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Determination of the fate of ^{13}C labelled exudates and rhizodeposit-C in two agricultural soils with different yield

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List of Abbreviations

(n)fum	(not) fumigated
c	Concentration
C_3	Plant with C_3 metabolism
C_4	Plant with C_4 metabolism
CFE	Chloroform-fumigation extraction
cm	Centimeter
C_{org}	Organic Carbon
DOC	Dissolved Organic Carbon
DOM	Dissolved Organic Matter
e.g.	for example
et al.	et alli
F	Fisher distribution
f	Fraction
g	Gram
GC	Gas chromatograph
Gt	Giga tons
h	Hour
ha	Hectare
HY	High yield
i.e.	that is
IRMS	Isotope ratio mass spectrometry
l	Liter
LC	Liquid chromatograph

LY	Low yield
m	Meter
M	Molar
MB(-C)	Microbial biomass (-carbon)
mbar	Millibar
mg	Milligram
ml	Milliliter
mM	Millimolar
n	Number of replicates
n.s.	not significant
ºC	Degrees Celsius
P	Level of Significance
PDB	PeeDee Belimnite
PE	Priming effect
R	Ratio
R^2	Coefficients of determination
r	Product moment correlation coefficient (Pearson's r)
SOM	Soil organic matter
t	Time
TOC	Total organic carbon
VPDB	Vienna PeeDee Belimnite
WEOC	Water extractable organic carbon
WEOM	Water extractable organic matter
z.B.	zum Beispiel
µm	Micrometer

Chapter 1

Introduction

Introduction

The organic fraction of soils accounts for a small but variable proportion of total soil mass. Soils consist to 90-98% of minerals, the rest comprises organic substances, so that organic matter is the second most important constituent in soils. Soils are the largest terrestrial carbon (C) pool, storing about 1600 Gt. This is roughly twice the amount of C in the atmosphere (760 Gt) and nearly three times the C amount stored in the vegetation cover (600 Gt) (Schlesinger and Andrews, 2000; Wang and Hsieh, 2002).

Despite the small amounts of organic matter in soils it is of great importance for soil properties and ecosystem functioning. Soil organic matter (SOM) acts for example as source for metabolic energy and nutrients, is responsible for stabilization of soils, and filters pollutants thereby preventing contamination of groundwater.

The soil solution contains varying amounts of dissolved organic matter (DOM), which is generally operationally defined by filtration. The threshold size to differentiate DOM from particulate organic matter is around 0.45 µm (Kalbitz et al., 2000; Zsolnay, 2003). The term water extractable organic matter (WEOM) is frequently used to specify that this material is obtained by shaking the soil with a 0.01 M $CaCl_2$ extractant, which mimics the ionic strength of the soil solution. DOM and WEOM are usually quantified with help of their C content amounting to roughly 50%. For this reason, DOM is often referred to as dissolved organic carbon (DOC) and water extractable carbon (WEOC).

Even though the contribution of DOM to total soil organic matter is small, it is responsible for processes as, for example, transport of metals and organic pollutants, mineral weathering, and podzolisation (Chantigny, 2003). The molecular composition of total soil organic matter is believed to be reflected in DOM, because the solid and soluble phases tend to be in a state of equilibrium (Zsolnay, 1996). Besides the older soil organic matter, fresh photosynthates are also considered as a source for DOM. It is still under discussion, which

source is of more importance in the production of DOM (McDowell, 2003). Sinks of DOM are microbial transformation and immobilization, mineralization, precipitation, and adsorption to the soil matrix (Guggenberger and Kaiser, 2003).

Following the description given above, photosynthetically-derived rhizodeposits including root exudates also serve as a source of DOM and can contribute significantly to this dissolved pool (Zsolnay, 1996; Chantigny, 2003; McDowell, 2003). Rhizodeposition consists of the total direct carbon released from plant roots into the soils. A maximum of 40% of plant primary production is assumed to be lost by rhizodeposition (Lynch and Whipps, 1990). It consists of several compounds ranging from water-soluble exudates over secretions and gases to sloughed root cells. The categorisation depends on the kind of the liberation (actively- or passively-mediated) from the roots to the soils (Lynch and Whipps, 1990; Meharg, 1994; Grayston et al., 1997). Since it is methodological impossible to separate the compounds released from each other, Uren and Reisenauer (1988) consider exudates as all soluble organic substances released by roots, regardless of the mode of their release.

The various functions of rhizodeposits or their components in soils can be summarized as follows:

- they enhance nutrient availability
- detoxify phytotoxic metals
- serve as allelochemicals
- act as signalling substances
- contribute to soil aggregate stabilization
- trigger priming effects
- supply carbon and energy for microorganisms (Kuzyakov et al., 2000; Traore et al., 2000; Hütsch et al., 2002).

The last point on this list is of major importance, since the microbial biomass is involved in the transformation of nutrients stored in soil organic matter, thereby producing CO_2 as a

relevant greenhouse gas. Moreover, microorganisms act as a short-term sink for rhizodeposit-C (Gregorich et al., 2000).

Priming effects are short-term changes in the turnover intensity of soil organic matter, induced by factors as, for example, plant cultivation or addition of organic substances to soils. Since these effects have an impact on the dynamics in the C cycle, they deserve attention when calculating balances in the C cycle. In case of an additional mineralization of SOM (relative to an untreated control) the term "positive priming effect" is used. Oppositely, one speaks of a "negative priming effect" when the decomposition of SOM is retarded (Helal and Sauerbeck, 1989; Kuzyakov et al., 2000). The processes leading to priming effects are not completely understood.

Due to its large size, soil organic matter plays a key role in the global C cycle. Increasing soil organic matter levels can reduce CO_2 concentration in the atmosphere and vice versa. Thus, a changing size of the SOM pool can affect the global climate (Kuzyakov and Cheng, 2001). To increase this pool size, a detailed knowledge of C-dynamics and processes in terrestrial ecosystems must be present. With these insights into the C cycle, soil organic matter fluxes become predictable and can finally be controlled. Sustainable management of soil organic matter especially in agricultural systems with special regard to C sequestration can be accomplished, when C-dynamics are determined in soils.

Therefore, the C-dynamics of rhizodeposits including root exudates as a potential source of organic matter has to be considered, too. The rhizosphere known as the plant-soil interface is the zone of high microbial activity due to a high C input from plants (Lynch and Whipps, 1990). Contrastingly, the "bulk" soil is not directly influenced by rhizodeposits (Toal et al., 2000). However, it has often been stated that our knowledge of the C-fluxes especially in the rhizosphere, i.e. input by rhizodeposit-C and the subsequent transformations, is restricted and highly fragmented (e.g. Kuzyakov, 2001; Hütsch et al., 2002; Kögel-Knabner, 2002; Liang et al., 2002; Farrar et al., 2003; Nguyen, 2003; Jones et al., 2004). Kögel-

Knabner (2002) stresses that despite rhizodeposition may constitute a substantial input of organic matter, exact data for soils are limited. Hagedorn et al. (2003) pointed out that it is unclear how much of the C coming into the soil will be stabilized in the long-term as soil organic matter and how much of it will be emitted as CO_2 (mineralization) to the atmosphere in the short-term. In this regard, Kalbitz et al. (2000) ascertain that the relationship between root-derived DOM to the DOM released from soils has not yet been unravelled, since there is a lack of direct measurements concerning root- and soil-derived DOM in soils.

This is caused by the fact that rhizodeposits in soils are not existent in a pure form, but as a mixture with the soil components. So, the experimental differentiation between these two C-sources is difficult and requires isotopic tracer techniques, which have been found to be very useful tools for investigating C-fluxes from plant roots to soils, because they allow the separation of root- and soil-derived C (Nguyen, 2003). The fast mineralization of rhizodeposition represents another methodological difficulty (Kuzyakov, 2001).

Most of the information concerning rhizosphere C flow has come from experiments conducted with ^{14}C as a tracer (Killham and Yeomans, 2001). Many labelling studies have been conducted in order to calculate complete carbon balances (Keith et al., 1986; Swinnen et al., 1994; Merbach et al., 1999). Some of the results have been compiled in a review by Kuzyakov and Domanski (2000) and great fluctuations in the rate of total fixed-C by plants transferred to soils have been reported therein. It has been estimated that about 20-30% of fixed-C is translocated below-ground. Roughly half of this amount is incorporated into the roots, one third is mineralized to CO_2 by the roots and associated microorganisms and the rest remains in soil and microorganisms. According to Jones et al. (2004) and Farrar et al. (2003) root exudation losses lie between 2-4% of total plant-assimilated C.

Apart from using the radiolabel ^{14}C to distinguish between plant- and soil-derived C, ^{13}C is also used at natural abundance and as a label (Meharg, 1994). The two naturally occurring isotopes are ^{12}C and ^{13}C, having a percentage of around 98.89% and 1.11% on all

carbon in nature. The $^{12}C/^{13}C$ ratios vary slightly around these values in natural materials (Farquhar et al., 1989; Boutton, 1996). The natural abundance data of ^{13}C are usually reported as *delta* (δ) values. Their unit is *per mil* (‰), since data are compared to the Cretaceous carbonate fossil *Bellemnitella americana* from the PeeDee Formation (PDB) in South Carolina, USA, as an internationally recognised standard (Barrie and Prosser, 1996). The standard has arbitrarily been set to 0‰, so $\delta^{13}C$ values lower than this designate a lower content of ^{13}C in the sample and vice versa. Since the original standard no longer exists, exact $\delta^{13}C$ values have been assigned to another carbonate. The resulting new scale is termed Vienna PDB (VPDB) (Werner and Brand, 2001).

One reason for the isotopic variations in plants is their metabolisms leading to a differently pronounced discrimination of the two isotopes during CO_2 assimilation. The natural abundance of ^{13}C is greater in C_4 compared to C_3 species. The enzyme ribulose bisphosphate carboxylase oxygenase (RuBisCo) reduces CO_2 in C_3 plants (Calvin cycle). The resulting $\delta^{13}C$ values range from –32‰ to –22‰, with a mean of –27‰. In C_4 plants, CO_2 is reduced by the enzyme phosphoenolpyruvate carboxylase (PEP), with resulting $\delta^{13}C$ values from –17‰ to –9‰ and a mean of –13‰ (Hatch-Slack cycle) (Balesdent et al., 1987; Boutton, 1996). Plants are the main source for soil organic matter (Kögel-Knabner, 2002). Consequently, the differences in the ^{13}C content of C_3 and C_4 plants are reflected in soil organic matter. This can be used to trace C-fluxes, determine contributions to several C pools in soils or the below-ground C turnover, and eventually calculate C balances. To apply the natural abundance ^{13}C label on a field-scale, a vegetation change must take place. Thus, a site previously cropped to a C_3 plant for a long time must be planted to a C_4 plant, or vice versa (Balesdent and Mariotti, 1996). Several studies have dealt with C-dynamics and contributions of plant-derived C to C pools in soils, using the natural ^{13}C abundance technique (Balesdent et al., 1988; Cheng, 1996; Qian and Doran, 1996; Flessa et al., 2000; Cheng et al., 2003; John et al., 2003). Recently, Yevdokimov et al. (2006) have grown oat plants under ^{13}C-CO_2 labelled

atmosphere in a greenhouse in order to trace the fate of their rhizodeposit-C. It is also possible to apply ^{13}C enriched substrates to soil, as has been done with ^{13}C labelled glucose (Mary et al., 1992; Wessels Perelo and Munch, 2005) or sucrose (Ekblad and Högberg, 2000).

Objectives of this study

As outlined above, below-ground C-flux is one of the most significant, but also least understood part of the global C cycle. Experiments were conducted under laboratory and greenhouse conditions in order to contribute to a deeper understanding of the soil C-dynamics especially in the rhizosphere. The temporal dynamics of exudates were determined, since no study has dealt with this before. The fate of rhizodeposition is still unclear and was also determined. Moreover, the processes occurring upon the addition of these substrates to soil were to be clarified with special regard to the influenced organic soil components.

The work was carried out in three studies, described in the following:

- In the first study a model system in the laboratory was used, where defined amounts of ^{13}C labelled natural (maize and wheat) exudate carbon were regularly applied to soil. The plants were chosen, since they represent major crops worldwide. The objective of the study was to determine the contribution of maize and wheat exudates during a 25-day incubation of upper material of an agricultural soil to the most relevant labile carbon pools: WEOC, microbial biomass, and CO_2.
- In the second study, the first experiment was repeated with ^{13}C labelled artificial instead of natural exudate. This experimental design offered the possibility to trace the fate of a defined mixture of organic compounds commonly found in exudates. The objective was the same as in the study with natural exudates, but upper material of two agricultural soils was taken and the incubation period was prolonged to 74 days. Furthermore, the addition of exudates was stopped after 56 days to determine whether there was still an exudate influence on the pools measured. The soils were chosen,

since it was assumed that their different yield pattern is reflected in their nutrient and C-fluxes.

- In the third study, a greenhouse experiment was conducted where maize and wheat plants were grown in pots filled with soil under a ^{13}C-CO_2 labelled atmosphere. The labelled CO_2 was incorporated into the plants. Consequently, rhizodeposition was also labelled. The aim of that study was to monitor the temporal dynamics of labelled rhizodeposits in the two agricultural soils also used in the second study. Besides the pools measured in the other studies, total organic carbon (C_{org}) was additionally determined to obtain a complete picture of the fate of rhizodeposits.

Another aspect was considered in all of the three studies. In experiments concerned with the determination the ^{13}C content of DOC, problems are encountered. Usually, laborious steps are necessary to oxidise liquid organic samples to CO_2, which is then isolated and purified with cryogenic distillation, followed by determination of its ^{13}C content (Potthoff et al., 2003). With these methods it is extremely time consuming to measure large sets of samples. A newly developed method by Krummen et al. (2004) overcomes this restriction. For the first time, this method is employed with soil extracts in the present work and the outcomes are evaluated.

Finally, the transferability of the laboratory data to those obtained in the greenhouse study is discussed to evaluate whether the observed dynamics and processes in the model experiments generally occur in a plant-soil system as well.

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Chapter 2

Determination of the fate of ^{13}C labelled maize and wheat exudates in an agricultural soil during a short-term incubation

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Summary

A broader knowledge of the contribution of carbon (C) released by plant roots (exudates) to soil is a prerequisite for optimising the management of organic matter in arable soils. This is the first study to show the contribution of constantly applied ^{13}C-labelled maize and wheat exudates to water extractable organic carbon (WEOC), microbial biomass-C (MB-C), and CO_2-C evolution during a 25-day-incubation of agricultural soil material. The CO_2-C evolution and respective $\delta^{13}C$ values were measured daily. The WEOC and MB-C contents were determined weekly and a newly developed method for determining $\delta^{13}C$ values in soil extracts was applied. Around 36% of exudate-C of both plants was recovered after the incubation, in the order WEOC < MB-C < CO_2-C for maize and MB-C < WEOC < CO_2-C for wheat. Around 64% of added exudate-C was not retrieved with the methods used here. Our results suggest that great amounts of exudates became stabilized in non-water extractable organic fractions. The amounts of MB-C stayed relatively constant over time despite a continuous exudate-C-supply, which is the prerequisite for a growing microbial population. A lack of mineral nutrients might have limited microbial growth. The CO_2-C mineralization rate declined during the incubation and this was probably caused by a shift in the microbial community structure. Consequently, incoming WEOC was left in the soil solution leading to rising WEOC amounts over time. In the exudate treated soil additional amounts of soil-derived WEOC (up to 110 µg g^{-1}) and MB-C (up to 60 µg g^{-1}) relative to the control were determined. We suggest therefore that positive priming effects (i.e. accelerated turnover of soil organic matter due to the addition of organic substrates) can be explained by exchange processes between charged, soluble C-components and the soil matrix. As a result of this exchange, soil-derived WEOC becomes available for mineralization.

Introduction

A detailed knowledge of carbon (C) flow in terrestrial ecosystems is crucial for understanding ecosystem functioning with respect to, for example, responses to anthropogenic pollution or climate change (Gregorich *et al.*, 2000). Sustainable management of soil organic matter, especially in agricultural systems, can only be accomplished when C-dynamics are known and become predictable.

Plants are the major source of C input to soil. Rhizodeposition is a part of this plant input. It consists of the compounds released directly from roots into soil. Depending on the active or passive release of these compounds by the roots, they are classified as water-soluble exudates, secretions, lysates, gases, or mucilage (Grayston *et al.*, 1997). Uren & Reisenauer (1988) define the term exudates as all soluble organic substances released by roots.

Exudates fulfil manifold functions and are subjected to different fates when entering the soil environment (Jones, 1999). Apart from the well-known fact of serving as an energy and C-source for microorganisms, they modify physico-chemical conditions in the rhizosphere in order to increase the availability for nutrients, thus playing an important role in plant nutrition (Lynch & Whipps, 1990). Moreover, they act as signalling substances between plants and microorganisms (Bertin *et al.*, 2003), contribute to soil aggregate stabilization (Traore *et al.*, 2000), and may influence the turnover of native soil organic matter (Kuzyakov *et al.*, 2000).

According to Jones *et al.* (2004) our understanding of the mechanistic processes involved in rhizodeposition is greatly fragmented. This is primarily due to methodological problems, since exudates exist in small concentrations in soil and are rapidly metabolized by microorganisms (Kuzyakov, 2001). Additionally, exudate-C forms a complex mixture with soil-C, making separation difficult. Consequently, the fate of C from rhizodeposits in soil is still unanswered (Hütsch *et al.*, 2002). In this regard, the contribution of root to soil dissolved organic carbon (DOC) is still unknown, as it has not yet been measured directly (Kalbitz *et al.*, 2000).

To circumvent the problems stated above, most studies have been conducted in the laboratory. Results from exudate-C impacts on, for example, soil organic matter (Nardi *et al.*, 2002) or on soil microbial community structure (Benizri *et al.*, 2002; Campbell *et al.*, 1997) have come from approaches based on solution cultures or on artificial rhizoexudates.

Apart from this, studies using $^{14}CO_2$ or $^{13}CO_2$ for plant labelling and subsequent monitoring of C allocation below-ground and CO_2 evolution either in the field or in the laboratory have been undertaken (Merbach *et al.*, 1999; de Neergaard & Magid, 2001; Kuzyakov & Cheng, 2001). These studies investigated the whole plant-root C input to soil. However, no study has dealt with the turnover of pure exudates, despite the determination of their relative contribution to labile soil organic matter fractions being often suggested. This is necessary in order to better understand below ground C-dynamics (Flessa *et al.*, 2000; Liang *et al.*, 2002).

To our knowledge, this is the first study to measure directly the dynamics of constantly applied pure plant exudates in the most relevant labile carbon pools in soil with the use of ^{13}C. The aim of our study was to determine the contribution of maize and wheat (as representatives of major crops worldwide) exudates to water extractable organic carbon (WEOC), microbial biomass, and CO_2 evolution during an incubation of upper soil material. The experimental approach was chosen because it was expected that most of the easily degradable exudates would be recovered in WEOC, microbial biomass, and CO_2.

Materials and methods

Production of ^{13}C labelled exudates

Plant culture and labelling

Maize (*Zea mays* L., Gavott) and wheat (*Tritivum aestivum* L., Petrus) were grown each in a hydroponic system in a greenhouse for four months. Seedlings were pre-germinated in the dark on moist filter paper. After one week, seedlings were transferred to 2.6 litre pots containing aerated nutrient solution with the following macroelements (in mM litre^{-1}): 0.7 K_2SO_4, 0.1 $CaCl_2$, 0.5 $MgSO_4$, 4 KNO_3, 0.02 $C_2H_{10}N_2O_4S \cdot FeSO_4$, 0.25 KH_2PO_4.

Microelements were added in the following concentrations (in µM litre^{-1}): 0.5 $MnSO_4$, 1 H_3BO_3, 0.5 $ZnSO_4$, 0.2 $CuSO_4$, 0.01 $(NH_4)_6Mo_7O_{24}$. The nutrient solution was renewed three times per week. Twelve pots containing 5 plants each were used for each plant species, making a total of 60 maize or wheat plants, respectively.

In order to obtain ^{13}C labelled exudates, wheat plants were grown under an airtight tent built of transparent plastic foil to separate the plants from the outer greenhouse atmosphere. The ^{13}C content of the CO_2 inside the tent was enriched with ^{13}C-CO_2 to 60-80‰ versus Vienna PeeDee Belemnite (VPDB) to a concentration of 300-400 µmol mol^{-1}. In the case of maize, no labelling was applied, and its natural ^{13}C content was used. Plant culture was performed with a photoperiod of 12 hours with 25/20°C day/night temperature.

Collection of exudates

After plants had grown for one-month, they were used daily to collect rhizoexudates over a 3-month period. Collection was done with the dipping method (Neumann & Romheld, 1999; Gransee & Wittenmayer, 2000). All plants were transferred from the pots containing nutrient solution to pots with 150 ml aerated bi-distilled water. Before transferring the plants from the nutrient solution to the water, roots were washed with distilled water to prevent nutrients from contaminating the collection media. The whole root system of the plants was immersed in the water for 2 hours and the released exudates were collected in the water. After the collection period the plants were relocated to the pots with nutrient solution. The maize and wheat exudate solutions were pooled separately and filtered through 0.4 µm pore-size polycarbonate filters to remove plant detritus and then concentrated in a vacuum rotary evaporator at 38˚C. The three months of exudate collection resulted in 40 ml of exudate solution for each plant species. The exudate solutions were deep frozen (–20˚C) in several portions, then thawed as required in order to pipette them onto the surface of the incubated soil. The corresponding C concentration was 1089.67 mg litre^{-1} with a $\delta^{13}C$ value of –9.1‰ VPDB and a C/N ratio of

1.5 for the maize exudate. The wheat exudate solution had the following characteristics: 1251.30 mg C litre^{-1} with a $\delta^{13}C$ value of –4.9‰ VPDB, and a C/N ratio of 2.8.

Incubation

Soil

The soil sampling was from a field with a maize-winter wheat rotation history at the agro-ecological research station in Scheyern, approximately 40 km north of Munich, Germany (48˚30'N, 11˚20'E). Soil material was collected from the upper 10 cm of a Cambisol and the field-fresh soil sieved to pass a 2-mm mesh. The silty loam soil had the following characteristics: clay 20%, silt 51%, sand 29%; bulk density 1.3 g cm^{-3}; pH ($CaCl_2$) 5.9; C_{org} 1.3% with a $\delta^{13}C$ of –25.6‰ VPDB, and total N 0.15%.

Experimental design (Incubation experiment)

Soil in aliquots equivalent to 5 g of dry matter was placed into 30 ml glass vials. Soil was pre-incubated over 3 weeks at a water-content equivalent to 60% water-filled pore space. In order to provide a continuous exudate-C supply to the soil during the 25-day-incubation, C additions were distributed for practical reasons as three doses per week. This gave a load of 46.7 or 53.6 µg g^{-1} soil day^{-1} for maize or wheat exudate-C, respectively. A control with distilled water addition to the soil instead of exudate was also run. To keep the soil at constant moisture content, samples in each vial were left in a desiccator at 15 mbar (absolute) for 50 minutes to induce a water loss of 0.5 ml, which was then replaced by the exudate solution or water, respectively. The temperature was kept constant at 14°C. At days 4, 11, 18, and 25 destructive soil sampling was conducted for each of the three treatments (control, maize, and wheat exudate treated soil) to determine microbial biomass-C and water extractable carbon. The first sampling took place on the fourth day of incubation, followed by weekly sampling. The CO_2-C evolution was determined daily except for the weekends from three randomly chosen vials of each treatment. The experiment was designed with three replicates, to give a

total of 36 vials. All results are expressed as equivalents to oven dried soil (105˚C for around 24 hours).

Analysis

Water extractable organic carbon (WEOC) concentration

WEOC was obtained by shaking the soil samples with 0.01 M $CaCl_2$ solution on an over-head shaker for 15 minutes at a soil (mass):solution (volume) ratio of 1:5 and subsequent filtration through 0.4 µm pore-size polycarbonate filters. The WEOC concentrations were determined on a Total Carbon Analyser (Shimadzu TOC 5050, Tokyo, Japan) by catalytic high temperature oxidation (Zsolnay, 2003).

Microbial biomass carbon (MB-C) concentration

The MB-C was determined by the chloroform-fumigation extraction method (Vance *et al.*, 1987) with 1 g of soil (0.5 g for fumigated and non-fumigated assay) in 4 ml of 0.5 M K_2SO_4 solution. Dissolved organic carbon (DOC) in the extracts was determined on a Shimadzu TOC 5050. The difference between DOC in fumigated and non-fumigated samples was divided by 0.45 to calculate MB-C (Joergensen, 1996).

^{13}C in WEOC and chloroform-fumigation extraction samples

The $^{13}C/^{12}C$ ratios in liquid samples were determined by a liquid chromatograph/isotope ratio mass spectrometer (LC/IRMS) (Thermo Finnigan LC IsoLink and MAT 253, Bremen, Germany) by an on-line method newly developed by Krummen *et al.* (2004). Ours is the first study to apply this method to soil extracts. The LC IsoLink worked in a mode that allows the bulk isotopic analysis of all water-soluble material. The samples were processed as follows: organic substances in the extracts were oxidized quantitatively to CO_2 by 0.45 M $Na_2S_2O_8$ and 8.5% H_3PO_4 solutions in a reaction chamber at 99.9°C. The CO_2 was separated from the liquid phase with a gas-exchange membrane and admitted to the IRMS in a stream of helium via an open split.

The ^{13}C values of the soil extracts determined were compared with values of an internal laboratory standard (benzoic acid solution) and a blank (solvent used for soil extraction), both of which were included in all sample measurements at regular intervals. The C concentrations of the standards were chosen according to the given concentrations of the soil extracts. Figure 1 shows the long-term stability of benzoic acid-^{13}C measurements, which were undertaken with different C concentrations in a 0.01 M $CaCl_2$ solution, as was also used for the soil WEOC extraction.

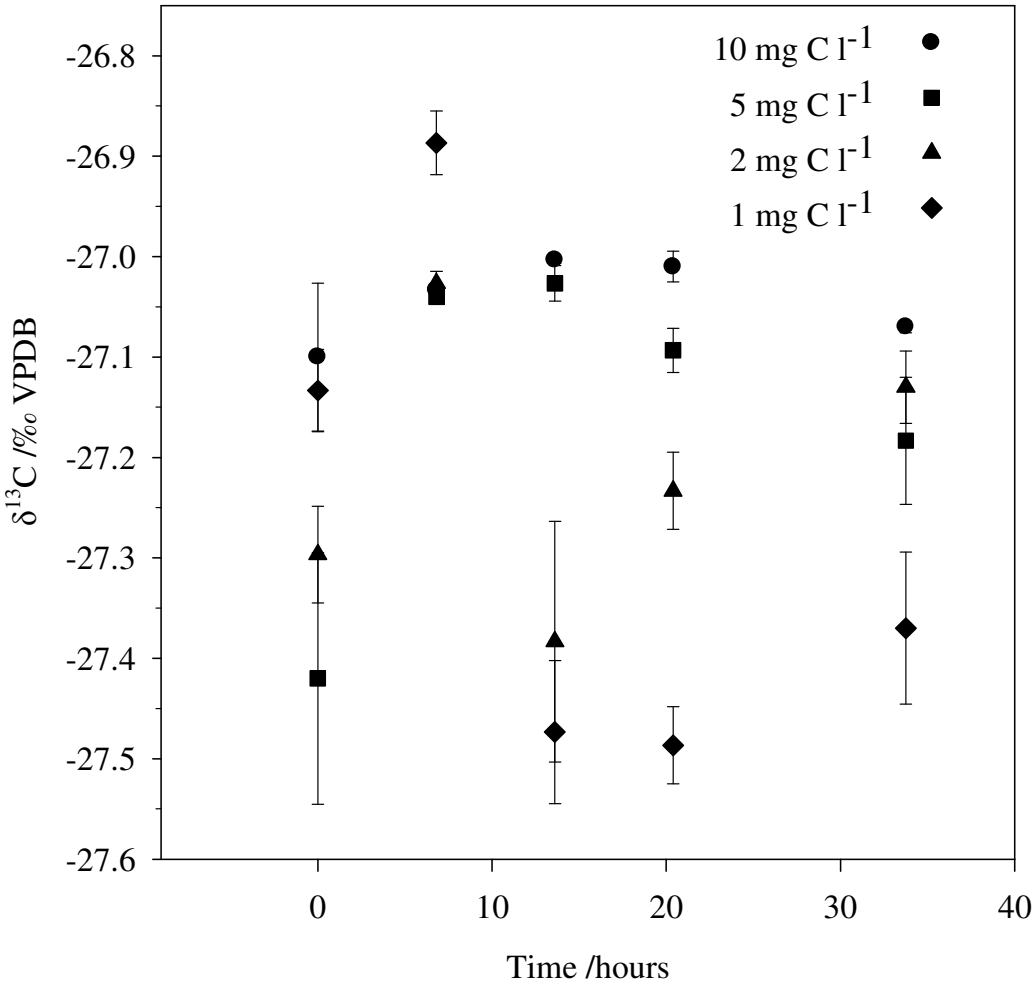

Figure 1 Benzoic acid-^{13}C standards measured in a sequence of soil extracts. The benzoic acid was dissolved in 0.01 M $CaCl_2$ solution which is also used for WEOC extraction. Error bars represent standard errors of the means (n = 3).

No directional trend could be observed over the measurement period at any C concentration level. In fact, the ^{13}C values for the respective C concentrations remained constant over time and differed only slightly from each other over a range of around 0.6‰. In the correction made for $\delta^{13}C$ values, the measurement signal of small values (1 mg C litre^{-1}) can equate to roughly 30% of the blank. However, it must be noted here that such small C concentrations hardly occur in bulk soil extracts.

These observations were also valid for the benzoic acid-^{13}C measurements in 0.5 M K_2SO_4 solution, the extracting agent for microbial biomass-C.

CO_2 and $^{13}CO_2$ in gaseous samples

During the incubation period, CO_2-concentrations and their corresponding $^{13}C/^{12}C$ ratios evolved from soil samples were determined on-line with a gas chromatography/isotope ratio mass spectrometer (GC/IRMS) (Finnigan MAT DeltaPlus, Bremen, Germany). Three randomly chosen vials were closed air-tight with a plastic lid with a rubber septum in its centre and placed in a water jacket adjusted to the incubation temperature (14°C). The rack was specially built to be mounted on a CombiPAL autosampler (CTC, Zwingen, Switzerland). The enrichment of CO_2 and respective $^{13}CO_2$ values in the headspace of the vials was determined with 5 measurements on each sample over a 9.5-hour-period. Samples were withdrawn from the vials' headspaces by a syringe on the autosampler and injected into the GC/IRMS. All sample values were compared with reference CO_2 at different concentrations. A regression line was fitted to the measured points ($R^2 > 0.95$) in order to calculate a CO_2 production rate. From this rate the CO_2 amounts per day were estimated and subsequently cumulated in order to obtain the total CO_2 amounts evolved on the respective samplings.

Calculations

The $\delta^{13}C$ values of the samples were expressed relative to the international VPDB standard:

$$\delta^{13}C\ (‰\ VPDB) = \left(\frac{R_{sample} - R_{VPDB}}{R_{VPDB}} \right) x\ 1000, \quad (1)$$

where $R = \frac{^{13}C}{^{12}C}$ and $R_{VPDB} = 0.0111802$ (Werner & Brand, 2001).

We calculated the $\delta^{13}C$ (‰ VPDB) of MB-C from the following mixing equation:

$$\delta^{13}MB\text{-}C = \frac{(c_{fum}\ x\ \delta^{13}C_{fum}) - (c_{nfum}\ x\ \delta^{13}C_{nfum})}{(c_{fum} - c_{nfum})}, \quad (2)$$

where c_{fum} and c_{nfum} = concentration (µg g^{-1}) of C in the fumigated and non-fumigated soils, respectively.

We calculated the fraction of C originating from the exudate ($f_{exudate}$) in MB-C, WEOC, or CO_2-C from:

$$f_{exudate} = \frac{(\delta^{13}C_{mix} - \delta^{13}C_{soil})}{(\delta^{13}C_{exudate} - \delta^{13}C_{soil})}, \quad (3)$$

where $\delta^{13}C_{mix}$ = composition of soil derived- and exudate-derived $\delta^{13}C$ (‰ VPDB), and $\delta^{13}C_{soil/exudate}$ = $\delta^{13}C$ (‰ VPDB) of soil or exudate, respectively.

We calculated the contribution of exudate-C ($c_{exudate}$) to WEOC, MB-C, or CO_2-C total concentration (µg g^{-1}) from:

$$c_{exudate} = f_{exudate}\ x\ c_{total}, \quad (4)$$

where c_{total} = total concentration (µg g^{-1}) of WEOC, MB-C, or CO_2-C, respectively.

The specific respiration rate measured as the metabolic quotient qCO_2 is an indicator of the efficiency of substrate use. It was calculated according to Anderson & Domsch (1990):

$$qCO_2 = \frac{\Delta CO_2\text{-}C_{total}}{MB\text{-}C}, \quad (5)$$

where ΔCO_2-C_{total} = CO_2-C – [CO_2-C from the previous sampling for a particular treatment over a specific time interval].

The priming effect (PE) was calculated according to Hamer & Marschner (2002). As a prerequisite for the determination of PE, the difference between soil derived CO_2-C of

exudate treated soil and the control CO_2-C must be significant on the basis of an unpaired *t*-test ($P < 0.05$) over the relevant time interval. The PE for this time span was calculated from:

$$PE\ (\%) = \frac{\Delta CO_2\text{-}C_{treatment} - \Delta CO_2\text{-}C_{control}}{\Delta CO_2\text{-}C_{control}} \times 100 \qquad (6)$$

where $\Delta CO_2\text{-}C_{treatment}$ = (soil-derived CO_2-C of exudate treated soil) – (soil-derived CO_2-C of exudate treated soil from previous sampling), and $\Delta CO_2\text{-}C_{control}$ = (control CO_2-C) – (control CO_2-C from previous sampling).

The absolute amounts of primed C were calculated by subtracting $\Delta CO_2\text{-}C_{control}$ from $\Delta CO_2\text{-}C_{treatment}$ for the relevant time intervals. This was also applied to WEOC and MB-C in order to calculate the effects of exudate addition on soil-derived C in these pools. These values are referred to as "net". It must be noted that the control of the first sampling was assumed to represent the soil status at time zero (*t*0).

Statistics

All results are expressed as the means of three replicates with standard errors. The data were subjected to an analysis of variance (ANOVA) for comparisons of the different C-fractions among each other over time.

Results

Significant incorporation of maize- or wheat-exudate derived C was detected in all three C pools investigated (Table 1, Figures 2 to 4). The utilisation pattern of both exudates showed similar dynamics apart from quantitative differences.

WEOC

Figure 2 shows that the WEOC of the control (soil without addition of exudates) was constant over the time of the experiment. The WEOC content in the exudate-treated soil was always significantly greater than in the control (Table 1). The amounts of exudate- and soil-derived WEOC extracted from the soil rose significantly from the third sampling on.

Table 1 Analysis of variance of water extractable organic carbon (WEOC), microbial biomass-C (MB-C), and CO_2-C data.

Source of variation	Degrees of freedom	Sum of squares	Mean square	*F*	*P*
Treatment					
Total WEOC	2	71655.810	35827.905	641.330	<0.001
Soil-derived WEOC	2	17295.929	8647.964	578.394	<0.001
Exudate-derived WEOC	1	310.896	310.896	10.525	0.005
Total MB-C	2	89208.712	44604.356	28.911	<0.001
Soil-derived MB-C	2	8459.796	4229.898	3.629	0.043
Exudate-derived MB-C	1	6187.161	6187.161	70.904	<0.001
Total CO_2-C	2	230720.283	115360.141	5791.420	<0.001
Soil-derived CO_2-C	2	13791.133	6895.566	1524.581	<0.001
Exudate-derived CO_2-C	1	3572.404	3572.404	176.378	<0.001
Sampling					
Total WEOC	3	66147.277	22049.092	394.685	<0.001
Soil-derived WEOC	3	10574.880	3524.960	235.757	<0.001
Exudate-derived WEOC	3	35913.002	11971.001	405.276	<0.001
Total MB-C	3	75593.288	25197.763	16.333	<0.001
Soil-derived MB-C	3	29747.139	9915.713	8.507	0.001
Exudate-derived MB-C	3	16529.923	5509.974	63.144	<0.001
Total CO_2-C	3	230725.380	76908.460	3861.032	<0.001
Soil-derived CO_2-C	3	43859.169	14619.723	3232.360	<0.001
Exudate-derived CO_2-C	3	110102.578	36700.859	1812.005	<0.001
Treatment x sampling					
Total WEOC	6	45742.994	7623.832	136.469	<0.001
Soil-derived WEOC	6	11471.533	1911.922	127.873	<0.001
Exudate-derived WEOC	3	666.161	222.054	7.518	0.002
Total MB-C	6	3308.560	551.427	0.357	0.898
Soil-derived MB-C	6	3188.710	531.452	0.456	0.833
Exudate-derived MB-C	3	3582.028	1194.009	13.683	<0.001
Total CO_2-C	6	33799.614	5633.269	282.807	<0.001
Soil-derived CO_2-C	6	4260.748	710.125	157.006	<0.001
Exudate-derived CO_2-C	3	4339.909	1446.636	71.424	<0.001
Residual					
Total WEOC	24	1340.761	55.865		
Soil-derived WEOC	24	358.840	14.952		
Exudate-derived WEOC	16	472.606	29.538		
Total MB-C	22	33941.511	1542.796		
Soil-derived MB-C	22	25641.794	1165.536		
Exudate-derived MB-C	14	1221.649	87.261		
Total CO_2-C	24	478.060	19.919		
Soil-derived CO_2-C	24	108.550	4.523		
Exudate-derived CO_2-C	16	324.068	20.254		

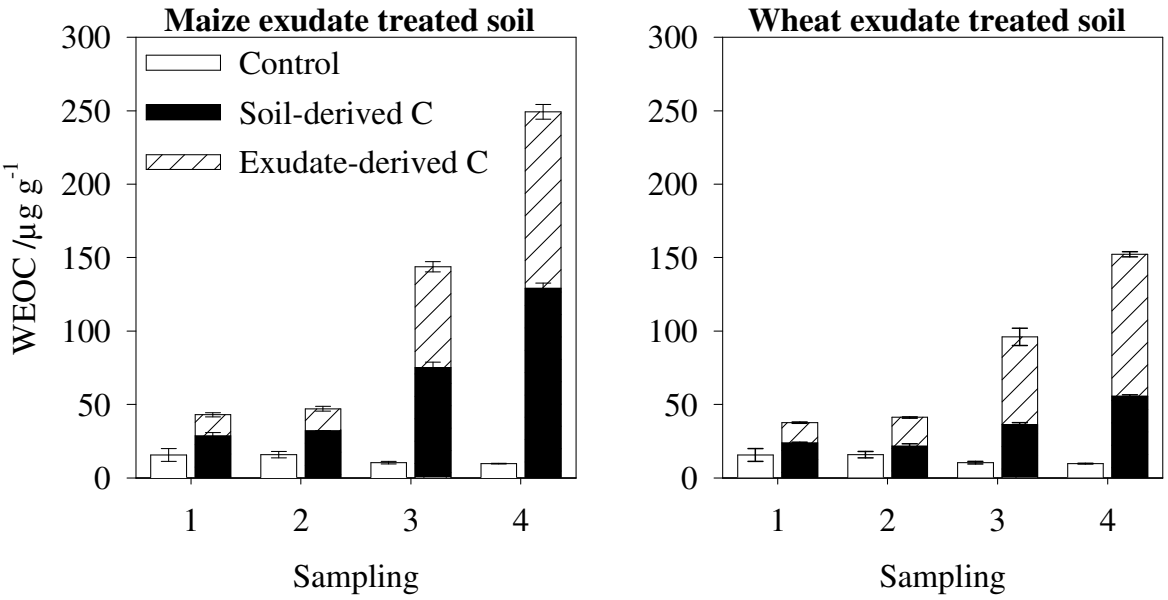

Figure 2 Amounts of WEOC from maize- and wheat-exudate derived C and of the respective soil-derived C. Error bars represent standard errors of the means (n = 3).

Microbial biomass

The microbial biomass-C (MB-C) of the control was significantly different over the course of the experiment. The MB-C content of the exudate-treated soil was always significantly greater than that of the control (Table 1, Figure 3). The biomass-C pool trends were comparable in both treatments. Remarkable growth of MB-C occurred only on the first two samplings. Thereafter, no significant increase of the microbial biomass was detected. At the end of the experiment, the microbial biomass consisted, to a significantly greater part, of maize or wheat exudate-derived C than on the first sampling. Newly built MB consisted mainly of exudate-derived C. However, on the first sampling in the wheat-exudate treated soil significant amounts of soil-derived C were incorporated into the microbial biomass. This is reflected in the significantly greater soil-derived MB-C values compared to the control. On the next sampling, there was a release of a part of this soil-derived C. Also in the maize-exudate treatment, soil-derived C tended to be incorporated into the microbial biomass and

was released on the last sampling. No significant change in the amount of soil-derived C in microbial biomass with both kinds of exudates was observed over the experimental period. The third sampling of maize-exudate treated soil was excluded from the statistical analysis, since only one value was available due to accidental discard of two samples.

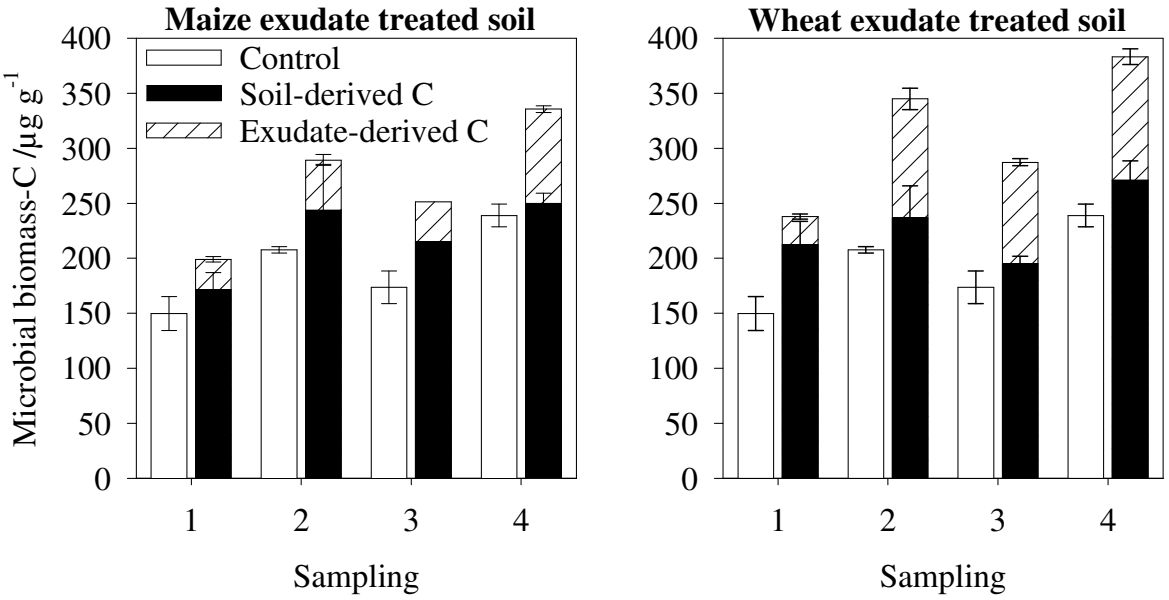

Figure 3 Amounts of microbial biomass-C from maize- and wheat-exudate derived C and of the respective soil-derived C. Error bars represent standard errors of the means (n = 3).

CO_2-C and qCO_2

The pattern of mineralization was similar for both incubated exudates with differing total amounts of CO_2-C production (Figure 4). As expected, the total CO_2 emissions were greater for exudate-treated soil than from the control. A significant increase occurred in the CO_2-C production from the control and in the total CO_2-C amounts from treated soil, accompanied by a rise in the respective exudate- and soil-derived CO_2-C fractions over time (Table 1). The mineralization rates of both treatments decreased as can be seen from the CO_2-C difference between two samplings. In maize-exudate treated soil, about 105 µg CO_2-C g^{-1} evolved between the first and second sampling, whereas only 36 µg CO_2-C g^{-1} were emitted between

the last two samplings. The corresponding values for wheat-exudate treated soil were 144 and 72 µg CO_2-C g^{-1}.

The major part of evolved CO_2-C came from the added exudates, with roughly a 3.5 fold greater maize-exudate derived CO_2-C evolution than from the associated soil-derived CO_2-C evolution on each sampling, except for the first sampling, which gave a larger factor. For wheat exudates, around 2.2 times more CO_2-C was emitted than from the associated soil-derived components.

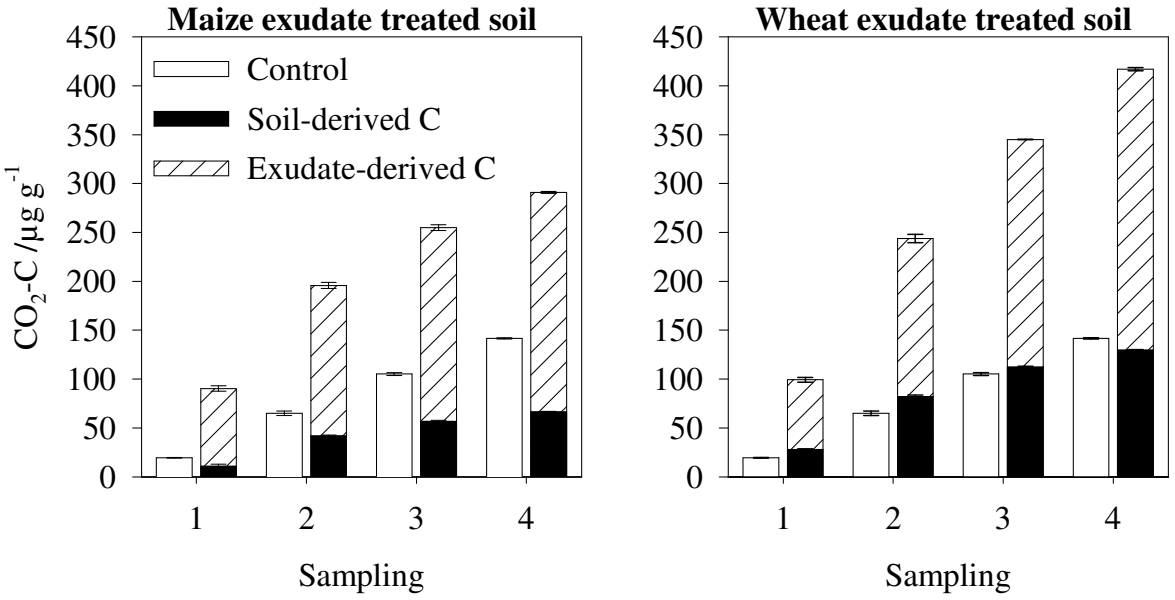

Figure 4 Amounts of CO_2-C from maize- and wheat-exudate derived C and of the respective soil-derived C. Error bars represent standard errors of the means (n = 3).

During the incubation, the metabolic quotient (qCO_2) of the control was around 0.2 µg CO_2-C $week^{-1}$ (µg MB-C)$^{-1}$. The qCO_2 values of exudate-treated soil decreased significantly over the incubation period (Figure 5).

Priming and net effects of exudate addition on soil-derived C

Negative priming effects were revealed on all samplings for maize-exudate treated soil and became significantly more pronounced during the incubation period. The net soil-derived

CO_2-C values also represented the actual amount of negatively primed C, which increased significantly over time (Table 2).

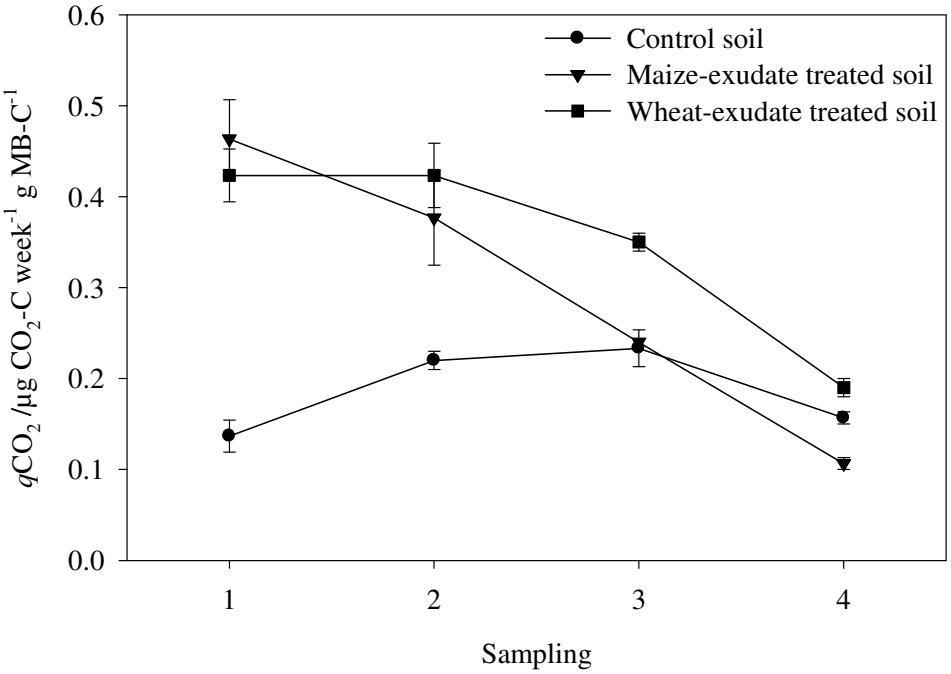

Figure 5 Metabolic quotient qCO_2 of control and exudate treated soil. Error bars represent standard errors of the means (n = 3).

Wheat-exudate treated soil showed significantly different positive priming effects on the first two samplings with no significant difference in the amount of primed C. On the last two samplings, negative priming was observed with significantly different amounts of primed C.

Table 2 also shows the net amounts of soil-derived C in the WEOC and microbial biomass pools compared to the control for the relevant samplings. Net soil-derived WEOC values increased significantly during the incubation. The corresponding values of MB-C show the amounts that were incorporated or released, respectively, from the microbial biomass during the incubation period.

Table 2 Net soil-derived WEOC, MB-C, CO_2-C amounts and priming effects of maize- and wheat-exudate treated soil over the course of the incubations. Values in parentheses are standard errors (n =3).

Sampling date	Maize				Wheat			
	WEOC	MB-C /µg g^{-1}	CO_2-C[a]	Priming / %	WEOC	MB-C /µg g^{-1}	CO_2-C[a]	Priming / %
1	13.16 (2.09)	21.87 (15.48)	–8.42 (2.02)	–43.04 (10.32)	8.37 (0.31)	62.56 (21.29)	8.47 (0.74)	43.29 (3.80)
2	3.13 (0.29)	14.10 (41.69)	–14.61 (0.73)	–32.08 (1.62)	–2.28 (1.42)	–33.50 (29.02)	8.58 (1.83)	18.84 (4.01)
3	48.38 (3.72)	5.62 (-)[b]	–25.35 (1.02)	–63.13 (2.54)	19.77 (1.41)	–7.53 (6.65)	–9.96 (0.95)	–24.82 (2.36)
4	54.65 (3.58)	–30.48 (9.04)	–26.57 (0.28)	–72.72 (0.76)	20.02 (0.94)	10.68 (17.41)	–18.98 (0.26)	–51.97 (0.71)

[a]Absolute amounts of primed C

[b]Only one value available

Fate of labelled exudates

To compare the fate of exudate-C among treatments after the incubation, the allocation of this C into the measured pools is presented as percent values in the overall balance (Figure 6).

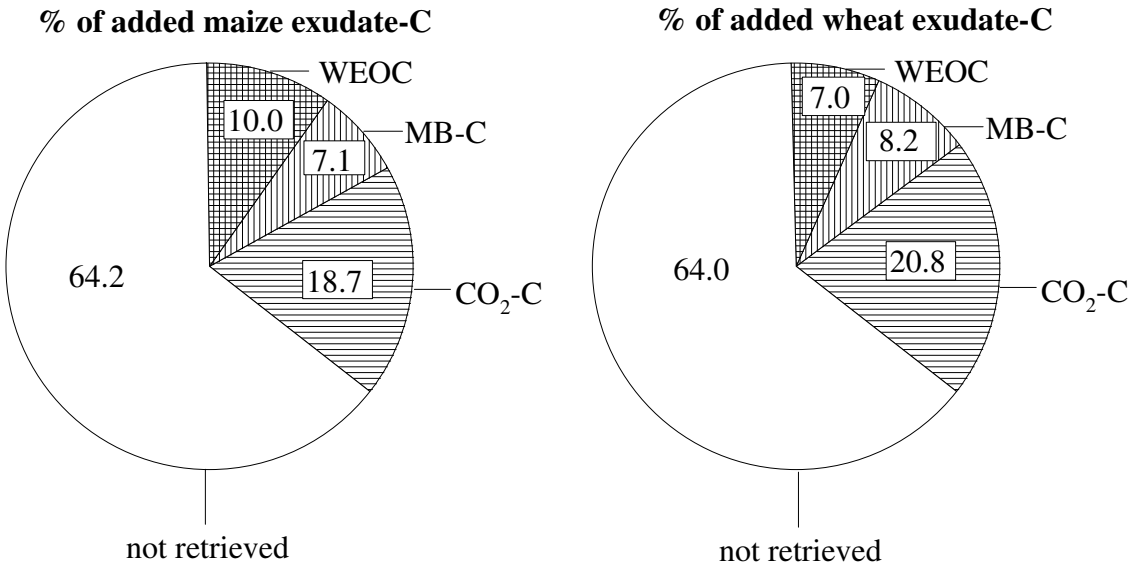

Figure 6 Percentages of added exudates recovered in the C pools investigated at the end of the incubations (n = 3).

On the single samplings, the percentages of added exudate-C in the measured pools were similar to those presented in the overall balances. The distribution of overall exudate-C for both exudates was comparable: around 36% was in the fractions, which were retrieved, and around 64% remained in the soil and were not extractable. The proportions of the two exudate types in the retrieved fractions differed. The fate of maize-exudate C was: WEOC < MB-C < CO_2-C. The values of wheat-exudate C were in the order: MB-C < WEOC < CO_2-C. Maize and wheat exudates showed significant differences from each other in the CO_2-C and WEOC pools.

Discussion

A direct comparison between the effects of maize and wheat exudates on soil is difficult as slightly different amounts of exudate-C were applied. Therefore, the general processes of exudate addition to soil are discussed instead of the impacts of contrasting plant species.

Major pathways of exudate- as well as soil-derived C could be determined in this study with the aid of stable isotope techniques. The new online-method was found to be a suitable tool for the determination of ^{13}C in soil extracts. The measurements were reproducible over time and very sensitive in measuring ^{13}C in extracts with very small C concentrations (down to 1 mg C litre^{-1}). Moreover, the method works very efficiently, since around 100 samples could be processed per day. The identification of soil- and exudate-C in the measured pools by the new online-method enables to understand their dynamics.

The C-dynamics observed could be explained by several of the following mechanisms. However, it seems reasonable to assume that no single but a combination of processes was responsible for the C-dynamics observed.

Influence of exudates on WEOC

It is well known that WEOC is the main energy source for microorganisms in soil (Zsolnay, 1996). In our study WEOC rose to the end of the incubation. This was partly due to a declining mineralization rate, which leaves incoming WEOC in the soil solution over time. A significant ($P < 0.01$) negative relationship was found between net WEOC and net CO_2-C production (maize exudate treated soil r = –0.91, wheat exudate treated soil r = –0.85). However, on a quantitative basis the net CO_2-C amounts do not entirely explain the rising soil-derived net WEOC amounts, as can be seen from Table 2.

Microbial metabolites were eventually measured as WEOC and may account for at least a small part of the rising amounts of both soil- and exudate-derived WEOC. The increasing soil-derived WEOC amounts can also be explained by the release of exoenzymes of microbial origin, which catalysed formerly insoluble C into a dissolved form (Paterson, 2003).

Fröberg *et al.* (2006) found soil-derived dissolved organic carbon (DOC) from exchange processes between solid soil organic matter and incoming DOC. In our study the additional amount of soil-derived WEOC relative to the control might also originate from an exchange between the soil matrix and added substrate-C. That means low molecular weight exudates exchange with soluble substances from the soil matrix, and this is probably a function of the added C-amount. The exudates used in this experiment would have included charged components, since binding to the solid phase occurs with charged clay or mostly metal hydroxides (Guggenberger & Kaiser, 2003; Kaiser & Guggenberger, 2000; Kaiser *et al.*, 2002; Kalbitz & Knappe, 1997). Uncharged components (e.g. glucose) are predominantly metabolized and not adsorbed (Jones *et al.*, 2004).

It is assumed that the adsorption capacity for organic compounds was exhausted from the third sampling on, where a significant rise in the WEOC amounts took place.

Influence of exudates on microbial biomass

The newly built microbial biomass consisted to a great extent of exudate-C. However, the proportion of soil-derived C in the microbial biomass of exudate-treated soil was greater than the control MB-C. The additional incorporated soil-derived C might have originated from the exchange processes stated above.

After the first sampling soil microbial biomass stayed constant over the incubation period despite a continuous exudate-C supply, which is the prerequisite for a growing microbial population. The growth of microbial biomass was not limited by a lack of nitrogen since it was available in sufficient amounts (data not shown). This is also reflected in the small C to N ratio of the added exudates. However, a deficiency of other mineral nutrients cannot be excluded. Helal & Sauerbeck (1986) pointed out that under conditions of sufficient C-supply, a lack of mineral nutrients may limit microbial growth.

According to the competitive exclusion principle, certain microorganisms might have been selectively promoted through the exudates added in this study. In general, these

saprophytic microbes are able to metabolize the given substrate rapidly due to a competitive advantage (Fontaine *et al.*, 2003). The fast germination of propagules combined with rapid growth, a suitable enzymatic system for the decomposition of the available substrate, the production of toxic metabolites, and the tolerance to inhibitors are factors that make those microbes ideal competitors for energy and nutrients (Curl & Truelove, 1986). Due to these (toxic) metabolites, other microbes may have been suppressed in their growth and activity and became dormant in this study. The remaining microorganisms might have been very well adapted to the specific conditions in the incubation system. Thus, they would consist of a narrow range of species with similar demands for resources and the ability to rapidly use the added exudates.

Influence of exudates on CO_2-C production

Dormant or resting microbes were triggered into activity on the first sampling as shown by a flush of CO_2-C in the exudate-treated soil compared to the control. However, the CO_2-C evolution rates declined over the course of the incubation despite a stable amount of microbial biomass in the soil. So, the decreasing CO_2 production rate over time cannot be accounted for by die-back of microbes. The qCO_2 values express the specific respiration rate and support the presumed shift in the microbial community structure, since qCO_2 decreased over the incubation period. The smaller qCO_2 values at the end compared to the beginning of the incubation period in the treated soil may indicate a mostly inactive microbial population and this is in line with the findings of Bottner *et al.* (1988). Others (Benizri *et al.*, 2002; Griffiths *et al.*, 1999) also suggested a shift in the microbial community structure with addition of exudates to soil over time.

The net soil-derived CO_2-C values show that gradually less soil-C was mineralized. It becomes obvious from the large amounts of respired exudate-C compared to soil-C that predominantly exudates were mineralized. Thus, exudates served as the main energy source for microorganisms.

Priming effects due to the addition of exudates

Similar to the well-known priming effect determined with help of CO_2 evolution (Kuzyakov *et al.*, 2000), a release of additional soil-derived C relative to the control was observed in the dissolved phase in this study. It is suggested here that due to the addition of exudate (fresh organic material), the dissolved organic matter from the soil matrix is liberated. This newly released material is then available for microorganisms and is eventually measured as soil-derived CO_2. This might also explain the contribution of soil-derived C to the microbial biomass, and the positive priming action observed in wheat-exudate treated soil on the first two samplings and in other studies (e.g. Fontaine *et al.*, 2004; Hamer & Marschner, 2005).

As a result of the use of exudate-C in preference of soil-C by microorganisms, negative priming effects occurred in both treatments on almost all samplings. This is supported by Kuzyakov (2002) who described preferential use of easily available (exudate) C over more recalcitrant (soil-derived) C as one possible mechanism of rhizosphere priming.

Fate of labelled exudates

The results reveal that 64% of the added exudates of both plants could not be recovered in the pools investigated (WEOC, microbial biomass, CO_2) or with the methods applied. This is surprising, since we assumed that it was possible to recover a large percentage of the easily degradable exudates in these labile C pools. Methodological deficiencies could account for this unidentified pool. For example, the microbial biomass-C cannot entirely be determined by the fumigation-extraction method and this is reflected in the inconsistent application of conversion factors found in the literature (Joergensen, 1996). However, this should explain only a small part of the difference.

Furthermore, unknown exudate-C amounts might have been adsorbed onto the soil matrix or fixed in organic structures and could not be extracted with one single extraction. Additionally, exudate-C also might have existed in a water-insoluble state and excluded from

WEOC extraction with the polar $CaCl_2$ solution used in this study. This form can either be a plant or soil microbial metabolite.

Discrimination against ^{13}C during microbial metabolism resulting in depleted CO_2 values did not appear in this study, as has been suggested by some authors (Mary *et al.*, 1992; Kristiansen *et al.*, 2004). This would have lead to an underestimation of the emitted exudate-C in the overall balance of our study. Consequently, CO_2 originating from soil-derived C would have been overestimated (apparent priming effect). In fact, respiration of ^{13}C-compounds dominated over the whole study as shown by the net CO_2-C balance. The negative priming effect that occurred on most of the samplings showed that ^{12}C-components were left in the soil solution rather than mineralized. After adding substrate to soil, Ekblad & Högberg (2000) found no shift in their CO_2-^{13}C values and this supports our results.

In our opinion, it is most probable that exudate-C was incorporated in the stable, non-water extractable organic fraction.

Conclusions

By using stable isotopes in the production of maize and wheat exudates, it was possible to show that exudates have more complex functions in the soil C-dynamics than just being an energy source for microorganisms. We also found that great amounts of exudates could become stabilized in non-water extractable organic fractions. We suggest that exchange processes between soluble, charged C-components and the soil matrix may induce positive priming effects. Further investigations of positive priming effects should also include soil physical processes (exchange of organic substances with the soil matrix) besides microbial effects on the release of surplus C from soil during the priming process.

The determination of the stable C pool will give valuable insight into the pathways of exudate-C in soil. This is necessary to elucidate the fate of exudates and eventually calculate complete mass balances. These calculations would help to reveal the influence of root exudates on carbon sequestration in soil, and therefore the contribution to global change.

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Chapter 3

Determination of the fate of constantly applied ^{13}C labelled artificial exudate-C in two agricultural soils with different yield

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Abstract

A broader knowledge of the contribution of carbon (C) released by plant roots (exudates) to soil is a prerequisite for optimising the management of organic matter in arable soils. This study was conducted to reveal the effects of ^{13}C labelled exudate (artificial mixture) that was constantly applied to upper soil material from two agricultural soils of the same location, but with different crop yields. The contribution of exudate-C to water extractable organic carbon (WEOC), microbial biomass-C (MB-C), and CO_2-C evolution was investigated during a 74-day-incubation. The WEOC, MB-C, and CO_2-C concentrations and the respective $\delta^{13}C$ values were determined regularly, and a newly developed method for determining $\delta^{13}C$ values in soil extracts was applied. In both soils, regardless of crop yield potential, significant incorporation of artificial exudate-derived C was observed in the MB-C pool and in CO_2-C, but not in the WEOC. Up to around 50% of the exudate-C amounts added were recovered in the order WEOC << MB-C < CO_2-C in both soils at the end of the incubation. Newly built microbial biomass consisted mainly of exudate-C, which substituted soil-derived C. Therefore, the formation of a new microbial structure is assumed. Correspondingly, the CO_2-C evolved from exudate-treated soils relative to the controls was dominated by exudate-C, showing a preferential mineralization of this substrate. Our results suggest that the remaining 50% of the exudate-C added became stabilized in non water-extractable organic fractions. This assumption was supported by the determination of the total organic C in the soils at the end of the incubation. In the exudate-treated soils, significantly more soil-derived C compared to the controls was found in the WEOC on almost all samplings and in the MB-C on the first sampling. It is concluded that the observed positive priming effects (i.e. accelerated turnover of soil organic matter due to the addition of organic substrates) can be explained by exchange processes between soluble C-components and the soil matrix.

Introduction

A detailed knowledge of carbon (C) flow in terrestrial ecosystems is crucial for understanding ecosystem functioning with respect to, for example, soil management, responses to anthropogenic pollution or climate change (Gregorich et al., 2000). Sustainable management of soil organic matter especially in agricultural systems can only be accomplished when C-dynamics are known and become predictable.

Exudates are a part of the total rhizodeposition released by plant roots. They comprise a mixture of compounds consisting mainly of sugars, amino acids, and organic acids (Uren and Reisenauer, 1988; Grayston et al., 1997). They are subjected to different fates when entering the soil and fulfil manifold functions (Jones, 1999). For example, they serve as an energy and C-source for microorganisms, modify physicochemical conditions in the rhizosphere leading to increasing availability for nutrients (Lynch and Whipps, 1990), act as signalling substances between plants and microorganisms (Bertin et al., 2003), stabilize soil aggregates (Grayston et al., 1997), and influence the turnover of native soil organic matter (Kuzyakov et al., 2000).

The fate of C from rhizodeposits in soil is still unanswered (Hütsch et al., 2002). This is primarily due to methodological problems, since exudates exist in small concentrations in soil and are rapidly metabolized by microorganisms (Jones et al., 2004). Thus, to obtain exudates sufficient for a long-term study is extremely difficult. Additionally, exudate-C forms a complex mixture with soil-C, making separation difficult. In this regard, the contribution of root-derived dissolved organic carbon (DOC) to the DOC released from the soil is still unknown, as it has not yet been measured directly (Kalbitz et al., 2000).

To circumvent the problems stated above, artificial rhizoexudate additions to soils have been undertaken. Results from such approaches have revealed, for example, the contribution of artificial exudates to soil aggregate stabilization (Traore et al., 2000), or on soil microbial community structure (Campbell et al., 1997; Griffiths et al., 1999). The

addition of single compounds commonly found in root exudates has recently been used to investigate priming effects in soil (Hamer and Marschner, 2005). However, no study has dealt with the turnover of pure exudates, despite the determination of their relative contribution to labile soil organic matter fractions being often suggested. This is necessary in order to better understand below ground C-dynamics (Flessa et al., 2000; Liang et al., 2002).

The present study was conducted to measure directly the dynamics of constantly applied artificial exudates into the most important labile carbon pools in soil with the use of ^{13}C. The aim of our study was to determine the contribution of simulated exudates to water extractable organic carbon (WEOC), microbial biomass, and CO_2 evolution during an incubation of upper soil material from two agricultural soils. These soils were chosen, since it was assumed that their nutrient and C-fluxes are different from each other, based on their different yield pattern. The experimental approach was chosen because it was expected that most of the easily degradable exudates would be recovered in WEOC, microbial biomass, and CO_2.

Material and methods

Production of ^{13}C labelled artificial exudates

The preparation of artificial exudates was adapted from Griffiths et al. (1999). The following substances commonly reported to occur in root exudates were mixed at a C-ratio given in brackets: glucose (1), fructose (1), sucrose (1), succinic acid (0.5), arginine (0.25), cysteine (0.25), serine (0.25), and benzoic acid (0.25). The organic compounds were 99 atom% ^{13}C labelled (purchased from SerCon Limited, Cheshire, England) and mixed with the respective unlabelled compounds to dilute their ^{13}C contents. The total concentration of the artificial exudate solution was 1130 mg C litre^{-1} with a $\delta^{13}C$ value +47.87‰ PDB, and a C/N ratio of 11.6.

Incubation

The soil sampling was from a field with potato - winter wheat – maize - winter wheat rotation history at the agro-ecological research station in Scheyern, approximately 40 km north of Munich, Germany (48°30', 11°20'E). A harvester equipped with a Global Positioning System and devices to record the yield amounts obtained data from this field over 4 years. As a result distinct stable areas of lower (LY) and higher yield (HY) were designated. Soil material was collected from the upper 10 cm of a Dystric Cambisol in the low yield area and of a Eutric Cambisol in the high yield area in spring 2004. The field-fresh soils were sieved to pass a 2-mm mesh. The LY soil had the following characteristics: clay 20%, silt 51%, sand 29%, pH ($CaCl_2$) 6.1, C_{org} 1.3% and total N 0.13%. The properties of the HY soil were as follows: clay 15%, silt 49%, sand 36%, pH ($CaCl_2$) 5.9, C_{org} 1.4%, and total N 0.14%.

Experimental design (Incubation experiment)

Soil in aliquots equivalent to 7 g of dry matter was filled in 30 ml glass vials. Soil was pre-incubated over 3 weeks at a water-content equivalent to 60% water-filled pore space. In order to provide a continuous artificial exudate-C supply to the soil, C additions were distributed for practical reasons as three doses per week after the pre-incubation period. This gave a load of 48.5 µg C g^{-1} soil day^{-1}. After 56 days, the substrate additions were stopped and the incubation was prolonged for further 18 days. This was done in order to determine whether exudate can still be detected in the measured pools. A control with distilled water addition to the soil instead of exudate was also run. To keep the soil at constant moisture content, samples in each vial were left in a desiccator at 15 mbar (absolute) for 70 minutes to induce a water loss of 0.7 ml, which was then replaced by the exudate solution or water, respectively. The temperature was kept constant at 14°C. Destructive soil sampling of five randomly chosen replicates was conducted for each of the treatments (controls, exudate-treated LY and HY soils) to determine microbial biomass-C and water-extractable carbon. The first sampling took place on the sixth day of incubation, followed by weekly sampling. The controls were also sampled on that day. Nevertheless, they were considered as starting point and used as

time zero (*t*0), as has also been done by Helal and Sauerbeck (1986). It was assumed that no change in the measured pools occurred during that time in these soils, where only water was added. CO_2-C evolution was determined daily (as described below) during the first incubation week. Thereafter, CO_2 determination was done twice a week on the days without exudate addition. All results are expressed as equivalents to oven dried soil (105˚C for around 24 h).

Analysis

WEOC was obtained by shaking the soil samples with 0.01 M $CaCl_2$ solution in an over-head shaker for 15 minutes at a soil:solution ratio of 1 (mass):5 (volume) and subsequent filtration through 0.45 µm pore-size polycarbonate filters. The WEOC concentrations were determined on a Total Carbon Analyser (Shimadzu TOC 5050, Tokyo, Japan) by catalytic high temperature oxidation (Zsolnay, 2003).

The microbial biomass carbon (MB-C) concentrations were determined by the chloroform-fumigation extraction method (CFE) (Vance et al., 1987) with 1 g of soil each for the fumigated and non-fumigated assay in 4 ml of 0.5 M K_2SO_4 solution. Dissolved organic carbon (DOC) in the extracts was determined on a Shimadzu TOC 5050. The difference between DOC in fumigated and non-fumigated samples was divided by 0.45 to calculate MB-C (Joergensen, 1996).

The total organic carbon (C_{org}) contents in all treatments were determined on sampling 10 in order to assess a possible influence of exudate on this pool. This single sampling was chosen, since it was at the end of the incubation. C_{org} was determined with an elementar analyser (Eurovector CN, Milan, Italy).

The $^{13}C/^{12}C$ ratios in liquid samples (WEOC, CFE) were determined by a liquid chromatograph/isotope ratio mass spectrometer (LC/IRMS) (Thermo Finnigan LC IsoLink and MAT 253, Bremen, Germany) by an on-line method newly developed by Krummen et al. (2004). The LC IsoLink worked in a mode that allows the bulk isotopic analysis of all water-soluble material. The samples were processed as follows: organic substances in the

extracts were oxidized quantitatively to CO_2 by 0.45 M $Na_2S_2O_8$ and 8.5% H_3PO_4 solution in a reaction chamber at 99.9°C. The CO_2 was separated from the liquid phase with a gas-exchange membrane and admitted to the IRMS in a stream of helium via an open split.

The ^{13}C values of the soil extracts determined were compared with values of an internal laboratory standard (benzoic acid solution) and a blank (solvent used for soil extraction), both of which were included in all sample measurements at regular intervals. The C concentrations of the standards were chosen according to the given concentrations of the soil extracts.

During the incubation period, CO_2-concentrations and their corresponding $^{13}C/^{12}C$ ratios evolved from soil samples were determined on-line with a gas chromatography/isotope ratio mass spectrometer (GC/IRMS) (Finnigan MAT DeltaPlus, Bremen, Germany). Five randomly chosen vials were closed air-tight with a plastic lid with a rubber septum and placed in a water jacket adjusted to the incubation temperature (14°C). The rack was specially built to be mounted on a CombiPAL autosampler (CTC, Zwingen, Switzerland). The enrichment of CO_2 and respective $^{13}CO_2$ values in the headspace of the vials was determined with 5 measurements on each sample over a 21-hour-period. Samples were withdrawn from the vials' headspaces by a syringe on the autosampler and injected into the GC/IRMS. A regression line was fitted to the measured points ($R^2 > 0.95$) in order to calculate a CO_2 production rate. From this rate the CO_2 amounts per day were estimated and subsequently cumulated in order to obtain the total CO_2 amounts evolved on the respective samplings.

Calculations

The $\delta^{13}C$ values of the samples were expressed relative to the international VPDB standard:

$$\delta^{13}C\ (‰\ \text{VPDB}) = \left(\frac{R_{\text{sample}} - R_{\text{VPDB}}}{R_{\text{VPDB}}} \right) \text{x}\ 1000, \qquad (1)$$

where $R = \frac{^{13}C}{^{12}C}$ and $R_{VPDB} = 0.0111802$ (Werner & Brand, 2001).

We calculated the $\delta^{13}C$ (‰ VPDB) of MB-C from the following mixing equation:

$$\delta^{13}\text{MB - C} = \frac{(c_{\text{fum}} \text{ x } \delta^{13}C_{\text{fum}}) - (c_{\text{nfum}} \text{ x } \delta^{13}C_{\text{nfum}})}{(c_{\text{fum}} - c_{\text{nfum}})}, \quad (2)$$

where c_{fum} and c_{nfum} = concentration (µg g^{-1}) of C in the fumigated and non-fumigated soils, respectively.

We calculated the fraction of C originating from the exudate ($f_{exudate}$) in MB-C, WEOC, or CO_2-C from:

$$f_{\text{exudate}} = \frac{(\delta^{13}C_{\text{mix}} - \delta^{13}C_{\text{soil}})}{(\delta^{13}C_{\text{exudate}} - \delta^{13}C_{\text{soil}})}, \quad (3)$$

where $\delta^{13}C_{mix}$ = composition of soil derived- and exudate-derived $\delta^{13}C$ (‰ VPDB), and $\delta^{13}C_{soil/exudate}$ = $\delta^{13}C$ (‰ VPDB) of soil or exudate, respectively.

We calculated the contribution of exudate-C ($c_{exudate}$) to WEOC, MB-C, or CO_2-C total concentration (µg g^{-1}) from:

$$c_{\text{exudate}} = f_{\text{exudate}} \text{ x } c_{\text{total}}, \quad (4)$$

where c_{total} = total concentration (µg g^{-1}) of WEOC, MB-C, or CO_2-C, respectively.

The priming effect (PE) was calculated according to Hamer & Marschner (2002). As a prerequisite for the determination of PE, the difference between soil-derived CO_2-C of exudate treated soil and the control CO_2-C must be significant on the basis of an unpaired *t*-test ($P < 0.05$) over the relevant time interval. The PE for this time span was calculated from:

$$\text{PE (\%)} = \frac{\Delta CO_2\text{-}C_{\text{treatment}} - \Delta CO_2\text{-}C_{\text{control}}}{\Delta CO_2\text{-}C_{\text{control}}} \text{ x } 100 \quad (5)$$

where ΔCO_2-$C_{treatment}$ = (soil-derived CO_2-C of exudate treated soil) – (soil-derived CO_2-C of exudate treated soil from previous sampling), and ΔCO_2-$C_{control}$ = (control CO_2-C) – (control CO_2-C from previous sampling).

The absolute amounts of primed C were calculated by subtracting ΔCO_2-$C_{control}$ from ΔCO_2-$C_{treatment}$ for the relevant time intervals. This was also applied to WEOC and MB-C in order to calculate the net effects of exudate addition on soil-derived C in these pools. It must

be noted that the control of the first sampling was assumed to represent the soil status at time zero (*t*0).

Statistics

All results are expressed as the means of five replicates with standard errors. The WEOC, MB-C, and CO_2-C content data were subjected to an analysis of variance to determine significant treatment, time, and soil effects on the different C-fractions of the pools investigated. An unpaired *t*-test was conducted to reveal significant differences between the percentages of exudate-C of the pools investigated in low compared to high yield soil. All tests were done at a significance level of $P < 0.05$.

Results

WEOC

The total WEOC concentrations of the exudate-treated soils as well as the soil-derived fraction were significantly greater than of the respective controls at almost all samplings (Figure 1, Table 1). The total, exudate-, and soil-derived WEOC concentrations showed significant temperal fluctuations over the course of the incubation. However, artificial exudate-C addition at a rate of 48.5 µg g^{-1} day^{-1} had almost no effect on WEOC in both soils during the observed period (Figure 1), since the differences between the treatments over time were consistently very small. Except for the samplings 4 and 6, all total values ranged around 12 to 13 µg g^{-1} in both soils.

Microbial biomass-C

The microbial biomass-C (MB-C) contents of the control soils ranged around 205 µg g^{-1} over the entire incubation period (Figure 2). At all samplings, the total MB-C concentrations of the exudate-treated soils were significantly greater than those of the controls. The soils showed a significant effect on the exudate-derived C-fraction, but not on the total and soil-derived MB-C (Table 1).

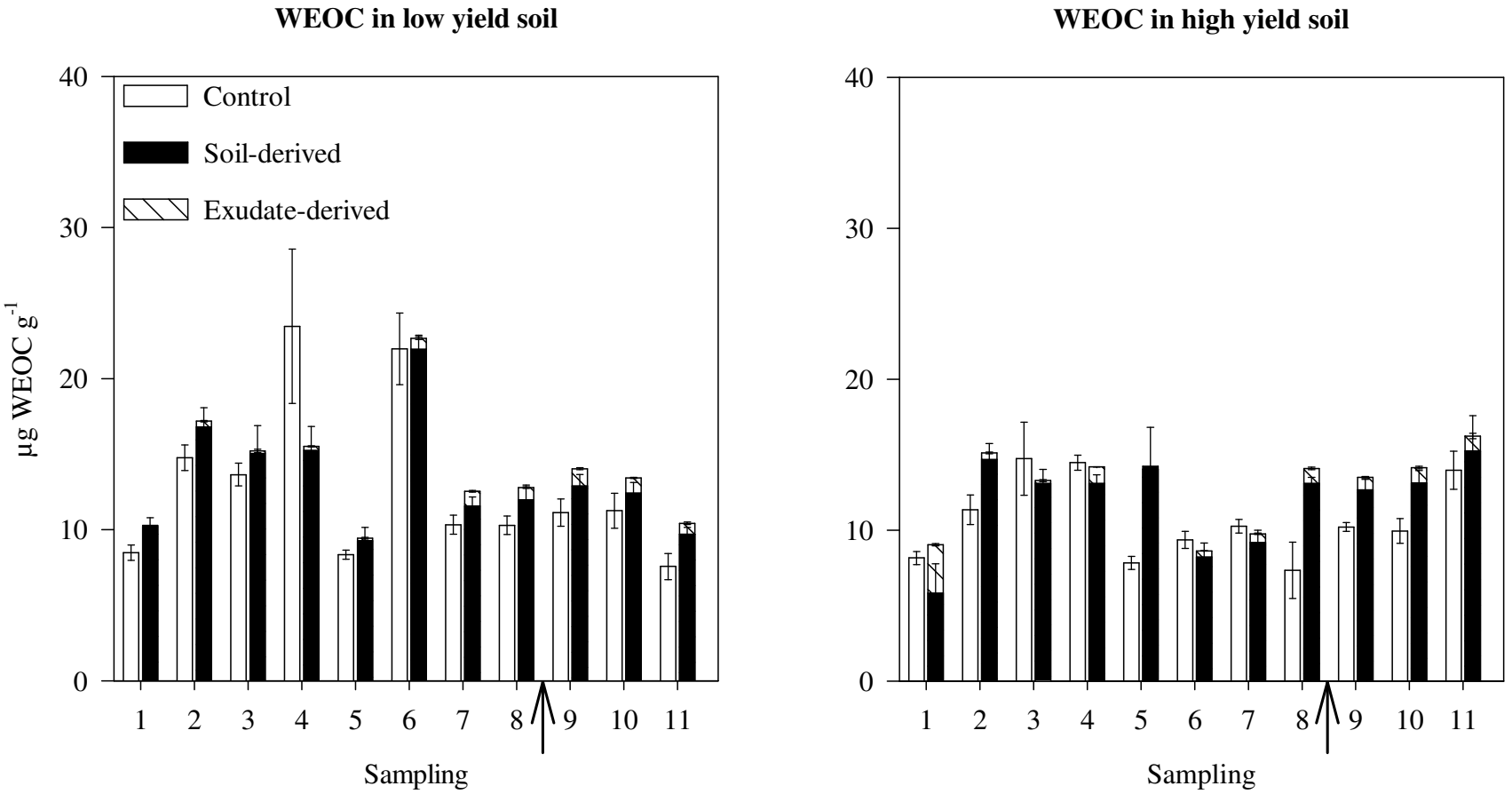

Figure 1 Amounts of WEOC from exudate-derived C and of the respective soil-derived C in low and high yield soil over a 74-day-incubation. Arrows show the stop of exudate additions. Error bars represent standard errors of the means (n = 5).

Table 1 Analysis of variance of water extractable organic carbon (WEOC), microbial biomass-C (MB-C), CO_2-C, and priming effect data.

Source of variation	Degrees of freedom	Sum of squares	Mean square	*F*	*P*
Total WEOC					
Treatment	1	121.496	121.496	14.420	<0.001
Sampling	10	1003.598	100.360	11.911	<0.001
Soil	1	128.930	128.930	15.302	<0.001
Treatment x sampling	10	229.602	22.960	2.725	0.004
Treatment x soil	1	12.420	12.420	1.474	0.227
Sampling x soil	10	991.116	99.112	11.763	<0.001
Treatment x sampling x soil	10	124.491	12.449	1.478	0.152
Residual	157	1322.848	8.426		
Soil-derived WEOC					
Treatment	1	46.822	46.822	5.683	0.018
Sampling	10	973.159	97.316	11.812	<0.001
Soil	1	125.723	125.723	15.260	<0.001
Treatment x sampling	10	198.422	19.842	2.408	0.011
Treatment x soil	1	11.702	11.702	1.420	0.235
Sampling x soil	10	962.289	96.229	11.680	<0.001
Treatment x sampling x soil	10	120.522	12.052	1.463	0.159
Residual	151	1244.024	8.239		
Exudate-derived WEOC					
Sampling	10	8.083	0.808	28.061	<0.001
Soil	1	0.018	0.018	0.627	0.431
Sampling x soil	10	0.977	0.098	3.390	0.001
Residual	74	2.132	0.029		
Total MB-C					
Treatment	1	2659886.579	2659886.579	2468.329	<0.001
Sampling	10	252328.202	25232.820	23.416	<0.001
Soil	1	1557.308	1557.308	1.445	0.231
Treatment x sampling	10	263930.251	26393.025	24.492	<0.001
Treatment x soil	1	2939.300	2939.300	2.728	0.101
Sampling x soil	10	14047.090	1404.709	1.304	0.233
Treatment x sampling x soil	10	9049.660	904.966	0.840	0.591
Residual	158	170261.777	1077.606		
Soil-derived MB-C					
Treatment	1	166031.006	166031.006	435.750	<0.001
Sampling	10	288388.706	28838.871	75.688	<0.001
Soil	1	774.173	774.173	2.032	0.156
Treatment x sampling	10	89258.244	8925.824	23.426	<0.001

Continued on the following page.

Table 1 Continued.

Source of variation	Degrees of freedom	Sum of squares	Mean square	*F*	*P*
Treatment x soil	1	170.861	170.861	0.448	0.504
Sampling x soil	10	7903.220	790.322	2.074	0.029
Treatment x sampling x soil	10	1782.172	178.217	0.468	0.909
Residual	158	60201.681	381.023		
Exudate-derived MB-C					
Sampling	10	1109930.277	110993.028	71.125	<0.001
Soil	1	8993.740	8993.740	5.763	0.019
Sampling x soil	10	9771.287	977.129	0.626	0.787
Residual	79	123282.431	1560.537		
Total CO_2-C					
Treatment	1	13277295.688	13277295.688	4527513.190	<0.001
Sampling	10	11879683.316	1187968.332	405093.207	<0.001
Soil	1	2382.922	2382.922	812.568	<0.001
Treatment x sampling	10	4843904.155	484390.416	165175.503	<0.001
Treatment x soil	1	8535.516	8535.516	2910.582	<0.001
Sampling x soil	10	8213.768	821.377	280.087	<0.001
Treatment x sampling x soil	10	13358.776	1335.878	455.530	<0.001
Residual	164	480.943	2.933		
Soil-derived CO_2-C					
Treatment	1	332.390	332.390	153.332	<0.001
Sampling	10	1475096.751	147509.675	68046.511	<0.001
Soil	1	68.299	68.299	31.506	<0.001
Treatment x sampling	10	1842.100	184.210	84.976	<0.001
Treatment x soil	1	2687.071	2687.071	1239.551	<0.001
Sampling x soil	10	579.460	57.946	26.731	<0.001
Treatment x sampling x soil	10	2388.734	238.873	110.193	<0.001
Residual	164	355.515	2.168		
Exudate-derived CO_2-C					
Sampling	10	9434025.926	943402.593	119443.543	<0.001
Soil	1	3063.229	3063.229	387.833	<0.001
Sampling x soil	10	9771.287	977.129	0.626	0.787
Residual	76	600.272	7.898		
Priming effect					
Sampling	10	10196.761	1019.676	137.885	<0.001
Soil	1	2580.076	2580.076	348.888	<0.001
Sampling x soil	4	191.563	47.891	6.476	<0.001
Residual	57	421.523	7.395		

The total amounts of MB-C rose significantly to about 172 µg g^{-1} in LY or 208 µg g^{-1} in HY from samplings 1 to 5 (34th day of incubation). Then, the MB-C concentrations stayed relatively constant followed by a significant drop after the addition of exudate stopped towards the level at the beginning of the incubation. On the first sampling, soil-derived C was significantly greater, and exudate-derived C was smaller than on all other samplings in both soils. After that, the soil-derived fraction of MB-C fell to a constant level of around 110 µg g^{-1} on sampling 6 until the end of the incubation in both soils. In contrast, exudate-derived C in the MB rose significantly to about 251 µg g^{-1} in LY and 386 µg g^{-1} in HY from samplings 1 to 8. This fraction dropped significantly on the last samplings.

CO_2-C

The exudate addition resulted in a significant increase of the CO_2-C emissions relative to the controls in both soils on all samplings. The differences of the total CO_2-C emissions between the controls were small but significantly greater in HY than in LY, except for the first two samplings of the incubation (Table 1, Figure 3). On sampling 11, the range between the controls of both soils amounted to around 10 µg g^{-1}, so the emission was 3.6% higher in the HY than in the LY control.

The total CO_2-C amounts of the exudate-treated soils were significantly different from each other throughout the incubation period. On sampling 5 the CO_2-C emitted was around 550 µg g^{-1} from both of the treated soils. Interestingly, before that sampling the emissions of HY were greater than those of LY. Thereafter, the situation changed and the CO_2-C amounts of the LY were with 1308 µg g^{-1} greater than those of HY with 1240 µg g^{-1} at the incubation end. The contributions of exudate-derived C to total CO_2-C rose constantly from 60% in LY and 50% in HY to around 76% in both soils during the incubation. The soil-derived CO_2-C proportions declined from 40% in LY and 50% in HY to around 24% in both soils.

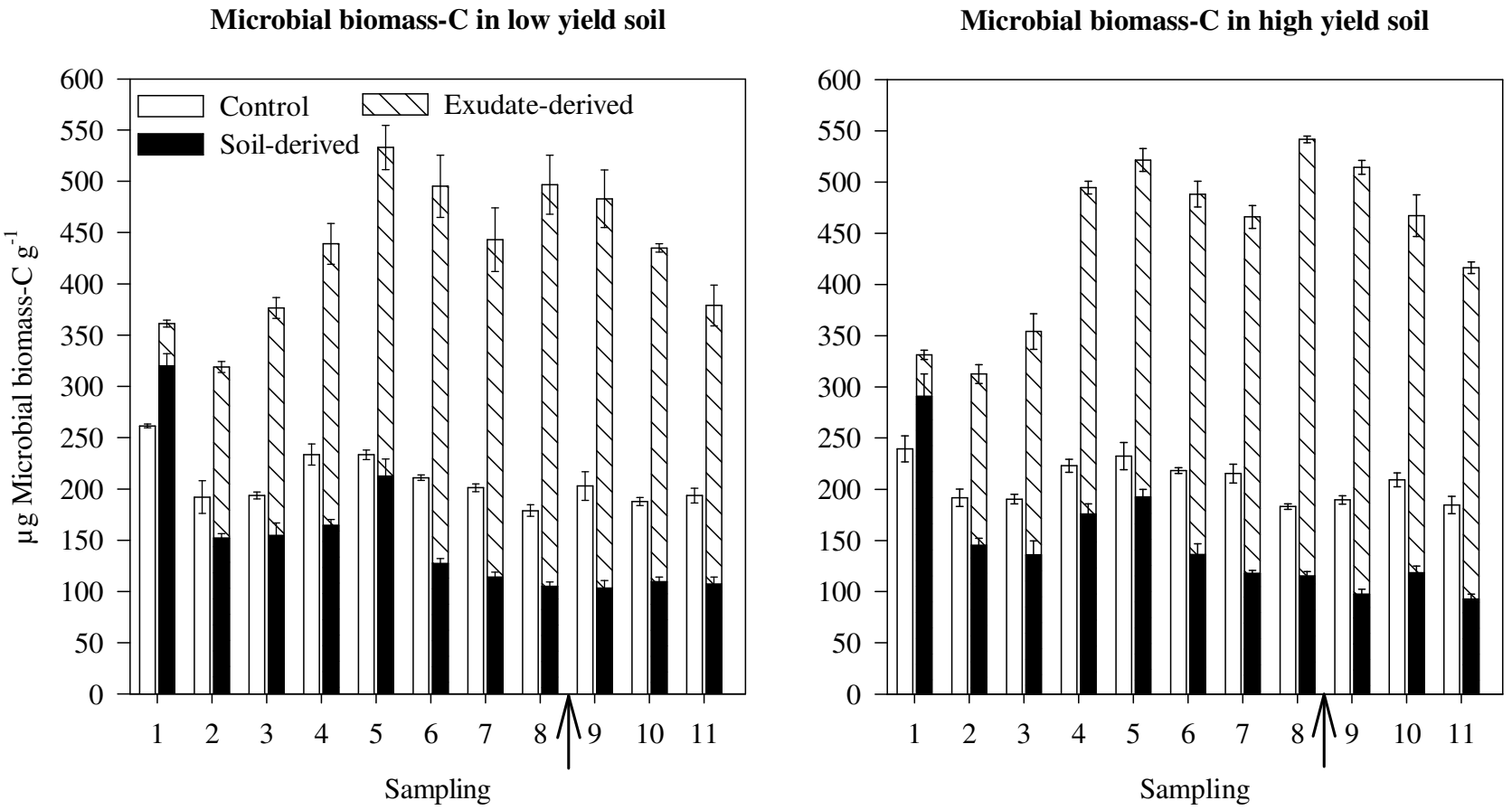

Figure 2 Amounts of microbial biomass-C from exudate-derived C and of the respective soil-derived C in low and high yield soil over a 74-day-incubation. Arrows show the stop of exudate additions. Error bars represent standard errors of the means (n = 5).

Priming and net effects of exudate addition on soil-derived C

Priming effects (PE) were revealed for both soils, but not on each sampling. Additionally, the primed C amounts were constantly very small in the considered time intervals (< 7 µg C g^{-1}), except for the first two samplings in HY (Table 1). In LY positive PE occurred from samplings 1 to 3 with a significant decline from 19.5 to 8.4%. At the end of the incubation period (samplings 10 and 11) the PEs significantly increased from 10.0 to 31.8%. On samplings 8 and 9 negative PEs were determined amounting to –6.9 and –9.9%, respectively (Table 1). The only positive PE observed in HY was on the first sampling with 75.4%. On sampling 2, the negative PE amount dropped significantly to –33.0%. Negative PE increased significantly from –4.5 to –27.8% on samplings 4 to 9 followed by a significant increase amounting to –8.0% on sampling 10. The net soil-derived CO_2-C values also represented the actual amount of primed C. These amounts were consistently very small (< 6 µg g^{-1}), except for the first two samplings in HY with 18 and –13 µg g^{-1}.

Table 2 also shows the net amounts of soil-derived C in the WEOC and microbial biomass pools compared to the controls for the considered samplings. The relatively stable amounts of WEOC over time were also reflected in the very small net amounts.

The corresponding values of MB-C show the amounts that were incorporated or being released, respectively, from the microbial biomass during the incubation period. The development of microbial biomass-C was striking at the beginning of the incubation. On the first sampling, the soil-derived fraction was 59 µg g^{-1} in LY or 52 µg g^{-1} in HY, respectively. On the next sampling, 98 µg g^{-1} of soil-derived C was liberated by the MB in both soils. The total influence of the observed priming effects on soil-derived C was calculated for the exudate-treated soils (Table 3). The addition of exudate-C caused positive C-balances in both of the treated soils, showing greater values in HY compared to LY. This indicates that a net gain of C occurred in both soils.

Table 2 Amounts of net soil-derived WEOC, MB-C, CO_2-C, and priming effects of exudate-treated low and high yield soils over the course of the incubation. Values in parentheses are standard errors (n = 5). Dashed line indicates the stop of exudate additions.

Sampling	Low yield soil				High yield soil			
	WEOC	MB-C	CO_2-C[a]	Priming	WEOC	MB-C	CO_2-C[a]	Priming
	($\mu g\ g^{-1}$)			(%)	($\mu g\ g^{-1}$)			(%)
1	1.81 (0.51)	58.55 (11.90)	4.72 (0.45)	19.48 (1.87)	–0.39 (0.12)	51.50 (21.72)	18.13 (4.65)	75.39 (19.33)
2	0.22 (1.27)	–98.41 (4.03)	2.58 (0.30)	6.91 (0.81)	3.73 (1.06)	–98.10 (6.74)	–12.72 (0.43)	–32.99 (1.13)
3	–0.63 (1.83)	0.90 (12.18)	2.85 (0.70)	8.37 (2.06)	–4.96 (0.91)	–20.32 (16.47)	0.11 (0.50)	n.s.
4	–9.52 (1.52)	–29.97 (5.61)	1.19 (0.44)	n.s.	0.26 (0.57)	19.76 (9.92)	–1.52 (0.23)	–4.51 (0.70)
5	9.13 (0.89)	48.29 (16.63)	0.36 (0.36)	n.s.	7.77 (2.59)	5.49 (12.79)	–1.71 (0.32)	–5.49 (1.01)
6	–0.93 (0.92)	–63.00 (4.89)	0.04 (0.34)	n.s.	–7.52 (0.92)	–42.12 (10.45)	–3.74 (0.12)	–13.35 (0.43)
7	1.26 (0.59)	–3.46 (4.84)	–0.95 (0.37)	n.s.	0.06 (0.81)	–15.54 (2.72)	–6.62 (0.03)	–23.20 (0.11)
8	0.44 (0.99)	13.30 (4.37)	–1.66 (0.30)	–6.92 (1.23)	4.99 (0.41)	29.40 (4.49)	–5.91 (0.22)	–23.67 (0.90)
9	0.09 (0.75)	–25.65 (7.30)	–2.20 (0.15)	–9.85 (0.68)	–1.45 (0.68)	–24.06 (4.88)	–6.43 (0.19)	–27.83 (0.81)
10	–0.60 (0.69)	21.22 (4.56)	2.04 (0.19)	10.03 (0.95)	0.69 (0.83)	1.29 (6.42)	–1.70 (0.15)	–7.96 (0.71)
11	0.96 (0.45)	–8.00 (6.69)	6.22 (0.35)	31.87 (1.81)	–1.89 (2.34)	–0.98 (4.91)	1.00 (0.11)	n.s.

n.s. not significant; [a]Absolute amounts of primed C

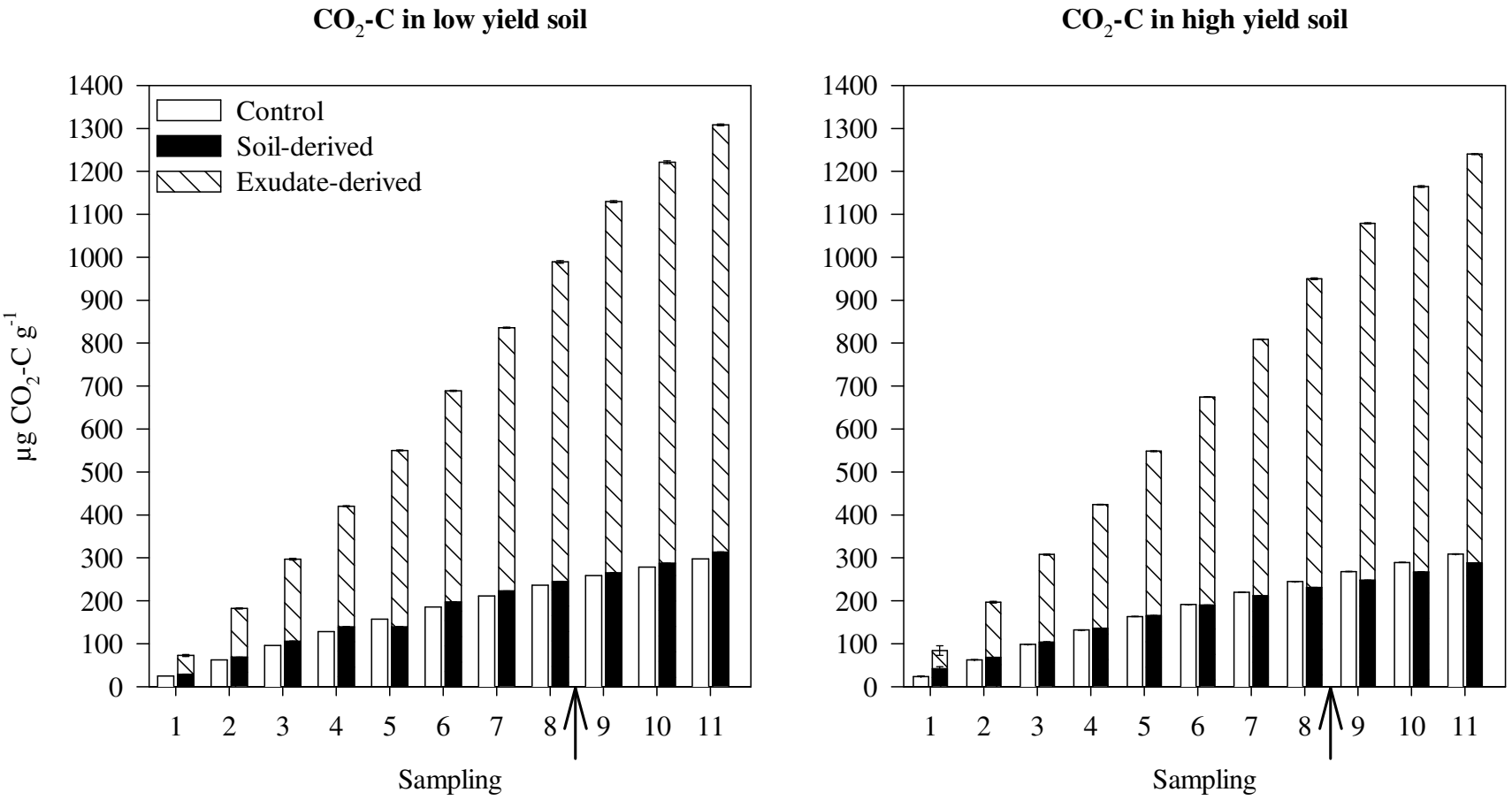

Figure 3 Amounts of CO_2-C from exudate-derived C and of the respective soil-derived C in low and high yield soil over a 74-day-incubation. Arrows show the stop of exudate additions. Error bars represent standard errors of the means (n = 5) (in most cases too small to be visible).

Table 3 C-balances of the exudate-treated soils after the incubation period.

Soil	Primed-C[a]	Mineralized exudate-C	Remaining exudate-C in soil[b]	Total mineralized-C	C-balance[c]
			($\mu g\ g^{-1}$)		
Low yield	15	995	1606	1308	298
High yield	–21	952	1649	1241	408

[a]Total amount of primed C after the incubation

[b]Added exudate-C – Mineralized exudate-C

[c]Remaining exudate-C – Total mineralized-C

Overall balance

To compare the fate of exudate-C applied in both soils, the allocation of this C into the pools investigated and the contribution to the CO_2 evolved is presented as percent values after the whole incubation period (Figure 4).

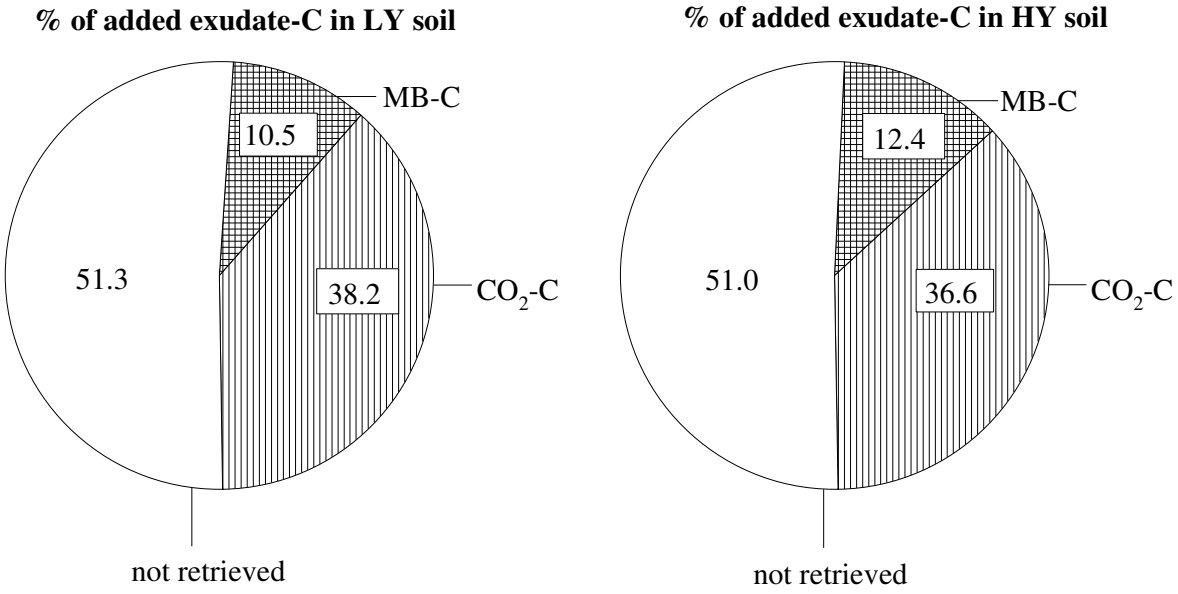

Figure 4. Percentages of exudates added recovered in the C pools investigated at the end of the incubations.

The amounts of exudate-C recovered in both soils were nearly the same and amounted to 50% in the order MB-C < CO_2-C. The share of WEOC amounts to the exudate-C balances was negligible in both soils (< 0.1%). MB-C values had a similar contribution to the balances in both soils and CO_2-C showed a small but significantly greater value in LY. The other 50% of the exudates added was not retrieved with the extraction methods used here.

To clarify the fate of C, which was not retrieved in the exudate-treated soils, the C_{org} contents from all treatments were determined on sampling 10 at the end of the incubation. In order to test the assumption that the not retrieved-C amounts were stabilized, these amounts were added to the C_{org} values of the untreated controls of both soils. These calculated C_{org} contents were almost identical to the measured ones of the exudate-treated samples (Table 4).

Table 4 The fate of not-retrieved exudate-C on sampling 10.

Soil	C_{org} control (%)[a]	Not retrieved exudate-C (µg g^{-1})	Calculated C_{org} (%)[ab]	Measured C_{org} (%)[a]
Low yield	1.24	1341	1.37	1.35
High yield	1.32	1354	1.46	1.45

[a]Reasseded by subtracting WEOC and MB-C amounts

[b]C_{org} control + Not retrieved exudate-C

Discussion

The pathways of artificial exudate-C as well as soil-derived C from exudate treated soils were determined in this study with the aid of stable isotope techniques. The outcomes are discussed in terms of the pools whereupon exudates could exert an immediate influence.

Development in the pools measured during exudate addition

Root exudates serve generally as a substrate for microorganisms (Lynch and Whipps, 1990; Zsolnay, 1996). Roughly 2600 µg exudate-C g^{-1} soil was added over the incubation period,

but the WEOC contents remained relatively constant at 12 to 13 µg g^{-1}. Obviously, almost the entire artificial exudate applied in this study was very efficiently incorporated in the microbial biomass, mineralized by microorganisms, or adsorbed to the soil matrix. Consequently, only very small exudate-C amounts were detected in the WEOC pool of the incubated soils.

The significantly greater amounts of soil-derived WEOC from the treated soils compared to the controls indicate an additional release of soluble soil-derived C-compounds. This might be due to the exudate added which adsorbs onto the soil matrix thereby exchanging soil-derived C. Results from other studies confirm this assumption, since soil-derived dissolved organic carbon (DOC) from exchange processes between solid soil organic matter and incoming DOC were also found (Fröberg et al., 2006; Marx et al., 2007).

Artificial exudate had a comparable impact on the microbial biomass in both soils. The total amounts of MB-C rose significantly to a maximum level on sampling 5. This seems to be the maximum MB content of these soils under the given conditions and is in accordance with van Veen et al. (1984) who assumed a specific biotic capacity for soils. Bottner et al. (1988) drew the same conclusion from their results.

The newly built microbial biomass in both of the exudate-treated soils consisted almost entirely of exudate-C as can be seen from the comparison with exudate-treated soils to the controls. However, on the first sampling significant amounts of soil-derived C-components were incorporated into the newly built microbial biomass. The additional amount of soil-derived C in the MB relative to the control might originate from an exchange between the soil matrix and substrate-C added as described for WEOC. The assumption is supported by the following values. On the first sampling, 37.1% in LY and 36.5% in HY of exudate-C was found in the pools investigated and in the CO_2 evolved, whereas the remaining percentages were not retrieved. This exudate fraction amounted absolutely to 142 µg C g^{-1} (LY) and 149 µg C g^{-1} (HY). In the likely case that these amounts were interacting with the soil matrix, they were presumably sufficient to exchange the soil-derived C, which was

incorporated into the MB. Only small amounts of additionally released soil-derived C were mineralized and this is proven by the primed C amounts. So, freshly released soil-derived C was available for incorporation into the microbial biomass.

On the next sampling followed a release of soil-derived C from the MB and an incorporation of exudate-C in the MB took place in both soils to the same amounts. The exchange process discussed occurred only at the commencement of the incubation. The amounts of soil-derived C in the microbial biomass of the exudate-treated soils were smaller than the control MB-C except for sampling 1. This indicates that soil-derived C was substituted by exudate-derived C in the microbial biomass. Most likely this C substitution was linked to a change in the microbial community structure in the treated soils.

This change in the microbial community structure is in line with the results of Griffiths et al. (1999). They showed a changing microbial community structure due to the addition of artificial exudates to soil. Also, Benizri et al. (2002) found a selection of a small specific microbial population by maize exudates accompanied by a decrease in soil microbial diversity. This is in accordance with Odum (1969) who described a few early species that are able to persist during the development of an ecosystem.

The CO_2-C evolved from exudate-treated soils compared to the controls was dominated by exudate-derived CO_2-C. This is a consequence of the adaptation of microbes to the exudate during the course of the incubation. Presumably, the newly built microbial biomass mineralized almost exclusively exudate-C. This preferential use of substrate-C might have led to negative priming effects on most of the samplings, as suggested by Kuzyakov (2002). Positive priming effects are commonly explained by microbial mediated processes, for example, the production of exoenzymes or microbial competition for energy and nutrients (Fontaine et al., 2003). It is concluded that the observed positive priming effects can also be explained by the above stated exchange processes between the soil organic matrix and exudates as observed here at the beginning of the incubation especially in the high yield soil.

However, the positive carbon balance of the exudate-treated soils shows that the primed C did not exceed the amount of exudate-C remaining in the soils.

Development in the measured pools after exudate addition

To monitor the development in the investigated pools after the exudate stop, the incubation period of the treated soils was prolonged for three weeks. This resembles the situation after harvest in the field, where no further exudates enter the soil. The stopped exudate flow was reflected in the sharply declining microbial activity and biomass values. However, even though exudate addition was stopped, obviously enough substrate had been stored and was now being released for respiration. This is proven by the detection of exudate-derived C in CO_2 at the end of the incubation. This material was either partly desorbed from the soil matrix or released from the dying microbial biomass. The latter can be seen in the fact that the net MB-C balance showed that exudate-derived C was released and became available for mineralization.

Stabilization of exudate-C

The similarity of calculated and measured C_{org} contents indicates that a stabilization of exudate-C in the treated soils occurred at least in the short-term. In this study exudates have more than the well-known substrate function for microorganisms. It was clearly shown with the use of stable isotopes that great amounts of exudate bind to the soil matrix and become stabilized in both soils to nearly the same amounts. Furthermore, it is assumed that exudates interact with non water-extractable organic matter.

The CO_2-C evolution was significantly greater in the LY compared to the HY soil explaining the lower C_{org} content of the former. In the long-term, more substrate is mineralized to CO_2-C in LY compared to the HY soil, and, thus, is not available for stabilization in soil. This assists the presumption that there are different C-fluxes in the soils investigated. Contradictory, Wessels Perelo and Munch (2005) using the same soil material in their study, found a greater microbial activity in HY compared to LY soil. This is most likely

due to the usage of other substrates in their incubation with ^{13}C labelled glucose. Interestingly, in the present study the CO_2 evolution was also greater in HY at the beginning, but the pattern reversed when a maximum content of microbial biomass due to a continuous exudate supply was present in both soils. So, the permanent substrate addition in this study reflected a more realistic situation to the field conditions, where also a steady C input of plants to soil is given.

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Chapter 4

Determination of the fate of ^{13}C labelled maize and wheat rhizodeposit-C in two agricultural soils in a greenhouse experiment under ^{13}C-CO_2 enriched atmosphere

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Abstract

A deeper understanding of the contribution of carbon (C) released by plant roots (rhizodeposition) to soil organic matter (SOM) can help to increase our knowledge of global C-cycling. These insights can eventually lead to sustainable management of SOM especially in agricultural systems. This study was conducted to determine the fate of ^{13}C labelled rhizodeposit-C of maize and wheat plants. They were grown in a greenhouse in permeable nylon bags filled with upper soil material from two agricultural soils of the same location, but with different crop yields. The bags were placed into pots, which were also filled with soil surrounding the bags. Soil inside the bags was considered as rhizosphere soil, wheras the one outside the bags represented bulk soil. The contributions of rhizodeposits to water extractable organic carbon (WEOC), microbial biomass-C (MB-C), CO_2-C evolution, and total organic carbon (C_{org}) were investigated during a 7-week growing period. The WEOC, MB-C, CO_2-C, C_{org} contents and the respective $\delta^{13}C$ values were determined regularly, and a newly developed method for determining $\delta^{13}C$ values in soil extracts was applied.

In both soils, regardless of crop yield potential, significant incorporation of rhizodeposition-derived C was observed in the MB-C, CO_2-C, and C_{org} pool, but not in the WEOC. The pattern of C incorporation into the different pools was the same for both soils with both plants, and rhizodeposit-derived C was recovered in the order MB-C < C_{org} < CO_2-C. This showed that rhizodeposits were mainly respired, but since C_{org} was the second largest pool of the overall balances, they were also stabilized in the soils at least in the short-term. It is suggested that the increased SOM mineralization observed in this study (positive priming effects) was probably induced by C exchange processes between the soil matrix and soluble rhizodeposits. Moreover, soluble rhizodeposit-C was detected in MB-C and CO_2-C evolved outside the direct root zone, showing the availability of these C-components in the bulk soil.

Introduction

Soils are the largest carbon (C) pool in terrestrial ecosystems. Any change in this pool can potentially affect the CO_2 concentration in the atmosphere and therefore influence the global climate (Wang and Hsieh, 2002). A deeper understanding of the soil organic matter (SOM) cycle can reveal, if it is a source or sink for CO_2. In addition, this understanding can give information about ecosystem functioning and global C-cycling and this helps to eventually predict and control SOM fluxes. With this knowledge, sustainable management of SOM, especially in agricultural systems, can be accomplished.

The rhizosphere - as opposed to the bulk soil - is known as the soil compartment with high microbial activity due to a high C input from plant roots (rhizodeposition) (Lynch and Whipps, 1990). Rhizosphere processes can play a key role in C sequestration and nutrient cycling in terrestrial ecosystems (Helal and Sauerbeck, 1989). Rhizodeposition comprises the total carbon directly released from plant roots into soils. A maximum of 40% of plant primary production is assumed to be lost by rhizodeposition (Lynch and Whipps, 1990). This root-derived material can comprise a main source of SOM (Kögel-Knabner, 2002). It consists of several organic compounds, as, for example, water-soluble root exudates, secretions, and lysates. They are classified in regard to their active or passive liberation from the roots (Whipps, 1990; Grayston et al., 1997).

The functions of rhizodeposits are manifold. For example, they are involved in the stabilization of soil aggregates, modify physico-chemical conditions in the rhizosphere leading to increasing availability for nutrients (Lynch and Whipps, 1990), and trigger priming effects, thereby influencing soil organic matter turnover (Helal and Sauerbeck, 1986; Fu and Cheng, 2002). The role of rhizodeposits as easily decomposable energy and C-source for microorganisms is often mentioned in literature (Kuzyakov et al., 2000; Butler et al., 2003). This stresses the functional importance of rhizodeposition in this regard, since microorganims

act as a source and sink of plant nutrients, thereby influencing ecosystem productivity (Butler et al., 2004).

The fate of C from rhizodeposits in soil is still unanswered (Hütsch et al., 2002). In this respect it is also uncertain how much of the C coming into the soils remains as SOM and how much is mineralized in the short-term, thus becoming relevant in a climate change perspective (Hagedorn et al., 2003).

The uncertainties concerning the dynamics of rhizodeposits are due to the small concentrations and fast mineralization of root-derived compounds in soils (Kuzyakov and Domanski, 2000). Since root- and soil-derived C is present as a complex mixture, isotope techniques can be used to separate these C-sources and trace their fluxes in soils, as has been done in several studies with natural ^{13}C abundance or ^{14}C, respectively (Flessa et al., 2000; Gregorich et al., 2000; Hütsch et al., 2002). Yevdokimov et al. (2006) used enriched ^{13}C-CO_2 for labelling plants and determined the C allocation below-ground.

However, our knowledge of below-ground C-dynamics including the rhizosphere is poorly understood and limited data sets are available in terms of turnover of whole rhizodeposits (Hütsch et al., 2002; Jones et al., 2004). The study was conducted to gain quantitative information about their dynamics in order to improve our understanding of SOM fluxes and C sequestration in soils as outlined above. The aim of the study was to determine the contribution of ^{13}C labelled maize or wheat rhizodeposits to water extractable organic carbon (WEOC), microbial biomass, CO_2 evolution, and total organic carbon (C_{org}) during an incubation of material from two agricultural soils with different yield. These soils were chosen, since it was assumed that their nutrient and C-fluxes are different from each other, based on their different yield pattern. To separate rhizosphere from bulk soil, plants were grown in pots in which the roots were isolated from the soil with special nylon tissue (Kuchenbuch and Jungk, 1982).

The experimental approach was chosen, because it was expected that the easily degradable rhizodeposits would almost completely be recovered in WEOC, microbial biomass, CO_2, and C_{org}.

Material and methods

Soil

The soil sampling was from a field with with potato - winter wheat – maize - winter wheat rotation history at the agro-ecological research station in Scheyern, approximately 40 km north of Munich, Germany (48°30', 11°20'E). A harvester equipped with a Global Positioning System and devices to record the yield amounts obtained data from this field over 4 years. As a result distinct stable areas of lower (LY) and higher yield (HY) were designated. Soil material was collected from the upper 10 cm of a Dystric Cambisol in the low yield area and of a Eutric Cambisol in the high yield area in summer 2004. The LY soil had the following characteristics: clay 20%, silt 51%, sand 29%, pH ($CaCl_2$) 6.1, C_{org} 1.3% and total N 0.13%. The properties of the HY soil were as follows: clay 15%, silt 49%, sand 36%, pH ($CaCl_2$) 5.9, C_{org} 1.4%, and total N 0.14%.

In this study the soils were used field-fresh and unsieved, but were separated from coarse plant residues and gravels. The soils were filled in bags made of nylon screen tissue with a 16 µm mesh size (Sefar Inc., Switzerland) containing 250 g soil (fresh weight). Three of those bags were placed into one pot (16 cm in diameter) with 865 g field-fresh soil surrounding the bags, making a total of 1615 g soil per pot. Soil moisture was adjusted to a water-content equivalent to around 50% water-filled pore space with a nutrient solution with the following macroelements (in mM litre^{-1}): 0.7 K_2SO_4, 0.1 $CaCl_2$, 0.5 $MgSO_4$, 4 KNO_3, 0.02 $C_2H_{10}N_2O_4S \cdot FeSO_4$, 0.25 KH_2PO_4. Microelements were added in the following concentrations (in µM litre^{-1}): 0.5 $MnSO_4$, 1 H_3BO_3, 0.5 $ZnSO_4$, 0.2 $CuSO_4$, 0.01 $(NH_4)_6Mo_7O_{24}$. The soils were pre-incubated in the pots over 3 weeks before they were planted.

Plant culture and labelling

Seeds of maize (*Zea mays* L., Gavott) and wheat (*Tritivum aestivum* L., Petrus) were pre-germinated in the dark on moist filter paper for one week. The seedlings were then transferred into the bags. Figure 1 shows exemplary the pot design with only one bag. In LY and HY, 35 maize and wheat plants were grown, making a total of 140 bags. The soil inside the bags was considered as rhizosphere soil, wheras the one outside the bags represented bulk soil. The bulk soils of the first sampling were considered as starting points and used as time zero (*t*0), as has also been done by Helal and Sauerbeck (1986). On all samplings, the values of the rhizosphere soils were related to these controls (*t*0) to show the development over the time of the growing period.

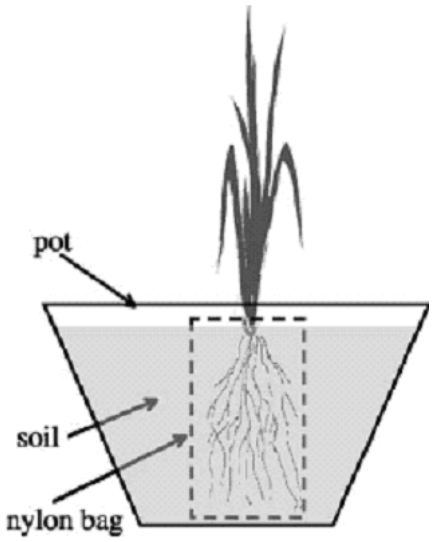

Figure 1 Experimental setup for separating rhizosphere from bulk soil in pots planted with maize and wheat (taken from Yevdokimov et al. (2006)).

Plants were grown for ten weeks under an airtight tent built of transparent plastic foil to separate the plants from the outer greenhouse atmosphere. The CO_2 concentration beneath the tent was measured continuously by infrared detection and was kept from 300 to 400 µmol mol^{-1}. To prevent a rising CO_2 concentration due to soil respiration the tent-air was pumped continuously through a washing flask filled with sodium hydroxide on support that absorbed

CO_2. In order to label the plants and consequently their rhizodeposition, CO_2 beneath the tent was continuously enriched with ^{13}C-CO_2. This was done by automatically dosing ^{13}C-CO_2 when the CO_2 concentration fell below 300 µmol mol^{-1}.

Plant culture was performed with a photoperiod of 12 hours with an average temperature of 20°C and relative humidity of nearly 100% inside the tent. The surface of the pots was covered with a perforated black plastic foil to avoid algal growth and to prevent soil from drying. Water content of the soils was checked once a week by weighing, but had to be adjusted with distilled water only once, since the humidity inside the tent was relatively high.

Incubation

Experimental design

Soil sampling started when plants were 3-weeks old. It was then expected that the roots were big enough to have a detectable influence on the soils in the bags. Soil sampling was continued weekly. On each sampling, the roots of five maize and five wheat plants grown in LY and HY were carefully separated from the rhizosphere soil inside the bags. The soil of each bag was thoroughly mixed before analysis. From the bulk soil, which was also mixed, five samples were taken. Soils of each treatment (LY control, HY control, planted LY, planted HY) in aliquots to 5 g fresh-weight were filled in 30 ml glass vials for determination of microbial biomass-C, water extractable organic C, and CO_2-C evolution. All results are expressed as equivalents to oven dried soil (105˚C for around 24 hours).

Analysis

Plant root weight

The plant roots harvested on each sampling as described above were gently cleaned with water from adhering soil and were then dried in an oven at 30˚C for around 48 hours. Each maize and wheat root was weighed separately.

Water extractable organic carbon (WEOC)

WEOC was obtained by shaking the soil samples with 0.01 M $CaCl_2$ solution on an over-head shaker for 15 minutes at a soil (mass):solution (volume) ratio of 1:4 and subsequent filtration through 0.45 µm pore-size polycarbonate filters. The WEOC concentration was determined on a Total Carbon Analyser (Shimadzu TOC 5050, Tokyo, Japan) by catalytic high temperature oxidation (Zsolnay, 2003).

Microbial Biomass

The microbial biomass carbon (MB-C) was determined by the chloroform-fumigation extraction (CFE) method (Vance et al., 1987) with 5 g of soil for the fumigated and non-fumigated assey in 20 ml of 0.5 M K_2SO_4 solution. Dissolved organic carbon (DOC) in the extracts was determined on a Shimadzu TOC 5050. The difference between DOC in fumigated and non-fumigated samples was divided by 0.45 to calculate MB-C (Joergensen et al., 1996).

Total organic carbon (C_{org}) and ^{13}C values of C_{org} and roots

The C_{org} content was determined with an elementar analyser Eurovector CN coupled with a gas chromatograph/isotope ratio mass spectrometer (GC/IRMS) (Finnigan MAT DeltaPlus, Bremen, Germany). MB-C was subtracted from C_{org}, in order to regard both C pools separately.

The dried roots were finely ground and processed as described for C_{org}.

^{13}C in WEOC and chloroform-fumigation extraction samples

The $^{13}C/^{12}C$ ratios in liquid samples were determined by a liquid chromatograph/isotope ratio mass spectrometer (LC/IRMS) (Thermo Finnigan LC IsoLink and MAT 253, Bremen, Germany) by an on-line method newly developed by Krummen et al. (2004). The LC IsoLink worked in a mode that allows the bulk isotopic analysis of all water-soluble material. On the LC IsoLink, the samples were processed as follows: organic substances in the extracts were oxidized quantitatively to CO_2 by 0.45 M $Na_2S_2O_8$ and 8.5% H_3PO_4 solutions in a reaction

chamber at 99.9°C. The CO_2 was separated from the liquid phase with a gas-exchange membrane and admitted to the IRMS in a stream of helium via an open split.

The ^{13}C values of the soil extracts determined were compared with values of an internal laboratory standard (benzoic acid solution) and a blank (solvent used for soil extraction), both of which were included in all sample measurements at regular intervals. The C concentrations of the standards were chosen according to the given concentrations of the soil extracts. The accuracy of this method has been presented for soil extracts by Marx et al (2007). The measurements were reproducible over time and sensitive in measuring ^{13}C in extracts with very small C concentrations around 1 mg C litre^{-1}.

CO_2 and $^{13}CO_2$ in gaseous samples

On each sampling, CO_2-concentrations and their corresponding $^{13}C/^{12}C$ ratios evolved from soil samples were determined on-line with a GC/IRMS. Five vials of each treatment were closed air-tight with a plastic lid with a rubber septum and placed in a water jacket adjusted to the incubation temperature (20°C). The rack was specially built to be mounted on a CombiPAL autosampler (CTC, Zwingen, Switzerland). The values of CO_2 and respective $^{13}CO_2$ enrichment in the headspace of the vials were determined with 5 measurements on each sample over a 26-hour-period. Samples were withdrawn from the vials' headspaces by a syringe on the autosampler and injected into the GC/IRMS. All sample values were compared with reference CO_2 at different concentrations. A regression line was fitted to the measured points ($R^2 > 0.95$) in order to calculate a CO_2 production rate. From this rate the CO_2 amounts per day were estimated and subsequently cumulated in order to obtain the total CO_2 amounts evolved on the respective samplings. The control CO_2-C amounts for the respective samplings were extrapolated by cumulating the CO_2-C emissions of *t*0.

Calculations

The $\delta^{13}C$ values of the samples were expressed relative to the international VPDB standard:

$$\delta^{13}C\ (‰\ VPDB) = \left(\frac{R_{sample} - R_{VPDB}}{R_{VPDB}} \right) x\ 1000, \quad (1)$$

where $R = \frac{^{13}C}{^{12}C}$ and $R_{VPDB} = 0.0111802$ (Werner & Brand, 2001).

We calculated the $\delta^{13}C$ (‰ VPDB) of MB-C from the following mixing equation:

$$\delta^{13}MB\text{-}C = \frac{(c_{fum}\ x\ \delta^{13}C_{fum}) - (c_{nfum}\ x\ \delta^{13}C_{nfum})}{(c_{fum} - c_{nfum})}, \quad (2)$$

where c_{fum} and c_{nfum} = concentration (µg g^{-1}) of C in the fumigated and non-fumigated soils, respectively.

We calculated the fraction of C originating from rhizodeposits ($f_{rhizodeposit}$) in MB-C, WEOC, CO_2-C, or C_{org} from:

$$f_{rhizodeposit} = \frac{(\delta^{13}C_{mix} - \delta^{13}C_{soil})}{(\delta^{13}C_{rhizodeposit} - \delta^{13}C_{soil})} \quad (3)$$

where $\delta^{13}C_{mix}$ = composition of soil-derived and rhizodeposit-derived ^{13}C (‰ VPDB), and $\delta^{13}C_{soil/rhizodeposit}$ = $\delta^{13}C$ (‰ VPDB) of soil or rhizodeposit, respectively. The $\delta^{13}C$ values of the rhizodeposit-C were assumed to be those of the roots.

We calculated the contribution of rhizodeposit-C ($c_{rhizodeposit}$) to WEOC, MB-C, CO_2-C, or C_{org} total concentration (µg g^{-1}) from:

$$c_{rhizodeposit} = f_{rhizodeposit}\ x\ c_{total} \quad (4)$$

where c_{total} = total concentration (µg g^{-1}) of WEOC, MB-C, CO_2-C, or C_{org}, respectively.

The priming effect (PE) was calculated according to Hamer and Marschner (2002). As a prerequisite for the determination of PE, the difference between soil-derived CO_2-C of planted soil and the control CO_2-C must be significant on the basis of an unpaired *t*-test ($P < 0.05$) over the respective time interval. The PE for this time span was calculated from:

$$PE\ (\%) = \frac{\Delta CO_2\text{-}C_{soil\text{-}derived} - \Delta CO_2\text{-}C_{control}}{\Delta CO_2\text{-}C_{control}}\ x\ 100 \quad (5)$$

where $\Delta CO_2\text{-}C_{soil\text{-}derived}$ = (soil-derived CO_2-C of planted soil) – (soil-derived CO_2-C of planted soil from previous sampling), and $\Delta CO_2\text{-}C_{control}$ = (control CO_2-C) – (control CO_2-C from previous sampling).

The absolute amounts of primed C were calculated by subtracting $\Delta CO_2\text{-}C_{control}$ from $\Delta CO_2\text{-}C_{soil\text{-}derived}$ for the relevant time intervals. These values are referred to as "net". It must be noted that the CO_2-C emissions of the controls (i.e. bulk soil) of the 1st sampling were assumed to represent the soil status at time zero (*t*0) as stated above, and that they were cumulated from sampling to sampling.

Statistics

All results are expressed as the means of five replicates with standard errors. An unpaired *t*-test was used to compare the $\delta^{13}C$ values of the planted soils with their respective controls (*t*0) in order to detect significant contributions of rhizodeposit-C to the C pools investigated on the different samplings.

The WEOC, MB-C, CO_2-C, and C_{org} content data were subjected to an ANOVA to determine significant plant, time, and soil effects on the different C-fractions of the pools investigated. Unpaired *t*-tests were conducted to reveal significant differences between the controls (*t*0) and the soil-derived fractions on the different samplings, and the percentages of rhizodeposit-C of the investigated pools in low compared to high yield soil. All tests were done at a significance level of $P < 0.05$.

Results

Root mass and $\delta^{13}C$ of the roots

In low yield soil, root growth tended to be smaller compared to the high yield soil (Figure 2). Furthermore, maize had greater root masses than wheat.

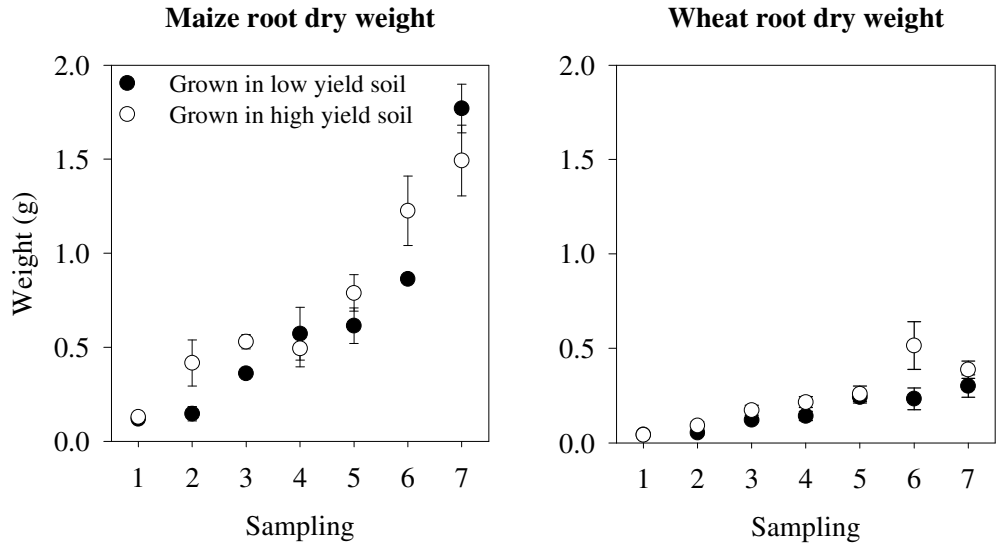

Figure 2 Dry root weight of maize and wheat plants grown in low and high yield soil materials during the course of the 7-week experiment. Error bars represent standard errors of the means (n = 5).

Table 1 shows increasing $\delta^{13}C$ values of maize and wheat roots from the beginning of the experimental period to sampling 5. Subsequently, the values for wheat roots decreased, whereas those of maize roots showed no clear trend. Nevertheless, the ^{13}C-enrichments of both plant roots were drastically greater at the end compared to the beginning of the experiment. The $\delta^{13}C$ values of maize roots were consistently greater than those of wheat.

WEOC

The plant rhizodeposit-C contributions to WEOC were considered to be negligible over the observed incubation period, although some contributions were detected on sampling 6 for maize (5.52 µg g^{-1}) and wheat (6.47 µg g^{-1}) planted low yield soil corresponding to the relatively high total WEOC amounts on this sampling. Maize planted low yield soil (1.34 µg g^{-1}) and wheat planted high yield soil (3.85 µg g^{-1}) showed also rhizodeposit-C contributions to WEOC on sampling 7. However, due to the small amounts and few contributions of root-derived components to WEOC only soil-derived WEOC is presented in Figure 2. The WEOC contents in both of the planted soils showed significant temporal

fluctuations (Table 2). Nevertheless, the WEOC contents were around 14 µg g^{-1}, irrespective of soils and plants.

Table 1 Values of $\delta^{13}C$ from maize and wheat roots grown in low and high yield soil materials during the course of the 7-week experiment. Values in parentheses are standard errors of the means (n = 5).

Sampling (week)	Low yield soil		High yield soil	
	Maize roots	Wheat roots	Maize roots	Wheat roots
	$\delta^{13}C$ (‰ VPDB)			
1	–8.7 (0.2)	–25.3 (0.2)	–4.4 (1.8)	-
2	–0.8 (4.5)	–19.5 (-)	3.9 (1.6)	–12.5 (2.4)
3	10.1 (5.8)	1.8 (1.0)	16.3 (1.1)	10.1 (1.2)
4	28.6 (5.3)	24.6 (0.0)	28.2 (4.2)	24.1 (3.7)
5	34.6 (2.2)	31.6 (2.0)	34.5 (3.8)	32.3 (0.1)
6	33.4 (2.2)	28.2 (3.6)	35.9 (1.1)	30.4 (1.1)
7	37.4 (2.0)	25.8 (5.3)	32.8 (1.7)	20.7 (1.2)

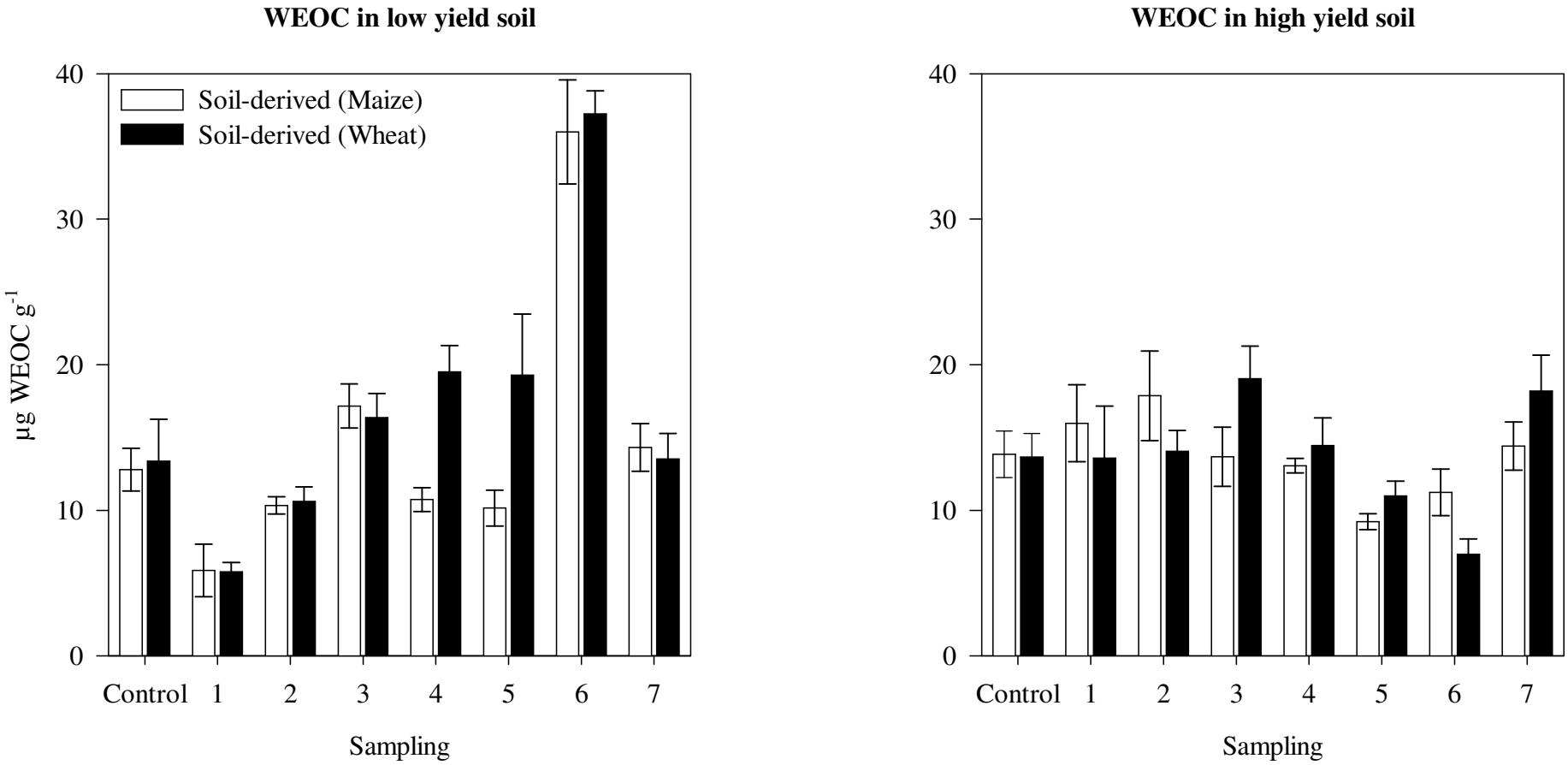

Figure 2 Amounts of WEOC from maize and wheat rhizodeposit-derived C and of the respective soil-derived C in low and high yield soil materials over the 7-week experimental period. Error bars represent standard errors of the means (n = 5).

Table 2 Analysis of variance of water extractable organic carbon (WEOC), microbial biomass-C (MB-C), CO_2-C, and C_{org} data.

Source of variation	Degrees of freedom	Sum of squares	Mean square	*F*	*P*
Total WEOC					
Plant	1	59.440	59.440	2.867	0.094
Sampling	6	1671.799	278.633	13.439	< 0.001
Soil	1	180.782	180.782	8.720	0.004
Plant x sampling	6	244.816	40.803	1.968	0.077
Plant x soil	1	39.259	39.259	1.894	0.172
Sampling x soil	6	3822.047	637.008	30.724	< 0.001
Plant x sampling x soil	6	211.567	35.261	1.701	0.129
Residual	99	2052.574	20.733		
Total MB-C					
Plant	1	6319.681	6319.681	7.292	0.008
Sampling	6	27792.973	4632.162	5.345	< 0.001
Soil	1	21112.541	21112.541	24.360	< 0.001
Plant x sampling	6	9762.495	1627.083	1.877	0.091
Plant x soil	1	188.784	188.784	0.218	0.642
Sampling x soil	6	44211.633	7368.606	8.502	< 0.001
Plant x sampling x soil	6	5408.656	901.443	1.040	0.404
Residual	106	91868.897	866.688		
Soil-derived MB-C					
Plant	1	461.498	461.498	0.866	0.354
Sampling	6	47558.321	7926.387	14.868	< 0.001
Soil	1	12959.587	12959.587	24.309	< 0.001
Plant x sampling	6	3470.695	578.449	1.085	0.376
Plant x soil	1	2646.597	2646.597	4.964	0.028
Sampling x soil	6	42849.053	7141.509	13.395	< 0.001
Plant x sampling x soil	6	7425.065	1237.511	2.321	0.038
Residual	102	54379.141	533.129		
Rhizodeposit-derived MB-C					
Plant	1	105.569	105.569	0.149	0.700
Sampling	6	23993.116	3998.853	5.645	0.000
Soil	1	666.986	666.986	0.942	0.335
Plant x sampling	5	16379.404	3275.881	4.624	0.001
Plant x soil	1	39.502	39.502	0.056	0.814
Sampling x soil	5	4332.707	866.541	1.223	0.305
Plant x sampling x soil	3	7016.817	2338.939	3.302	0.024
Residual	84	59507.638	708.424		

Continued on the following page.

Table 2 Continued.

Source of variation	Degrees of freedom	Sum of squares	Mean square	*F*	*P*
Total CO_2-C					
Plant	1	316134.534	316134.534	752.065	< 0.001
Sampling	6	4918228.380	819704.730	1950.027	< 0.001
Soil	1	56437.543	56437.543	134.261	< 0.001
Plant x sampling	6	104809.368	17468.228	41.556	< 0.001
Plant x soil	1	29757.555	29757.555	70.791	< 0.001
Sampling x soil	6	46787.181	7797.864	18.551	< 0.001
Plant x sampling x soil	6	16175.240	2695.873	6.413	< 0.001
Residual	98	41194.837	420.355		
Soil-derived CO_2-C					
Plant	1	22050.975	22050.975	95.008	< 0.001
Sampling	6	977152.561	162858.760	701.688	< 0.001
Soil	1	50857.976	50857.976	219.125	< 0.001
Plant x sampling	6	6769.915	1128.319	4.861	< 0.001
Plant x soil	1	34.683	34.683	0.149	0.700
Sampling x soil	6	9111.022	1518.504	6.543	< 0.001
Plant x sampling x soil	6	578.516	96.419	0.415	0.867
Residual	98	22745.390	232.096		
Rhizodeposit-derived CO_2-C					
Plant	1	558496.767	558496.767	1515.719	< 0.001
Sampling	6	1538546.127	256424.355	695.917	< 0.001
Soil	1	761.372	761.372	2.066	0.154
Plant x sampling	5	51245.243	10249.049	27.815	< 0.001
Plant x soil	1	31482.359	31482.359	85.441	< 0.001
Sampling x soil	6	22107.354	3684.559	10.000	< 0.001
Plant x sampling x soil	5	9698.808	1939.762	5.264	< 0.001
Residual	93	34267.692	368.470		
Total C_{org}					
Plant	1	263600.978	263600.978	0.381	0.538
Sampling	6	5080379.296	846729.883	1.223	0.300
Soil	1	61649005.198	61649005.198	89.066	< 0.001
Plant x sampling	6	5289098.342	881516.390	1.274	0.275
Plant x soil	1	383875.184	383875.184	0.555	0.458
Sampling x soil	6	4334303.731	722383.955	1.044	0.401
Plant x sampling x soil	6	1524577.024	254096.171	0.367	0.898
Residual	109	75447121.851	692175.430		

Continued on the following page.

Table 2 Continued.

Source of variation	Degrees of freedom	Sum of squares	Mean square	*F*	*P*
Soil-derived C_{org}					
Plant	1	17212.838	17212.838	0.025	0.875
Sampling	6	6557351.555	1092891.926	1.571	0.163
Soil	1	55241448.782	55241448.782	79.388	< 0.001
Plant x sampling	6	6747195.240	1124532.540	1.616	0.150
Plant x soil	1	178723.158	178723.158	0.257	0.613
Sampling x soil	6	3812947.788	635491.298	0.913	0.488
Plant x sampling x soil	6	1390030.575	231671.763	0.333	0.918
Residual	106	73759187.938	695841.396		
Rhizodeposit-derived C_{org}					
Plant	1	88649.143	88649.143	7.215	0.010
Sampling	4	14330.605	3582.651	0.292	0.882
Soil	1	58851.912	58851.912	4.790	0.034
Plant x sampling	2	75278.002	37639.001	3.063	0.056
Plant x soil	1	66068.374	66068.374	5.377	0.025
Sampling x soil	3	32164.800	10721.600	0.873	0.462
Residual	47	577512.233	12287.4943		

Microbial biomass-C (MB-C)

In the maize planted soils, rhizodeposit-C contributed to the total MB-C throughout the experiment, except for sampling 3 in LY. In wheat planted soils, these contributions were observed on samplings 2 and from 4 to 7 in LY, and from sampling 3 in HY. The contributions were smallest on sampling 1 in both maize planted soils. Thereafter, the amounts of maize-rhizodeposition C in the MB varied irregularly. In wheat planted low yield soil, strongly scattering values in a great range were observed. Contrastingly, in wheat planted high yield soil the contributions of rhizodeposit-C to total MB-C were relatively stable (Figure 3).

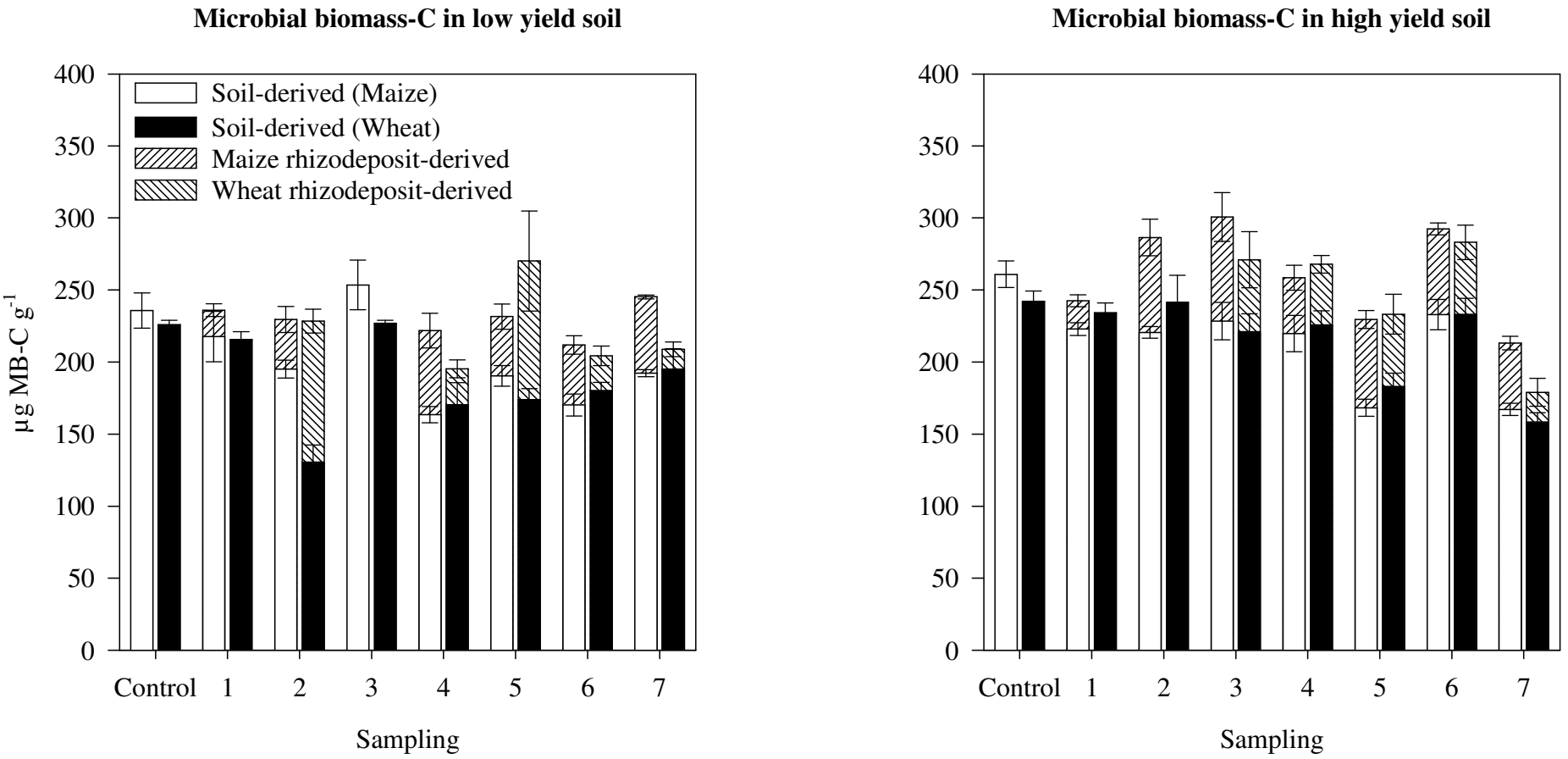

Figure 3 Amounts of MB-C from maize and wheat rhizodeposit-derived C and of the respective soil-derived C in low and high yield soil materials over the 7-week experimental period. Error bars represent standard errors of the means (n = 5).

The total MB-C amounts in both of the planted soils showed significant temporal fluctuations (Table 2). The concentrations of MB-C in planted soils were on a similar level to those of the controls. The mean total MB-C content was around 240 µg g^{-1}, with a minimum value of around 180 µg g^{-1} in wheat planted high yield soil on sampling 7 and a maximum value of around 300 µg g^{-1} in maize planted high yield soil on sampling 3. The plant, sampling, and soil interactions had a significant effect on the rhizodeposit- and soil-derived C-fractions in the microbial biomass (Table 2).

The soil-derived C-fractions of the planted soils revealed significantly smaller values than the controls (*t*0). Soil-derived MB-C values of maize and wheat planted soils were significantly greater in HY compared to LY (Table 2).

CO_2-C

Maize rhizodeposits contributed significantly to the CO_2 evolutions over the whole experimental period in both soils, whereas rhizodeposits of wheat contributed to the CO_2 emissions from the second sampling on (Figure 4).

The CO_2 emissions from the maize planted soils were significantly greater than those from the wheat planted soils. From the maize planted LY the CO_2-C emissions were significantly greater than from maize planted HY at the beginning of the experiment (Table 2). After staying on a similar level, the emission pattern turned and was higher in HY than in LY on sampling 7. From wheat planted LY the CO_2 emissions were greater than from the wheat planted HY.

Strongly significant correlations ($P < 0.01$) were calculated between root weight and rhizodeposit-derived CO_2-C. In LY the values amounted to r = 0.78 for maize and r = 0.71 for wheat. The corresponding values for HY were r = 0.86 and r = 0.81, respectively.

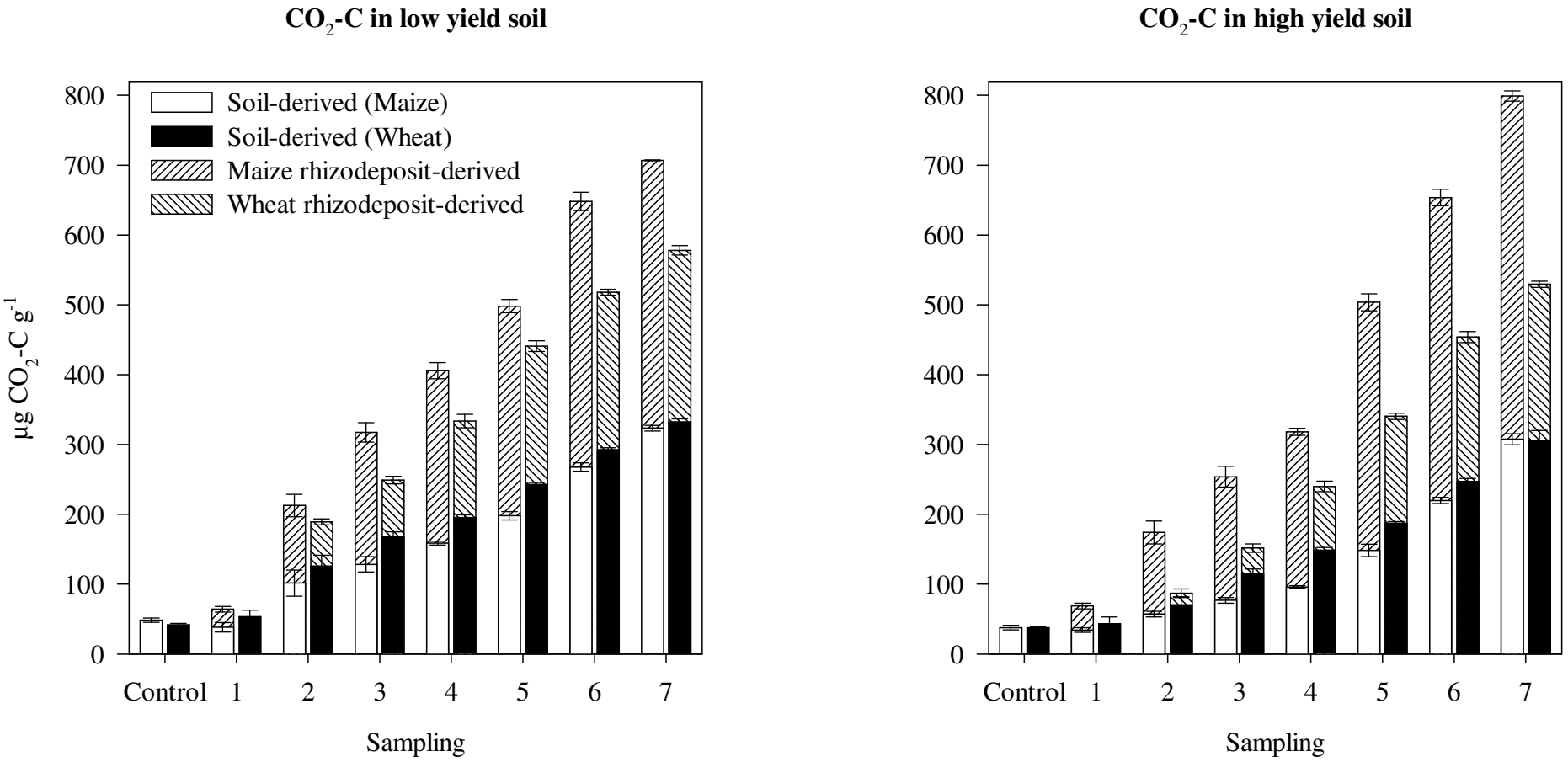

Figure 4 Amounts of CO_2-C from maize and wheat rhizodeposit-derived C and of the respective soil-derived C in low and high yield soil materials over the 7-week experimental period. Error bars represent standard errors of the means (n = 5).

At the end of the experiment, the soil-derived CO_2-C evolutions in both of the planted soils rose to roughly 310 µg g^{-1}. The interaction between soil, sampling, and plant had a significant effect on the rhizodeposit-derived CO_2-C emission (Table 2). The rhizodeposit-derived CO_2-C emission amounted to 380 µg g^{-1} in maize planted LY, being significantly smaller than in HY with 490 µg g^{-1}. The corresponding values for wheat planted soils were significantly smaller than in the maize planted soils during the experimental period, amounting to 245 or 225 µg CO_2-C g^{-1} in LY or HY, respectively.

Priming and net effects of rhizodeposition on soil derived CO_2-C

The addition of organic substances to soils can accelerate (positive priming) or retard (negative priming) the mineralization of soil organic matter. Positive (+) and negative (–) priming effects (PE) were mainly revealed in maize planted HY, namely on the samplings 2 to 4, and on samplings 6 and 7. PE occurred in maize planted low yield soil only on samplings 4 and 6. In wheat planted soils, such an effect was detectable on sampling 4 in LY and on sampling 6 in HY (Table 3).

The net soil-derived CO_2-C values also represented the actual amount of primed C. These values tended to turn from negative to positive amounts in both of the maize planted soils, and this effect was more pronounced in HY.

C_{org}

Incorporation of rhizodeposits into C_{org} was revealed by significant differences between the ^{13}C values of planted soils and their respective controls on the following samplings. Maize and wheat rhizodeposits contributed from sampling 3 to 7 and on samplings 5 and 7, respectively, to total C_{org} in low yield soil. The contributions of maize and wheat rhizodeposits to C_{org} in high yield soil was observed on samplings 4 to 7 and 4 to 5, respectively (Table 4).

Table 3 Net soil derived CO_2-C amounts and priming effects of maize and wheat planted low and high yield soils over the experimental period. Values in parentheses are standard errors of the means (n = 5).

Sampling	Low yield				High Yield			
	Maize	Wheat	Maize	Wheat	Maize	Wheat	Maize	Wheat
	Net soil-derived CO_2-C[a]		Priming effect		Net soil-derived CO_2-C[a]		Priming effect	
	(mg g^{-1})		(%)		(mg g^{-1})		(%)	
1	–9.99 (6.83)	11.56 (9.34)	n.s.	n.s.	–3.43 (3.18)	6.24 (2.82)	n.s.	n.s.
2	14.69 (8.86)	30.63 (15.42)	n.s.	n.s.	–15.08 (3.92)	–10.51 (11.20)	–39.78 (10.33)	n.s.
3	–21.66 (10.79)	0.06 (6.75)	n.s.	n.s.	–18.06 (4.09)	7.40 (6.03)	–47.67 (10.80)	n.s.
4	–18.02 (2.57)	–14.65 (3.67)	–37.15 (5.31)	–34.88 (8.75)	–18.93 (1.73)	–4.97 (4.28)	–49.96 (4.56)	n.s.
5	–9.38 (5.96)	5.40 (2.61)	n.s.	n.s.	14.60 (8.95)	1.05 (2.37)	n.s.	n.s.
6	21.32 (5.83)	7.64 (2.73)	43.94 (12.02)	n.s.	33.60 (4.28)	22.12 (4.04)	88.65 (11.31)	58.62 (10.71)
7	7.17 (4.04)	–2.16 (4.34)	n.s.	n.s.	49.65 (8.05)	21.36 (13.68)	131.02 (21.25)	n.s.

[a]Absolute amounts of primed C

n.s. not significant

Table 4 Amounts of total and rhizodeposit-derived C_{org} from maize and wheat planted low and high yield soil over the experimental period. Values in parentheses are standard errors of the means (n = 5).

Sampling	Low yield				High Yield			
	Maize	Wheat	Maize	Wheat	Maize	Wheat	Maize	Wheat
	Total C_{org}		Rhizodeposit-derived C_{org}		Total C_{org}		Rhizodeposit-derived C_{org}	
	(mg g^{-1})		(mg g^{-1})		(mg g^{-1})		(mg g^{-1})	
Control (*t* 0)	12.88 (0.60)	13.54 (0.24)	0	0	14.14 (0.56)	13.81 (0.35)	0	0
1	14.15 (0.22)	13.83 (0.50)	0	0	14.89 (0.36)	14.76 (0.53)	0	0
2	13.18 (0.17)	13.18 (0.15)	0	0	15.25 (0.66)	14.71 (0.92)	0	0
3	13.38 (0.31)	13.02 (0.09)	0.13 (0.04)	0	14.43 (0.29)	14.38 (0.39)	0	0
4	13.19 (0.29)	13.08 (0.28)	0.12 (0.03)	0	14.94 (0.29)	14.05 (0.32)	0.19 (0.04)	0.15 (0.04)
5	13.16 (0.04)	13.68 (0.33)	0.15 (0.09)	0.13 (0.04)	14.78 (0.28)	14.84 (0.35)	0.35 (0.07)	0.09 (0.01)
6	13.19 (0.33)	13.74 (0.36)	0.17 (0.06)	0	14.04 (0.18)	14.87 (0.38)	0.30 (0.06)	0
7	13.15 (0.16)	12.98 (0.11)	0.18 (0.01)	0.06 (0.02)	15.24 (0.51)	14.61 (0.17)	0.41 (0.08)	0

The soil factor showed a significant influence on the total, soil-, and rhizodeposit-derived C_{org} content. The soil was the only factor that had a significant effect on the soil-derived C_{org} content (difference between total and rhizodeposition-derived C_{org} in Table 4). Moreover, for the plant factor and the interaction of plant and soil a significant effect on rhizodeposit-derived C_{org} was revealed (Table 2).

Significantly greater total C_{org} values were found in maize planted high yield compared to low yield soil with a mean difference of 1.6 mg g^{-1}. C_{org} in wheat planted HY soil showed significantly greater values with a mean difference of about 1.4 mg g^{-1}. The mean maize rhizodeposit-derived C_{org} in HY was 0.31 mg g^{-1} and was significantly higher than the LY one with 0.15 mg g^{-1}. The same was true for wheat rhizodeposit-derived C_{org}, where the values amounted to 0.09 and 0.12 mg g^{-1} in LY and HY, respectively.

Contributions of rhizodeposit-C to microbial biomass, CO_2, and C_{org}

Absolute amounts of rhizodeposit-C in the measured pools and in CO_2 as described above are compiled in Table 5 as per cent values of the respective total amounts. Consequently, the presented data reflect the development of the absolute amounts.

The contribution of maize rhizodeposits to total MB-C was between 15-26%, except for the first sampling and sampling 3 in LY. Wheat rhizodeposits contributed to total MB-C between 12-20%, except for some differing values in LY. Rhizodeposits had the greatest contribution to CO_2-C compared to MB-C and C_{org}, being generally higher in maize than in wheat planted soil. The C_{org} values tended to be higher in maize planted soils in comparison to wheat planted ones. Additionally, HY tended to show higher values than LY.

Overall balance

The fate of rhizodeposit-C in both soils after the whole experimental period was calculated by summing up the rhizodeposit-derived C values of MB-C, CO_2-C, and C_{org} on the last sampling (in wheat planted high yield soil C_{org} on sampling 5 was taken). In maize planted low yield soil the total rhizodeposit-C input amounted to 617 µg C g^{-1} and in high yield soil

947 µg C g^{-1}. For wheat planted soils the rhizodeposit-C input was 317 and 332 µg g^{-1}, respectively. These values were then referred separately to MB-C, CO_2-C, and C_{org} (Figure 5). As a consequence of the lacking contribution of rhizodeposit-derived C to WEOC, it is not presented in the balances.

Table 5 Contribution of maize and wheat rhizodeposit-C to microbial biomass, CO_2, and C_{org} in low and high yield soil. Values in parentheses show standard errors of the means (n = 5).

Sampling	Low yield soil					
	Maize			Wheat		
	MB-C	CO_2-C	C_{org}	MB-C	CO_2-C	C_{org}
	(%)			(%)		
1	8.00 (1.93)	40.52 (5.63)	0	0	0	0
2	14.75 (3.59)	52.48 (7.70)	0	42.40 (4.30)	34.16 (4.31)	0
3	36.84 (11.50)	59.42 (3.53)	1.01 (0.34)	2.19 (0.74)	32.51 (2.10)	0
4	25.48 (3.48)	60.73 (1.04)	0.91 (0.18)	12.35 (2.87)	41.22 (2.02)	0
5	17.63 (3.44)	60.18 (1.47)	1.10 (0.65)	31.95 (8.20)	44.84 (0.89)	0.94 (0.27)
6	19.71 (3.09)	58.61 (1.18)	1.28 (0.47)	11.76 (3.25)	43.50 (0.65)	0
7	21.58 (0.60)	54.23 (0.31)	1.36 (0.05)	6.43 (2.14)	42.45 (0.68)	0.44 (0.14)
	High yield soil					
1	7.85 (1.51)	49.71 (4.61)	0	0	0	0
2	22.59 (3.76)	66.15 (4.60)	0	0	19.35 (7.17)	0
3	23.29 (4.39)	69.19 (2.67)	0	17.46 (6.10)	23.67 (3.94)	0
4	15.14 (3.32)	69.79 (0.80)	1.26 (0.30)	15.04 (0.63)	37.88 (2.13)	1.26 (0.30)
5	26.61 (2.38)	70.57 (0.56)	2.35 (0.44)	20.33 (4.54)	44.93 (0.58)	0.58 (0.10)
6	20.26 (0.66)	66.31 (0.64)	2.12 (0.43)	17.56 (3.92)	45.48 (0.57)	0
7	21.49 (1.61)	61.52 (0.35)	2.68 (0.51)	12.28 (1.42)	42.21 (0.77)	0

The pattern of C incorporation into the different pools was the same for both soils with both plants, and rhizodeposit-derived C was recovered in the order MB-C < C_{org} < CO_2-C. The relative mineralization to CO_2 for both of the rhizodeposits was significantly greater in LY than in HY. The wheat planted soils showed additionally significantly greater relative microbial activity than the maize planted ones.

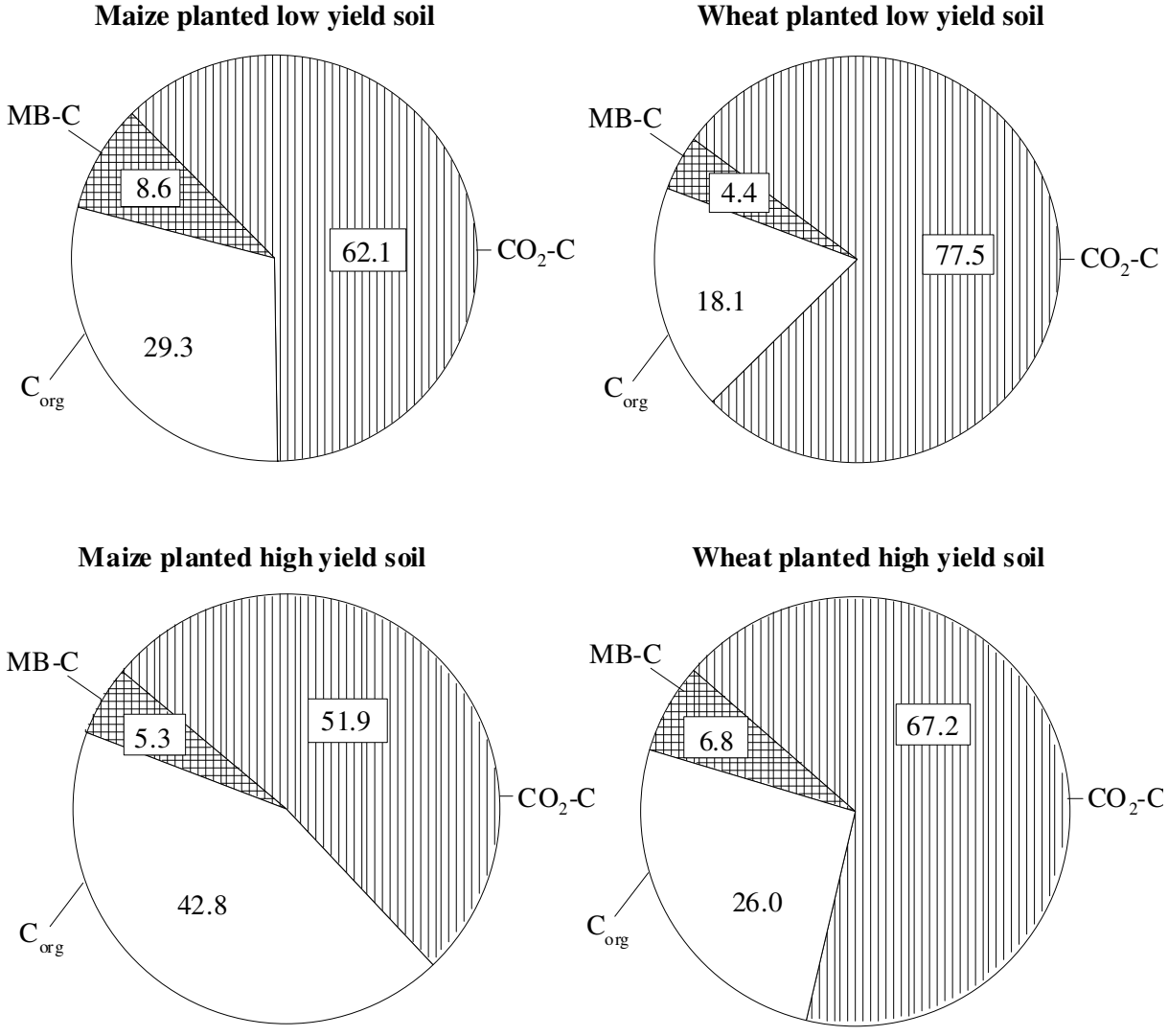

Figure 5 Percentages of rhizodeposit-C recovered in the investigated C pools and in CO_2 at the end of the experiment.

The relative contributions of MB-C to the total balances were similar in both soils with both plants (around 5%), except in LY for maize-derived MB-C, which was with 8.6% significantly greater than the wheat treatment.

$\delta^{13}C$ values in CO_2 and microbial biomass of bulk and rhizosphere soil

Figure 6 illustrates that maize- and wheat-rhizodeposits obviously exerted an influence not only on the rhizosphere soils in the nylon bags, but also on the bulk soil surrounding these water and air permeable bags. This is indicated by the course of bulk soil $\delta^{13}C$ values, which showed an intermediate position between the controls at *t*0 and the rhizosphere soil. The values were generally greater in CO_2 than in the microbial biomass.

The ^{13}C values increased from the beginning of the experiment and reached their maximums on samplings 4 and 5, followed by a decrease. This development reflected the $^{13}CO_2$ content in the tent atmosphere. Initially, the amounts of CO_2 consumed by the plants induced more $^{13}CO_2$ doses (and therefore greater ^{13}C content) to the tent atmosphere as at the end of the experiment. Due to the regular samplings at this time, the amounts of plants and consequently the fixed CO_2 became gradually lesser, so that no further $^{13}CO_2$ was dosed to the tent atmosphere. Additionally, soil respiration diluted the ^{13}C-enriched CO_2 to an isotopically lighter value compared to the middle of the experiment.

Discussion

Maize and wheat plants incorporated ^{13}C in their tissues, shown by the increasing ^{13}C enrichments of the roots over the experiment. Consequently, the rhizodeposits were also ^{13}C labelled. The greater $\delta^{13}C$ values of maize relative to wheat roots are due to the different metabolisms of the plant species. Except for WEOC, all investigated C pools and CO_2 were affected by the rhizodeposits of both plants.

Development in the pools investigated during the growing period

It can be seen from the results that apparently only soil-derived C constituted WEOC. However, this does not necessarily mean that plant-derived WEOC is absent. According to

Gregorich et al. (2000) the isotopic composition of WEOC is dominated by soil-derived components, due to its equilibrium with the native soil-C.

In conclusion, the lack of differences in the ^{13}C contents between planted soils and the controls led to the fact that plant-derived C was not detected in the WEOC pool. In this regard, Yevdokimov et al. (2006) reported small values with a contribution of 1.8% of root-derived C to WEOC, indicating the fast utilisation of this very active water-soluble C substrate. Liang et al. (2002) measured also a small contribution of maize rhizodeposits to WEOC. Additional to the microbial use, the substrate can also be adsorbed to the soil matrix, thus being withdrawn from the WEOC pool (Guggenberger and Kaiser, 2003). Furthermore, the ^{13}C enrichments of the plants and consequently of rhizodeposit-C might have been too small to detect any difference between rhizodeposit- and soil-derived WEOC. Soil strongly adhering to the roots was not included in the WEOC analysis due to the method used here. This can also be responsible for the absence of soluble root-derived compounds in total WEOC.

The microbial biomass was on a similar level in both soils with both plants. Surprisingly, unlike in other studies (Helal and Sauerbeck, 1986; Helal and Sauerbeck, 1989) no growth of the microbial biomass in the planted soils compared to the controls occurred in this experiment. Moreover, microbial biomass was lower than in comparable works. This can be attributed to the use of unsieved soils, where the conditions for microbial population, for example, the nutritional status or the surface area, were not favourable for greater growth rates. Yevdokimov et al. (2006) used sieved soil, which was rewetted two days before the commencement of their experiment. This led to a drastically higher amount of microbial biomass-C amounting to roughly 450-650 µg g^{-1} on day 30 to 50, using the same Eutric Cambisol (HY) soil as in the present study. Additionally, as already mentioned above the soil sticking to the roots was excluded from analysis.

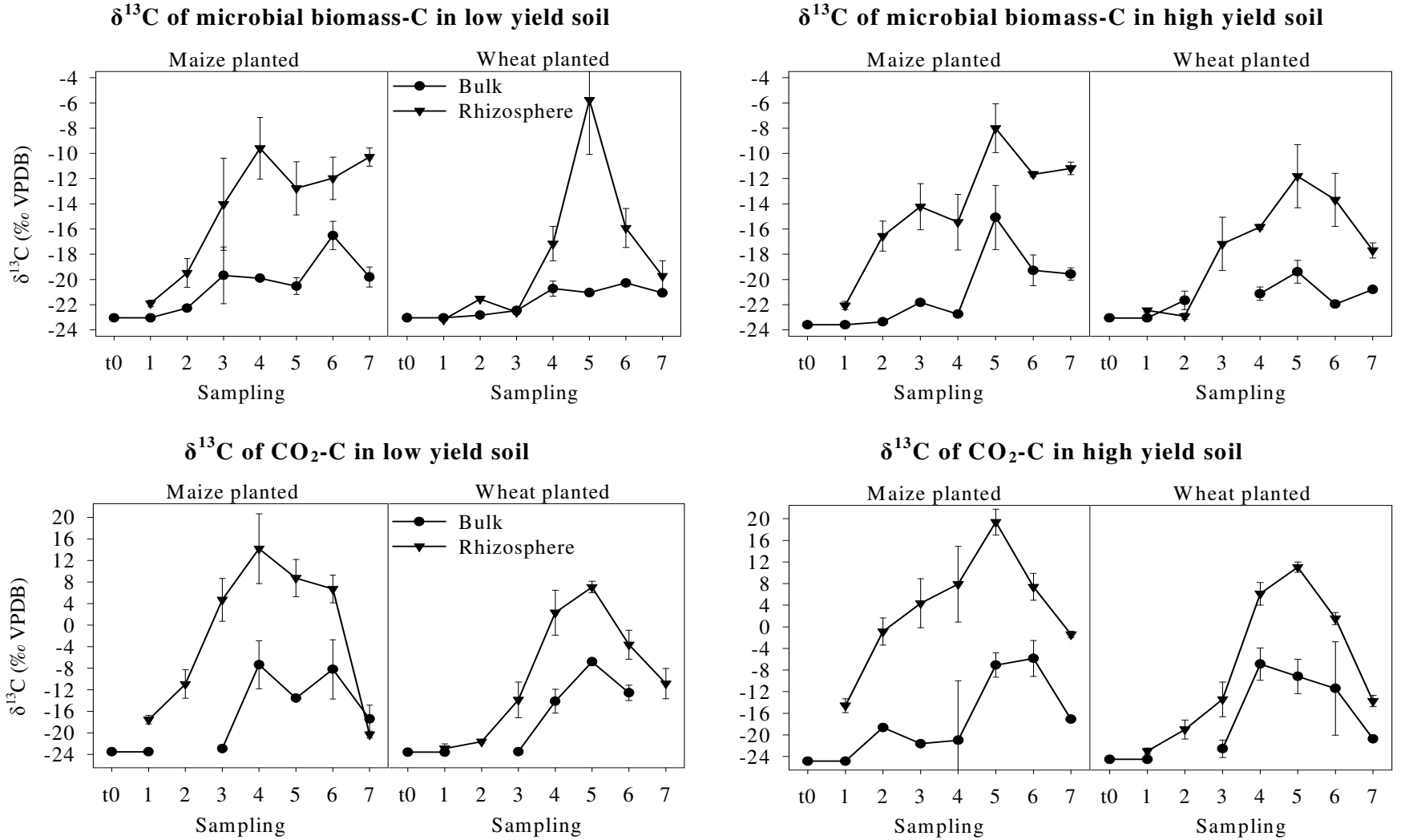

Figure 6 $\delta^{13}C$ values from microbial biomass-C and CO_2 in maize and wheat planted bulk and rhizosphere soil of low and high yield areas. Error bars represent standard errors of the means (n = 5).

But exactly this minor part of soil is considered to be mostly influenced by rhizodeposits inducing the rhizosphere effect and a greater microbial population (Curl and Truelove, 1986; Rees et al., 2005).

The amounts of soil-derived C in the microbial biomass of the planted soils were smaller than those of the controls and this suggests a substitution of soil-C by rhizodeposit-derived C. It is conceivable that the C substitution occurred concurrently with a change in the microbial community structure as observed by other authors. For example, Kandeler et al. (2002) found the bacterial community structure affected by maize root deposits. Also, Benizri et al. (2002) showed a selection of a small specific microbial population by maize exudates accompanied by a decrease in soil microbial diversity. In this regard it is assumed that metabolites of newly established members (consisting of rhizodeposit-derived C) of the microbial community suppressed previously established members (consisting of soil-derived C). Maybe this suppression induced a release of soil-borne components from the microbial biomass leading to the lower soil-derived values in the microbial biomass of planted soils compared to the controls.

The CO_2-C emissions of the planted soils compared to the controls over time were dominated by rhizodeposit-derived CO_2-C. It seems reasonable to assume that wheat contributed to the total CO_2 emissions in a similar manner as maize at the beginning of the experiment (Figure 4), but the differences of ^{13}C in CO_2 between the controls (*t*0) and the wheat planted soils were not yet big enough to differentiate between the two C-sources: soil and rhizodeposition. Consequently, the C input of wheat rhizodeposition would have been underestimated. On the other hand, rhizodeposition might have been overestimated in this study, because the contribution of dead roots and the turnover of labelled microbial biomass to CO_2 were not accounted for. However, also Rees et al. (2005) considered root mortality prior to flowering to be negligible for their calculations. Which of the assumptions concerning the quantity of rhizodeposition were of more importance remains unclear.

Discrimination against ^{13}C during the microbial metabolism resulting in depleted CO_2-^{13}C values might also have appeared in this study as suggested by some authors (Mary et al., 1992; Kristiansen et al., 2004). This would have led to an underestimation of the rhizodeposit-C emitted in the present study. However, Ekblad and Högberg (2000) found no shift in the CO_2-^{13}C values in their study. This shows the difficulties in predicting the circumstances under which isotopic fractionation occurs.

Moreover, the CO_2 determinations were conducted without the direct plant influence, since roots were separated from the soils before the measurements. Thus, the continuous C input from plant roots was lacking and so microbial activity was probably smaller than with direct root contact. Due to the experimental design used here, the contributions of rhizodeposits to the measured pools can be underestimated, since not the entire soil in the bags was influenced by root C loss.

Kuzyakov (2002) described a preferential use of easily available (rhizodeposit) C over more recalcitrant (soil-derived) C, or the inhibition of microbial activity due to the addition of toxic substances to soil as possible mechanisms of inducing a negative rhizosphere priming effect. The preferential use of rhizodeposit-derived C is shown by the dominance of this C in CO_2. The suppression of microbes feeding on soil-derived C by the toxic metabolites of other members of the microbial community can be another explanation of the observed negative priming effect, leading to gradually lesser use of soil-derived C. Furthermore, the preferential use of substrate C and the suppression of microbes using soil-derived C can occur concurrently.

Kuzyakov et al. (2000) proposed that exoenzymes can decompose soil organic matter, thereby inducing a positive priming effect. The energy input from rhizodeposits during the experiment was the prerequisite for microorganisms to produce such exoenzymes. This input increased during the growing period, since rhizodeposition seems to increase linearly with root mass (Darrah, 1996). According to the yield pattern of the high yield soil, there tended to

occur greater root growth and therefore greater C input compared to the low yield soil. The observed change from negative to positive priming effects during the growing period corresponds to the increasing energy input. These effects were mainly detected in maize planted soil, and here chiefly in HY, where the rhizodeposition was greatest. The greater C input of maize compared to wheat suggests that the plant species affects the C deposition as well.

An additional mechanism that can explain a positive priming effect is postulated in the following. It is reported that WEOC, including dissolved-rhizodeposit C binds to the solid phase via clay and metal hydroxides (Kalbitz and Knappe, 1997; Kaiser and Guggenberger, 2000; Kaiser et al., 2002; Guggenberger and Kaiser, 2003). It is suggested here that in our study occurred an exchange of C between the soil matrix and the soil solution. This is supported by Fröberg et al. (2006) and Marx et al. (2007) who found soil-derived dissolved organic carbon (DOC) from exchange processes between solid soil organic matter and incoming DOC. Assuming that the proposed exchange is a function of the added C amount, a higher rhizodeposition rate also means a higher potential to exchange material from the soil matrix. This soil-derived C is then available for respiration. Hence, the use of this additionally available substrate can lead to a positive priming effect, as observed in this study.

Similar as for total WEOC, rhizodeposit-C presumably contributed to the total C_{org} contents of both soils even at the beginning of the experiment, but the ^{13}C content was not sufficiently different from that of the soil and could therefore not be determined.

Contribution of rhizodeposition to microbial biomass and C_{org}

The contribution of rhizodeposit-C to the total concentrations of the measured pools in relative terms is comparable with that of other studies found in relevant literature. Liang et al. (2002) conducted a greenhouse study with maize plants grown in pots filled with soil. In the first 28 days, they found 9 to 25% of rhizodeposit-derived C in the MB-C and 1.3 to 3.0% in the C_{org} pool over a comparable time period as in our experiment. This range fits well to the

contributions of rhizodeposits to MB-C and C_{org} observed in the present study. Merckx et al. (1986) showed in their work with ^{14}C labelled maize and wheat plants grown in soil columns that the contribution of root-derived C to MB-C increased from 8 to 20% after six weeks, and this is in perfect accordance with the values observed here. Yevdokimov et al. (2006) found oat plant rhizodeposits contributing to MB-C in the range from 9 to 19% in a similar study as the present one, and this is also comparable with our values. Helal and Sauerbeck (1986) found 15% of plant-C incorporated into the microbial biomass in a pot experiment planted with ^{14}C labelled maize for 30 days. They pointed out that this value is in the range of the utilisation efficiencies of substrate use by microorganisms.

Extension of the rhizosphere

The results indicated a strong influence of root-derived C on MB-C and CO_2-C in the bulk soil outside the bags. The course of ^{13}C values in bulk and rhizosphere soils showed that most likely soluble exudates reached farther from the direct root zone, thereby influencing the carbon composition of microbial biomass and CO_2 of the bulk soil. Helal and Sauerbeck (1986) also found root-derived C far away from the direct root vicinity. Kuzyakov et al. (2003) used a similar approach as the latter authors with ^{14}C labelled maize plants grown in pots where rooted soil was separated from non rooted one with monofilament gauze. The maximal extension of the rhizosphere was thereby shown to be 10 mm from the root. However, they did not determine the microbial biomass, where fixation of ^{14}C originating from exudates might have been observable farther from the roots.

CO_2 fixing bacteria were not considered to play a significant role in transferring the ^{13}C label to the bulk soil. Also Butler et al. (2004) found no autotrophic activity in their study when exposing soil to ^{13}C labelled CO_2. Nevertheless, it cannot be ruled out that fungi transferred ^{13}C labelled components to their mycorrhizal hyphae which penetrated into the bulk soil.

Difference of the fate of rhizodeposit-C between high and low yield soil

The results clearly demonstrated that most incoming root material was mineralized shown by the significant relationship between root weight (rhizodeposition) and rhizodeposit-derived CO_2-C evolution. Referred to the C input through rhizodeposits, more substrate was mineralized to CO_2-C in LY compared to the HY soil, and this material is not available for stabilization in soil. This is reflected by the greater C_{org} content of HY, showing that organic material has accumulated in the soil of this field area. Wessels Perelo and Munch (2005) incubated the same soil materials as in this study with white mustard and found also a higher microbial activity in LY compared to HY soil. They hypothesized that microbial populations were in a different physiological state due to the different characteristics in both soils. This supports the assumption that there are different C-fluxes in the investigated soils.

Conclusions

By using stable isotopes, it was possible to determine the quantitative contributions from maize and wheat rhizodeposition to the major carbon pools in soil. Rhizodeposit-C was detected in MB-C and CO_2-C evolved outside the direct root zone, showing the availability of these C-components also in the bulk soil. It is suggested that the increased SOM mineralization observed in this study (positive priming effects) was probably induced by C exchange processes between the soil matrix and soluble rhizodeposits. This shows that, besides microbial effects, positive priming effects can also be triggered by soil physical processes. We determined great amounts of rhizodeposits stabilized in the C_{org} pool at least in the short-term. Thus, despite the high degradability of rhizodeposits, they might also contribute to C sequestration in soils. The magnitudes of rhizodeposit-C in the investigated pools and CO_2 were different between the two soils irrespective of the plant species. The rhizodeposit-C-fluxes seem to be influenced by several soil characteristics as, for example, texture or microbial community structure.

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Chapter 5

Summary discussion and conclusions

Summary discussion and conclusions

The fate of natural (maize and wheat) exudate-C, artificial exudate-C, or rhizodeposit-C, respectively, was determined in experiments conducted under lab and greenhouse conditions with ^{13}C measurements in order to trace the C-fluxes of the substrates and the soil being influenced by the C input. In contrast to methods, where laborious and time consuming steps are necessary to oxidize organics with subsequent purification of CO_2 and determination of ^{13}C (Potthoff et al., 2003), the application of the newly developed powerful method by Krummen et al. (2004) can process more samples in a much shorter time.

The general processes due to C additions to soil are comparable between the three studies. The outcomes are discussed in terms of similarities and dissimilarities of the conducted experiments for the pools measured and the effects observed.

Influence of added exudates and rhizodeposits on microbial biomass and activity

Substantial amounts of substrate carbon were incorporated into the soil microbial biomass, shown by the exudate/rhizodeposit-derived-C balances in all of the three experiments. This was accompanied by microbes being triggered into activity upon the additions of substrates, indicated by a flush of CO_2-C. The increase of microbial activity was present from the first sampling in the exudate experiments. Also, the microbial activity in planted soils started to be significantly greater than from the unplanted controls in the study with rhizodeposits from the second sampling on, suggesting that a remarkable C input by plants was given.

The CO_2-C emissions relative to the controls were dominated by exudate/rhizodeposit-derived CO_2-C. Thus, the newly built microbial biomass mineralized almost exclusively substrate-C, proving that the added C served as the main energy source for microorganisms.

Growth of microbial biomass

In all of the studies, the MB-C contents of the soils were not permanently increasing despite a continuous C input was given and this is the prerequisite for a growing microbial population.

The maximum content of microbial biomass differed among the experiments. The occurrence of a stable microbial biomass content in the soils treated with different kinds of substrate supports the view of a specific biotic capacity reported in relevant literature (van Veen et al., 1984; Bottner et al., 1988). Helal and Sauerbeck (1986) suggested that a deficiency of essential mineral nutrients can restrict microbial growth, if C is not the limiting factor. Since a sufficient C-supply was given in the experiments, a lack of other nutrients was likely to control the growth of microbial biomass.

Change in microbial community structure

In the incubations with exudates, newly built microbial biomass consisted mainly of exudates presumably causing a change in the microbial structure. A decline of soil-derived C in the microbial biomass and a concurrently incorporation of artificial exudate- or rhizodeposit-C into the latter took place. This indicates a substitution of soil-derived C by substrate-C in the microbial biomass. The C-substitution also suggests a change in the microbial community structure. Members of the new microbial community might have been specialized on the substrates added and this is shown by their preferential mineralization. A changing microbial community structure after the addition of several substrates has frequently been reported in literature (Griffiths et al., 1999; Kozdroj and van Elsas, 2000; Benizri et al., 2002; Kandeler et al., 2002).

Negative priming effects

As a consequence of the prevailing use of substrate-derived C by microbes, soil-derived C mineralization was reduced leading to negative priming effects in all studies. The mostly negative soil-derived C values in the net CO_2 balances show the retarded mineralization of the soil compounds. Kuzyakov (2002) explained the occurrence of negative priming effects by the preferential microbial use of easily available C over more recalcitrant (soil-derived) C. So, the substrates added included all nutrients required for the maintenance of the microbial biomass.

A further explanation can be that metabolites of newly established members of the microbial community suppressed previously established ones leading to a reduced usage of soil-derived components.

Positive priming effects

Also positive priming effects were observed, especially at the beginning of the incubation periods of the exudate experiments and at the end of the study with rhizodeposits. In the latter this effect was detected when the rhizodeposition and therefore energy input was greatest. According to Hamer and Marschner (2005) sufficient C input may lead to an increasing production of energetically expensive exoenzymes by microorganisms due to the compensation of energy limitation. In this manner a positive priming effect may be induced, since these enzymes are able to decompose soil organic matter.

Here, it is additionally suggested that an exchange of C between the soil matrix and soil solution occurred. It is well known that water extractable organic carbon (WEOC) adsorbs to clay minerals and metal hydroxides (Kaiser and Guggenberger, 2000; Kalbitz et al., 2000; Kaiser et al., 2002). Naturally, soil-WEOC includes exudates or rhizodeposits used in the three different studies. It is supposed that desorption of soil-derived C occurred upon the adsorption of incoming dissolved-C from the applied substrates. This desorbed soil-derived C becomes accessible to the microbial biomass that is specialized on this kind of substrate. So, the mineralization of this additionally available C can lead to a positive priming effect. Fröberg et al. (2006) investigated dissolved organic carbon (DOC) fluxes in Norway spruce stands and found that significant amounts of DOC in the studied B horizon originated from exchange processes between solid soil organic matter (SOM) and incoming DOC. They pointed out that such sorption/desorption processes have rarely been discussed in literature so far.

Although not detected here (data not shown), a significant difference in WEOC quality was observed in a field study dealing with the same soils, but on a much larger scale than in

the present experiment (Zeller, 2006). There it was shown by fluorescence spectroscopy that water-soluble C was more humified in HY compared to LY, irrespective of season and crop influences. This might partly be due to the higher C input in HY through rhizodeposits reflected by the higher above ground biomass compared to LY. Following the proposed hypothesis of exchange processes, the incoming C-compounds in HY exchanged more humified soil-derived material than in LY and this may be responsible for the observed difference in the WEOC quality.

The effects of incoming C tended to be more pronounced in the high yield soil. However, presuming that priming effects are microbially mediated, a different community pattern between the low and high yield soil can also explain the different quantities in primed C observed in the artificial exudate and rhizodeposit studies. To verify the hypothesis that sorption may be responsible for positive priming effects, experiments with sterile soil must be carried out. This would eliminate the influence of microorganisms on the processes underlying the priming action.

The dynamics of soil-derived C in the microbial biomass of the exudate experiments provided further evidence for the assumption that sorption processes as well as new stable SOM formation occurred during the incubations. Besides the incorporation of exudate-C in the newly built microbial biomass, also significant amounts of soil-derived C were concurrently incorporated into the microbial biomass in all natural and artificial exudate treatments on the first sampling. The origin of the soil-derived material can be explained by the same sorption/desorption processes as stated above.

Differences in the observed C-dynamics

The quality of the natural and artificial exudates and the rhizodeposits was apparently different from each other, and this became obvious from the differently pronounced dynamics in the pools investigated and from the CO_2 emissions. The different quality of the two exudate types and the rhizodeposits was reflected in the quantitatively different mineralization and

incorporation patterns. The C:N ratio of maize exudates was 1.5, that of wheat exudate was 2.8 and that of artificial exudate amounted to 11.6. The detailed composition of natural exudates was not determined. However, the lower C:N ratio of natural compared to artificial exudates indeed indicated a much higher N content in maize and wheat exudate. This suggests that the natural exudates included amino acids to a great extend.

Obviously, almost the entire artificial exudate and the rhizodeposits were very efficiently incorporated or mineralized by microorganisms or adsorbed to the soil matrix. Consequently, they were not detected in the WEOC pools from these studies. In contrast to this, remarkable amounts of exudate and additional soil-derived material were detected in the WEOC pool from the study conducted with natural exudates. On the one hand this shows that some components of the natural exudates were relatively stable against decomposition. On the other hand, besides organic compounds also inorganic anions (for example phosphate, sulphate, chlorite, bicarbonate) were presumably exuded in small amounts as well (Uren and Reisenauer, 1988). These anions are known to compete with dissolved organic compounds for adsorption sites (Gu et al., 1994; Kalbitz et al., 2000), and may thereby have partly desorbed soil-derived C. This can have occurred in addition to the assumed C desorption due to natural exudate addition discussed above.

Plants produce several different types of root exudates (Bertin et al., 2003). According to Uren (2000) there are several plant waste products among the exudates. In the model study with maize and wheat exudates these waste products had possibly no substrate value for microorganisms, so that they accumulated in the soil solution, or exchanged soil-derived C-compounds, or suppressed microorganisms in their activity. Nevertheless, Kuzyakov (2002) pointed out that these exuded substances are neither plant waste products nor energy losses for the plant, but an evolutionary developed mechanism of indirect symbiosis with rhizosphere microorganisms.

In all studies, CO_2-C always had the biggest proportions of the substrate-C recovered, stressing the function of exudates/rhizodeposits as easily available substrate for microorganisms. Contrasting to the exudate experiments, where the not retrieved pool was biggest, CO_2-C had the largest proportion on the overall C balance in the rhizodeposit study.

In the exudate experiments, most of the added C (> 50%) was not retrieved with the methods applied. This C amount was most likely in a water-insoluble form or adsorbed to the soil matrix, i.e. potentially detectable in the total organic carbon (C_{org}) pool. The C_{org} values shown in the overall C balances of the rhizodeposit study suggest that they were indeed present in a more stable pool. This suggests that the applied exudates were potentially detectable in the model experiments as well. Hence, C adsorption may have analogously occurred under laboratory conditions. This is proven by the C_{org} determination in the study with artificial exudates on sampling 10, where the previously unretieved C amounts were recovered.

The negative priming effect was more pronounced in the incubation with natural exudates compared to artificial exudate. In the incubation with the latter substrate, the effect was stronger in high yield than in low yield soil. This stresses the different quality of the exudate types on the one hand, and the different C-fluxes in both of the soil types on the other hand.

Differences between exudates and rhizodeposits studies

The following striking differences between the effects occurred with addition of exudates and rhizodeposits to the soils were observed. It was shown that the substrates added in all studies were partly adsorbed to the soil, but in the exudates experiments the adsorbed amounts were greater than of the rhizodeposit study. No growth of the microbial biomass on the rhizodeposits took place, whereas a clear increase of this C pool occurred upon the addition of exudates. Furthermore, the initial effect of large soil-derived C incorporation into the

microbial biomass as detected in the exudates experiments was not observed in the study with rhizodeposits.

A reason proposed for this is that the soil in the direct vicinity to the root was not considered in the analysis due to the experimental design applied in the rhizodeposit study. This soil adhering to the roots might indeed have shown similar effects as described above, but the differences of ^{13}C between the unplanted control and the planted soils was not sufficient to differentiate between soil-derived and rhizodeposit-C. In other words the soil in the nylon bags representing the rhizosphere of the rhizodeposit study included too much of material that was not influenced by plant root deposits. In this regard Gregorich et al. (2000) pointed out that the isotopic composition of WEOC is dominated by components of the relatively large solid organic matter pool from which WEOC is derived. This dominance of soil-derived components can easily superpose the presence of C from a different origin.

Consequently, an underestimation of the C input through rhizodeposits can be assumed since the values on a daily basis were very low in comparison to literature data. The amounts estimated for rhizodeposition in the greenhouse study were much lower than the amounts of exudates added. The deposition was in a range of about 7 µg C g^{-1} soil d^{-1} in wheat planted low yield soil and around 19 µg C g^{-1} soil d^{-1} in maize planted high yield soil. According to De Nobili et al. (2001) even small amounts of exudates may stimulate microorganisms to stronger SOM decomposition, thus influencing the soil C-dynamics. However, the values found here were drastically lower than those reported in literature. For example, Trofymow et al. (1987) mentioned an exudation rate of 100 µg C g^{-1} soil day^{-1} and Cheng (1996) even calculated 500-1500 µg C g^{-1} soil day^{-1}. The lowest reported value is 50 µg C g^{-1} soil day^{-1} (Griffiths et al., 1999). The present results suggest that the contributions of rhizodeposits to the pools measured and to CO_2 were underestimated due to the diluting effects of bulk soil.

Moreover, the tendency of negative priming or a net negative soil-derived CO_2 balance with small values was observed in the rhizodeposit study. A distinct negative priming pattern as in the exudate experiments was probably superposed by the diluting effects of additionally present uninfluenced soil in the rhizosphere bags.

Furthermore, the additional C_{org} amounts relative to the controls at the first sampling of the rhizodeposit experiment consisted only of soil-derived C. The only source of this C was found to be the microbial biomass, releasing only some 20 to 40 µg C g^{-1} soil on this sampling, but the C_{org} content increased in an order of magnitude greater (milligrams). The ^{13}C values of the incoming rhizodeposits were apparently not yet sufficiently different from those of the soil due most likely to the initially small C input, making a differentiation between the two C-sources with help of ^{13}C impossible.

Final conclusions

The exudate studies conducted in the laboratory showed that high proportions of added exudates (> 50%) were in a water-insoluble state or became stabilized (by adsorption) at least in the short-term. Surprisingly, despite the high degradability of exudates or rhizodeposits, they contribute to C-sequestration in soils in this study at least in the short-term. It seems therefore that exudates are more than just an energy source for microorganisms, i.e. they have more functions in the C-cycle as activating the microbial biomass pool where nutrients are stored.

However, the addition of exudates to soil in the experiments was conducted only over a short period of time. Moreover, the results of the incubation with artificial exudate showed clearly that exudates were mineralized after their addition was stopped. This proves a release of exudate that was most likely previously adsorbed or present in the microbial biomass. It is therefore necessary to investigate the exudate dynamics over a longer term to elucidate their role in C-sequestration, and this may help mitigate issues concerning global change.

In the exudate experiments processes were clarified under controlled substrate additions and observed on a finer scale than in the greenhouse study with rhizodeposits. A small soil volume was completely subjected to exudate influence and considered as rhizosphere soil, whereas rhizodeposits were probably unevenly distributed in the greenhouse study. The results of the exudate experiments reflected the situation in the direct vicinity of actively exuding roots. Therefore the effects discussed above were clearly observable in the exudate studies, but are supposed to happen in the rhizosphere soils from the rhizodeposit experiment as well. The estimation of the relative contribution of plant rhizodeposits was shown to be different from that obtained in the exudate experiments, revealing a different quality of the substrates added. Thus, it is suggested here to conduct measurements that are concerned with quantitative contributions of below-ground C-fluxes with plant-soil systems in greenhouse studies or *in situ*. In conclusion, the processes occurring upon substrate addition within the major C pools and CO_2 can be elucidated in model experiments with different kinds of easily available exudate.

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Summary

The rhizosphere is known as the soil compartment that is affected by plant roots. This zone is characterized by large C-fluxes due to the high input of root-derived compounds (rhizodeposition), being easily available for microorganisms. Rhizodeposition comprises all components released directly from the root to the soil, as, for example, water-soluble exudates, which consists mainly of carbohydrates, amino- and organic acids, or sloughed-off root cells. The fate of C from rhizodeposits in soil is still unanswered. A broader knowledge of the contribution of carbon (C) released by plant roots to soil can help to increase our knowledge of global C-cycling with particular regard to climate relevant CO_2. The aim of this work was to determine with different approaches the dynamics of rhizodeposits in the major C pools in soil. The experimental approaches were chosen because it was expected that the easily degradable exudates and rhizodeposits would almost completely be recovered in the measured pools and in CO_2.

This is the first study to reveal the contributions of constantly applied ^{13}C labelled natural (maize and wheat) or artificial (mixture of several C-compounds) exudates to water extractable organic carbon (WEOC), microbial biomass-C (MB-C), and CO_2-C evolution during incubations with material of two agricultural soils with different yields (low or high yield soil). An additional greenhouse study was conducted to reveal effects of ^{13}C labelled rhizodeposits of maize and wheat plants grown in the same soils as stated above on WEOC, MB-C, CO_2-C, and total organic carbon (C_{org}) during a 49-day growing period. These soils were chosen, since it was assumed that their nutrient and C-fluxes are different from each other, reflected in their different yield pattern. Due to methodological limitations, natural exudates were only applied to the soil with low yield during a 25-day-incubation. The incubation with artificial exudates was conducted over 74 days. After 56 days, the substrate additions were stopped and the incubation was prolonged for further 18 days. This was done

in order to determine whether exudate can still be detected in the investigated pools and in CO_2. The WEOC, MB-C, and CO_2-C concentrations and their respective $\delta^{13}C$ values were measured regularly in all studies. The same was done for C_{org} in the rhizodeposit experiment. A newly developed method for determining $\delta^{13}C$ values in soil extracts (WEOC and MB-C) was applied. The new online-method was found to be a suitable tool for the determination of ^{13}C values in soil extracts, since it was reproducible over time, sensitive in measuring ^{13}C, and working very efficiently.

Around 36% of the natural exudate-C of both plants was recovered after the incubation, in the order WEOC < MB-C < CO_2-C for maize and MB-C < WEOC < CO_2-C for wheat. Around 64% of added exudate-C was not retrieved with the methods used here and was presumably transferred to a non-water soluble form. The amounts of MB-C stayed relatively constant while those of WEOC rose and the CO_2-C mineralization rate declined during the incubation. In the exudate treated soil additional amounts of soil derived WEOC and MB-C were determined relative to the control.

In both soils incubated with artificial exudate remarkable amounts of artificial exudate-derived C was observed in MB-C and in CO_2-C, but not in WEOC. Up to around 50% of the added exudate-C amounts were recovered in the order WEOC << MB-C < CO_2-C in both soils at the end of the incubation. Around 50% of added exudate-C was presumably in a non-water extractable form. This assumption was supported by the determination of total organic C in the soils at the end of the incubation, where the respective amounts were recovered.

The exudate-derived MB-C values had a similar contribution to the overall balance in both soils. The CO_2-C emission showed a significantly greater value in the low yield soil, supporting the assumption of different C-fluxes in the investigated soils. The stopped exudate flow after 56 days was reflected in the sharply declining CO_2-C and microbial biomass values. However, even though exudate addition was stopped, exudate-derived C was detected in MB-

C and CO_2 at the end of the incubation. Obviously, the exudate-derived C stored in the microbial biomass or adsorbed to the soil matrix was now being released for mineralization. In both of the maize and wheat planted soils rhizodeposit-derived C was determined in MB-C, CO_2-C, and C_{org}, but not in WEOC. The pattern of C incorporation into the different pools and CO_2 was the same for both soils with both plants. The amounts of rhizodeposit-C were recovered in the order MB-C < C_{org} < CO_2-C.

In the incubations with exudates, newly built microbial biomass consisted mainly of exudates-C, presumably causing a change in the microbial structure. In the experiments with artificial exudate and with rhizodeposits, a decline of soil-derived C from the microbial biomass and a concurrently incorporation of substrate-derived C took place. This indicates a substitution of soil-derived C by substrate-C. Correspondingly, the CO_2-C evolutions compared to that of the controls were dominated by exudate/rhizodeposit derived CO_2-C. As a consequence of the prevailing use of substrate-derived C, soil-derived C mineralization was reduced (negative priming effect). The suppression of microbes feeding on soil-derived C by the (toxic) metabolites of other members of the microbial community can be another explanation of the observed negative priming effect.

Also positive priming effects (i.e. accelerated turnover of soil organic matter due to the addition of organic substrates) were observed especially at the beginning of the incubation periods of the exudate experiments and at the end of the study with rhizodeposits. In the soils treated with exudates, additional amounts of soil-derived WEOC and MB-C relative to the controls were determined. It is suggested that these soil-derived C amounts originated from an exchange between the soil matrix and the added substrate. The organic material liberated in this way became available for microorganisms and was eventually measured as soil-derived CO_2. Positive priming-effects might be explained by exchange processes between soluble C-compounds and the soil matrix.

Surprisingly, our results show that more than a half of the added exudates became stabilized in non-water extractable organic fractions. The rhizodeposits were mainly mineralized. The magnitudes of rhizodeposit-C in the investigated pools and CO_2 were different between the two soils irrespective of the plant species. The rhizodeposit-C-fluxes seem to be influenced by several soil characteristics or microbial mediated processes. Since C_{org} was the second largest pool of the overall balances, rhizodeposits were also stabilized at least in the short-term. So, despite the high degradability of exudates or rhizodeposits, they can contribute to C-sequestration in soils.

Zusammenfassung

Die Rhizosphäre ist allgemein die Zone des Bodens, die durch Pflanzenwurzeln beeinflusst wird. In ihr finden beträchtliche Kohlenstoffflüsse infolge der Abscheidung mikrobiell leicht verfügbarer Wurzelabscheidungen (Rhizodeposition) statt. Rhizodeposition umfasst die von der Wurzel direkt in den Boden abgegebenen Verbindungen, wie beispielsweise wasserlösliche Exsudate, die hauptsächlich aus Zuckern, Amino- und organischen Säuren bestehen, oder abgestorbene Wurzelzellen. Es ist noch weitgehend unbekannt, wie rhizodepositionsbürtiger Kohlenstoff (C) zum Gesamt-C in Böden beiträgt. Genaue Kenntnisse dieses Verhältnisses sind bedeutsam für ein umfassenderes Prozessverständnis im C-Kreislauf mit Berücksichtigung des klimarelevanten CO_2. Ziel dieser Arbeit war es daher mit unterschiedlichen Ansätzen die Dynamik von Wurzelabscheidungen in den wichtigsten C Pools im Boden zu bestimmen. Die experimentellen Ansätze wurden unter der Annahme gewählt, dass zum Boden gegebene leicht abbaubare Exsudate bzw. Rhizodepositionen in den gemessenen Pools und im CO_2 fast vollständig wiedergefunden werden.

Dies ist die erste Studie, in der die Anteile von regelmäßig zugegebenen ^{13}C markierten natürlichen (Mais und Weizen) beziehungsweise künstlichen (Mischung von mehreren C-Verbindungen) Exsudaten zum wasserextrahierbaren organischen Kohlenstoff (WEOC), mikrobiellen Biomasse-C (MB-C) und zur CO_2-C Entwicklung während Inkubationen mit Material von zwei landwirtschaftlichen Böden mit unterschiedlicher Ertragstruktur (Hoch- und Niederertrag) bestimmt wurden. Zusätzlich wurde ein Gewächshausversuch durchgeführt, um Effekte von ^{13}C markierten Rhizodepositionen von Mais- und Weizenpflanzen, die in den oben genannten Böden wuchsen, auf WEOC, MB-C, CO_2-C und organischen Gesamt-C (C_{org}) während einer 49-tägigen Wachstumsphase der Pflanzen aufzudecken. Die Böden wurden ausgewählt, da sich ihre Nährstoff- und Kohlenstoffflüsse vermutlich voneinander unterscheiden, was sich in ihrem unterschiedlichen

Ertragsmuster spiegelt. Aufgrund von methodischen Einschränkungen wurde nur der Niederertragsboden mit natürlichen Exsudaten über 25 Tage inkubiert. Der Versuch mit künstlichen Exsudaten wurde über 74 Tage durchgeführt. Nach 56 Tagen wurde die Substratgabe zu den Böden gestoppt und die Inkubation für weitere 18 Tage fortgesetzt. Mit diesem Ansatz sollte festgestellt werden, ob Exsudat auch in diesen 18 Tagen in den gemessenen Pools sowie im CO_2 nachweisbar war. Die WEOC, MB-C und CO_2-C Konzentrationen sowie die jeweiligen $\delta^{13}C$ Werte wurden in den drei Studien regelmäßig gemessen. Beim Versuch mit Mais- und Weizenrhizodeposition wurden zusätzlich die C_{org} Gehalte und jeweiligen $\delta^{13}C$ Werte regelmäßig gemessen. Um die $\delta^{13}C$ Werten in den Bodenextrakten (WEOC und MB-C) zu bestimmen wurde eine neuentwickelte Online-Methode getestet. Diese Methode lieferte reproduzierbare Ergebnisse über die Zeit, arbeitete sehr empfindlich und effizient, und erwies sich somit als geeignet für die Bestimmung von $^{12}C/^{13}C$ Verhältnissen in Flüssigextrakten.

Natürlicher Exsudat-C beider Pflanzen wurde zu etwa 36% nach der Inkubation, in der Reihenfolge WEOC < MB-C < CO_2-C für Mais und in MB-C < WEOC < CO_2-C für Weizen bestimmt. Etwa 64% des applizierten Exsudat-C konnte nicht mit den hier angewendeten Methoden bestimmt werden und wurde vermutlich in eine nicht wasserextrahierbare Form überführt. Die MB-C Gehalte blieben verhältnismäßig konstant, wohingegen die WEOC Gehalte anstiegen und die CO_2-C Mineralisierungsraten während der Inkubation sanken. Im mit natürlichem Exsudat inkubierten Boden wurden erhöhte Mengen von bodenbürtigem WEOC und MB-C im Verhältnis zur Kontrolle festgestellt.

In beiden mit künstlichem Exsudat behandelten Böden konnten nennenswerte Mengen des exsudatbürtigen C im MB-C und im CO_2-C gefunden werden. Der Exsudatanteil im WEOC war dagegen gering. Am Ende der Inkubation wurde etwa 50% der applizierten Exsudat-C Menge in der Reihenfolge WEOC << MB-C < CO_2-C bestimmt. Die anderen ca. 50% der applizierten Exsudat-C Menge waren vermutlich in einer nicht wasserextrahierbaren

Form. Diese Annahme wurde durch die Bestimmung von organischem Gesamt-C in den Böden am Ende der Inkubation mit künstlichen Exsudaten gestützt, in denen die zuvor nicht gefundenen C-Mengen bestimmt wurden.

In den beiden untersuchten Böden hatten die exsudatbürtigen MB-C Werte einen ähnlichen Beitrag zur C-Gesamtbilanz. Die CO_2-C Emission zeigte einen erheblich höheren Wert im Niederertragsboden, was damit die Annahme der voneinander unterschiedlichen C-Flüsse in den untersuchten Böden stütze. Die nach 56 Tagen gestoppte Exsudatgabe spiegelte sich in den deutlich abfallenden Werten der mikrobiellen Aktivität und der mikrobiellen Biomasse. Obwohl die Exsudatgabe gestoppt wurde, konnte exsudatbürtiger C im MB-C und CO_2 am Ende der Inkubation nachgewiesen werden. Offensichtlich wurde das in der mikrobiellen Biomasse gespeicherte oder an der Bodenmatrix adsorbierte künstliche Exsudat-C nach Exsudatstopp teilweise wieder für die Mineralisierung freigesetzt.

In den mit Mais und Weizen bepflanzten Böden konnte rhizodepositionsbürtiger C im MB-C, CO_2-C und C_{org} nachgewiesen werden, jedoch nicht im WEOC. Das Muster des C-Einbaus in die unterschiedlichen Pools und in das CO_2 war dasselbe in beiden Böden mit beiden Pflanzen. Die Mengen des rhizodepositionsbürtigen C wurden in der Reihenfolge MB-C < C_{org} < CO_2-C bestimmt.

In den Inkubationen mit natürlichen und künstlichen Exsudaten bestand die neu gebildete mikrobielle Biomasse hauptsächlich aus Exsudat-C, was vermutlich mit einer Änderung der Struktur der mikrobiellen Gemeinschaft einherging. In den Versuchen mit künstlichem Exsudat und mit den Rhizodepositionen fanden Abnahmen der Anteile von bodenbürtigen C in der mikrobiellen Biomasse und Einbau von Substrat-C statt. Dieses lässt erkennen, dass es zu einer Substitution von bodenbürtigem C durch Substrat-C kam. Entsprechend wurden die CO_2-C Emissionen relativ zu den Kontrollen durch das Exsudat/Rhizodepositionbürtige CO_2-C dominiert. Als Folge der vorherrschenden Veratmung von Substrat-C wurde die Mineralisierung von bodenbürtigem C verringert (negativer

Priming-Effekt). Außerdem könnte es sein, dass die (toxischen) Stoffwechselprodukte von Mitgliedern der mikrobiellen Gemeinschaft andere Mikroorganismenarten, die bodenbürtigen C veratmen, unterdrückten.

Auch positive Priming-Effekte (d.h. erhöhter Umsatz der organischen Bodensubstanz durch Zugabe von organischen Substraten) wurden besonders am Anfang der Inkubationsperioden der Exsudatexperimente und am Ende der Studie mit Rhizodepositionen beobachtet. Im mit natürlichen Exsudaten inkubierten Boden wurden erhöhte Mengen bodenbürtiger WEOC und MB-C im Verhältnis zu den Kontrollen festgestellt. Es wird postuliert, dass diese zusätzlichen bodenbürtigen C Mengen von einem Austausch zwischen der Bodenmatrix und dem zugegebenen Substrat stammten. Das dadurch freigesetzte organische Material war dann für Mikroorganismen verfügbar und konnte letztendlich als bodenbürtiges CO_2 gemessen werden. Positive Priming-Effekte könnten daher auch durch Austauschprozesse zwischen löslichen C-Bestandteilen und der Bodenmatrix erklärt werden.

Überraschenderweise zeigen die Exsudatversuche, dass mehr als die Hälfte der applizierten Exsudate in den wasserunlöslichen organischen Fraktionen stabilisiert wurden. Die Rhizodepositionen wurden hauptsächlich mineralisiert. Die Menge des Rhizodeposition-C in den gemessenen Pools und im CO_2 variiert unabhängig von der Pflanzenart zwischen den beiden untersuchten Böden. Die Rhizodeposition-C Flüsse scheinen daher von verschiedenen Bodeneigenschaften oder mikrobiologischen Prozessen gesteuert zu werden. Da C_{org} den zweitgrößten Pool der Gesamtbilanz darstellte, wurden die Rhizodepositionen aber auch - zumindest kurzfristig - stabilisiert. Trotz ihrer leichten Verfügbarkeit können Exsudate bzw. Rhizodepositionen damit zur C-Rückbindung (Sequestration) in Böden beitragen.

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Appendix

Chapter 2

Table 1 Amounts of WEOC from control and exudate treated soil.

Sampling	Control		
	WEOC	MB-C	CO_2-C
		($\mu g\ g^{-1}$)	
1	11.93	69.24	19.37
	10.69	54.56	20.26
	24.11	78.31	19.05
2	20.00	92.93	69.13
	14.16	91.60	61.62
	12.99	95.92	64.53
3	9.57	86.05	104.22
	9.50	83.43	108.13
	11.94	64.85	103.37
4	9.30	98.81	141.65
	10.12	114.78	142.99
	9.68	108.94	140.68

Sampling	Maize								
	WEOC			MB-C			CO_2-C		
	Total	Soil-derived	Exudate-derived	Total	Soil-derived	Exudate-derived	Total	Soil-derived	Exudate-derived
				($\mu g\ g^{-1}$)					
1	38.88	26.95	11.93	206.58	177.13	29.45	85.99	11.80	74.19
	40.42	26.36	14.06	164.95	142.42	22.53	91.27	7.36	83.91
	49.82	32.89	16.92	225.45	195.16	30.29	93.80	14.26	79.55
2	50.12	32.43	17.69	268.58	220.28	48.30	191.02	41.39	149.63
	43.48	31.45	12.03	222.16	186.13	36.03	195.37	43.53	151.84
	47.45	32.16	15.29	377.17	324.72	52.45	200.78	41.27	159.51
3	140.31	73.87	66.44	251.24	215.17	36.07	256.58	56.77	199.81
	133.43	69.22	64.22	-	-	-	260.93	58.68	202.26
	157.54	81.95	75.58	-	-	-	247.40	55.15	192.25
4	241.91	125.02	116.89	353.62	263.46	90.16	288.92	66.35	222.57
	239.48	125.88	113.60	312.52	232.84	79.68	293.06	67.31	225.75
	266.08	136.17	129.90	340.56	253.73	86.83	290.71	66.83	223.88

Continued on the following page.

Table 1 Continued.

Sampling	Wheat								
	WEOC			MB-C			CO_2-C		
	Total	Soil-derived	Exudate-derived	Total	Soil-derived	Exudate-derived	Total	Soil-derived	Exudate-derived
	($\mu g\ g^{-1}$)								
1	38.57	24.49	14.08	204.73	181.84	22.89	97.11	26.55	70.56
	36.64	23.93	12.72	283.66	253.27	30.39	104.87	28.90	75.97
	37.43	23.42	14.01	225.45	201.70	23.75	96.28	28.63	67.65
2	44.15	24.07	20.09	413.43	294.84	118.59	252.55	82.91	169.64
	40.60	22.19	18.41	295.80	207.27	88.53	245.01	84.84	160.17
	38.72	19.18	19.54	325.60	208.29	117.31	233.70	78.66	155.04
3	81.92	33.43	48.49	292.56	198.68	93.88	343.94	110.94	233.00
	101.10	37.93	63.17	301.03	204.43	96.60	347.10	114.14	232.97
	105.02	37.27	67.76	268.34	182.23	86.11	344.00	111.88	232.12
4	157.43	57.42	100.01	415.65	293.96	121.69	420.25	130.01	290.24
	148.76	54.29	94.47	399.35	282.43	116.92	415.43	129.37	286.07
	150.48	55.06	95.42	335.04	236.95	98.09	414.76	130.23	284.53

Table 2 $\delta^{13}C$ values from WEOC and MB-C of control and exudate treated soil.

Sampling	$WEO^{13}C$			$MB\text{-}^{13}C$		
	Control	Maize	Wheat	Control	Maize	Wheat
	(‰ VPDB)					
1	-27.3	-21.8	-19.2	-20.7	-22.1	-20.1
	-27.5	-21.0	-19.6	-29.1	-22.2	-20.1
	-	-21.2	-19.0	-23.1	-22.2	-19.0
2	-	-21.3	-17.5	-23.4	-20.8	-18.1
	-27.5	-22.7	-17.5	-22.8	-21.1	-17.8
	-28.3	-21.9	-16.3	-23.9	-21.4	-16.7
3	-28.8	-19.4	-14.6	-23.3	-	-14.1
	-28.0	-19.2	-13.8	-23.0	-	-
	-29.2	-19.3	-13.3	-23.7	-20.8	-15.1
4	-27.2	-18.4	-13.0	-7.1	-26.1	-17.8
	-27.2	-18.5	-13.0	-14.1	-23.4	-19.9
	-26.7	-18.3	-13.0	-24.6	-14.3	-18.9

Table 3 qCO_2 values of control and exudate treated soil.

Sampling	qCO_2		
	Control	Maize	Wheat
	µg CO_2-C $week^{-1}$ (µg MB-C)$^{-1}$		
1	0.13	0.42	0.47
	0.17	0.55	0.37
	0.11	0.42	0.43
2	0.24	0.37	0.37
	0.21	0.47	0.49
	0.21	0.29	0.41
3	0.20	0.24	0.34
	0.23	-	0.34
	0.27	-	0.37
4	0.17	0.10	0.18
	0.15	0.12	0.18
	0.15	0.10	0.21

Table 4 Net soil-derived WEOC, MB-C, CO_2-C amounts and priming effects of exudate treated soil.

Sampling	Maize				Wheat			
	WEOC	MB-C	CO_2-C	Priming	WEOC	MB-C	CO_2-C	Priming
		(µg g^{-1})		(%)		(µg g-1)		(%)
1	11.37	27.42	-7.76	-39.65	8.92	32.13	6.99	35.72
	10.79	-7.28	-12.20	-62.36	8.35	103.56	9.34	47.75
	17.32	45.46	-5.30	-27.11	7.85	51.99	9.07	46.39
2	3.55	-9.33	-15.28	-33.56	-0.02	24.54	9.36	20.55
	2.57	-43.48	-13.14	-28.85	-1.90	-63.03	11.28	24.78
	3.28	95.11	-15.40	-33.82	-4.91	-62.01	5.10	11.20
3	47.24	5.62	-25.45	-63.38	16.99	-3.97	-11.34	-28.25
	42.58	-	-23.54	-58.62	21.50	1.78	-8.15	-20.29
	55.32	-	-27.06	-67.40	20.83	-20.41	-10.40	-25.91
4	50.65	-17.03	-27.05	-74.04	21.85	33.53	-18.84	-51.58
	51.50	-47.66	-26.09	-71.42	18.72	21.99	-19.49	-53.34
	61.80	-26.76	-26.56	-72.71	19.49	-23.49	-18.62	-50.98

Table 5 Percentages of added exudates recovered in the investigated C pools.

	Maize				Wheat			
	WEOC	MB-C	CO_2-C	not retrieved	WEOC	MB-C	CO_2-C	not retrieved
Added-C ($\mu g\ g^{-1}$)	1198.40				1376.49			
	9.59	7.92	17.96	64.54	6.53	9.52	21.63	62.32
%	8.83	6.24	19.42	65.50	6.98	7.73	21.03	64.26
	11.65	8.85	18.71	60.79	7.55	7.21	19.88	65.36

Chapter 3

Table 6 Amounts of WEOC, MB-C, and CO_2-C from controls.

	Control					
	WEOC		MB-C		CO_2-C	
Sampling	Low yield	High yield	Low yield	High yield	Low yield	High yield
	($\mu g\ g^{-1}$)					
1	9.13	7.86	255.81	225.76	24.53	24.33
	9.35	6.93	263.64	271.17	23.94	23.70
	9.17	7.70	-	249.17	24.83	25.41
	6.58	9.00	263.58	253.57	23.00	24.49
	8.16	9.28	262.59	197.23	24.89	22.29
2	13.45	8.48	235.37	179.32	62.02	62.97
	12.90	14.51	142.03	206.09	61.28	63.36
	17.44	11.77	215.09	217.17	62.09	62.56
	14.02	11.52	187.28	174.75	60.13	61.43
	16.04	10.47	180.09	181.51	62.40	62.65
3	13.68	10.94	190.24	177.31	95.93	98.90
	14.57	10.26	193.17	-	94.63	99.46
	15.93	21.38	183.93	198.36	95.83	98.44
	12.00	19.85	203.32	195.30	95.95	97.39
	12.05	11.21	197.20	190.39	95.71	99.06
4	28.93	-	214.02	223.44	128.48	133.34
	8.44	-	230.36	-	127.27	131.98
	25.47	11.09	262.80	231.41	127.84	132.71
	-	14.94	226.80	232.17	130.21	131.01
	32.93	14.33	-	204.56	128.35	132.79

Continued on the following page.

Table 6 continued.

Sampling	Control					
	WEOC		MB-C		CO_2-C	
	Low yield	High yield	Low yield	High yield	Low yield	High yield
	($\mu g\ g^{-1}$)					
5	8.94	8.07	224.68	235.14	157.35	163.56
	8.22	7.57	-	196.08	158.21	162.72
	8.69	8.84	234.14	221.95	158.94	163.64
	7.56	6.80	240.95	230.02	158.85	163.77
	-	-	-	-	157.07	164.02
6	20.51	-	-	216.76	186.06	191.50
	16.06	9.98	213.23	223.51	186.33	191.66
	26.81	8.09	203.09	215.71	186.11	191.20
	28.16	8.75	215.14	209.58	184.93	191.64
	18.33	10.59	212.11	225.50	185.83	191.79
7	12.35	11.51	197.74	188.00	212.55	220.85
	10.44	9.79	191.05	222.57	211.86	221.20
	8.47	-	197.56	243.90	212.99	219.92
	9.86	9.45	212.72	208.19	211.39	220.33
	10.52	10.27	206.23	213.74	211.79	218.11
8	-	8.33	193.36	185.40	237.05	245.68
	11.60	8.49	192.01	178.88	235.78	244.91
	10.86	10.03	170.63	187.05	234.75	244.16
	8.72	9.82	167.05	189.78	236.98	244.91
	10.00	-	170.97	174.87	236.12	245.63
9	-	9.91	188.20	188.90	259.64	268.44
	9.90	-	224.59	196.65	257.78	268.52
	-	9.52	188.00	196.08	258.26	268.05
	12.91	10.56	167.91	191.78	258.05	268.60
	10.59	10.81	245.17	174.56	258.71	267.29
10	14.40	9.65	175.65	198.54	279.65	289.74
	13.29	12.20	183.35	224.68	278.20	289.37
	9.32	8.68	198.65	200.10	278.75	288.98
	11.03	11.38	187.30	227.11	278.82	289.69
	8.25	7.82	193.53	195.56	278.67	290.00
11	-	11.15	176.60	202.94	299.12	309.01
	10.03	14.15	-	195.48	298.39	310.93
	6.03	18.23	191.76	194.07	299.41	309.09
	7.26	11.62	211.38	173.56	297.03	308.09
	6.95	14.70	193.90	156.68	297.76	308.97

Table 7 Amounts of WEOC from artificial exudate treated soils.

Sampling	Artificial exudate					
	WEOC					
	Low yield			High yield		
	Total	Soil-derived	Exudate-derived	Total	Soil-derived	Exudate-derived
	($\mu g\ g^{-1}$)					
1	10.54	10.38	0.16	9.28	9.28	-
	9.07	-	-	7.83	7.82	0.01
	11.96	11.70	0.26	8.21	7.94	0.28
	9.73	9.57	0.15	7.63	7.53	0.10
	9.75	9.50	0.25	12.20	-	-
2	15.86	15.54	0.32	18.13	17.69	0.44
	18.72	18.17	0.55	16.76	16.18	0.58
	21.12	20.74	0.38	12.29	12.03	0.26
	13.44	13.17	0.27	15.36	14.87	0.49
	16.82	16.38	0.44	13.02	12.64	0.38
3	13.37	13.39	-	14.57	14.24	0.34
	22.24	21.82	0.41	13.90	13.69	0.21
	12.42	12.42	-	12.00	11.87	0.13
	16.32	15.89	0.43	10.51	10.28	0.23
	11.75	11.75	0.01	15.40	15.44	-
4	19.67	19.30	0.37	13.81	-	-
	12.44	12.26	0.18	-	-	-
	18.64	18.28	0.36	12.24	12.02	0.22
	15.29	15.06	0.23	13.53	13.31	0.22
	11.54	11.38	0.16	14.19	13.95	0.24
5	-	-	-	9.68	9.30	0.38
	8.87	8.69	0.18	21.33	20.26	1.06
	11.34	11.00	0.34	17.50	16.76	0.74
	7.16	7.03	0.13	10.66	-	-
	10.38	10.34	0.03	11.01	10.54	0.47
6	20.84	20.21	0.62	11.15	10.76	0.39
	23.25	22.33	0.92	6.97	6.59	0.37
	23.95	23.33	0.62	8.74	8.30	0.44
	-	-	-	-	-	-
	-	-	-	7.63	7.25	0.38
7	13.36	-	-	10.77	10.28	0.49
	13.83	12.92	0.91	12.27	11.57	0.70
	13.01	12.21	0.80	8.37	7.85	0.53
	11.20	10.53	0.67	9.83	9.17	0.66
	11.35	10.62	0.72	7.52	7.06	0.46

Continued on the following page.

Table 7 Continued.

Sampling	Artificial exudate					
	WEOC					
	Low yield			High yield		
	Total	Soil-derived	Exudate-derived	Total	Soil-derived	Exudate-derived
	($\mu g\ g^{-1}$)					
8	13.24	12.46	0.78	14.61	13.64	0.97
	9.41	8.65	0.76	14.91	13.76	1.15
	11.99	11.28	0.70	-	-	-
	15.64	14.65	0.99	13.72	12.96	0.76
	13.75	12.82	0.92	13.09	12.00	1.09
9	13.40	12.57	0.83	14.92	14.15	0.77
	12.78	12.10	0.68	11.57	10.72	0.86
	15.24	-	-	12.74	11.93	0.81
	16.12	15.11	1.01	15.29	14.28	1.01
	12.66	11.84	0.82	12.99	12.30	0.70
10	14.08	12.97	1.11	15.26	14.21	1.05
	13.17	12.14	1.03	13.83	12.82	1.01
	11.40	10.58	0.81	10.82	10.03	0.79
	12.74	11.73	1.01	15.15	13.85	1.30
	15.75	14.74	1.01	15.66	14.63	1.03
11	9.92	9.34	0.58	17.48	16.22	1.26
	10.73	9.93	0.80	25.35	23.81	1.54
	9.06	8.56	0.50	12.07	11.36	0.72
	12.19	11.27	0.92	11.78	11.01	0.77
	10.26	9.43	0.82	14.44	13.83	0.61

Table 8 Amounts of MB-C from artificial exudate treated soils.

Sampling	Artificial exudate					
	MB-C					
	Low yield			High yield		
	Total	Soil-derived	Exudate-derived	Total	Soil-derived	Exudate-derived
	($\mu g\ g^{-1}$)					
1	375.72	341.77	33.95	400.89	344.94	55.95
	399.31	350.43	48.89	359.05	324.87	34.19
	349.75	300.10	49.65	345.70	302.54	43.16
	327.59	287.79	39.80	258.71	229.71	29.00
	354.23	319.68	34.54	292.41	252.36	40.05

Continued on the following page.

Table 8 Continued.

Sampling	Artificial exudate					
	MB-C					
	Low yield			High yield		
	Total	Soil-derived	Exudate-derived	Total	Soil-derived	Exudate-derived
	($\mu g\ g^{-1}$)					
2	319.12	146.53	172.59	301.48	160.45	141.03
	328.27	161.13	167.14	-	-	-
	310.12	161.39	148.73	305.12	137.08	168.03
	314.83	150.54	164.29	312.69	131.10	181.60
	321.89	140.95	180.94	330.61	152.07	178.54
3	435.20	172.94	262.26	326.70	95.56	231.14
	383.75	173.11	210.64	406.82	154.68	252.14
	366.28	155.17	211.11	308.50	145.16	163.34
	321.70	107.73	213.98	405.33	148.84	256.49
	375.24	164.09	211.15	322.58	72.90	249.69
4	419.61	165.66	253.95	-	-	-
	397.93	171.23	226.71	506.45	175.25	331.21
	474.47	143.66	330.80	504.47	193.16	311.31
	414.37	165.67	248.70	472.76	158.82	313.94
	489.12	176.60	312.52	-	-	-
5	448.18	182.95	265.24	485.01	198.16	286.85
	569.24	262.11	307.13	517.23	179.37	337.86
	525.93	169.76	356.17	543.07	216.21	326.86
	507.25	217.00	290.26	521.46	176.48	344.98
	614.17	231.24	382.93	541.06	192.71	348.34
6	464.92	125.73	339.19	515.61	156.25	359.36
	455.80	129.38	326.42	483.81	137.44	346.37
	460.09	133.75	326.35	507.00	111.28	395.72
	596.09	109.48	486.61	438.11	114.37	323.74
	499.54	137.88	361.66	496.02	162.29	333.73
7	538.07	113.68	424.39	475.57	118.02	357.54
	463.94	104.67	359.27	418.96	109.35	309.61
	365.78	127.02	238.76	486.36	124.38	361.98
	432.98	102.04	330.94	452.52	114.82	337.70
	414.71	122.34	292.37	496.47	122.72	373.75
8	434.44	102.38	332.06	-	-	-
	575.97	111.91	464.07	544.06	123.79	420.27
	565.97	112.14	453.83	544.36	113.05	431.31
	486.06	109.53	376.52	536.48	108.67	427.81
	420.59	89.00	331.60	-	-	-

Continued on the following page.

Table 8 Continued.

Sampling	Artificial exudate					
	MB-C					
	Low yield			High yield		
	Total	Soil-derived	Exudate-derived	Total	Soil-derived	Exudate-derived
	($\mu g\ g^{-1}$)					
9	462.49	94.12	368.37	502.94	83.17	419.77
	455.32	110.13	345.20	-	-	-
	436.81	111.43	325.37	517.18	102.85	414.32
	493.95	121.10	372.85	504.21	104.34	399.87
	566.29	79.78	486.51	532.29	99.67	432.61
10	-	-	-	399.49	111.33	288.16
	426.76	105.98	320.77	506.07	116.30	389.77
	446.56	123.07	323.49	460.17	106.26	353.91
	442.07	104.45	337.62	536.66	143.09	393.56
	424.52	104.30	320.22	433.39	115.02	318.37
11	357.32	112.70	244.62	-	-	-
	323.46	113.60	209.87	-	-	-
	370.73	86.81	283.92	415.56	102.58	312.98
	417.79	97.71	320.08	419.86	88.08	331.78
	425.02	125.02	300.00	413.68	87.63	326.05

Table 9 Amounts of CO_2-C from artificial exudate treated soils.

Sampling	Artificial exudate					
	CO_2-C					
	Low yield			High yield		
	Total	Soil-derived	Exudate-derived	Total	Soil-derived	Exudate-derived
	($\mu g\ g^{-1}$)					
1	75.84	29.86	45.98	85.95	30.00	55.95
	72.59	28.47	44.12	-	-	-
	-	-	-	86.44	43.28	43.16
	-	-	-	81.64	52.63	29.00
	69.98	28.54	41.43	82.82	42.77	40.05
2	185.28	69.74	115.54	194.12	66.93	127.19
	181.59	68.76	112.83	199.18	69.05	130.12
	181.31	68.98	112.33	198.33	68.04	130.29
	182.68	69.08	113.59	194.51	67.99	126.52
	180.52	67.87	112.65	-	-	-

Continued on the following page.

Table 9 Continued.

Sampling	Artificial exudate					
	CO_2-C					
	Low yield			High yield		
	Total	Soil-derived	Exudate-derived	Total	Soil-derived	Exudate-derived
	($\mu g\ g^{-1}$)					
3	296.97	105.27	191.71	311.88	105.85	206.03
	297.68	105.73	191.95	306.20	103.51	202.69
	302.04	108.32	193.72	307.65	104.12	203.53
	296.52	105.44	191.08	308.38	104.51	203.88
	292.98	104.05	188.93	305.16	102.87	202.29
4	421.71	140.15	281.56	424.39	136.07	288.32
	422.59	141.26	281.33	425.56	136.98	288.58
	420.43	139.53	280.90	423.02	135.76	287.26
	417.80	138.78	279.02	423.66	136.18	287.48
	419.41	139.12	280.28	424.52	136.84	287.68
5	551.96	170.54	381.43	547.30	165.06	382.25
	-	-	-	550.06	166.77	383.29
	550.31	170.13	380.18	548.86	165.71	383.15
	550.43	169.60	380.82	549.71	166.31	383.40
	548.40	168.87	379.54	546.68	165.31	381.37
6	692.43	198.83	493.60	-	-	-
	690.25	197.79	492.46	675.32	190.35	484.97
	687.23	196.95	490.28	674.79	190.17	484.62
	687.26	197.01	490.25	673.93	189.77	484.16
	687.35	197.39	489.96	674.12	190.14	483.98
7	834.64	222.29	612.35	809.56	211.96	597.60
	837.59	223.17	614.42	-	-	-
	836.71	223.83	612.88	807.99	212.07	595.91
	833.81	222.35	611.46	-	-	-
	-	-	-	808.67	212.01	596.66
8	987.74	245.22	742.52	953.20	231.87	721.32
	995.25	246.33	748.92	948.22	230.82	717.40
	985.65	244.50	741.15	948.45	230.70	717.74
	989.01	245.11	743.90	951.39	231.28	720.11
	988.24	245.17	743.07	947.58	230.73	716.85
9	1130.77	265.85	864.92	1077.49	247.52	829.97
	1131.18	265.53	865.65	1080.65	248.13	832.52
	1130.87	265.56	865.31	-	-	-
	1128.08	265.16	862.92	1078.60	247.66	830.95
	1125.78	264.99	860.79	-	-	-

Continued on the following page.

Table 9 Continued.

Sampling	Artificial exudate					
	CO_2-C					
	Low yield			High yield		
	Total	Soil-derived	Exudate-derived	Total	Soil-derived	Exudate-derived
	($\mu g\ g^{-1}$)					
10	1226.58	288.40	938.18	1163.57	267.24	896.33
	1223.24	287.99	935.25	1165.23	267.73	897.50
	1217.35	287.33	930.03	1162.27	267.14	895.13
	1217.48	287.43	930.04	1163.84	267.20	896.64
	1221.94	287.80	934.14	1168.13	267.88	900.25
11	1309.75	313.91	995.84	1240.73	288.16	952.57
	1311.71	314.47	997.24	-	-	-
	1308.66	313.88	994.78	1239.80	288.29	951.51
	1305.69	312.76	992.94	1238.32	287.78	950.55
	1304.94	312.67	992.27	1241.24	288.18	953.06

Table 10 Percentages of added artificial exudates recovered in the investigated C pools.

	Low yield				High yield			
	WEOC	MB-C	CO_2-C	not retrieved	WEOC	MB-C	CO_2-C	not retrieved
Added-C ($\mu g\ g^{-1}$)	2601.09				2601.09			
%	0.01	7.82	38.77	53.40	0.04	8.87	37.25	53.84
	0.05	6.43	38.81	54.71	0.09	13.50	36.71	49.71
	0.02	8.82	38.07	53.10	0.02	11.73	36.54	51.71
	0.04	13.95	37.85	48.15	0.04	13.94	36.00	50.02
	0.02	15.21	37.70	47.07	0.00	14.17	36.48	49.35

Table 11 Amounts of C_{org} on sampling 10 from controls and artificial exudate treated soils.

	Low yield		High yield	
	Control	Artificial exudate	Control	Artificial exudate
C_{org} (%)	1.29	1.36	1.40	1.56
	1.21	1.33	1.38	1.54
	1.24	1.44	1.37	1.50
	1.26	1.40	1.37	1.48
	1.32	1.44	1.32	1.44

Table 12 $\delta^{13}C$ values from WEOC and MB-C of controls and artificial exudate treated soils.

Sampling	Control				Artificial exudate			
	WEOC		MB-C		WEOC		MB-C	
	Low yield	High yield	Low yield	High yield	Low yield	High yield	Low yield	High yield
	(‰ VPDB)				(‰ VPDB)			
1	-27.18	-26.06	-24.18	-21.48	-25.90	-	-17.26	-13.08
	-26.89	-25.75	-23.98	-23.70	-	-26.08	-14.96	-16.22
	-29.34	-26.01	-22.21	-23.11	-25.44	-23.69	-13.57	-14.13
	-25.78	-27.20	-24.31	-23.36	-25.87	-25.19	-15.03	-15.03
	-26.11	-25.97	-23.96	-23.19	-25.12	-27.46	-16.75	-13.27
2	-26.16	-27.54	-22.16	-22.39	-24.44	-24.84	15.83	10.58
	-26.69	-25.00	-21.26	-22.35	-23.74	-24.06	13.62	11.85
	-26.46	-26.73	-22.15	-21.50	-24.57	-25.06	11.56	16.39
	-24.56	-27.32	-21.54	-22.39	-24.43	-24.27	14.51	18.49
	-25.64	-26.69	-22.38	-22.35	-23.97	-24.47	17.32	15.64
3	-26.55	-24.80	-22.40	-24.33	-27.26	-24.52	19.99	27.07
	-27.09	-25.48	-20.63	-	-25.78	-25.13	16.23	20.83
	-26.16	-26.89	-22.61	-22.65	-	-25.44	18.15	14.41
	-28.89	-26.92	-22.83	-23.14	-25.20	-24.62	24.38	21.76
	-27.20	-27.12	-22.93	-22.87	-27.13	-26.42	17.19	31.80
4	-26.67	-	-22.16	-22.10	-24.77	-	20.18	-
	-	-	-22.18	-	-25.09	-24.29	17.69	23.64
	-26.22	-27.18	-22.35	-22.98	-24.74	-24.62	26.64	21.06
	-25.67	-26.90	-22.36	-21.86	-25.05	-24.72	19.83	24.35
	-26.14	-23.69	-	-21.66	-25.15	-24.68	22.55	-

Continued on the following page.

Table 12 Continued.

Sampling	Control				Artificial exudate			
	WEOC		MB-C		WEOC		MB-C	
	Low yield	High yield	Low yield	High yield	Low yield	High yield	Low yield	High yield
	(‰ VPDB)				(‰ VPDB)			
5	-27.09	-27.29	-22.24	-22.22	-	-24.55	19.26	19.27
	-27.13	-27.45	-	-20.88	-25.40	-23.73	15.60	23.59
	-26.13	-28.37	-22.32	-23.19	-24.71	-24.30	25.25	20.00
	-27.91	-28.08	-22.10	-22.00	-25.61	-	17.89	24.18
	-26.49	-26.24	-	-22.36	-26.71	-24.27	21.48	22.94
6	-26.14	-26.54	-	-21.88	-23.91	-24.69	28.87	26.63
	-25.98	-27.89	-22.38	-22.42	-23.19	-23.27	27.93	27.96
	-	-27.56	-22.54	-22.42	-24.20	-23.50	27.45	32.49
	-26.50	-27.49	-22.22	-21.76	-23.83	-	34.97	29.57
	-25.84	-26.97	-22.35	-22.63	-23.69	-23.59	28.48	24.94
7	-28.77	-27.05	-22.18	-22.36	-	-24.11	33.02	30.42
	-28.52	-27.04	-22.26	-22.41	-23.36	-23.22	32.01	29.52
	-	-27.98	-22.67	-22.01	-23.68	-22.77	23.46	29.89
	-28.42	-27.82	-22.47	-22.53	-23.82	-22.47	31.30	30.03
	-27.77	-27.66	-22.58	-22.91	-23.53	-22.86	27.13	30.49
8	-29.44	-30.18	-21.68	-22.43	-23.44	-23.41	31.35	33.10
	-25.18	-27.03	-22.33	-22.58	-21.79	-22.59	34.25	31.88
	-27.56	-29.33	-22.35	-22.47	-23.46	-22.53	33.98	33.28
	-29.94	-27.65	-22.08	-22.25	-23.11	-24.25	32.08	33.64
	-27.45	-28.09	-22.63	-22.26	-22.83	-22.08	33.04	32.81
9	-28.39	-28.02	-22.40	-22.42	-22.69	-23.08	34.15	36.27
	-25.96	-27.28	-22.18	-21.50	-23.36	-21.39	31.56	30.56
	-28.21	-25.46	-22.85	-22.63	-	-22.19	30.67	33.92
	-28.32	-26.64	-22.76	-22.39	-22.67	-21.98	31.34	33.35
	-26.02	-27.23	-7.62	-22.43	-22.48	-22.91	38.37	34.73

Continued on the following page.

Table 12 Continued.

Sampling	Control				Artificial exudate			
	WEOC		MB-C		WEOC		MB-C	
	Low yield	High yield	Low yield	High yield	Low yield	High yield	Low yield	High yield
	(‰ VPDB)				(‰ VPDB)			
10	-28.46	-29.16	-22.49	-22.64	-22.56	-23.23	36.17	28.18
	-28.76	-26.96	-22.55	-22.96	-22.58	-22.89	30.33	31.63
	-28.88	-29.23	-22.55	-22.76	-23.11	-22.88	28.41	31.55
	-27.48	-29.17	-22.95	-23.05	-22.53	-21.92	31.19	29.03
	-29.26	-27.76	-23.17	-22.53	-23.66	-23.44	30.52	29.12
11	-28.27	-27.56	-22.01	-22.26	-23.71	-22.62	25.69	36.20
	-26.89	-28.03	-	-22.54	-22.53	-23.49	23.18	33.45
	-29.01	-	-22.60	-22.52	-23.97	-23.59	31.40	30.52
	-28.67	-28.30	-22.42	-22.60	-22.41	-23.15	31.42	33.13
	-28.01	-28.55	-22.76	-22.11	-22.06	-24.89	27.19	32.98

Table 13 Net soil-derived WEOC, MB-C, CO_2-C amounts and priming effects of artificial exudate treated soils.

Sampling	Artificial exudate							
	WEOC		MB-C		CO_2-C		Priming	
	Low yield	High yield	Low yield	High yield	Low yield	High yield	Low yield	High yield
	($\mu g\ g^{-1}$)						(%)	
1	1.90	-	80.36	105.56	5.63	5.95	23.22	24.75
	-	-0.33	89.02	85.48	4.23	-	17.45	-
	3.22	-0.22	38.70	63.16	-	19.23	-	79.99
	1.09	-0.63	26.39	-9.67	-	28.59	-	118.91
	1.02	-	58.28	12.98	4.31	18.73	17.78	77.90
2	-1.03	6.74	-103.99	-82.82	3.43	-13.79	9.18	-35.78
	1.59	5.22	-89.39	-	2.45	-11.67	6.56	-30.27
	4.16	1.08	-89.13	-106.19	2.68	-12.68	7.16	-32.90
	-3.40	3.91	-99.99	-112.17	2.78	-12.73	7.43	-33.02
	-0.20	1.69	-109.57	-91.20	1.57	-	4.19	-
3	-2.29	-3.83	19.23	-48.19	2.35	1.79	6.91	n.s.
	6.14	-4.37	19.40	10.94	2.81	-0.55	8.27	n.s.
	-3.26	-6.19	1.46	1.41	5.41	0.06	15.89	n.s.
	0.21	-7.78	-45.98	5.10	2.53	0.45	7.43	n.s.
	-3.93	-2.62	10.39	-70.85	1.14	-1.19	3.34	n.s.
4	-5.57	-	-28.87	-	1.57	-1.82	n.s.	-5.39
	-12.61	-	-23.31	19.26	2.68	-0.90	n.s.	-2.68
	-6.60	-0.82	-50.87	37.18	0.95	-2.13	n.s.	-6.31
	-9.81	0.47	-28.86	2.84	0.20	-1.70	n.s.	-5.06
	-13.00	1.11	-17.93	-	0.55	-1.04	n.s.	-3.09
5	-	2.86	18.62	-	1.11	-2.49	n.s.	-7.98
	8.55	13.81	97.79	-5.83	-	-0.77	n.s.	-2.48
	10.86	10.31	5.43	31.01	0.71	-1.83	n.s.	-5.87
	6.89	-	52.67	-8.72	0.18	-1.23	n.s.	-3.94
	10.20	4.09	66.92	-	-0.56	-2.23	n.s.	-7.16
6	-2.67	-4.99	-64.52	-22.19	1.28	-	n.s.	-
	-0.56	-9.16	-60.87	-41.01	0.24	-3.50	n.s.	-12.49
	0.44	-7.45	-56.50	-67.17	-0.60	-3.68	n.s.	-13.12
	-	-	-80.76	-64.07	-0.54	-4.08	n.s.	-14.56
	-	-8.50	-52.37	-16.15	-0.17	-3.71	n.s.	-13.24
7	-	1.15	-3.73	-15.37	-1.57	-6.67	n.s.	-23.38
	2.61	2.44	-12.74	-24.05	-0.69	-	n.s.	-
	1.90	-1.28	9.61	-9.02	-0.03	-6.56	n.s.	-23.00
	0.22	0.04	-15.37	-18.58	-1.51	-	n.s.	-
	0.31	-2.07	4.92	-10.68	-	-6.62	n.s.	-23.22

Continued on the following page.

Table 13 Continued.

Sampling	Artificial exudate							
	WEOC		MB-C		CO_2-C		Priming	
	Low yield	High yield	Low yield	High yield	Low yield	High yield	Low yield	High yield
			($\mu g\ g^{-1}$)				(%)	
8	0.92	5.55	10.68	-	-1.71	-5.12	-7.11	-20.49
	-2.89	5.67	20.21	38.02	-0.60	-6.17	-2.50	-24.71
	-0.25	-	20.45	27.27	-2.42	-6.29	-10.10	-25.18
	3.11	4.86	17.84	22.90	-1.82	-5.71	-7.59	-22.86
	1.29	3.90	-2.70	-	-1.75	-6.26	-7.30	-25.08
9	-0.24	0.03	-34.84	-38.40	-1.77	-6.69	-7.92	-28.92
	-0.72	-3.41	-18.84	-	-2.09	-6.07	-9.37	-26.25
	-	-2.20	-17.53	-18.71	-2.06	-	-9.20	-
	2.30	0.15	-7.86	-17.23	-2.46	-6.55	-11.00	-28.31
	-0.97	-1.83	-49.18	-21.89	-2.63	-	-11.76	-
10	-0.06	1.79	-	-5.79	2.65	-1.90	13.02	-8.90
	-0.89	0.40	17.75	-0.82	2.24	-1.41	11.04	-6.61
	-2.45	-2.39	34.84	-10.85	1.57	-2.00	7.75	-9.34
	-1.29	1.43	16.22	25.98	1.68	-1.94	8.28	-9.07
	1.71	2.21	16.07	-2.09	2.05	-1.26	10.09	-5.90
11	0.60	-0.91	-2.46	-	6.60	1.06	33.79	n.s.
	1.19	6.68	-1.57	-	7.15	-	36.63	n.s.
	-0.18	-5.78	-28.35	8.84	6.56	1.19	33.62	n.s.
	2.52	-6.12	-17.45	-5.66	5.44	0.68	27.88	n.s.
	0.69	-3.30	9.85	-6.11	5.35	1.08	27.41	n.s.

n.s. not significant

Chapter 4

Table 14 Amounts of WEOC from planted soils.

Sampling	Low yield		High yield	
	WEOC		WEOC	
	Maize	Wheat	Maize	Wheat
	($\mu g\ g^{-1}$)		($\mu g\ g^{-1}$)	
Control (t0)	15.40	21.75	10.02	9.55
	11.59	11.79	19.01	18.96
	9.82	11.26	13.18	13.14
	10.07	8.75	11.36	11.56
	17.08	-	15.66	15.09

Continued on the following page.

Table 14 Continued.

Sampling	Low yield		High yield	
	WEOC		WEOC	
	Maize	Wheat	Maize	Wheat
	(μg g^{-1})		(μg g^{-1})	
1	7.67	5.94	14.73	17.45
	4.07	-	25.36	8.10
	-	-	17.44	7.30
	-	6.79	12.11	9.14
	-	4.58	10.27	25.91
2	10.19	13.89	29.38	14.44
	10.12	9.45	13.88	9.95
	9.37	8.47	12.21	15.67
	9.38	9.52	18.77	16.17
	12.58	11.79	15.13	-
3	19.73	19.86	17.65	13.63
	14.95	18.40	18.95	26.35
	18.65	14.36	13.18	21.83
	20.21	12.91	9.24	16.74
	12.32	-	9.36	16.65
4	7.77	14.27	-	12.20
	12.31	19.83	12.99	19.46
	12.17	22.54	-	9.98
	10.50	16.83	12.23	18.44
	10.96	24.11	13.96	12.22
5	6.94	13.74	10.46	14.65
	10.34	34.97	9.62	10.28
	-	16.38	7.86	11.38
	10.32	11.15	-	9.99
	13.01	20.22	8.93	8.67
6	45.22	41.05	8.77	11.03
	37.00	-	9.20	6.84
	26.73	35.44	8.08	6.40
	41.92	38.50	16.03	5.34
	29.10	33.96	14.08	5.22
7	12.94	12.77	17.42	20.01
	19.73	18.46	19.01	23.05
	12.85	10.23	12.20	11.43
	15.97	9.56	13.32	-
	10.12	16.62	10.10	18.27

Table 15 Amounts of MB-C from planted low yield soil.

Sampling	Low yield					
	MB-C					
	Maize			Wheat		
	Total	Soil-derived	Rhizodeposit-derived	Total	Soil-derived	Rhizodeposit-derived
	($\mu g\ g^{-1}$)					
Control (t0)	189.95	-	-	227.42	-	-
	236.55	-	-	227.82	-	-
	238.56	-	-	231.30	-	-
	256.25	-	-	217.21	-	-
	257.47	-	-	-	-	-
1	279.57	256.16	23.41	226.78	226.78	-
	265.02	259.65	5.37	223.02	223.02	-
	186.80	169.16	17.65	219.54	219.54	-
	227.03	195.63	31.40	213.19	213.19	-
	221.78	207.81	13.97	195.16	195.16	-
2	229.89	212.18	17.72	227.96	146.63	81.34
	233.27	175.55	57.72	239.02	-	-
	250.00	195.63	54.37	241.18	150.32	90.86
	219.52	202.90	16.62	217.77	98.46	119.31
	215.08	189.27	25.80	216.33	126.66	89.67
3	194.79	-	-	226.61	218.23	8.38
	294.73	126.80	167.93	223.69	216.48	7.22
	248.93	205.37	43.57	233.89	231.49	2.39
	248.97	208.26	40.71	223.16	221.38	1.78
	280.09	121.73	158.36	-	-	-
4	209.51	153.92	55.58	241.27	217.21	24.06
	226.90	179.10	47.80	133.02	127.17	5.85
	271.96	167.57	104.39	184.24	147.70	36.54
	218.94	168.79	50.15	224.22	183.89	40.33
	181.73	148.07	33.66	194.16	175.63	18.53
5	234.47	211.90	22.57	310.29	158.54	151.75
	247.58	181.69	65.89	243.44	202.89	40.55
	226.02	202.58	23.44	375.54	169.88	205.66
	236.66	180.11	56.56	212.44	167.57	44.86
	213.18	175.54	37.63	208.71	170.55	38.16
6	202.40	163.46	38.94	205.04	172.54	32.50
	216.40	194.66	21.74	-	-	-
	213.86	177.92	35.94	205.77	176.76	29.01
	205.35	148.56	56.78	202.17	191.40	10.78
	221.31	166.42	54.89	-	-	-

Continued on the following page.

Table 15 Continued.

Sampling	Low yield					
	MB-C					
	Maize			Wheat		
	Total	Soil-derived	Rhizodeposit-derived	Total	Soil-derived	Rhizodeposit-derived
	($\mu g\ g^{-1}$)					
7	240.59	185.23	55.36	194.40	191.06	3.34
	-	-	-	236.28	226.87	9.41
	247.89	193.09	54.79	257.39	225.53	31.87
	246.68	195.36	51.32	172.11	153.68	18.43
	245.73	195.58	50.15	184.14	177.99	6.16

Table 16 Amounts of MB-C from planted high yield soil.

Sampling	High yield					
	MB-C					
	Maize			Wheat		
	Total	Soil-derived	Rhizodeposit-derived	Total	Soil-derived	Rhizodeposit-derived
	($\mu g\ g^{-1}$)					
Control (t0)	265.49	-	-	252.20	-	-
	247.24	-	-	262.33	-	-
	243.79	-	-	242.84	-	-
	253.37	-	-	221.86	-	-
	294.55	-	-	231.08	-	-
1	245.14	221.96	23.18	241.00	241.00	-
	214.63	209.16	5.47	249.45	249.45	-
	259.09	231.71	27.38	243.12	243.12	-
	259.71	233.10	26.61	226.08	226.08	-
	234.00	218.89	15.10	211.13	211.13	-
2	258.07	225.64	32.43	255.70	255.70	-
	303.29	227.42	75.88	172.91	172.91	-
	-	-	-	265.15	265.15	-
	302.10	209.78	92.32	279.95	279.95	-
	282.12	219.48	62.65	233.72	233.72	-
3	274.50	199.96	74.54	259.51	178.88	80.63
	309.61	215.87	93.74	256.11	251.39	4.72
	367.39	244.69	122.70	337.96	228.71	109.25
	240.87	210.05	30.82	257.59	235.06	22.53
	310.94	271.11	39.83	243.50	211.11	32.38

Continued on the following page.

Table 16 Continued.

Sampling	High yield					
	MB-C					
	Maize			Wheat		
	Total	Soil-derived	Rhizodeposit-derived	Total	Soil-derived	Rhizodeposit-derived
	($\mu g\ g^{-1}$)					
4	248.61	204.13	44.48	245.07	212.15	32.91
	279.33	268.12	11.20	245.50	208.04	37.46
	260.45	198.05	62.41	275.42	-	-
	260.65	215.75	44.90	273.79	232.73	41.06
	243.52	212.82	30.70	299.65	250.28	49.37
5	221.22	151.01	70.20	171.56	155.93	15.62
	242.50	168.66	73.84	258.91	210.77	48.14
	206.76	165.45	41.31	224.64	188.91	35.73
	241.21	188.43	52.78	273.28	173.43	99.85
	236.27	167.77	68.50	237.56	186.46	51.10
6	310.51	241.67	68.84	258.18	212.71	45.47
	309.97	250.61	59.36	273.20	241.68	31.52
	295.06	236.78	58.28	293.92	224.74	69.18
	293.11	-	-	292.49	272.89	19.61
	253.24	202.64	50.60	297.73	213.17	84.56
7	190.37	155.99	34.38	160.08	141.46	18.62
	-	-	-	171.18	-	-
	224.65	176.03	48.61	176.30	156.09	20.21
	223.41	165.85	57.56	204.09	170.75	33.34
	214.44	170.46	43.98	183.15	165.37	17.78

Table 17 Amounts of CO_2-C from planted low yield soil.

Sampling	Low yield							
	CO_2-C							
	Maize				Wheat			
	Control	Total	Soil-derived	Rhizodeposit-derived	Control	Total	Soil-derived	Rhizodeposit-derived
	($\mu g\ g^{-1}$)							
1	44.82	57.2	40.95	16.25	42.90	71.83	71.83	-
	52.84	88.87	64.09	24.78	39.21	-	-	-
	38.77	44.32	26.73	17.59	36.83	47.82	47.82	-
	51.21	68.16	31.41	36.75	49.10	41.06	41.06	-
	54.88	62.11	29.39	32.72	41.97	-	-	-
2	93.32	214.25	55.22	159.03	84.90	-	-	-
	101.35	235.71	143.70	92.00	81.21	210.46	154.21	56.25
	87.27	188.65	90.98	97.68	78.84	162.11	91.83	70.28
	99.71	-	-	-	91.11	205.48	150.21	55.27
	103.38	212.23	116.93	95.30	83.98	179.91	108.55	71.36
3	141.82	299.6	126.38	173.22	126.91	-	-	-
	149.85	-	-	-	123.21	234.45	162.10	72.35
	135.78	313.37	123.09	190.28	120.84	255.14	162.87	92.27
	148.22	323.15	158.20	164.95	133.11	248.28	159.69	88.59
	151.88	333.91	106.53	227.38	125.98	259.20	188.40	70.80
4	190.33	384.10	153.09	231.01	168.91	325.86	193.87	131.99
	198.35	404.93	156.47	248.46	165.22	317.54	208.45	109.08
	184.28	-	-	-	162.85	361.07	197.98	163.09
	196.72	441.18	162.38	278.80	175.12	320.82	190.58	130.24
	200.39	393.04	164.18	228.86	167.99	343.32	187.19	156.13

Continued on the following page.

Table 17 Continued.

Sampling	Low yield							
	CO_2-C							
	Maize				Wheat			
	Control	Total	Soil-derived	Rhizodeposit-derived	Control	Total	Soil-derived	Rhizodeposit-derived
	($\mu g\ g^{-1}$)							
5	238.83	508.82	178.67	330.15	210.92	468.20	242.19	226.00
	246.86	505.81	193.59	312.23	207.22	452.85	251.24	201.62
	232.79	492.69	200.87	291.82	204.85	434.87	245.85	189.03
	245.22	490.46	214.93	275.54	217.12	424.05	239.86	184.19
	248.89	493.18	202.71	290.47	209.99	425.10	235.94	189.16
6	287.33	635.97	271.23	364.74	252.92	523.06	284.41	238.65
	295.36	638.70	262.32	376.38	249.22	527.14	293.78	233.36
	281.29	659.16	287.99	371.17	246.85	510.74	291.56	219.18
	293.73	683.98	252.79	431.19	259.12	518.74	301.50	217.24
	297.4	623.49	265.51	357.98	251.99	510.81	292.05	218.77
7	335.84	693.93	311.02	382.91	294.92	609.53	341.89	267.63
	343.87	701.17	317.62	383.56	291.23	572.49	318.68	253.80
	329.79	714.40	329.31	385.09	288.86	563.42	329.80	233.62
	342.23	710.88	327.41	383.47	301.13	582.25	341.79	240.47
	345.9	714.61	332.85	381.77	294.00	562.41	330.36	232.05

Table 18 Amounts of CO_2-C from planted high yield soil.

Sampling	High yield							
	CO_2-C							
	Maize				Wheat			
	Control	Total	Soil-derived	Rhizodeposit-derived	Control	Total	Soil-derived	Rhizodeposit-derived
	($\mu g\ g^{-1}$)							
1	31.83	76.67	29.09	47.59	35.52	38.83	38.83	-
	40.97	77.83	45.68	32.15	36.70	39.45	39.45	-
	32.95	64.08	28.90	35.19	41.44	47.78	47.78	-
	48.54	59.09	37.22	21.87	33.69	49.80	49.80	-
	35.19	67.28	31.44	35.83	41.29	-	-	-
2	69.73	201.76	47.98	153.79	73.25	68.67	59.74	8.92
	78.86	154.29	62.64	91.65	74.43	86.34	84.67	1.67
	70.84	189.14	53.75	135.38	79.17	88.91	50.80	38.11
	86.43	-	-	-	71.42	70.05	50.74	19.31
	73.08	151.99	64.78	87.21	79.02	122.03	108.12	13.91
3	107.62	254.94	90.98	163.96	110.98	152.33	96.00	56.33
	116.76	288.76	66.85	221.91	112.16	152.95	127.17	25.78
	108.74	264.65	75.92	188.74	116.90	155.66	116.54	39.12
	124.33	210.87	79.96	130.91	109.15	147.36	110.76	36.60
	110.98	251.01	71.87	179.14	116.75	151.21	129.25	21.96
4	145.52	314.41	99.40	215.01	148.71	237.66	152.40	85.26
	154.65	-	-	-	149.89	225.12	140.92	84.20
	146.63	329.27	94.14	235.13	154.63	267.50	147.52	119.98
	162.22	316.97	92.21	224.76	146.88	230.17	139.59	90.58
	148.87	312.33	98.56	213.77	154.48	239.63	163.09	76.53

Continued on the following page.

Table 18 Continued.

Sampling	High yield							
	CO_2-C							
	Maize				Wheat			
	Control	Total	Soil-derived	Rhizodeposit-derived	Control	Total	Soil-derived	Rhizodeposit-derived
	($\mu g\ g^{-1}$)							
5	183.41	492.70	145.05	347.65	186.44	325.02	181.37	143.65
	192.55	-	-	-	187.62	345.84	184.65	161.18
	184.53	452.01	126.58	325.43	192.36	345.99	189.46	156.53
	200.12	552.01	169.70	382.30	184.61	357.92	195.39	162.54
	186.77	517.91	152.98	364.93	192.21	328.27	186.54	141.73
6	221.3	630.31	208.61	421.71	224.17	436.91	244.13	192.78
	230.44	-	-	-	225.35	-	-	-
	222.42	683.87	220.62	463.26	230.09	442.39	241.96	200.42
	238.01	630.78	221.70	409.08	222.34	488.24	259.37	228.88
	224.66	669.53	229.35	440.18	229.94	448.21	243.85	204.36
7	259.2	744.57	279.58	464.99	261.90	480.12	266.70	213.42
	268.34	821.39	325.41	495.99	263.08	-	-	-
	260.32	821.22	314.34	506.88	267.82	528.96	309.98	218.97
	275.91	819.30	317.85	501.45	260.07	556.00	323.17	232.83
	262.56	787.96	300.88	487.08	267.67	553.16	325.80	227.36

Table 19 Amounts of C_{org} from planted low yield soil.

Sampling	Low yield					
	C_{org}					
	Maize			Wheat		
	Total	Soil-derived	Rhizodeposit-derived	Total	Soil-derived	Rhizodeposit-derived
	($mg\ g^{-1}$)					
Control (t0)	10.92	-	-	13.99	-	-
	12.81	-	-	14.02	-	-
	12.42	-	-	13.03	-	-
	14.18	-	-	13.77	-	-
	14.06	-	-	12.91	-	-
1	14.69	14.69	-	15.39	15.39	-
	13.38	13.38	-	13.46	13.46	-
	14.01	14.01	-	14.60	14.60	-
	14.26	14.26	-	12.87	12.87	-
	14.40	14.40	-	12.85	12.85	-
2	12.94	12.94	-	13.01	13.01	-
	-	-	-	13.10	13.10	-
	13.46	13.46	-	12.82	12.82	-
	12.82	12.82	-	13.30	13.30	-
	13.50	13.50	-	13.69	13.69	-
3	13.34	13.31	0.04	13.04	13.04	-
	12.46	12.23	0.23	13.11	13.11	-
	14.23	14.07	0.16	12.69	-	-
	12.98	12.96	0.02	13.25	13.25	-
	13.88	13.66	0.22	13.03	13.03	-
4	14.19	13.99	0.19	13.85	13.85	-
	12.43	12.30	0.13	13.45	13.45	-
	13.15	13.15	-	12.20	12.20	-
	13.30	13.22	0.09	13.12	13.12	-
	12.91	12.83	0.07	12.81	12.81	-
5	13.07	13.05	0.03	12.56	12.41	0.15
	13.22	13.12	0.09	13.38	13.37	0.01
	-	-	-	14.49	14.24	0.25
	-	-	-	13.89	13.73	0.16
	13.18	12.86	0.31	14.10	14.01	0.09
6	12.15	12.13	0.02	14.15	14.15	-
	14.21	14.11	0.10	13.10	13.10	-
	13.32	13.19	0.12	14.95	14.95	-
	13.29	12.92	0.38	13.27	13.27	-
	12.96	12.73	0.23	13.21	13.21	-

Continued on the following page.

Table 19 Continued.

Sampling	Low yield					
	C_{org}					
	Maize			Wheat		
	Total	Soil-derived	Rhizodeposit-derived	Total	Soil-derived	Rhizodeposit-derived
	(mg g^{-1})					
7	13.59	13.39	0.20	13.26	13.22	0.04
	13.07	12.89	0.17	13.21	13.16	0.05
	12.69	-	-	12.93	12.84	0.09
	13.02	12.85	0.17	12.67	12.57	0.10
	13.38	13.38	-	12.81	12.81	0.00

Table 20 Amounts of C_{org} from planted high yield soil.

Sampling	High yield					
	C_{org}					
	Maize			Wheat		
	Total	Soil-derived	Rhizodeposit-derived	Total	Soil-derived	Rhizodeposit-derived
	(mg g^{-1})					
Control (t0)	12.93	-	-	12.83	-	-
	12.70	-	-	14.08	-	-
	15.30	-	-	13.46	-	-
	15.17	-	-	14.97	-	-
	14.60	-	-	13.73	-	-
1	14.18	14.18	-	14.42	14.42	-
	14.94	14.94	-	13.98	13.98	-
	15.03	15.03	-	13.52	13.52	-
	16.13	16.13	-	16.51	16.51	-
	14.17	14.17	-	15.35	15.35	-
2	14.31	14.31	-	16.70	16.70	-
	15.24	15.24	-	14.43	14.43	-
	15.41	15.41	-	16.06	16.06	-
	13.72	13.72	-	14.93	14.93	-
	17.57	17.57	-	11.42	11.42	-
3	13.96	13.96	-	14.52	14.52	-
	13.61	13.61	-	12.99	12.99	-
	14.46	14.46	-	15.29	15.29	-
	15.16	15.16	-	14.23	14.23	-
	14.96	14.96	-	14.89	14.89	-

Continued on the following page.

Table 20 Continued.

Sampling	High yield					
	C_{org}					
	Maize			Wheat		
	Total	Soil-derived	Rhizodeposit-derived	Total	Soil-derived	Rhizodeposit-derived
	(mg g^{-1})					
4	13.96	13.90	0.06	13.19	13.12	0.07
	15.74	15.65	0.10	13.67	13.64	0.03
	14.82	14.56	0.27	15.03	14.82	0.22
	14.99	14.73	0.27	14.51	14.29	0.22
	15.18	14.93	0.25	13.85	13.61	0.23
5	14.72	14.26	0.46	16.04	15.94	0.10
	14.26	14.03	0.23	13.92	13.80	0.12
	15.64	15.06	0.57	14.41	14.37	0.04
	15.15	14.93	0.23	15.01	14.91	0.10
	14.15	13.88	0.26	14.83	14.76	0.07
6	13.74	13.63	0.12	15.86	15.38	-
	14.61	14.21	0.40	15.57	15.34	-
	14.02	13.58	0.44	14.24	14.20	-
	13.60	13.41	0.20	14.82	14.79	-
	14.25	13.90	0.35	13.86	-	-
7	15.31	14.65	0.66	14.53	14.53	-
	14.94	14.74	0.20	14.62	14.62	-
	13.59	13.18	0.42	14.26	14.26	-
	16.71	16.39	0.32	14.40	14.40	-
	15.66	15.23	0.43	15.22	15.22	-

Table 21 $\delta^{13}C$ values from WEOC of planted soils.

Sampling	$WEO^{13}C$			
	Low yield		High yield	
	Maize	Wheat	Maize	Wheat
	(‰ VPDB)			
Control (t0)	-27.87	-25.91	-26.70	-27.74
	-24.93	-25.81	-22.42	-24.37
	-28.07	-26.26	-26.46	-26.68
	-27.21	-25.03	-23.74	-25.65
	-20.46	-	-24.51	-25.94

Continued on the following page.

Table 21 Continued.

Sampling	WEO^{13}C			
	Low yield		High yield	
	Maize	Wheat	Maize	Wheat
	(‰ VPDB)			
1	-24.58	-25.78	-25.77	-20.24
	-25.81	-	-26.15	-23.27
	-	-	-29.55	-
	-	-24.22	-24.59	-
	-	-24.59	-25.00	-24.21
2	-26.54	-21.89	-22.03	-25.11
	-26.10	-27.06	-26.63	-26.67
	-24.46	-23.77	-27.22	-23.51
	-21.65	-24.76	-26.20	-23.60
	-26.69	-23.69	-22.23	-
3	-20.18	-26.06	-25.33	-24.80
	-27.62	-25.76	-25.19	-20.96
	-21.06	-26.74	-	-25.81
	-23.61	-25.70	-25.05	-25.27
	-23.63	-	-25.59	-23.89
4	-26.72	-24.29	-	-17.16
	-26.76	-21.69	-25.96	-24.85
	-23.85	-26.29	-	-26.16
	-22.52	-20.82	-22.35	-23.79
	-26.16	-23.23	-20.15	-22.66
5	-24.62	-26.35	-23.15	-23.06
	-23.51	-23.95	-23.13	-26.55
	-	-28.06	-	-26.83
	-26.84	-24.16	-	-25.33
	-25.16	-20.80	-23.24	-26.39
6	-13.61	-16.48	-24.31	-26.47
	-15.26	-	-25.07	-26.06
	-17.72	-19.46	-23.36	-24.19
	-19.49	-14.51	-21.32	-24.85
	-17.07	-17.55	-25.12	-24.56
7	-24.85	-26.37	-18.78	-17.42
	-18.04	-19.59	-17.17	-11.28
	-20.21	-25.62	-24.51	-20.34
	-19.22	-24.67	-22.25	-
	-17.58	-22.99	-23.75	-18.57

Table 22 $\delta^{13}C$ values from MB-C of planted soils.

Sampling	MB-^{13}C			
	Low yield		High yield	
	Maize	Wheat	Maize	Wheat
	(‰ VPDB)			
Control (t0)	-22.96	-22.80	-23.76	-22.72
	-22.76	-22.50	-23.46	-23.21
	-23.30	-23.32	-23.65	-22.39
	-23.17	-23.56	-23.54	-23.07
	-	-	-	-23.90
1	-21.79	-23.16	-21.48	-21.94
	-22.76	-	-23.12	-22.27
	-21.67	-22.86	-21.57	-22.56
	-21.14	-23.33	-21.63	-22.78
	-22.16	-23.40	-22.55	-22.70
2	-21.33	-21.78	-20.15	-23.18
	-16.02	-	-17.51	-23.23
	-17.63	-21.71	-13.22	-22.52
	-22.03	-21.11	-14.82	-22.19
	-20.38	-21.58	-17.08	-23.49
3	-24.55	-22.16	-12.37	-12.75
	-7.46	-22.31	-10.95	-22.45
	-16.24	-22.77	-10.52	-11.64
	-17.63	-22.85	-18.84	-20.18
	-4.31	-22.89	-18.49	-18.90
4	-8.68	-18.29	-15.01	-16.23
	-12.17	-20.95	-21.60	-15.86
	-1.42	-13.59	-8.84	-
	-9.34	-14.47	-13.15	-15.98
	-16.33	-18.49	-18.71	-15.28
5	-18.24	2.24	-3.45	-18.01
	-8.21	-13.29	-7.87	-12.77
	-16.79	6.90	-14.36	-14.25
	-8.09	-11.50	-9.64	-2.83
	-12.52	-13.22	-4.74	-11.17
6	-10.69	-14.74	-11.09	-13.50
	-17.38	-11.64	-11.60	-16.83
	-14.24	-15.36	-11.84	-11.22
	-8.62	-21.06	-	-19.48
	-8.96	-16.79	-12.12	-7.42

Continued on the following page.

Table 22 Continued.

Sampling	MB-^{13}C			
	Low yield		High yield	
	Maize	Wheat	Maize	Wheat
	(‰ VPDB)			
7	-8.85	-22.20	-12.35	-17.97
	-11.47	-21.10	-10.03	-
	-8.25	-16.44	-11.90	-18.26
	-11.55	-17.18	-9.93	-15.95
	-11.35	-21.76	-11.72	-18.61

Table 23 $\delta^{13}C$ values from CO_2 of planted soils.

Sampling	$^{13}CO_2$			
	Low yield		High yield	
	Maize	Wheat	Maize	Wheat
	(‰ VPDB)			
Control (t0)	-24.35	-24.02	-25.61	-24.60
	-22.28	-24.39	-23.78	-23.07
	-24.13	-23.72	-25.28	-25.68
	-23.79	-23.45	-25.37	-24.43
	-23.17	-22.48	-24.33	-24.93
1	-19.13	-24.36	-10.09	-24.11
	-19.44	-	-16.41	-23.47
	-17.55	-23.91	-13.66	-22.91
	-15.89	-24.48	-17.32	-21.53
	-15.85	-22.20	-15.47	-
2	-3.32	-	1.16	-18.12
	-12.30	-22.14	-7.25	-23.89
	-	-20.95	-0.56	-14.90
	-15.41	-22.13	7.25	-15.79
	-12.86	-21.34	-5.02	-22.33
3	-0.28	-2.87	0.35	-2.82
	15.46	-19.37	16.07	-19.18
	7.50	-12.43	7.57	-11.72
	-7.66	-12.82	-10.74	-12.60
	8.36	-21.90	8.57	-20.82
4	10.68	2.17	6.35	5.79
	11.31	-13.15	-13.67	7.79
	34.27	8.30	23.97	8.77
	19.87	3.21	22.16	10.08
	-5.31	10.90	0.65	-1.76

Continued on the following page.

Table 23 Continued.

Sampling	$^{13}CO_2$			
	Low yield		High yield	
	Maize	Wheat	Maize	Wheat
	(‰ VPDB)			
5	17.88	10.58	22.10	11.79
	13.47	8.02	-	14.16
	8.13	4.59	12.33	10.81
	-2.44	5.13	20.19	10.14
	6.50	6.89	22.89	8.35
6	6.76	3.06	6.10	-1.25
	8.98	2.03	-	-
	0.07	-6.02	14.35	0.93
	14.84	-11.06	2.50	4.14
	2.74	-6.26	6.62	2.26
7	-23.17	-0.82	-1.80	-12.13
	-19.46	-11.18	-3.17	-
	-18.56	-13.92	0.18	-16.63
	-20.93	-10.59	-1.81	-12.29
	-22.36	-17.85	-0.46	-13.93

Table 24 $\delta^{13}C$ values from C_{org} of planted soils.

Sampling	$^{13}C_{org}$			
	Low yield		High yield	
	Maize	Wheat	Maize	Wheat
	(‰ VPDB)			
Control (t0)	-25.83	-25.59	-25.82	-25.44
	-25.54	-25.69	-25.56	-25.64
	-25.73	-25.87	-25.52	-25.67
	-25.36	-25.54	-25.82	-25.81
	-25.62	-25.78	-25.61	-25.31
1	-25.22	-25.63	-26.14	-25.88
	-25.88	-	-25.74	-25.91
	-25.64	-26.02	-25.42	-25.96
	-25.44	-25.79	-25.82	-
	-25.81	-25.93	-25.90	-25.69
2	-25.49	-25.76	-25.77	-24.83
	-25.13	-25.75	-25.74	-25.81
	-25.63	-25.69	-25.08	-25.18
	-25.69	-25.64	-25.42	-25.59
	-25.61	-25.64	-23.76	-25.62

Continued on the following page.

Table 24 Continued.

Sampling	$^{13}C_{org}$			
	Low yield		High yield	
	Maize	Wheat	Maize	Wheat
	(‰ VPDB)			
3	-25.51	-25.35	-25.67	-25.72
	-25.06	-25.60	-25.67	-26.01
	-25.15	-25.47	-25.14	-26.02
	-25.55	-25.69	-25.24	-25.86
	-25.05	-25.57	-25.10	-25.86
4	-24.85	-25.80	-25.45	-25.30
	-25.05	-25.43	-25.34	-25.48
	-	-25.31	-24.52	-24.91
	-25.20	-25.47	-24.55	-24.83
	-25.39	-25.20	-24.99	-24.74
5	-25.49	-25.06	-23.62	-25.22
	-25.15	-25.64	-24.81	-25.07
	-24.45	-24.72	-23.89	-25.40
	-25.06	-25.04	-24.68	-25.19
	-24.20	-25.33	-24.41	-25.31
6	-25.52	-25.37	-25.17	-23.86
	-25.19	-24.98	-23.90	-24.74
	-25.10	-25.12	-23.72	-25.43
	-24.07	-25.91	-24.76	-25.46
	-24.57	-25.36	-24.21	-25.62
7	-24.76	-25.53	-23.14	-
	-24.76	-25.49	-24.78	-25.33
	-	-25.30	-23.78	-25.43
	-24.78	-25.24	-24.46	-
	-	-25.69	-24.04	-25.41

Table 25 Net soil-derived CO_2-C amounts and priming effects of planted soils.

Sampling	Low yield				High yield			
	CO_2-C		Priming		CO_2-C		Priming	
	Maize	Wheat	Maize	Wheat	Maize	Wheat	Maize	Wheat
	($\mu g\ g^{-1}$)		(%)		($\mu g\ g^{-1}$)		(%)	
1	-7.55	29.83	-7.55	29.83	-8.81	1.10	-23.25	2.92
	15.58	-	15.58	-	7.79	1.72	20.55	4.56
	-21.77	5.81	-21.77	5.81	-9.00	10.05	-23.74	26.64
	-17.09	-0.95	-17.09	-0.95	-0.68	12.07	-1.78	31.99
	-19.12	-	-19.12	-	-6.45	-	-17.03	-
2	-31.79	-	-31.79	-	-24.39	-21.58	-64.35	-58.18
	56.68	58.64	56.68	58.64	-9.72	3.34	-25.66	7.88
	3.96	-3.74	3.96	-3.74	-18.61	-30.53	-49.11	-81.89
	-	54.64	-	54.64	-	-30.59	-	-82.05
	29.92	12.98	29.92	12.98	-7.58	26.79	-20.01	70.04
3	-23.83	-	-23.83	-	-4.20	-12.54	-11.08	-33.24
	-	-6.11	-	-6.11	-28.33	18.63	-74.77	49.37
	-27.12	-5.34	-27.12	-5.34	-19.26	8.00	-50.84	21.21
	7.98	-8.52	7.98	-8.52	-15.22	2.21	-40.16	5.87
	-43.68	20.19	-43.68	20.19	-23.31	20.70	-61.51	54.88
4	-23.96	-16.40	-23.96	-16.40	-15.61	-1.28	-41.19	-3.38
	-20.58	-1.81	-20.58	-1.81	-	-12.76	-	-33.81
	-	-12.28	-	-12.28	-20.87	-6.16	-55.06	-16.32
	-14.68	-19.69	-14.68	-19.69	-22.80	-14.09	-60.17	-37.33
	-12.87	-23.08	-12.87	-23.08	-16.45	9.42	-43.41	24.97

Continued on the following page.

Table 25 Continued.

Sampling	Low yield				High yield			
	CO_2-C		Priming		CO_2-C		Priming	
	Maize	Wheat	Maize	Wheat	Maize	Wheat	Maize	Wheat
	($\mu g\ g^{-1}$)		(%)		($\mu g\ g^{-1}$)		(%)	
5	-28.87	4.57	-28.87	4.57	11.08	-5.06	29.23	-13.41
	-13.95	13.62	-13.95	13.62	-	-1.78	-	-4.72
	-6.67	8.23	-6.67	8.23	-7.40	3.03	-19.52	8.02
	7.39	2.24	7.39	2.24	35.73	8.95	94.29	23.73
	-4.82	-1.68	-4.82	-1.68	19.00	0.11	50.15	0.28
6	24.57	-0.61	24.57	-0.61	22.14	18.92	58.41	50.15
	15.67	8.76	15.67	8.76	-	-	-	-
	41.34	6.54	41.34	6.54	34.15	16.75	90.11	44.40
	6.14	16.48	6.14	16.48	35.22	34.15	92.95	90.52
	18.86	7.03	18.86	7.03	42.87	18.64	113.14	49.41
7	-5.46	7.23	-5.46	7.23	21.62	-18.36	57.06	-48.66
	1.14	-15.98	1.14	-15.98	67.44	-	177.98	-
	12.84	-4.86	12.84	-4.86	56.38	24.93	148.77	66.06
	10.94	7.12	10.94	7.12	59.88	38.11	158.03	101.00
	16.37	-4.30	16.37	-4.30	42.92	40.74	113.26	107.98

Table 26 Percentages of rhizodeposit-C recovered in the investigated C pools after the growing period.

	Low yield					
	Maize			Wheat		
	MB-C	CO_2-C	C_{org}	MB-C	CO_2-C	C_{org}
Added-C (µg g^{-1})		616.86			316.15	
	8.98	62.07	32.05	1.06	84.56	13.08
	8.58	62.18	27.85	2.97	80.19	16.68
%	8.88	62.43	29.28	10.07	73.81	28.59
	8.32	62.17	27.93	5.82	75.98	31.59
	8.13	61.89	29.28	1.95	73.31	0.33

	High yield					
	Maize			Wheat		
	MB-C	CO_2-C	C_{org}	MB-C	CO_2-C	C_{org}
Added-C (µg g^{-1})		947.21			332.01	
	3.63	49.09	69.87	5.61	64.28	29.80
	7.03	52.36	21.55	6.77	67.21	36.57
%	5.13	53.51	43.97	6.09	65.95	13.03
	6.08	52.94	33.57	10.04	70.13	30.06
	4.64	51.42	45.20	5.35	68.48	20.63

Table 27 Percentages of rhizodeposit-C recovered in the investigated C pools in low yield soil on all samplings.

Sampling	Low yield					
	MB-C		CO_2-C		C_{org}	
	Maize	Wheat	Maize	Wheat	Maize	Wheat
	(%)					
1	8.37	-	28.41	-	-	-
	2.03	-	27.88	-	-	-
	9.45	-	39.69	-	-	-
	13.83	-	53.92	-	-	-
	6.30	-	52.68	-	-	-
2	7.71	35.68	74.23	-	-	-
	24.74	-	39.03	26.73	-	-
	21.75	37.67	51.78	43.35	-	-
	7.57	54.79	-	26.90	-	-
	12.00	41.45	44.90	39.66	-	-
3	-	-	57.82	-	0.29	-
	-	-	-	30.86	1.86	-
	-	-	60.72	36.16	1.11	-
	-	-	51.04	35.68	0.18	-
	-	-	68.10	27.31	1.60	-

Continued on the following page.

Table 27 Continued.

Sampling	Low yield					
	MB-C		CO_2-C		C_{org}	
	Maize	Wheat	Maize	Wheat	Maize	Wheat
	(%)					
4	26.53	9.97	60.14	40.51	1.35	-
	21.07	4.40	61.36	34.35	1.05	-
	38.38	19.83	-	45.17	-	-
	22.91	17.99	63.19	40.60	0.67	-
	18.52	9.54	58.23	45.48	0.57	-
5	9.63	48.91	64.89	48.27	0.22	1.17
	26.61	16.66	61.73	44.52	0.71	0.08
	10.37	54.76	59.23	43.47	-	1.69
	23.90	21.12	56.18	43.44	-	1.13
	17.65	18.28	58.90	44.50	2.38	0.65
6	19.24	15.85	57.35	45.63	0.15	-
	10.05	-	58.93	44.27	0.72	-
	16.81	14.10	56.31	42.91	0.94	-
	27.65	5.33	63.04	41.88	2.82	-
	24.80	-	57.42	42.83	1.76	-
7	23.01	1.72	55.18	43.91	1.45	0.31
	-	3.98	54.70	44.33	1.31	0.40
	22.10	12.38	53.90	41.46	-	0.70
	20.80	10.71	53.94	41.30	1.32	0.79
	20.41	3.35	53.42	41.26	-	0.01

Table 28 Percentages of rhizodeposit-C recovered in the investigated C pools in high yield soil on all samplings.

Sampling	High yield					
	MB-C		CO_2-C		C_{org}	
	Maize	Wheat	Maize	Wheat	Maize	Wheat
	(%)					
1	9.46	-	62.07	-	-	-
	2.55	-	41.31	-	-	-
	10.57	-	54.92	-	-	-
	10.25	-	37.01	-	-	-
	6.45	-	53.26	-	-	-
2	12.57	-	76.22	12.99	-	-
	25.02	-	59.40	1.93	-	-
	-	-	71.58	42.86	-	-
	30.56	-	-	27.57	-	-
	22.21	-	57.38	11.40	-	-

Continued on the following page.

Table 28 Continued.

Sampling	High yield					
	MB-C		CO_2-C		C_{org}	
	Maize	Wheat	Maize	Wheat	Maize	Wheat
	(%)					
3	27.15	31.07	64.31	36.98	-	-
	30.28	1.84	76.85	16.86	-	-
	33.40	32.33	71.32	25.13	-	-
	12.80	8.75	62.08	24.84	-	-
	12.81	13.30	71.37	14.52	-	-
4	17.89	13.43	68.39	35.87	0.44	0.52
	4.01	15.26	-	37.40	0.63	0.19
	23.96	-	71.41	44.85	1.79	1.44
	17.23	15.00	70.91	39.35	1.78	1.48
	12.61	16.48	68.44	31.94	1.65	1.67
5	31.73	9.10	70.56	44.20	3.13	0.62
	30.45	18.59	-	46.61	1.59	0.87
	19.98	15.91	72.00	45.24	3.66	0.30
	21.88	36.54	69.26	45.41	1.49	0.66
	28.99	21.51	70.46	43.17	1.87	0.46
6	22.17	17.61	66.91	44.12	0.85	3.02
	19.15	11.54	-	-	2.73	1.47
	19.75	23.54	67.74	45.30	3.16	0.27
	-	6.70	64.85	46.88	1.43	0.20
	19.98	28.40	65.74	45.59	2.45	-
7	18.06	11.63	62.45	44.45	4.32	-
	-	-	60.38	-	1.37	-
	21.64	11.46	61.72	41.40	3.06	-
	25.76	16.34	61.20	41.88	1.90	-
	20.51	9.71	61.82	41.10	2.73	-

Table 29 Root dry weight and $\delta^{13}C$ values from roots of planted soils.

Sampling	Root dry weight				$\delta^{13}C$ of roots			
	Low yield		High Yield		Low yield		High Yield	
	Maize	Wheat	Maize	Wheat	Maize	Wheat	Maize	Wheat
	(g)				(‰ VPDB)			
1	0.20	0.04	0.12	0.03	-8.03	-	-1.18	-
	0.03	0.05	0.16	0.04	-9.03	-	-4.72	-
	0.13	0.04	0.13	0.04	-8.43	-25.10	-	-25.10
	0.12	0.04	0.11	0.05	-9.30	-	-	-
	0.11	0.04	0.12	0.06	-8.93	-25.58	-7.27	-25.58
2	0.28	0.09	0.21	0.08	-	-	-	-7.66
	0.13	0.07	0.22	0.03	5.36	-19.51	0.75	-
	0.17	0.01	0.39	0.13	1.85	-	-	-14.74
	0.06	0.06	0.31	0.13	-9.59	-	5.14	-15.09
	0.10	0.04	0.27	0.10	-	-	5.78	-
3	0.37	0.08	0.66	0.16	-	0.73	17.77	-
	0.35	0.12	0.45	0.09	4.30	-0.42	18.17	-
	0.30	0.14	0.46	0.20	15.87	3.18	15.56	12.27
	0.47	0.14	0.58	0.17	-	-	13.61	9.88
	0.32	0.14	0.50	0.24	-	3.61	-	8.19
4	1.04	0.19	0.75	0.22	31.11	-	24.41	27.80
	0.42	0.05	0.33	0.17	-	-	26.44	-
	0.71	0.16	0.71	0.13	33.30	-	38.02	20.50
	0.47	0.16	0.39	0.29	36.80	24.61	37.07	-
	0.22	0.15	0.29	0.27	13.21	24.62	15.24	-

Continued on the following page.

Table 29 Continued.

Sampling	Root dry weight				$\delta^{13}C$ of roots			
	Low yield		High Yield		Low yield		High Yield	
	Maize	Wheat	Maize	Wheat	Maize	Wheat	Maize	Wheat
	(g)				(‰ VPDB)			
5	0.44	0.32	1.13	0.18	26.90	28.66	39.91	32.40
	0.43	0.14	0.68	0.36	32.69	35.53	28.05	-
	0.81	0.21	0.64	0.18	37.27	-	22.67	-
	0.78	0.27	0.61	0.23	39.56	-	40.22	-
	-	0.28	0.89	0.35	36.57	30.70	41.46	32.22
6	0.86	0.38	1.96	0.42	41.20	29.32	32.84	31.24
	0.80	0.32	1.07	0.36	33.34	32.52	39.07	30.98
	0.84	0.26	0.99	0.32	29.38	31.42	35.97	27.26
	0.91	0.07	1.10	-	29.13	14.20	37.52	-
	0.91	0.14	1.01	0.46	33.74	33.73	33.87	32.02
7	1.31	0.18	1.91	0.30	38.65	-	38.71	-
	1.89	0.31	1.07	0.41	37.91	-	31.16	-
	1.82	0.42	1.92	0.33	43.91	30.30	30.46	18.83
	2.09	0.44	1.49	0.56	32.24	31.70	29.47	20.45
	1.74	0.16	1.07	0.35	34.26	15.27	34.36	22.82

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