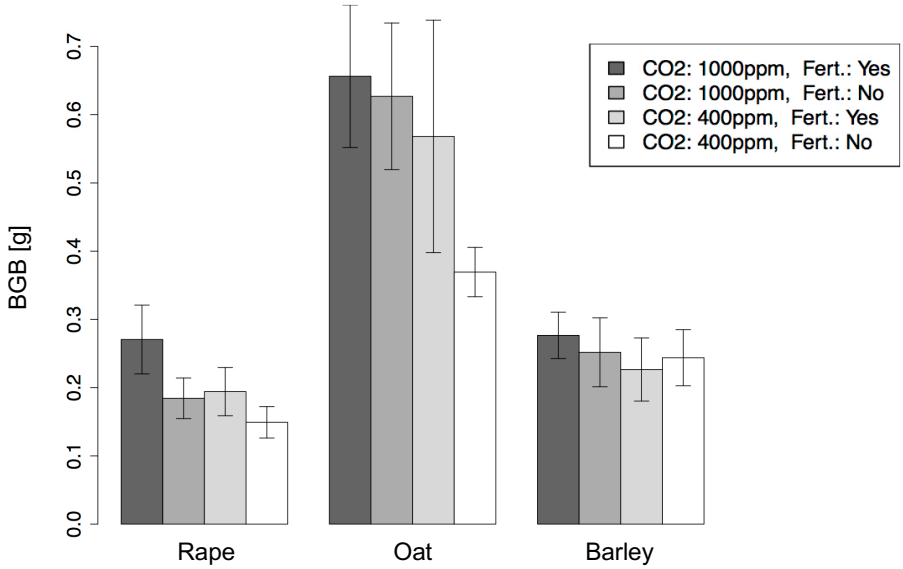


Figure 14: Mean and standard error of the BGB of the different treatments.

As the AGB, the below ground biomass (BGB), which refers to the weight of dry roots in g, showed a strong difference between the plan species as well (Figure 14; Table 5). Oat clearly had the highest BGB with a mean of 0.55 g, ranging from 0.11 g to 1.01 g. Rape and barley developed similar amounts of BGB, however, less than half of the BGB of oat. The mean BGB of rape was 0.20 g (min: 0.09 g; max: 0.45 g) and the mean BGB of barley was 0.25 g (min: 0.1 g; max: 0.45 g).

In contrast to the AGB, neither the CO_2 nor the fertilizer treatment had a significant effect on the total BGB (Table 5). However, the root C [g/kg dry soil], which was analyzed only for soil depth 0-12 cm and 23.5-35 cm did show a significant effect of the CO_2 and fertilization treatment (Table 6). The higher CO_2 environment increased the mean root C content by 29.4% and the fertilization lead to a 23.5% higher mean root C content. The following subchapter takes a closer look at the vertical root distribution.

Table 5: Mean and standard deviation of BGB and results of ANOVA and post-hoc test.

	CO_2 level (n.s.)		Fertilizer (n.s.)		Plant species (***)		
	1000ppm	400ppm	Yes	No	Rape	Oat	Barley
∅ BGB [g]	0.37	0.29	0.37	0.29	0.20	0.55	0.25
Standard Deviation	(±0.23)	(±0.21)	(±0.26)	(±0.18)	(±0.09)	(±0.26)	(±0.09)
Post-hoc test	*a*	*a*	*a*	*a*	*b*	*a*	*b*

Table 6: Mean and standard deviation of root C [g/kg dry soil] and results of ANOVA and post-hoc test.

	CO_2 level (***)		Fertilizer (*)		Plant species (***)		
	1000ppm	400ppm	Yes	No	Rape	Oat	Barley
∅ root C	0.22	0.17	0.21	0.17	0.19	0.26	0.13
Standard Deviation	(±0.15)	(±0.13)	(±0.16)	(±0.13)	(±0.17)	(±0.15)	(±0.07)
Post-hoc test	*a*	*b*	*a*	*b*	*b*	*a*	*c*

4.2.1 Below Ground Biomass per Soil Depth

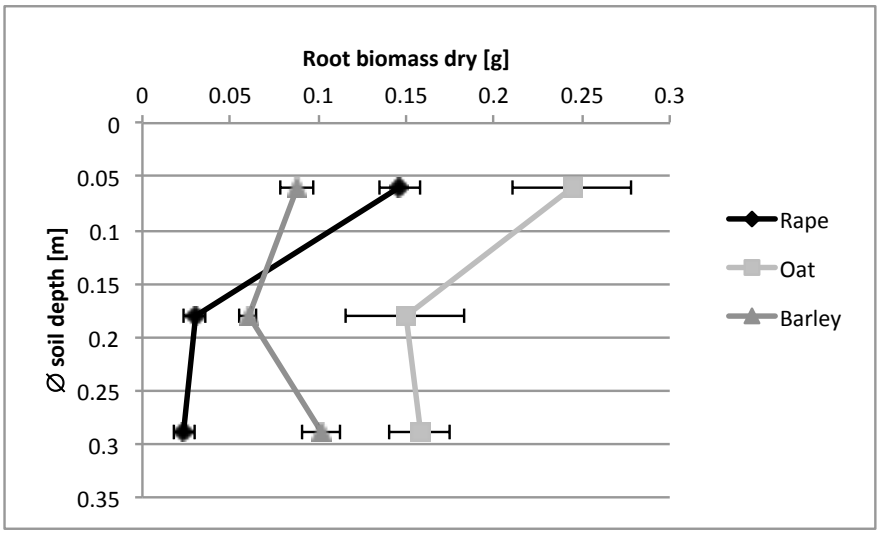


Figure 15: Mean and standard error of the BGB over soil depth of the different plant species.

Even though oat has twice as many roots than rape, Figure 15 shows that they have a similar relative root distribution over the soil profile. Both have the largest BGB in the upper soil depth (0-12cm) with a mean of 0.15 g of dry roots in rape and 0.24 g in oat. Furthermore, they have significantly less BGB in the middle and lowest soil depths (Table 7). However, the vertical root distribution of rape is more extreme. Rape allocated 75% of the total BGB in the

upper soil depth and allocated only 15% and 10% to the middle and lower soil depths respectively. By contrast, oat developed 44% of the BGB in the upper soil depth and 27% in the middle and 29% of the BGB in the lowest soil depth.

Table 7: Mean and standard deviation of BGB per soil depth and results of ANOVA and post-hoc test.

	soil depth (**)		
	0 – 12 cm	12 - 23.5 cm	23.5 – 35 cm
∅ BGB rape [g]	0.15	0.03	0.02
Standard Deviation	(±0.05)	(±0.03)	(±0.02)
Post-hoc test	*a*	*b*	*b*
∅ BGB oat [g]	0.24	0.15	0.16
Standard Deviation	(±0.15)	(±0.07)	(±0.07)
Post-hoc test	*a*	*b*	*b*
∅ BGB barley [g]	0.09	0.06	0.10
Standard Deviation	(±0.04)	(±0.02)	(±0.05)
Post-hoc test	*a*	*b*	*a*

Barley has with 0.1 g or 40% the biggest BGB in the lowest soil depth (23.5-35cm) and nearly as much in the upper depth (0.09 g; 36%). Barley shows in the middle soil depth (12-23.5 cm) the least BGB with a mean of 0.06 g, which represents 24% of the total BGB of barley (Table 7).

While Fertilizer had no effect on the total BGB, there was one exception considering the soil depths separately. The fertilizer treatment increased the BGB of rape in the upper depth by 42% (Table 8). Fertilized rape samples had a mean BGB of 0.17 g, ranging from 0.09 g to 0.28 g. However, not fertilized rape samples had a mean BGB of 0.12 g, ranging from 0.08 g to 0.17 g.

Table 8: Mean BGB of rape in 0-12 cm soil depth and results of ANOVA and post-hoc test.

	Fertilizer (*)	
	Yes	No
∅ BGB rape [g]	0.17	0.12
Standard Deviation	(±0.06)	(±0.03)
Post-hoc test	*a*	*b*

4.3 Root:Shoot Ratio

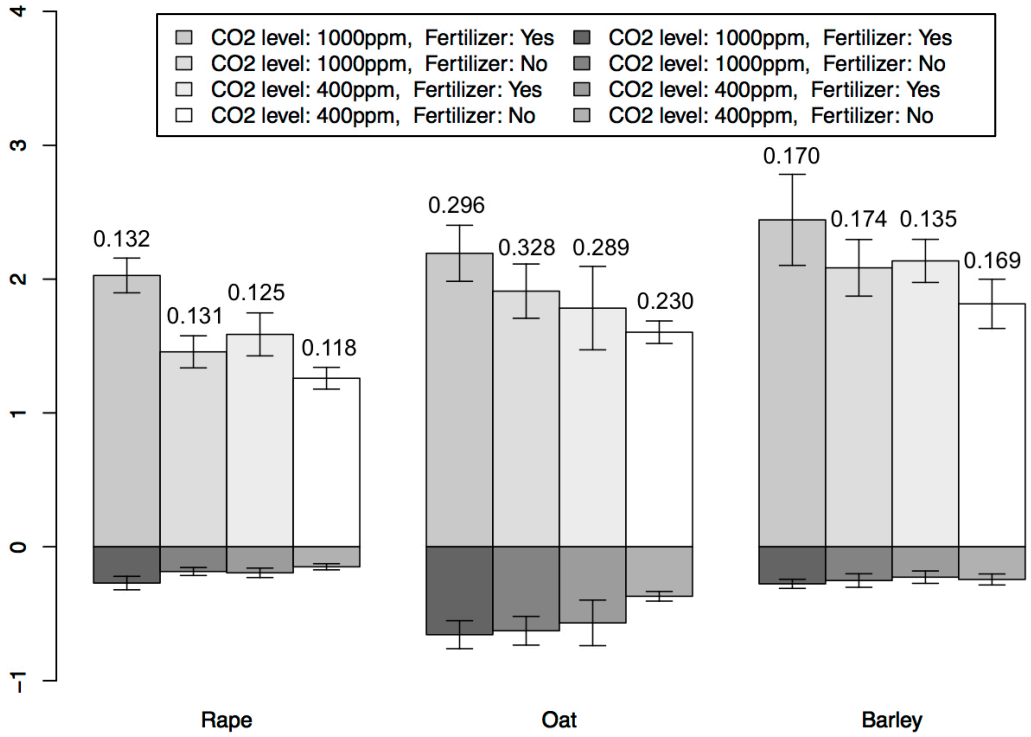


Figure 16: Mean and standard error of the AGB and the BGB and R:S ratio of the different treatments (indicated on top of the bars).

The Root:Shoot (R:S) ratio varied according to the Crops (Table 9). Rape and barley showed a similar mean R:S ratio of 0.13 (min: 0.07; max: 0.19) and 0.16 (min: 0.05; max: 0.36) respectively. By contrast, oat had a higher R:S ratio with a mean of 0.28, ranging from 0.16 to 0.47, which is largely due to the larger BGB of oat (Figure 16).

Table 9: Mean and standard deviation of Root:Shoot ratio and results of ANOVA and post-hoc test.

	CO_2 level (n.s.)		Fertilizer (n.s.)		**Plant species (***)**		
	1000ppm	400ppm	Yes	No	Rape	Oat	Barley
∅ R:S ratio	0.20	0.18	0.19	0.19	0.13	0.28	0.16
Standard Deviation	(±0.10)	(±0.09)	(±0.11)	(±0.08)	(±0.09)	(±0.26)	(±0.09)
Post-hoc test	*a*	*a*	*a*	*a*	*b*	*a*	*b*

4.4 Root and Rhizodeposition Input into Soil

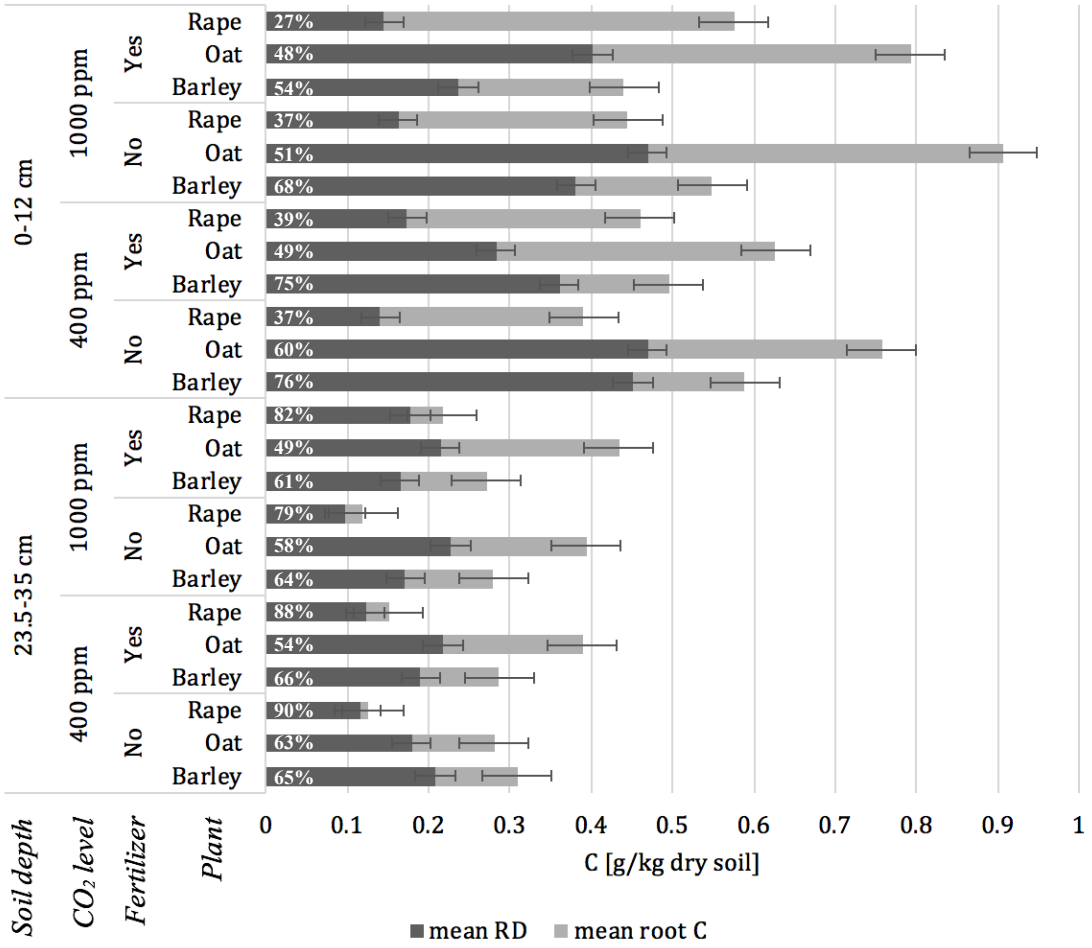


Figure 17: Rhizodeposition and below ground biomass with the standard error of the different treatments.

Figure 17 shows the mean amount of root C and rhizodeposition (RD) in g per kg of dry soil per sample. It is visible that the sum of the two components is decreasing over the soil depth. As already described in chapter 4.2.1, the root biomass is smaller in the lowest soil depth 23.5- 35 cm compared to the upper soil depth 0-12 cm, except for barley. The RD, however, is significantly smaller in the lower soil depth in all three plant species. Table 10 shows that in the soil depth 1 (0-12 cm), the RD is on average 0.30 g C/kg dry soil, ranging from 0.08 g C/kg dry soil to 0.74 g C/kg dry soil. In contrast, in the soil depth 3 (23.5-35 cm) the mean RD was at 0.18 g C/kg dry soil (min: 0.03 g C/kg dry soil; max: 0.40 g C/kg dry soil).

Moreover, the RD is plant specific (Table 10). Rape showed significantly the lowest RD with a mean of 0.14 g C/kg dry soil (min: 0.04 g C/kg dry soil; max: 0.25g C/kg dry soil). Oat and barley had a similar amount of RD with a mean of 0.31 g C/kg dry soil and 0.27 g C/kg dry soil respectively. The RD of oat varied between 0.03 g C/kg dry soil and 0.74 g C/kg dry soil, while the RD of barley varied between 0.06 g C/kg dry soil and 0.61 g C/kg dry soil.

Additionally, it is worth mentioning that the barley samples produced on average nearly as much RD as the oat samples, while having on average less than half the amount of dry roots than the oat samples (see chapter 4.2).

Table 10: Mean and standard deviation of rhizodeposition [g C/kg dry soil] and results of ANOVA and post-hoc test. Soil depths 1 and 3 stand for 0 – 12 cm and 23.5 – 35 cm soil depth respectively.

	CO_2 level (n.s.)		**Fertilizer (n.s.)**		**Plant species (***)**			**Soil depth (***)**	
	1000ppm	400ppm	Yes	No	Rape	Oat	Barley	1	3
∅ RD	0.24	0.24	0.23	0.26	0.14	0.31	0.27	0.30	0.18
Standard Deviation	(±0.14)	(±0.15)	(±0.12)	(±0.17)	(±0.05)	(±0.17)	(±0.14)	(±0.17)	(±0.08)
Post-hoc test	*a*	*a*	*a*	*a*	*b*	*a*	*a*	*a*	*b*

Furthermore, while the CO_2 treatment had no significant effect on the RD, there was an interaction between the soil depth and the fertilizer treatment. Table 11 shows that fertilized samples had a 21% lower mean RD in the soil depth 0-12 cm, compared to the not fertilized samples. However, the fertilizer had no significant effect on the RD in the soil depth 23.5-35 cm.

Table 11: Interaction of soil depth and fertilizer treatment in rhizodeposition.

	Interaction soil depth : Fertilizer (*)			
Soil depth	0 – 12 cm		23.5 – 35 cm	
Fertilizer	Yes	No	Yes	No
∅ RD	0.27	0.34	0.18	0.17
Standard Deviation	(±0.13)	(±0.19)	(±0.09)	(±0.07)
Post-hoc test	*b*	*a*	*c*	*c*

4.4.1 Ratio between the Rhizodeposition and Root C

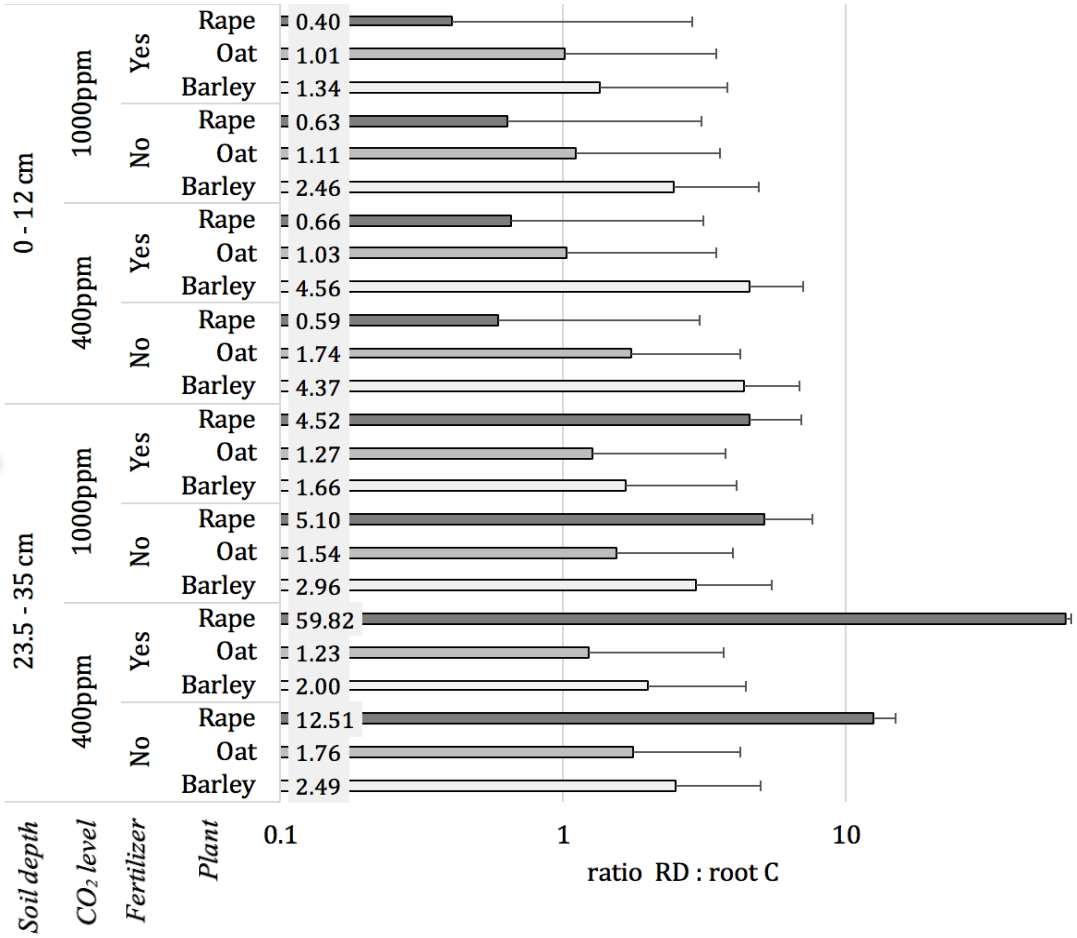


Figure 18: Rhizodeposition : root C ratio with the standard error of the different treatments.

The RD: root C ratio is significantly dependent on the plant species (Table 12). Rape clearly has the highest ratio with a mean of 11.14, ranging from 0.17 to 133.55. This is largely due to the fact that the rape samples in the lowest soil depth had, with a mean of 0.02 g of dry roots, very little root biomass (see chapter 4.2.1), which results in a very high RD : root C ratio (Figure 18). These values distort the overall statistical analysis of the RD: root C ratio (Table 12). Therefore, the statistical analysis was in a second step conducted individually per plant species.

	CO_2 level (*)		**Fertilizer (n.s.)**		**Plant species (**)**			**Soil depth (**)**	
	1000ppm	400ppm	Yes	No	Rape	Oat	Barley	1	3
∅ ratio	1.83	7.65	6.74	2.97	11.14	1.34	2.73	1.67	8.36
Standard Deviation	(±1.82)	(±23.13)	(±23.54)	(±3.65)	(±29.66)	(±0.65)	(±2.26)	(±1.94)	(±0.08)
Post-hoc test	*b*	*a*	*a*	*a*	*a*	*b*	*b*	*b*	*a*

Table 12: Mean and standard deviation of rhizodeposition : root C ratio and results of ANOVA and post-hoc test. Soil depths 1 and 3 stand for 0 – 12 cm and 23.5 – 35 cm soil depth respectively.

As already mentioned above, the rape samples showed a strong depth effect due to the little root biomass in the lowest soil depth (Table 13). The mean RD : root C ratio of rape in the soil depth 0-12 cm is 0.57, ranging from 0.17 to 1.05. However, the mean ratio of the soil depth 23.5-35 cm is 25.24. The values varied strongly from 1.07 to 133.55.

Table 13: Mean and standard deviation of RD : root C ratio of rape and results of ANOVA and post-hoc test. Soil depths 1 and 3 stand for 0 – 12 cm and 23.5 – 35 cm soil depth respectively.

	CO_2 level (n.s.)		**Fertilizer (n.s.)**		**Soil depth (**)**	
	1000ppm	400ppm	Yes	No	1	3
∅ ratio rape	2.16	18.70	18.44	4.25	0.57	25.24
Standard Deviation	(±2.64)	(±39.04)	(±41.52)	(±5.81)	(±0.25)	(±42.00)
Post-hoc test	*a*	*a*	*a*	*a*	*b*	*a*

In contrast, the RD : root C ratio of the oat and barley samples did not show a significant soil depth effect (Table 14; Table 15). Furthermore, even though the differences are not significant, it is worth mentioning that the barley and oat samples showed a lower mean RD : root C ratio in the fertilized treatments. The mean RD : root C ratios were 27% and 22% lower in the oat and barley samples respectively.

However, the mean RD : root C ratio was still significantly (***) different between the oat and the barley samples. The oat samples had a lower mean ratio of 1.34 (min: 0.45; max: 2.90) and the barley samples had a mean RD : root C ratio of 2.73, ranging from 0.48 to 11.85. This means that the average RD : root C ratio is more than twice as high in the barley samples as in the oat samples.

Table 14: Mean and standard deviation of RD : root C ratio of oat and results of ANOVA and post-hoc test. Soil depths 1 and 3 stand for 0 – 12 cm and 23.5 – 35 cm soil depth respectively.

	CO_2 level (n.s.)		**Fertilizer (n.s.)**		**Soil depth (n.s.)**	
	1000ppm	400ppm	Yes	No	1	3
∅ ratio oat	1.22	1.44	1.14	1.56	1.23	1.45
Standard Deviation	(±0.69)	(±0.60)	(±0.59)	(±0.66)	(±0.63)	(±0.67)
Post-hoc test	*a*	*a*	*a*	*a*	*a*	*a*

Table 15: Mean and standard deviation of RD : root C ratio of barley and results of ANOVA and post-hoc test. Soil depths 1 and 3 stand for 0 – 12 cm and 23.5 – 35 cm soil depth respectively.

	CO_2 level (n.s.)		Fertilizer (n.s.)		Soil depth (n.s.)	
	1000ppm	400ppm	Yes	No	1	3
∅ ratio barley	2.12	3.35	2.39	3.07	3.18	2.28
Standard Deviation	(±1.66)	(±2.62)	(±2.38)	(±2.14)	(±2.68)	(±1.69)
Post-hoc test	*a*	*a*	*a*	*a*	*a*	*a*

4.5 Priming Effects

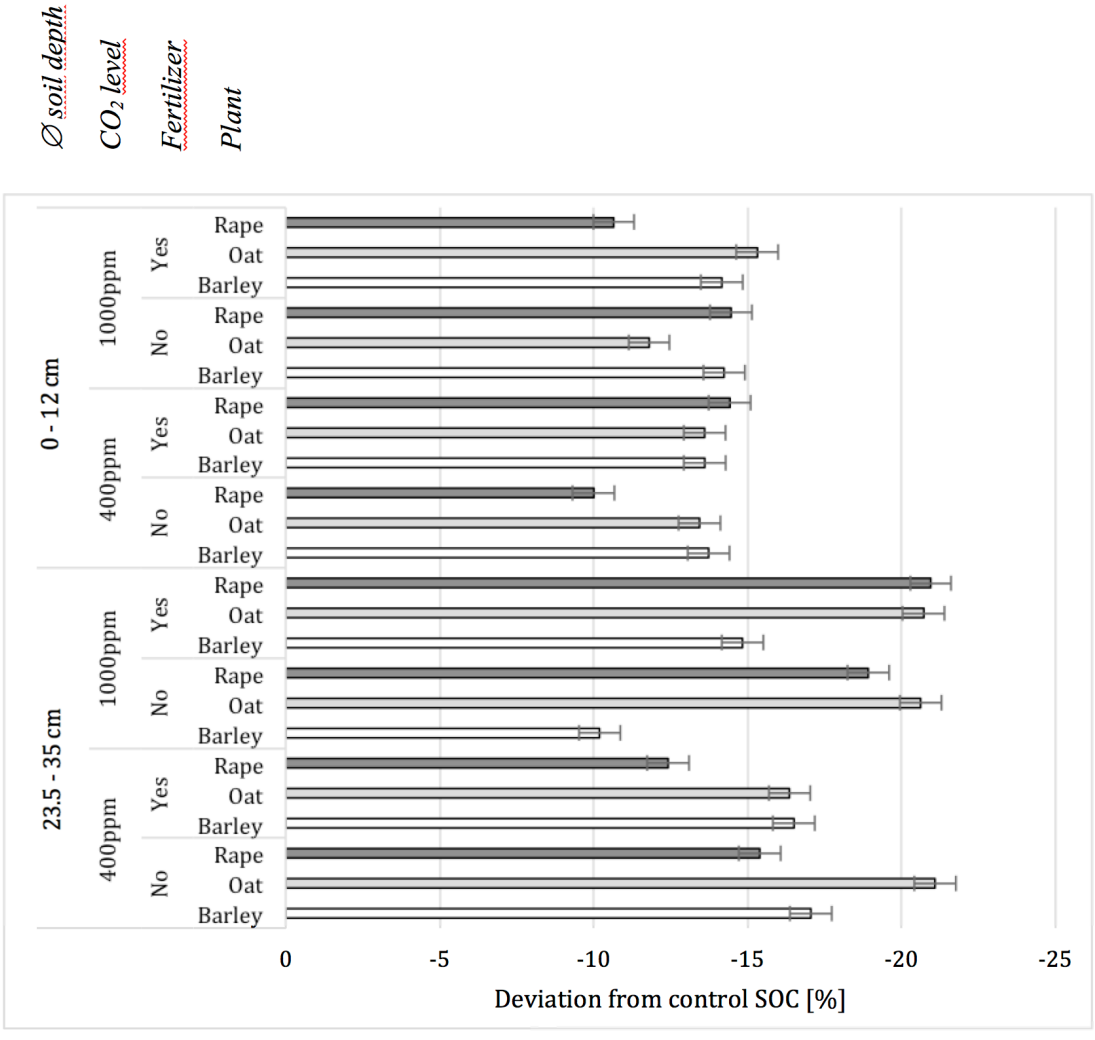


Figure 19: Priming effect in % of the initial soil C of the different treatments.

All the samples showed a positive PE (Figure 19). Thus, the soil C content after the MICE experiment was lower compared to the initial C content of the soil (1.97% C). This

breakdown of some of the preexisting SOM is generally referred to as positive priming effect (Weil & Brady, 2017). The results ranged from -6.75 g C / kg dry soil to -0.45 g C / kg dry soil, which accounts for -34.34% to -2.30% of the initial soil C respectively. The PE did neither significantly differ between the CO_2 level, the fertilizer nor the plant species treatment. Only soil depth had an influence on the PE. In rape and oat, the PE was significantly higher in soil depth 3 (23.5-35 cm) compared to soil depth 1 (0-12 cm). The barley samples showed the same vertical distribution of the PE. However, the difference was statistically not significant (Table 18).

Table 16 shows that samples with rape had a mean PE of -2.44 g C / kg dry soil in soil depth 1, ranging from -4.49 g C / kg dry soil to -1.17 g C / kg dry soil. This accounts on average for a loss of 12.39% of the initial soil C in soil depth 1. By contrast, in soil depth 3 there was an average loss of 16.08% of soil C. This represents a mean reduction of 3.16 g C / kg dry soil (min: -5.24 g C / kg dry soil; max: -1.18 g C / kg dry soil).

Table 16: Mean and standard deviation of the priming effect [g C/kg dry soil] in the rape samples and results of ANOVA and post-hoc test. Soil depths 1 and 3 stand for 0 – 12 cm and 23.5 – 35 cm soil depth respectively.

	CO_2 level (n.s.)		**Fertilizer (n.s.)**		**Soil depth (*)**	
	1000ppm	400ppm	Yes	No	1	3
∅ PE rape	-2.99	-2.54	-2.65	-2.84	-2.44	-3.16
Standard Deviation	(±1.05)	(±1.11)	(±0.96)	(±1.22)	(±0.85)	(±1.26)
Post-hoc test	*a*	*a*	*a*	*a*	*a*	*b*

Oat had a higher negative PE than rape with a mean of -2.68 g C / kg dry soil in soil depth 1, ranging from -4.17 to -0.78 g C / kg dry soil (Table 17). This accounts for an average loss of 13.63% soil C. The positive PE in soil depth 3 was in oat also higher with a mean of -3.86 g C / kg dry soil (min: -6.75 g C / kg dry soil; max: -1.51 g C / kg dry soil), accounting for a loss of 19.65% of soil C.

Table 17: Mean and standard deviation of the priming effect [g C/kg dry soil] in the oat samples and results of ANOVA and post-hoc test. Soil depths 1 and 3 stand for 0 – 12 cm and 23.5 – 35 cm soil depth respectively.

	CO_2 level (n.s.)		Fertilizer (n.s.)		Soil depth (*)	
	1000ppm	400ppm	Yes	No	1	3
∅ PE oat	-3.38	-3.17	-3.24	-3.30	-2.68	-3.86
Standard Deviation	(±1.35)	(±1.44)	(±1.56)	(±1.21)	(±0.84)	(±1.58)
Post-hoc test	*a*	*a*	*a*	*a*	*a*	*b*

Barley also has a higher PE in soil depth 3 with a mean of -2.91 g C / kg dry soil compared to soil depth 1 (mean: -2.74 g C / kg dry soil). This accounts for -14.79% and -13.94% of the initial soil C respectively. However, in contrast to oat and rape this difference is statistically not significant (Table 18).

Table 18: Mean and standard deviation of the priming effect [g C/kg dry soil] in the barley samples and results of ANOVA and post-hoc test. Soil depths 1 and 3 stand for 0 – 12 cm and 23.5 – 35 cm soil depth respectively.

	CO_2 level (n.s.)		Fertilizer (n.s.)		Soil depth (n.s.)	
	1000ppm	400ppm	Yes	No	1	3
∅ PE barley	-2.66	-2.89	-2.89	-2.75	-2.74	-2.91
Standard Deviation	(±1.24)	(±1.20)	(±1.37)	(±1.07)	(±1.20)	(±1.26)
Post-hoc test	*a*	*a*	*a*	*a*	*a*	*a*

4.6 Fertilizer Effects

The following subchapters describe parameters, which can be linked to the N availability. These are the number of tillers, the chlorophyll content, the C:N ratio, the total amount of N and the NO_3^- leaching.

4.6.1 Fertilizer Effects on Above Ground Biomass

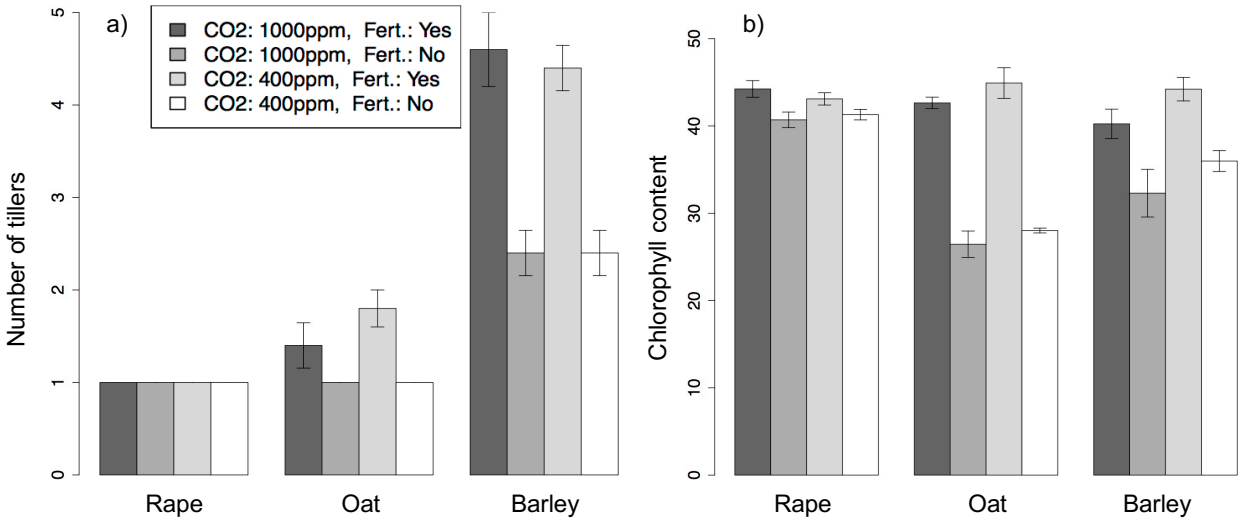


Figure 20: Mean and standard error of the number of tillers (a) and the upper chlorophyll content (b) of the different treatments.

Oat and barley samples increased their number of tillers significantly (***) with the addition of N fertilizer (Figure 20a). Not fertilized oat samples did not do any tillering. By contrast, fertilized oat samples had an average of 1.6 tillers per sample. In barley the difference was bigger. While not fertilized samples had on average 2.4 tillers per sample, fertilized ones had an average of 4.5 tillers per sample. Rape samples showed no difference between the fertilization treatments. No rape plants showed tillering (Figure 20a).

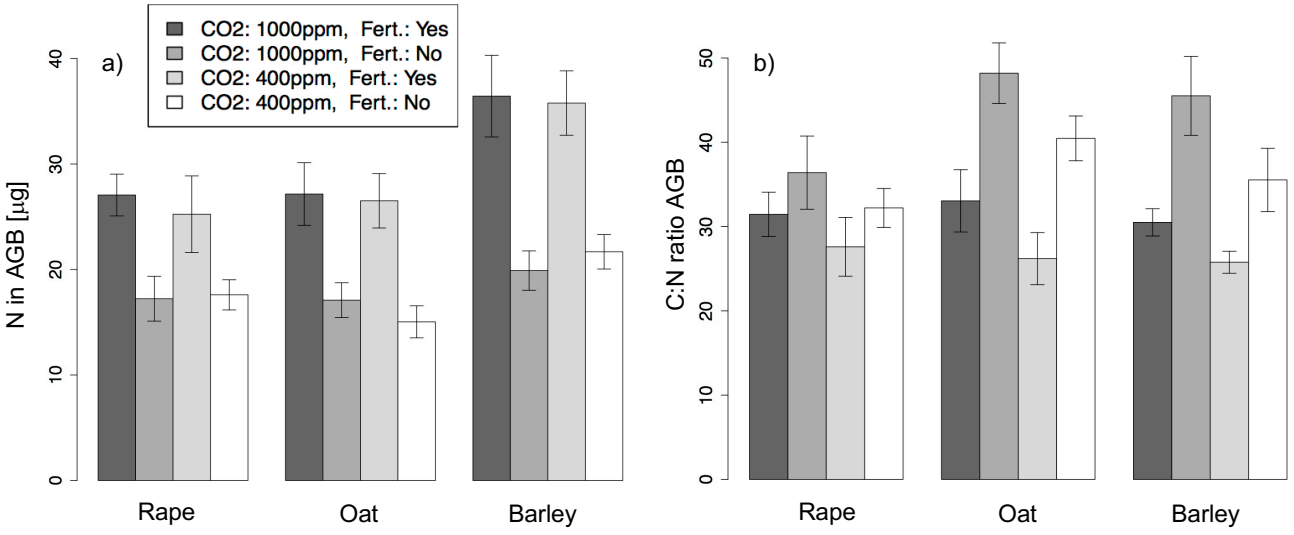


Figure 21: Mean and standard error of the total N [µg] in the above ground biomass (a) and the C:N ratio of the above ground biomass (b) the different treatments.

Fertilization had a similar effect on the chlorophyll content of the upper leaves of the plant (***). However, in contrast to the tillering, the difference in the chlorophyll content due to fertilization was higher in oat than barley and rape (Figure 20b). Oat samples without fertilizer had on average a chlorophyll content of 27.32, while the fertilized oat samples had one of 43.78, which is an increase of 60%. Barley showed a lower increase of +24%, with a mean of the fertilized samples of 42.23 compared to the not fertilized ones of 34.14. The fertilizer treatment had the lowest effect on rape. Fertilized rape samples had on average a chlorophyll content of 43.67, while not fertilized samples had one of 41.00. This results in an increase of 7% due to fertilization.

Table 19 shows that the total N content in the AGB was plant specific. Barley had with a mean of 28.45 µg (min: 12.99 µg; max: 45.14 µg) a higher N content in the AGB than rape and oat, which had an average N content in the AGB of 21.78 µg and 21.68 µg respectively. The N content in rape varied between 12.47 µg and 38.41 µg, while oat samples varied between 9.79 µg and 38.08 µg.

Furthermore, while the CO_2 treatment had no significant effect on the total N content in the AGB, the fertilizer treatment had a significant effect (Table 19). Fertilized samples contained on average 29.70 µg N, ranging from 17.20 µg to 45.14 µg. By contrast, not fertilized samples had on average 18.12 µg N, ranging from 9.79 µg to 27.13 µg. This is an increase of 64% of N in the AGB due to fertilization. Figure 21a shows that the fertilizer effect was particularly strong in barley.

Table 19: Mean and standard deviation of the total N [µg] in the above ground biomass and results of ANOVA and post-hoc test.

	CO_2 level (n.s.)		**Fertilizer (***)**		**Plant species (***)**		
	1000ppm	400ppm	Yes	No	Rape	Oat	Barley
∅ total N [µg]	24.39	23.64	29.70	18.12	21.78	21.68	28.45
Standard Deviation	(±8.69)	(±8.48)	(±7.80)	(±4.09)	(±6.74)	(±7.30)	(±9.71)
Post-hoc test	*a*	*a*	*a*	*b*	*b*	*b*	*a*

Table 20 shows that the C:N ratio in the AGB was not plant specific. However, the fertilizer treatment had a significant effect. Fertilized samples had a mean C:N ratio of 29.09, ranging from 15.42 to 41.76. In contrast, not fertilized samples had a mean C:N ratio of 39.43 (min: 26.37; max: 56.10). The fertilizer effect was particularly strong in oat and barley samples (Figure 21b).

Moreover, the CO_2 treatment significantly influenced the C:N ratio in the AGB (Table 20). The samples, which grew in the 1000 ppm atmosphere, had a significantly higher C:N ratio with a mean of 37.15 (min: 22.08; max: 56.10). However, the samples of the 400 ppm CO_2 treatment had a mean of 31.30, ranging from 15.42 to 47.50.

Table 20: Mean and standard deviation of the C:N ratio in the above ground biomass and results of ANOVA and post-hoc test.

	CO_2 level (**)		**Fertilizer (***)**		**Plant species (n.s.)**		
	1000ppm	400ppm	Yes	No	Rape	Oat	Barley
∅ C:N ratio	37.15	31.30	29.09	39.43	31.92	36.39	34.33
Standard Deviation	(±9.89)	(±8.02)	(±6.31)	(±9.22)	(±7.47)	(±10.48)	(±9.94)
Post-hoc test	*a*	*b*	*b*	*a*	*a*	*a*	*a*

4.6.2 Fertilizer Effects on Below Ground Biomass

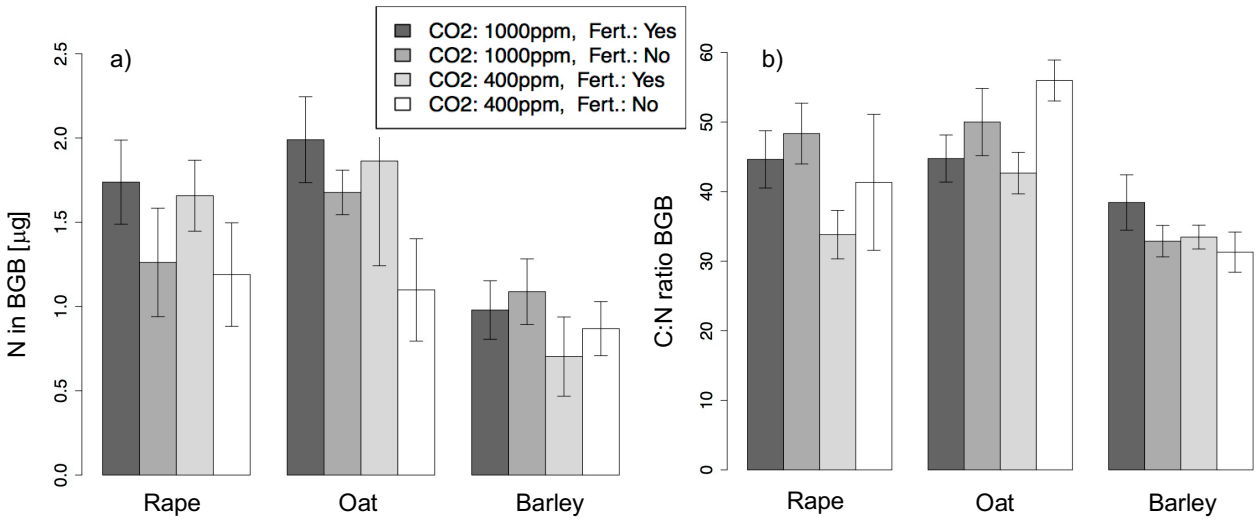


Figure 22: Mean and standard error of the total N [µg] in the below ground biomass (a) and the C:N ratio of the below ground biomass (b) the different treatments.

In contrast to the total N content of the AGB, the fertilizer treatment had no significant effect on the N content of roots in soil depth 0-12 cm (Table 21). Neither did the CO_2 treatment. However, the N content of the roots in the soil depth 1 (0-12 cm) is plant specific (Figure 22a). Roots in the soil depth 1 of the rape and oat samples had a similar amount of N, with a mean of 1.46 µg and 1.66 µg respectively. The values of the rape samples varied between 0.42 µg and 2.47 µg and the oat samples between 0.41 µg and 3.78 µg. However, the N content of the roots in the soil depth 1 was significantly lower in the barley samples (Table 21). They had on average 0.91 µg of N, ranging from 0.13 µg to 1.84 µg.

Table 21: Mean and standard deviation of the N content [µg] in the roots in the soil depth 0-12 cm and results of ANOVA and post-hoc test.

	CO_2 level (n.s.)		Fertilizer (n.s.)		Plant species (**)		
	1000ppm	400ppm	Yes	No	Rape	Oat	Barley
∅ N [µg] depth 1	1.45	1.23	1.49	1.18	1.46	1.66	0.91
Standard Deviation	(±0.60)	(±0.81)	(±0.82)	(±0.56)	(±0.62)	(±0.86)	(±0.42)
Post-hoc test	*a*	*a*	*a*	*a*	*a*	*a*	*b*

While the CO_2 and the fertilizer treatments had an effect on the C:N ratio of the AGB, they had no significant effect on the root C:N ratio in the soil depth 0-12 cm (Table 22). By contrast, the C:N ratio of the roots in the soil depth 1 (0-12cm) is plant specific. Oat roots had the highest C:N ratio with a mean of 48.26, ranging from 33.47 to 62.33. Roots of rape samples had a significantly lower C:N ratio with a mean of 42.03 (min: 25.39; max: 79.88). Figure 22b shows, that the roots in soil depth 1 of barley had significantly the lowest C:N ratio with an average of 34.02, ranging from 20.19 to 52.74.

Table 22: Mean and standard deviation of the root C:N ratio in the soil depth 0-12 cm and results of ANOVA and post-hoc test.

	CO_2 level (n.s.)		Fertilizer (n.s.)		Plant species (***)		
	1000ppm	400ppm	Yes	No	Rape	Oat	Barley
∅ C:N ratio depth 1	42.94	39.76	39.63	43.07	42.03	48.26	34.02
Standard Deviation	(±9.70)	(±12.91)	(±8.37)	(±13.89)	(±13.47)	(±8.78)	(±6.43)
Post-hoc test	*a*	*a*	*a*	*a*	*b*	*a*	*c*

4.6.3 NO_3^- Leaching

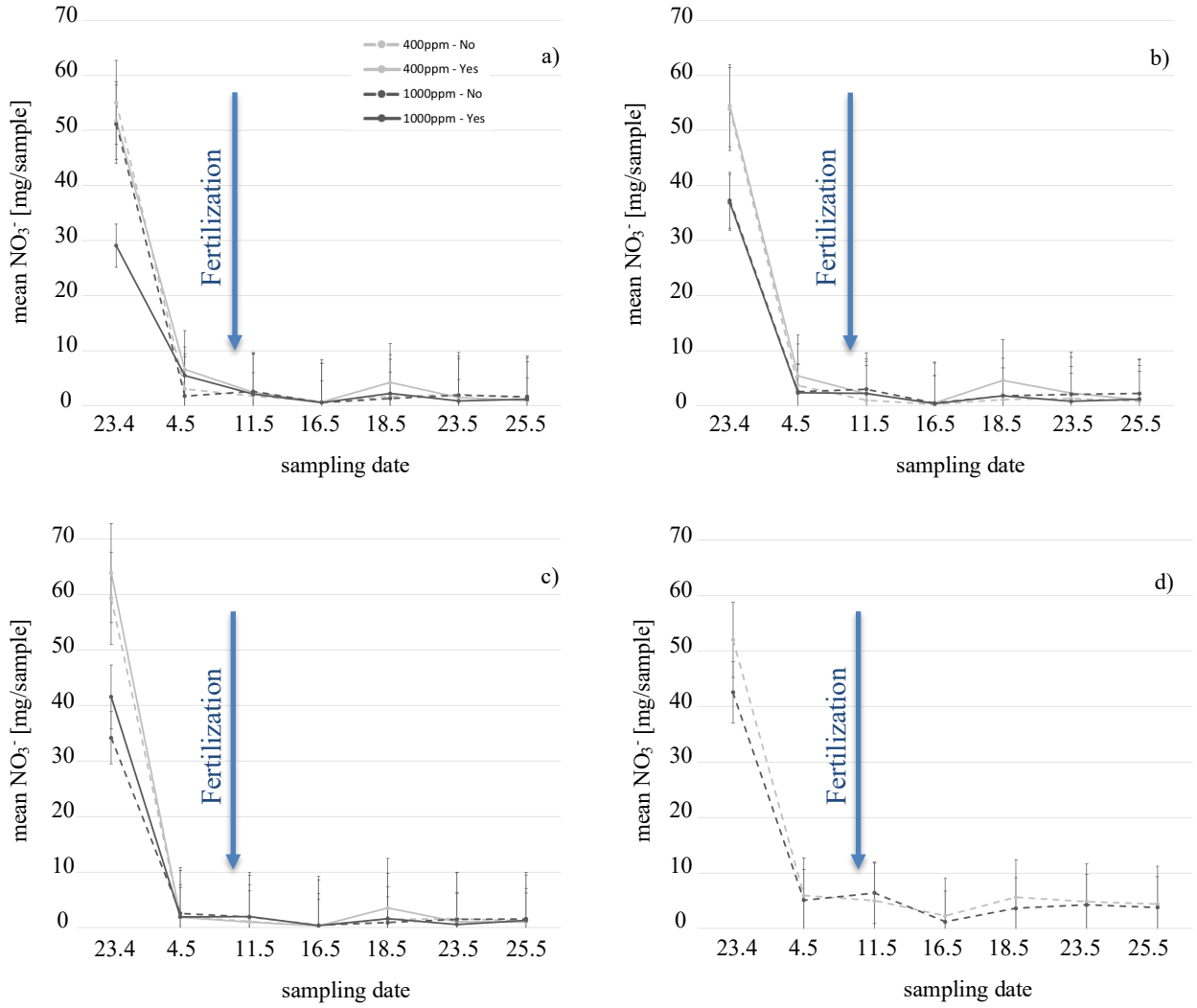


Figure 23: Time series of the mean and standard error of the NO_3^- leaching [mg/sample] of rape (a), oat (b), barley (c) and the control soil (d) of the different treatments. The striped lines indicate the samples without added fertilizer.

Figure 23 shows that there was a flush of nitrate (NO_3^-) in the beginning of the experiment in all the plant species including the control soil. The flush was significantly higher in the 400 ppm CO_2 atmosphere with a mean of 55.78 mg NO_3^- per sample, ranging from 20.8 mg NO_3^- to 113.4 mg NO_3^- per sample. In contrast, in the 1000 ppm CO_2 atmosphere, the mean was at 39.1 mg NO_3^- per sample. The values varied between 15.37 and 113.94 mg NO_3^- per sample. However, after this first flush, there is no CO_2 effect visible. Furthermore, the fertilization treatment, which was applied on the 9th of May 2018, had no visible effect on the NO_3^- leaching.

The time series of the different plant species show a similar leaching dynamic with comparable NO_3^- quantities. By contrast, the NO_3^- leaching of the control soil was visibly higher. The control soil samples leached on average 74.89 mg NO_3^- per sample over the whole sampling period, the values varied between 46.53 mg NO_3^- and 107.19 mg NO_3^- per sample. The planted samples, however, leached on average 59.04 mg NO_3^- per sample, ranging from 22.35 mg NO_3^- to 125.34 mg NO_3^- per sample. Hence, the planted samples leached on average 48.09 kg N per hectare over the sampling period, while the control soil samples leached on average 61.01 kg N per hectare over the sampling period.

5 Discussion

The following subchapters discuss the findings of this work and put them into the relevant scientific context. The differences between the plant species are discussed in the first subchapter. Observations about soil depth, atmospheric CO_2 levels and fertilizer treatments will then follow in separate subchapters.

5.1 Plant Specific Effects

The plant species treatment had a considerable effect on the above- and below ground biomass, the R:S ratio, the RD and the N content. Foremost, the plant species showed different above and below ground C allocation strategies and different C assimilation efficiencies. The following three paragraphs show and discuss the observed characteristics of the individual crop species.

Rape: Rape samples assimilated C the least efficiently. This shows in the smallest above and below ground biomass as well as the smallest amount of RD. By contrast, the crop showed a relatively efficient N take up. Rape assimilated the same overall amount of N than oat. This is rather surprising, considering the taproot structure of rape and the fact that the BGB of rape is less than half the amount of the BGB of oat. This suggests that there are other factors next to the root type and the quantity of BGB defining N absorption.

Oat: On the contrary to the N uptake, oat assimilated C the most efficiently. Oat developed more than double the amount of BGB than rape and barley and developed 18% more AGB than the rape specie. The high BGB of oat shows that the oat specie transferred the assimilated C to the roots very actively. As BGB has been reported to contribute more to SOM (Kätterer et al., 2011; Rasse et al., 2005), the oat specie seems the first choice to increase SOM. Due to the high BGB, oat showed with 0.28 a higher R:S ratio than rape (0.13) and barley (0.16). The observed R:S ratios are in the expected range of crops, which show lower R:S ratios compared to grasses as they are bred to maximize yield. For example, Bolinder et al. (2007) reported a mean S:R ratio of crops of 5 with values ranging from 1.1 to 10.7. A S:R ratio of 5 refers to a R:S ratio of 0.2. Additionally, oat did not only develop the most BGB, they also released the highest amount of RD to the soil (0.31 g C/kg dry soil). This could be due to the high root surface area of oats, which can be assumed due to the high BGB and the branched root structure. Jones et al. (2009) reported that the root surface area is an important factor influencing root exudation.

Barley: Barley allocated C preferably in the AGB. While they showed on average 55% less BGB than oat, they developed 13% more AGB than oat, which is the highest amount of AGB of the three crops. This strong preference to allocate C in the AGB could be a result of long-

term breeding for yield production (Johanna Pausch & Kuzyakov, 2017). Surprisingly, these observations are not in line with the results of a similar study with nearly identical growing conditions. Huber (2018) reported a different C allocation in barley. The author observed half of the AGB and a much bigger BGB than observed in this study. Therefore, the R:S ratio was more than ten times higher in Huber's study. These different results suggest that there are likely important factors influencing the plant-soil system that were not yet considered. However, even though the BGB of barley was rather small in this study accounting for half the size of the BGB of oat, barley released with 0.27 g C per kg dry soil nearly as much RD as oat (0.31 g C/kg dry soil). Therefore, the RD : root C ratio of barley is twice as high in barley than in oat. Additionally, barley developed the longest roots. Barley was the only specie, which accumulated roots at the bottom of the 35 cm tube at the end of the experiment. The deeper rooting depth of barley compared to rape and oat was also observed by Fan et al. (2016). Such morphological traits of the root system are important to be considered. Deep-rooting, for example, has been reported to enhance N acquisition (Saengwilai et al., 2014). This study supports the correlation between the rooting depth and the N acquisition, as barley showed the highest overall N content. The ability of barley to develop deep roots might go back to its origins, which are predominantly hot and dry environments, where deep roots are of advantage to get water access (Dawson et al., 2015). Moreover, deep roots are reported to not only increase the access to water and N, but also play an important role in increasing SOM, which is key to mitigate climate change (Kell, 2011; Lynch & Wojciechowski, 2015).

All species: This work observed a substantially higher C allocation to RD compared to roots in all three plant crops. RD accounted on average for 60% of the total root-derived C. By contrast, most studies reported a higher C allocation to roots than to RD. Over 80% of the studies that Pausch & Kuzyakov (2017) looked at, reported a higher C allocation to roots than to RD. It is likely that the continuous labeling method, which was used in this study, detects more RD, as Friedli et al. (2017) reported an even higher relative proportion of RD to the root C using the same continuous ^{13}C labeling technique under controlled conditions. The authors observed between 74 and 94% RD of the root-derived C in Swiss wheat varieties. This could mean that RD has so far been underestimated in most studies. However, it is also likely that the RD is slightly overestimated as small roots, which were not picked up by hand may end up in the RD pool. Nevertheless, at least they are counted as root-derived C and are not just left out of the picture.

Overall, the experiment showed that the three different plant species had different C and N assimilation and distribution capacities. Other studies also reported that different species or varieties can perform differently not only on the above ground but also below ground on the same soil (Hirte et al., 2018; Ontl et al., 2013; Thorup-Kristensen et al., 2009). However, it is

interesting that even though the three species assimilated different amounts of N, the NO_3^- leaching was not species dependent. Therefore, the crop choice does not play an important role when it comes to NO_3^- leaching. Moreover, even though the crop choice seems an important parameter in maximizing the C input to agricultural soil, the PE was not influenced by the different species in this study. This is not in line with the study conducted by Zhu et al. (2014). The authors reported that sunflowers showed a consistently higher intensity of rhizosphere priming than soybeans. The fact that Zhu et al. (2014) used a legume and a non-legume, while this study used three non-legumes, might explain the different outcome. The authors explain that the N-fixing capacity of soybean nodules reduces the N demand in the rhizosphere, which could then lead to a reduced N mining from SOM. It is, however, interesting that in this study N fertilization had no effect on the PE. The only significant change in the PE was observed with soil depth, no other treatment showed a significant effect on SOM priming. This contrasts with some of the previous findings. Cheng & Kuzyakov (2005), for example, reported a higher SOM priming in dicotyledons, which include rape, than in monocotyledons, the category of oat and barley. In general, the results of this work suggest that neither higher atmospheric CO_2 concentrations in the future nor N fertilization or the crop choice will influence C stocks in agricultural soils.

5.2 Effects of Soil Depth

The parameters BGB distribution over soil depth, RD and PE changed through the soil profile. Chapter 4.2.1 showed that the vertical distribution of the root biomass varied significantly between the different plant species. Due to the similar root systems of oat and barley (see chapter 3.1), one would expect them to have a similar vertical root biomass distribution. However, even though oat developed on average more than twice the amount of BGB than rape and they have a very different root system, they showed a similar vertical root biomass distribution. Both species developed the most root biomass in the upper soil depth (0-12 cm), while having considerably less root biomass in the soil depths below. Barley showed a similar root biomass distribution than oat and rape in the soil depths 0-12 cm and 12-23.5 cm. However, in contrast to oat and rape, barley developed as much root biomass in the soil depth 23.5-35 cm than in the first soil depth. Therefore, the vertical root biomass distribution of barley is more even compared to the ones of rape and oat. However, as mentioned in the previous subchapter, the barley samples already developed deeper roots, which accumulated at the bottom of the 35 cm growth tube. Consequently, it is probable that all three plant species show a similar vertical root biomass distribution pattern with the most root biomass in soil depth 0-12 cm and less root biomass in deeper soil depths. Fan et al. (2016) confirms this finding. They even reported that oat, barley and rape develop 50% of their total BGB in the first 12 cm soil depth. Moreover, they developed 67-76% of their roots in the upper 30 cm of

the soil profile. This shows that the tube length of 35 cm used in this experiment provides enough depth for the majority of the roots to develop. However, due to limited amount of space, this study fails to provide information about the deeper roots and their effects on SOM priming. Furthermore, it is to mention that the plant roots were also constrained in the width of the tubes with a diameter of 5.8 cm. Therefore, it would be interesting to analyze the root distribution of rape, oat and barley under field conditions.

Similarly to the overall root biomass distribution, which showed more BGB in soil depth 0-12 cm and less BGB in soil depth 23.5-35 cm, the rhizodeposition (RD) differed accordingly between these two soil depths. The RD was 67% higher in the upper soil depth (0-12 cm) compared to the lowest soil depth (23.5-35 cm). Therefore, the RD : root C ratio did not change in the vertical soil profile. Except for the rape samples, which were most likely distorted due to the very small amount of roots found in the lowest soil depth (see chapter 4.4.1). These results suggest that the amount of C released to the soil as RD depends on the amount of root C.

Living roots and their rhizodeposits were reported to enhance soil C mineralization by 27-245% (Zhu et al., 2014). Huber (2018), who used a comparable soil and the same barley variation, found a PE of 5-10%. This study found a mean positive PE of 15 %. A mean reduction of 15% of the initial soil C still seems a rather large C loss. However, one has to keep in mind that the plants grew in a small tube (925 cm^3). Consequently, probably most of the soil was influenced by root activities. Therefore, a large part of the soil can be classified as rhizosphere (McNear, 2013). In consequence, the quantity of bulk soil in this experiment was below average field conditions. Thus, it is probable that this result is a zoom-in into the rhizosphere, where it is possible that the positive PE is in that range. Another explanation for this rather strong positive PE could be that the soil temperature was higher during the experiment (~19-24 °C) than in the field in the beginning of March in Switzerland, which could have led to an increased microbe activity. Zhu & Cheng (2011) reported that a 5°C warming of the soil increased the positive PE up to threefold. Therefore, rising temperatures in the future could still increase the soil C mineralization, even though the higher atmospheric CO_2 concentration itself did not influence the PE.

Furthermore, all samples showed a consistent positive priming effect with rather small variations in the C loss within the replicates (*see chapter 4.5*). More precisely, all samples lost between 2.30% and 34.34 % of the initial soil C during the experiment. A positive PE was probable, as it was more frequently reported than the negative PE (Cheng et al., 2014; Zhu & Cheng, 2011). Moreover, all plant species showed a significantly higher mean PE in soil depth 23.5-35 cm compared to the soil depth 0-12 cm. Barley showed the same picture as well, but it was not statistically significant. This higher PE in the lowest soil depth is

surprising, as the RD and the root biomass were the highest in the first soil depth. The observed soil depth effect suggests that there are likely other factors in addition to the presence of roots and the quantity of RD influencing C stocks in agricultural soils. Keiluweit et al. (2015) for example, reported that oxalic acid, which is a common root exudate, promotes C loss by liberating organic compounds from protective associations with minerals. The authors explain that this indirect mechanism can accelerate C loss more by enhancing microbial access to previously mineral-protected compounds. These findings suggest that the RD quantity alone is not a sufficient parameter to predict priming. The RD quality seems to play a role in the soil C stock dynamics as well. Therefore, it could well be that the RD quality in the soil depth 23.5-35 cm differed from the one in the soil depth 0-12cm. This led in consequence to a higher PE in the lowest soil depth, where the least amount of root derived C was put into the soil. However, this is only a hypothesis and needs further research.

5.3 Effects of Different Atmospheric CO_2 Levels

In short, the CO_2 treatment had a considerable influence on the AGB and the C:N ratio of the AGB. Moreover, different CO_2 levels showed an effect on root C. However, the connection of the CO_2 level and certain below ground parameters is ambiguous as the following discussion will show. Additionally, the CO_2 treatment influenced considerably the NO_3^- leaching, although in an unexpected way.

Chapter 4.1 showed that an increase of the atmospheric CO_2 level led to a higher AGB. This so-called carbon fertilization effect was already reported in previous studies (Kang et al., 2002; Manderscheid & Weigel, 2007). More precisely, this study showed that an increase of 600 ppm CO_2 (from 400 ppm to 1000 ppm) resulted in an 18.8% higher dry AGB. This increase lies in the range of similar studies. Manderscheid & Weigel (2007), for example, conducted a field study of wheat grown over two years at 400 ppm and 680ppm. The CO_2 enrichment enhanced the final dry AGB by 8.6% under well-watered conditions. However, some experiments showed a much higher effect of CO_2 fertilization. Kang et al. (2002), for instance, conducted an experiment with pot-grown wheat in 350 ppm and 700 ppm CO_2. They observed an increase of shoot dry matter of well-watered spring wheat of 47.16%.

In contrast to Kang et al. (2002), who also reported an increase of 42.64% of root biomass due to CO_2 fertilization, this study did not observe any significant effect of CO_2 fertilization on the BGB. Also, the root:shoot ratio was not significantly influenced by the atmospheric CO_2 level. These observations are surprising, because some authors do not only report an increased BGB in an elevated CO_2 atmosphere, but even report that BGB increased more than the AGB (Prior et al., 1994; Wittwer, 1978). Rogers et al. (1994) summarized several studies and stated that “virtually all studies (=87%) found that root dry weight increased under

elevated atmospheric CO_2, regardless of species or study conditions." This study did observe a higher BGB and a higher root:shoot ratio in a higher CO_2 environment, however, the effects were not statistically significant. By contrast, the mean root C content was significantly increased by 29.4% due to the higher atmospheric CO_2 concentration.

The C:N ratio of the AGB and the BGB show a similar picture. On the one hand, the mean C:N ratio of the AGB rose from 31.30 in a 400 ppm CO_2 atmosphere to 37.15 in a 1000 ppm CO_2 atmosphere. Other studies observed higher C:N ratio in plants grown in high CO_2 environments as well (Cotrufo et al., 1998). On the other hand, the C:N ratio of the BGB was not affected by the atmospheric CO_2 concentration, which confirms the picture of the BGB.

These observations indicate that CO_2 fertilization of barley, oat and rape crops could fix more CO_2 in a future with a higher atmospheric CO_2 level. However, the effect on the BGB was not as big as reported by other authors (Kang et al., 2002). Therefore, the contribution of these plant species to the negative feedback on the climate might not be as important as suggested by Kang et al. (2002). Since root C is more persistent in soil with residence times twice as high as those of AGB (Kätterer et al., 2011; Rasse et al., 2005). In addition to the atmospheric CO_2 concentration, increasing temperatures are also reported to influence plant growth and microbial decomposition of SOM. At low temperatures, SOM is thought to accumulate, while at temperatures between 25 and 35°C, decomposition surpasses plant growth, which would lead to a lower SOM accumulation than in cooler soils (Weil & Brady, 2017). As the atmospheric CO_2 concentration is correlated to the temperature, CO_2 fertilization might not be an adequate strategy to mitigate climate change.

Moreover, the NO_3^- leaching hypothesis is also linked to the atmospheric CO_2 concentration. The hypothesis states that in a higher CO_2 environment, less N is leached. The hypothesis is based on the assumption that CO_2 fertilized plants produce more biomass, which was the case in this study, and would in consequence need more N. Thus, less N will be leached. The NO_3^- leaching figures (*see chapter 4.6.3*) showed, however, another picture. The difference in the NO_3^- leaching between the atmospheric CO_2 levels came from the first NO_3^- flush in the beginning of the experiment. At that point the plants were only sown 11 days prior and were still very small. Therefore, it can be assumed that this difference was induced by another factor than N demand due do plant growth. Torbert et al. (1996) reported as well that elevated CO_2 significantly decreases the NO_3^- leaching in both soybean and grain sorghum. The authors observed that the decomposition of SOM was the primary source of the NO_3^- leaching. Therefore, it can be hypothesized that the microbial activity and thus the SOM decomposition was reduced at the beginning of the experiment due to the elevated CO_2 concentration. Thus, this could have led to the lower flush of NO_3^- in the higher CO_2 environment in the beginning of the experiment. However, further research is needed to

confirm this hypothesis. The NO_3^- flush itself was likely induced through enhanced nitrification. Weil & Brady (2017) state that nitrifying organisms perform best, when temperatures are between 20 and 30 °C and perform very slowly if the soil is cold. The authors explain further that a sudden aeration of the soil by tillage can also cause a flush of soil nitrate production. Both conditions were met at the beginning of the experiment and thus likely caused the NO_3^- flush. There was an increase of temperature at the start of the experiment, and the soil was well aerated during the root picking before the experiment.

5.4 Effects of N Fertilization

Similar to the effects of different atmospheric CO_2 levels, also the effects of N fertilization show a different picture on the above- and below ground parameters. N fertilization showed a positive effect on above ground plant parameters like AGB, the number of tillers, the chlorophyll content in the leaves, the N content and the C:N ratio. By contrast, N fertilization did, aside from one exception, not influence the BGB (*see chapters 4.2 and 4.2*). Moreover, while N fertilization did not influence the total RD, the RD in the soil depth 0-12 cm was influenced by the N treatment.

Regarding the above ground plant parameters, the number of tillers in barley and oat increased significantly with N fertilization. Studies have shown that N is required for tiller development and that in consequence a reduced tiller formation is an N deficiency symptom in barley and oat (GRDC, 2017a, 2017b). The difference in the number of tillers was the strongest in barley. Even though the supplementary tillers were smaller and thinner than the main stem, they still carried additional ears. This means that N fertilization did not only increase the number of tillers in oat and barley, but it would probably also increase crop yield. Hough (1990) confirms that N is a key nutrient for determining yield of rape, oat and barley. An increased plant productivity measured in tons of grain due to N fertilization was also reported by Weil & Brady (2017). This was expected, as increasing yield due to N fertilization is basically the main reason for its use. Moreover, N fertilization also increased the chlorophyll content in the upper leaves of all three plant species. This increased leaf greenness due to N fertilization was also reported by Weil & Brady (2017). However, the N fertilization effect was much smaller on the chlorophyll content of the rape samples than of the oat and barley samples. Blackmer & Schepers (1995) reported that the chlorophyll concentration in corn is positively correlated with the leaf N concentration and N sufficiency. In this work, however, chlorophyll content did not well indicate the N fertilization effect on the AGB or the N content in the AGB.

Even though the chlorophyll content did not predict well the N content in the AGB, N fertilization still had a strong effect on the N content in the AGB in all three plant species.

Fertilized samples contained on average 64% more N than not fertilized ones. This high increase and the observed chlorosis on the lower leaves of the not fertilized samples indicate that the plants without N fertilization were likely N limited. The term chlorosis refers to the appearance of yellowish or pale green leaf colors due to an N deficiency (Weil & Brady, 2017). Another fact speaking for an N limited environment in this experiment is that there was no difference in the NO_3^- leaching between the fertilized and the not fertilized samples after the application of mineral N fertilizer.

Moreover, the C:N ratio was also changed with N fertilization. Due to the higher N content in the AGB, the C:N ratio in the AGB decreased on average from 39.43 to 29.09 because of N fertilization. Studies have shown that biomass with a low C:N ratio is generally faster decomposed due to microbial N demand (Weil & Brady, 2017). Therefore, one could assume that the AGB of fertilized plants will be decomposed faster and will thus contribute less to the soil C stock.

Furthermore, N fertilization increased not only significantly the N content in the AGB, but also increased the AGB itself by 20.8%. A higher AGB due to N fertilization is a well-known phenomenon. Furthermore, the CO_2 fertilization effect on the AGB was clearly limited by N. This was visible in the samples, which grew in the higher CO_2 environment, but were not treated with mineral N fertilizer. They showed a similar AGB than the samples, which were treated with mineral N but grew in the lower CO_2 atmosphere. This interaction between the C and the N cycle was also reported by Stitt & Krapp (1999). For the future, this observation suggests that the full C sink potential of the vegetation can only be leveraged if N is not limited. However, N limitations are reported to be widespread in both unmanaged and managed vegetation (Luo et al., 2004; Reich et al., 2006). Therefore, some authors conclude that N supply is an important constraint on the C sink potential of vegetation. For example, Thornton et al. (2007) reported that climate models, which only consider the C cycle alone overestimate the total C uptake by the vegetation due to CO_2 fertilization. Therefore, the future atmospheric CO_2 concentration predicted by C only models is underestimated. The authors report that models, which consider the interaction between the C and the N cycles, provide a more accurate estimation for future atmospheric CO_2 concentrations.

However, plant-soil-interaction with nutrients is more complex than that. As already mentioned, roots have been reported to play a more important role in C sequestration (Kätterer et al., 2011; Rasse et al., 2005). In consequence, it is crucial to look at the N fertilization effect on the BGB as well. This study, however, showed that N fertilization had in almost all cases no significant effect on the BGB. Also, Otto et al. (2009), who analyzed the root system distribution of sugar cane in relation to N fertilization did not find any effect of N fertilization rate on root biomass either. Furthermore, several other studies reported that

root biomass was similar or even higher in organic than in conventional farming systems (Chirinda, et al., 2012; Hirte et al., 2018). The fact that in most cases N fertilization influenced significantly shoot but not root biomass suggests that root biomass is not directly linked to crop productivity (Hirte et al., 2018; Koevoets et al., 2016; Palta & Yang, 2014). However, there was one exception. N fertilization increased the BGB of rape in the soil depth 0-12 cm by 42%. By contrast, N fertilization had no effect on the root biomass in soil depths below 12 cm. Overall, this study is in line with the findings of Hirte et al. (2018), which stated that in order to enhance the BGB input to soil for C sequestration, the crop choice is more important than the N fertilization intensity. Furthermore, in contrast to the AGB, the C:N ratio of the BGB was not significantly influenced by N fertilization.

Last but not least, the N mining hypothesis states that with no added fertilizer, the RD will increase in order to get the plants access to organic N. Chapter 4.4 showed that while there was no significant effect of N fertilization on the total RD, there was an interaction between the soil depth and the fertilizer treatments influencing RD. In the soil depth 0-12cm, not fertilized plants released on average 26% more RD than fertilized ones. This result supports the microbial N mining hypothesis. This result is in line with Phillips et al. (2011), who reported that a high N availability reduces the portion of C allocated to RD. However, the higher RD in the first soil depth in not fertilized samples did, surprisingly, not influence PE. This is not in line with the study of Fontaine et al. (2004), which reported that nutrient addition decreased SOM priming. However, Cheng et al. (2003), who conducted a greenhouse experiment with wheat and soybean, did not find an influence of nutrient addition on SOM priming either. Furthermore, in the soil depth 23.5-35 cm, the RD was in general lower and the fertilizer treatment had no influence on the RD quantity, which does not support the N mining hypothesis. Additionally, as explained in chapter 5.2, it was surprising that the positive PE was the highest, where RD was the lowest.

6 Conclusion

This thesis has shown different interactions between the C and the N cycles. For example, this study confirmed its biomass hypothesis that more N fertilizer will lead to a higher above ground biomass in an elevated CO_2 environment. Both atmospheric CO_2 and N fertilization independently lead to a higher AGB, while the highest AGB was observed in the samples, which were treated with both a higher CO_2 environment and N fertilizer. However, it was interesting that these two treatments had, with one exception, no effect on the BGB. This finding highlights the importance of taking roots into account when research about climate change mitigation strategies is conducted. Therefore, studies which only focus on above ground plant parameters show an insufficient picture.

Furthermore, the plant species hypothesis stated that branched rooting systems take up N more efficiently. This work showed a very interesting insight into the connection between root structures and N uptake. Neither the root 'type' (taproot of rape vs. branched roots of barley and oat), nor the quantity of BGB played an important role in determining the overall N content. This work suggests that the important factor in the N uptake is rooting depth, as barley was the specie with the deepest roots and the highest N content. However, as the root growth was restricted in this experiment, field studies with no restricted root growth are needed to further test this hypothesis.

Another important interaction between the C and the N cycles is suggested by the N mining hypothesis. This study can confirm the N mining hypothesis in the soil depth 0-12 cm with caution, where not fertilized samples showed a significantly higher RD. However, this was not the case in the soil depth 23.5-35 cm. There, the RD in all samples, regardless the N fertilization treatment, was the lowest. Furthermore, it was unexpected that the PE was the highest in the soil depth 23.5-35 cm, where the RD was the lowest. This result suggests that one cannot only consider the RD quantity to deepen the current understanding of the factors inducing PE. However, investigating further research into the RD quality might enhance this understanding.

Last but not least, the NO_3^- leaching hypothesis assumed that in a higher CO_2 environment, less NO_3^- is leached. However, even though the total NO_3^- leached was lower in the higher CO_2 environment, this hypothesis can only be confirmed with caution. The difference in NO_3^- leaching between the two different CO_2 levels is due to the NO_3^- flush at the beginning of the experiment, when the plants were still very small (<2 cm). After this initial NO_3^- flush, there was no significant difference of NO_3^- leaching visible between the two CO_2 levels. The difference in the NO_3^- leaching during the initial flush is most likely due to a decrease in microbial activity in the higher CO_2 environment, as the microbes were not yet adapted to the

1000 ppm CO_2 concentration. However, this is only a hypothesis and needs further research to be confirmed. Based on this hypothesis no change in NO_3^- leaching is expected in a future with a higher atmospheric CO_2 concentration.

7 Limitations

Even though this master thesis provided interesting insights into the interactions between the C and the N cycle in the plant-soil-system, there are also some limitations. First of all, in order to better understand the role of the atmospheric CO_2 in the plant-soil-system and to ensure comparability with the master thesis of N. Huber, the 'climate' treatment consisted only of different atmospheric CO_2 levels. However, it is widely known that atmospheric CO_2 concentrations are positively correlated with temperature. Therefore, a 'climate' treatment combining higher CO_2 levels with higher temperatures would have provided more realistic results. However, one would not have been able to associate the effects to either the CO_2 level or the temperature.

Furthermore, despite picking the roots of the grassland very thoroughly before the experiment, the sampled soil still contained some weed seeds. In consequence, there was weed growth in some samples (Figure 24). The presence of the weed roots could have influenced the results through additional BGB and RD and through competition for nutrients.

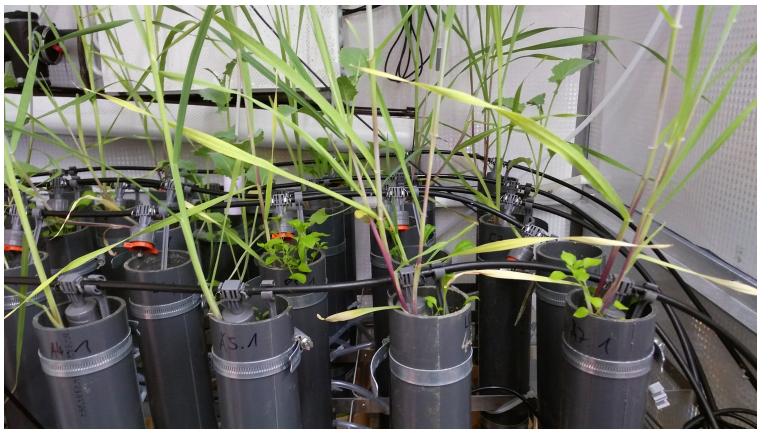


Figure 24: Weed growth

Moreover, in this study the RD might be slightly overestimated to the expense of the BGB. As the finest roots, which were not picked by hand, add to the RD pool instead of the BGB. However, this methodical challenge was already reported by other studies (Hirte et al., 2018; Pausch & Kuzyakov, 2017).

In addition, this experiment was highly manipulated. Mainly the root growth was limited by the tubes and the observation period did not cover one full plant cycle. Therefore, the results of this study should be considered as a first step, which can then be followed by field research.

8 Outlook

As this study reported a high RD fraction of the total root-derived C (60%), it would be interesting to analyze if relative RD is in the same range under field conditions, where root growth is not limited. Furthermore, it is worth investigating into how stable this C is in the soil. Moreover, this study showed that looking at RD quantities alone is not sufficient to understand drivers of SOM priming. Therefore, it would be particularly interesting and valuable to investigate more in the different RD qualities and its potential effects on SOM priming.

Even though the relationship between RD and PE still needs further research, this work showed well, with the consistent positive PE of 2-34%, that SOM decomposition can be increased through the presence of roots. Therefore, as already proposed by Cheng et al. (2014) plant-soil interactions should be included with other parameters, such as soil temperature and soil moisture, as significant controlling factors of SOM decomposition.

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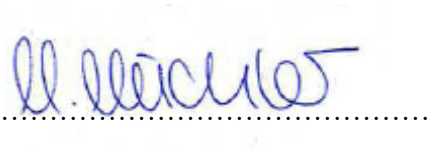
10 Personal Declaration

I hereby declare that the submitted thesis is the result of my own, independent work. All external sources are explicitly acknowledged in the thesis.

Zürich, 28.01.2019 

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