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Fast incorporation of root-derived lipids and fatty acids into soil – Evidence from a short term multiple $^{14}CO_2$ pulse labelling experiment

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ABSTRACT

Plant-derived lipids are regarded to be mainly incorporated into soil via above ground biomass. The contribution of root-derived lipids to soil organic matter (SOM) is not easily accessible, so this incorporation pathway is mostly underestimated, whereas it is common knowledge that the contribution of rhizodeposits to SOM is of major importance for the turnover of organic carbon. Not only the contribution, but also the incorporation rates and turnover time of exclusively root-derived lipids remain unknown. We determined for the first time the incorporation rates of rhizodeposit-derived lipids into soil planted with *Lolium perenne*, using a multiple $^{14}CO_2$ pulse labelling experiment carried out under controlled laboratory conditions. Additionally, we accessed differences in lipid composition between the rhizosphere and root-free soil to evaluate the direct contribution of root-derived lipids to SOM. The lipid composition in the rhizosphere clearly showed a greater abundance of microbial lipids like $C_{16:1}$ and $C_{18:1}$, as well as root-derived $C_{18:2+3}$ fatty acids (FAs) than the initial and root-free soil. The incorporation rates of total lipids (k_{Lip}) and FAs (k_{FA}) based on ^{14}C data revealed a very fast incorporation into SOM (rhizosphere: k_{Lip} 0.82 year^{-1}; k_{FA} 0.31 year^{-1}; root-free soil: k_{Lip} 0.70 year^{-1}; k_{FA} 0.48 year^{-1}) after the first ^{14}C pulse for young plants. Thereafter, incorporation rates decreased until the end of the experiment (rhizosphere: k_{Lip} 0.17 year^{-1}; k_{FA} 0.03 year^{-1}; root-free loess: k_{Lip} 0.11 year^{-1}; k_{FA} 0.06 year^{-1}). The incorporation rates resulting from the ^{14}C pulse labelling experiment are comparable to turnover rates of total, i.e. above ground and root-derived, and lipids from field experiments using ^{13}C labelling approaches. The fast allocation of root-derived lipids to substrate beneath, and distant from, roots gives new insights into the carbon incorporation of OM on a molecular level. This implies that incorporation of lipid compounds, especially into soil deeper than the uppermost few centimetres or the ploughing layer, is mainly due to root-derived OM, in contrast to common knowledge.

1. Introduction

Incorporation and turnover of plant-derived lipids into soil have been frequently studied and reveal mean residence times of lipid compounds in soils in the range of several decades (Cayet and Lichtfouse, 2001; Wiesenberg et al., 2004, 2008a; Quénéa et al., 2006). Long term turnover and age of lipids in soil are commonly studied using radiocarbon dating (Bol et al., 1996; Rethemeyer et al., 2004; Kramer and Gleixner, 2006), modification of ^{13}C signature after C_3/C_4 vegetation change (Cayet and Lichtfouse, 2001; Wiesenberg et al., 2004; Quénéa et al., 2006) or ^{13}C modifications derived from free air CO_2 enrichment experiments using ^{13}C depleted CO_2 (Wiesenberg et al., 2008a). These methods are based on changes in isotopic signature of $\Delta^{14}C$ or $\delta^{13}C$ in C_{org} and lipids close to natural abundance and imply minor isotopic changes in soil C detectable on a year to decade range. Thus, the approaches are not appropriate for determining short term changes in plant-derived lipids in soil on a day to month scale. Some recent studies described short term changes on a week to month scale in soil lipid composition via experiments under controlled conditions and combining biomarker with ^{13}C and ^{14}C pulse labelling techniques (Lichtfouse et al., 1995; Wiesenberg et al., 2009, 2010). However, the dynamics of plant-derived lipids in soil within shorter periods on a day to week scale have not been reported. Whereas short term incorporation of plant-derived lipids into soil was difficult to follow, even on a monthly scale only by determining changes in abundances of individual components (Wiesenberg et al., unpublished results), application of isotopic (^{13}C, ^{14}C) pulse labelling techniques revealed a high potential for following short term changes in soil OM pools (Kuzyakov and Domanski, 2000; Nguyen, 2003), even on a molecular level (Wiesenberg et al., 2009, 2010). By combining lipid analysis and ^{14}C labelling, a high sensitivity was obtained for determining such changes on a day to week scale (Wiesenberg et al., 2010).

It remains unclear whether root-derived lipids contribute a major part to the soil lipid pool. The traditional opinion relates mainly to plant-derived lipid incorporation into soil via litterfall (Lichtfo-

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use et al., 1994; Cayet and Lichtfouse, 2001) or atmospheric deposition (Conte et al., 2003). Recent studies have implied analysis of root lipids for the correlation of plant biomass with SOM (e.g. Wiesenberg et al., 2004; Otto and Simpson, 2006; Jansen and Nierop, 2009; Kuhn et al., 2009). Nevertheless, the dynamics of root-derived lipids remain unknown, i.e. whether there is a faster incorporation than from litterfall or if the incorporation rates of root-derived lipids might be in a same range as those from above ground biomass. Attempts to assess the contribution of root-derived C to soil lipids are scarce (Feng and Simpson, 2007) and did not reveal information concerning short term dynamics.

In order to investigate short term incorporation of root-derived total lipids and FAs as a sub-fraction of total lipids, *Lolium perenne* plants were grown under controlled conditions. Several $^{14}CO_2$ isotopic pulse labels were applied and ^{14}C signals in C_{org}, lipids and FAs were traced in the soil in order to determine the incorporation of root-derived OM. While lipid distribution patterns were expected to reveal only marginal changes on a day to week scale, the ^{14}C signal of lipids incorporated into soil after several isotopic pulses was expected to follow the short term dynamics of OM.

2. Materials and methods

2.1. Experimental and sampling

L. perenne [L.] was chosen as a typical, widespread grass from temperate climates. The growing season of this perennial plant strongly depends on climatic conditions and averages around 6 months per year. The lipid composition (Dove et al., 1996; Wiesenberg et al., 2008b) and below ground allocation of bulk C under this grass species (Kuzyakov et al., 1999; Domanski et al., 2001) are well known, whereas the below ground allocation of lipid components is not known. *L. perenne* was grown under controlled laboratory conditions on loess from Nussloch (SW Germany) in polycarbonate filtration devices ("CombiSart", Sartorius AG, Germany) and fertilized with modified Hoagland nutrient solution (Hoagland and Arnon, 1950; Gocke et al., unpublished results). Loess was chosen as growing substrate because of structural and physical properties similar to loamy soils (Kuzyakov et al., 2006), whereas the organic carbon content (C_{org} 0.3 mg g^{-1}) and microbial activity are very low. Hence, little interference from loess OM with freshly incorporated plant biomass could be expected (Wiesenberg et al., 2010). Three pots per sampling date were initially planted with *L. perenne*, accounting for 15 pots in total. Starting from an age of 59 days after germination, the plants received five ^{14}C isotopic pulses at 407 kBq (equivalent to 2.442×10^7 dpm) in 5 day intervals by labelling in an atmosphere enriched in $^{14}CO_2$. To avoid direct input of above ground biomass and of $^{14}CO_2$ into loess, the plant pots were sealed around the shoots 1 day before the first $^{14}CO_2$ pulse label was applied. Growing conditions and the labelling technique have been described in detail elsewhere (Kuzyakov et al., 2006; Gocke et al., unpublished results). Briefly, plants were labelled in a $^{14}CO_2$ atmosphere by dissolving $Na_2^{14}CO_3$ in H_2SO_4 and pumping the produced $^{14}CO_2$ into the closed acrylic glass chamber equipped with an internal ventilation unit for the equal distribution of the CO_2. The plants were exposed for 5 h to $^{14}CO_2$ until the labelled CO_2 was completely consumed. As previously described, these short term pulse labels do not influence the plant composition (Wiesenberg et al., 2009). Between the ^{14}C pulses the plants continued to grow outside the labelling chamber under controlled conditions with natural atmospheric ^{14}C concentration. An aliquot of the homogenized loess sample was kept as a reference for lipid composition and termed initial loess.

Three planted pots were sampled 5 days after each ^{14}C pulse. Shoots were cut and roots were separated from loess with tweezers. While the loess almost free of roots was termed root-free loess, the loess adjacent to roots was separated from roots by washing and filtration of the solution and was termed rhizosphere loess. All samples were dried at 60 °C and ground in a ball mill. The sample set from one representative pot per sampling date was subjected to lipid analysis.

2.2. Lipid extraction, separation and analysis

Total root biomass (0.6–2.4 g), as well as part of rhizosphere (10–20 g) and root-free/initial loess samples (ca. 100 g) were extracted for free lipids via Soxhlet extraction for at least 40 h using a solvent mixture of CH_2Cl_2/MeOH (93:7; v:v; Wiesenberg et al., 2004, 2010). After extraction, the solvent mixture was reduced by rotary evaporation. Extracts were re-dissolved with CH_2Cl_2 and aliquots were transferred to scintillation vials for ^{14}C liquid scintillation counting. FAs were separated from the remaining lipid extract on a KOH-coated silica gel column (Wiesenberg et al., 2009). Neutral lipids were eluted first with CH_2Cl_2, followed by FAs as a second fraction using CH_2Cl_2/HCO_2H (99:1; v:v). The solvent was completely removed after elution. After re-dissolving the FA fraction in CH_2Cl_2, an aliquot was transferred to a scintillation vial. Another aliquot was subjected to gas chromatography with flame ionisation detection (GC–FID; Agilent 7890). Defined amounts of a deuteriated standard (d_{39}-*n*-C_{20} FA) were added to the FA fractions, before they were silylated using BSTFA [*N,O*-bis(trimethylsilyl)trifluoroacetamide] prior to GC–FID analysis.

2.3. ^{14}C liquid scintillation counting

To analyse ^{14}C incorporated into plant biomass, shoot and root samples were weighed into ceramic cups and combusted in an oven (Feststoffmodul 1300, AnalytikJena) at 800 °C under continuous O_2 flow. Loess samples (rhizosphere and root-free loess) were combusted at 1200 °C. CO_2 released by combustion was trapped in NaOH and ^{14}C activity was measured in 1 ml aliquots mixed with 2 ml scintillation cocktail (Rotiszint EcoPlus, Carl Roth) using a 1450 LSC & Luminescence Counter (MicroBeta TriLux, Perkin Elmer Inc.). Because of lower ^{14}C activity in loess than in plant biomass, loess samples were measured in 6 ml aliquots mixed with 12 ml Rotiszint using a LS 6500 multi-purpose scintillation counter (Beckman). ^{14}C incorporated into loess OM ($^{14}C_{org}$) was calculated as the difference between total ^{14}C recovered in loess (by combustion, see above) and ^{14}C incorporated into loess $CaCO_3$ by recrystallization with root-derived CO_2. To analyse ^{14}C activity only in loess $CaCO_3$, loess samples were dissolved in H_3PO_4, and the CO_2 released from $CaCO_3$ was trapped in NaOH (Gocke et al., unpublished results) and ^{14}C measured as above.

Three aliquots each of total extracts and FAs (10 μg) were split from the total fractions and measured in triplicate for ^{14}C activity. After transferring lipid fractions to scintillation vials, the solvent was completely removed. Thereafter, FAs were re-dissolved in 2 m MeOH and 4 ml Rotiszint were added. ^{14}C activity of lipids and FAs, as well as background of the respective solvent blanks, were measured after decay of chemiluminescence using LS 6500 a multi-purpose scintillation counter (LS 6500; Wiesenberg et al., 2010).

3. Results and discussion

3.1. FA composition

The distribution pattern of FAs in roots of *L. perenne* revealed a strong predominance of *n*-C_{16} FAs, large amounts of unsaturated $C_{18:1-3}$ and a predominance of even long chain (>C_{18}) *n*-FAs

(Fig. 1A). The distribution confirms previous studies of grass roots (Wiesenberg et al., 2004; Wiesenberg and Schwark, 2006).

Unplanted, initial loess was dominated by n-C_{16} and long chain FAs maximizing at n-C_{28} (Fig. 1A). The initial loess lacked unsaturated FAs. The low predominance of even vs. odd numbered long chain FAs originates from strongly degraded plant-derived FAs and is related to the absence of any recently incorporated plant biomass (Wiesenberg et al., 2004).

After the experiment corresponding to 12 weeks growth, the root-free loess samples revealed a slight enrichment in very long chain acids (>n-C_{26}) and also in n-C_{16} and $C_{18:1}$ acids (Fig. 1B). While the very long chain acids are derived from roots, the short chain acids can be attributed to microbial as well as plant remains (Harwood and Russell, 1984). In root-free loess, unsaturated C_{16} FAs could not be determined, indicating an absence of living microorganisms (Harwood and Russell, 1984). Hence, the root-derived very long chain FAs denote that part of the root-free loess was rooted during the growth of *Lolium*. Resulting from the ongoing modification of the root system, part of the roots died during plant growth and was therefore not part of the rhizosphere at the sampling date.

Within the rhizosphere, the abundance of most long chain acids (>n-C_{18}) decreased similarly to n-C_{16}, whereas the abundance of especially unsaturated $C_{16:1-2}$ and $C_{18:1-3}$ FAs increased vs. the initial loess (Fig. 1B). The increase in polyunsaturated $C_{18:2-3}$ FAs in the rhizosphere is due to the presence of fresh roots, whereas the increase in $C_{16:1-2}$ and partially $C_{18:1}$ can be related to the presence of microorganisms feeding on rhizodeposits (Kuzyakov and Schneckenberger, 2004). This might explain the deficit in n-C_{16} within the rhizosphere as microorganisms degrade fresh, and co-metabolize old, plant related compounds in loess, including n-C_{16}, which is slightly more readily degradable than long chain FAs (Wiesenberg et al., 2008a). The decrease in long chain FAs in the rhizosphere can be related to the co-metabolic degradation of 'old' loess FAs by way of utilization of freshly incorporated root-derived FAs by microorganisms (Blagodatskaya and Kuzyakov, 2008). The changes in the FA composition in the rhizosphere and in root-free loess compared to initial loess can be attributed to different

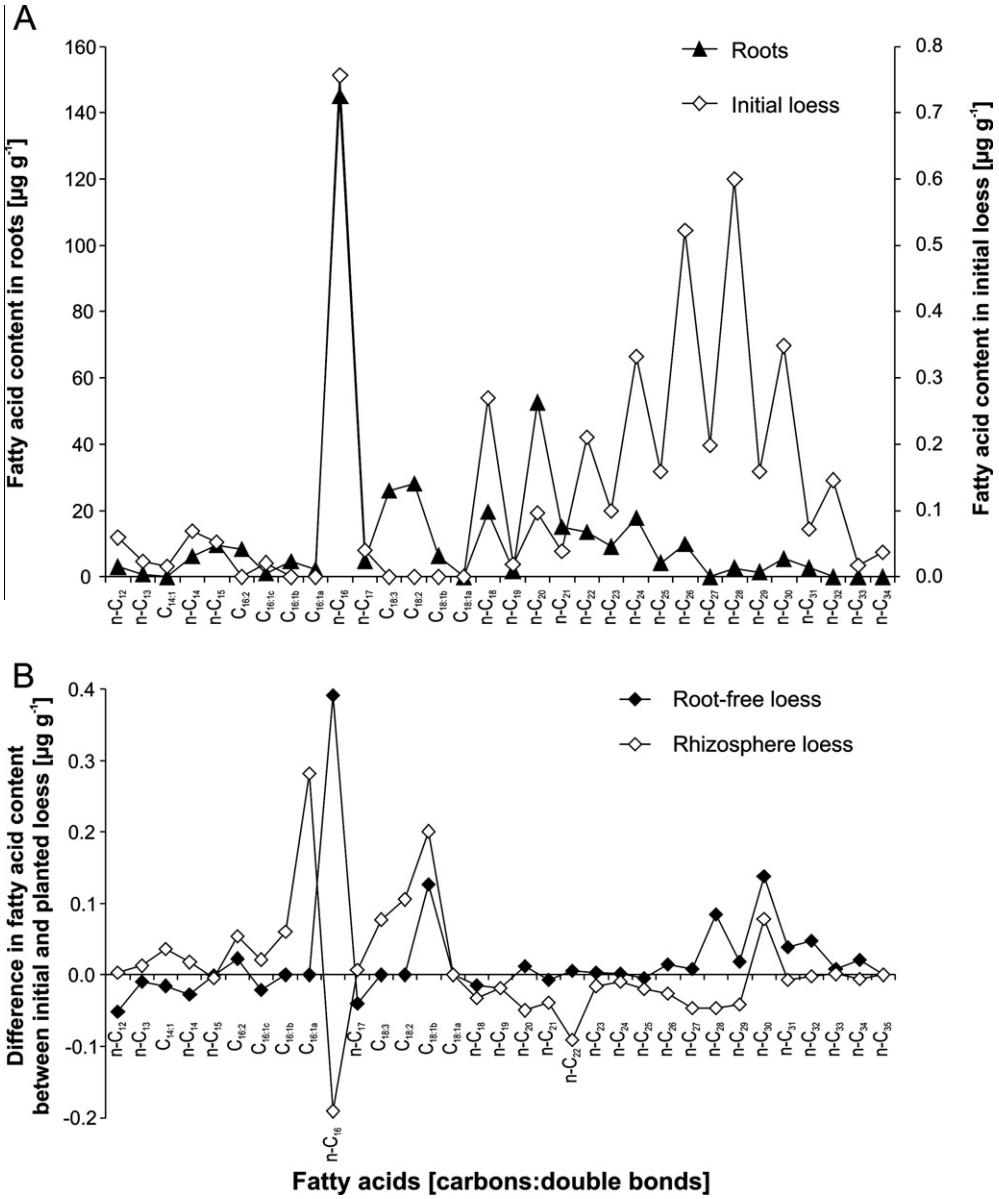

Fig. 1. FA composition of initial loess and root tissues (A). Changes in FA abundance in rhizosphere and root-free loess are given for the final sampling in the experiment (B).

sources of biomass i.e. dead root fragments in root-free loess and microorganisms and fresh root biomass in the rhizosphere, confirming previous findings not using molecular markers (Kuzyakov and Schneckenberger, 2004). Although the separation method for rhizosphere sampling does not allow clear separation between rhizosphere and root-free soil, the lipid distribution pattern clearly indicates different OM contents in both samples.

3.2. Incorporation of ^{14}C label into loess

Labelling of *L. perenne* in a $^{14}CO_2$ atmosphere produced shoot tissues with ^{14}C activity between 8.8 and 46.9 $\times$ 10^6 dpm g^{-1} in shoots and between 0.4 and 9.9 $\times$ 10^6 dpm g^{-1} in root biomass (Table 1), whereas ambient ^{14}C values were close to zero. Depending on plant growth stage and therefore changing incorporation and respiration of assimilated $^{14}CO_2$, ^{14}C activity in plant tissues did not increase linearly with increasing number of ^{14}C pulses. However, the almost constant proportions of ^{14}C in total lipids and FAs in shoots when related to $^{14}CO_{org}$ in shoots suggest that the general mechanisms of lipid biosynthesis remained almost uniform during the experiment. The comparatively high ^{14}C activity in lipids vs. the absolute amount of lipids in plant tissue (generally <10% of plant biomass correspond to extractable lipids) can be related to the fact that major parts of more mobile C pools in plants like sugars are re-utilized during the 5 day periods after the isotopic pulses. This led to depletion in ^{14}C values in these C pools when compared to more stable pools in plants like lipids.

FAs account for 19–31% of the ^{14}C activity in the total lipids (Table 1), which corresponds to the mass portion of FAs (unpublished data). Therefore, the whole extractable lipid pool seems to be homogeneously labelled in shoots after all the ^{14}C pulses.

A decrease in ^{14}C activity was observed from root tissues over rhizosphere towards root-free loess. ^{14}C activity of C_{org} in rhizosphere was up to 2.3 times that in root-free loess (Table 1). Generally, the ^{14}C activity of lipids and FAs was higher in rhizosphere than in root-free loess. The data indicate an incorporation of lipids into both, substrate adjacent to and distant from roots, which was not restricted to FAs. Hence, rhizodeposition of lipids took place, not only in the rhizosphere, which was sampled at the end of the experiment, but also at places where the roots grew earlier. Also, uncertainties in the separation of rhizosphere and root-free soil contribute to this result. Furthermore, root-free loess contained molecular markers indicating the presence of dead root fragments, which must derive from formerly incorporated roots that died before sampling and therefore were not part of the intact rhizosphere anymore. Despite the operationally defined separation of rhizosphere and root-free substrate, clear differences in ^{14}C values and lipid composition were observed in both sample sets.

3.3. Incorporation rates of lipids and FAs

Based on the ^{14}C activity, the incorporation/turnover rates of root-derived C_{org}, lipids and FAs can be assessed in rhizosphere and root-free loess. According to calculations used for estimation of turnover rate in soil (e.g. Balesdent et al., 1987; Wiesenberg et al., 2004), the fraction of incorporated ^{14}C signal in rhizosphere/root-free loess is calculated ($f_{incorporated}$):

$$f_{incorporated} = \left({}^{14}C_{labelled\ Rh/RF} - {}^{14}C_{initial\ Rh/RF}\right) \times \left({}^{14}C_{labelled\ root} - {}^{14}C_{initial\ root}\right)^{-1} \quad (1)$$

where $^{14}CO_{labelled\ Rh/RF}$ is the ^{14}C activity of labelled rhizosphere or root-free loess after isotopic pulse labelling and $^{14}CO_{initial\ Rh/RF}$ the initial ^{14}C activity of the corresponding compartment; $^{14}CO_{labelled\ root}$ corresponds to the ^{14}C activity of the roots after ^{14}C pulse labelling and $^{14}CO_{initial\ root}$ as the initial ^{14}C activity in roots.

Table 1
Normalized ^{14}C activity (dpm g^{-1} C_{org}) for individual plant and loess compartments after application of 1–5 ^{14}C pulses.

Carbon pool	Received ^{14}C pulses [Number of pulses] (days after 1st pulse)	Shoots [10^6 dpm g^{-1} shoot C_{org}] (% of $^{14}CO_{org}$ shoots)	Roots [10^3 dpm g^{-1} root C_{org}] (% of $^{14}CO_{org}$ roots)	Rhizosphere loess [10^3 dpm g^{-1} rhizosphere C_{org}] (% of $^{14}CO_{org}$ rhizosphere)	Root-free loess [10^3 dpm g^{-1} root-free loess C_{org}] (% of $^{14}CO_{org}$ root-free loess)
C_{org}		8.8	352.8	112.1	47.8
	1 (5)				
		33.1	7 101.8	1 760.1	1 022.3
	2 (10)				
		32.7	3 677.7	1 613.7	893.8
	3 (15)				
		35.0	5 361.7	1 421.3	1 362.0
	4 (20)				
		46.9	9 855.7	3 190.3	2 113.1
	5 (25)				
Total lipids		3.3 (37)	24.5 (7)	4.0 (4)	3.4 (7)
	1 (5)				
		8.0 (24)	343.0 (5)	76.9 (4)	58.4 (6)
	2 (10)				
		7.5 (23)	77.7 (2)	38.7 (2)	36.9 (4)
	3 (15)				
		6.7 (19)	242.2 (5)	70.2 (5)	38.4 (3)
	4 (20)				
		12.1 (26)	1 279.4 (13)	113.6 (4)	73.5 (4)
	5 (25)				
FAs		0.6 (7)	10.1 (3)	1.5 (1)	2.3 (5)
	1 (5)				
		2.5 (8)	106.1 (2)	28.3 (2)	21.3 (2)
	2 (10)				
		2.3 (7)	20.1 (1)	13.8 (1)	10.9 (1)
	3 (15)				
		2.0 (6)	81.5 (2)	19.6 (1)	12.4 (1)
	4 (20)				
		3.4 (7)	386.0 (4)	21.1 (1)	37.0 (2)
	5 (25)				

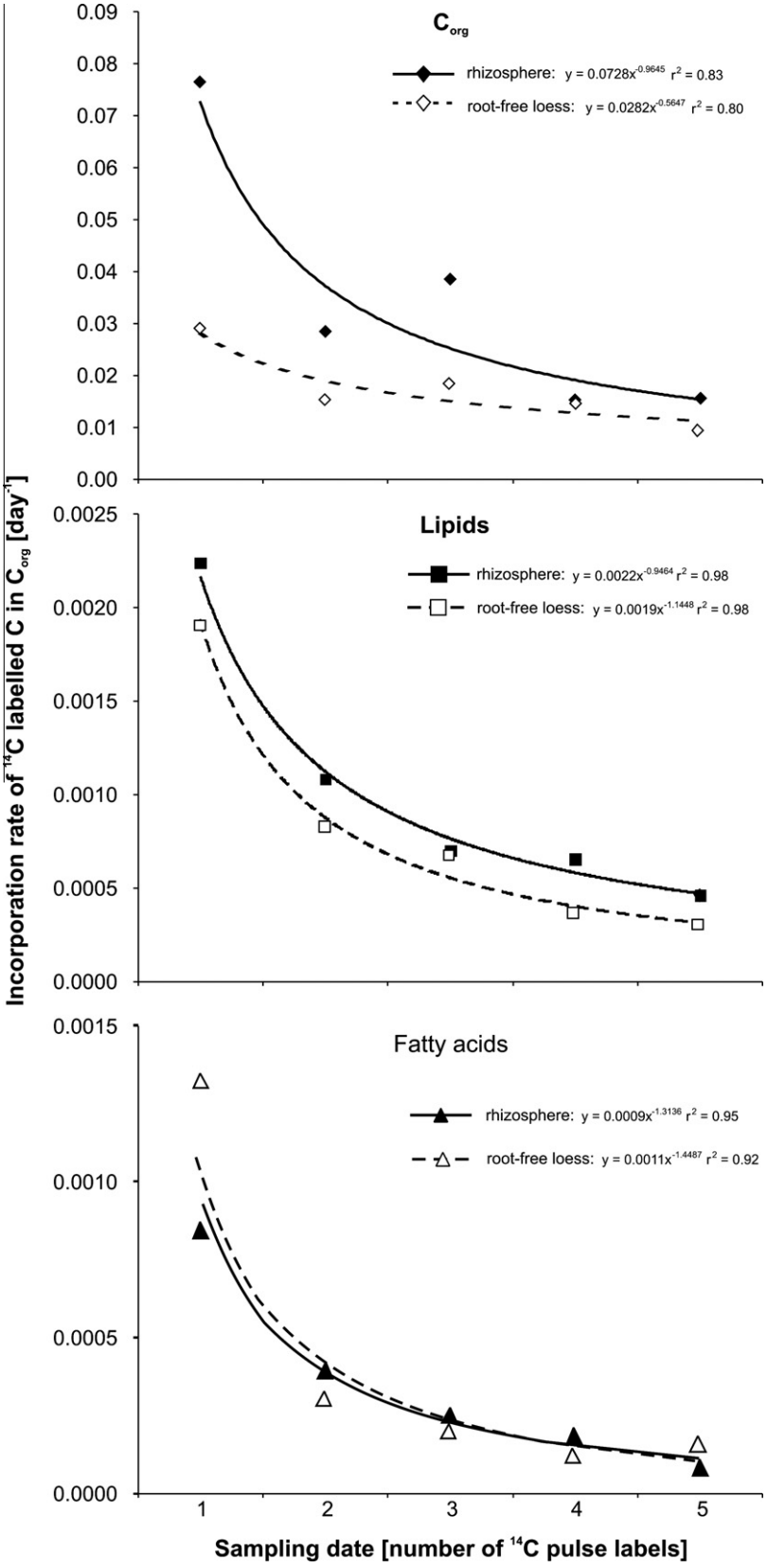

Fig. 2. Incorporation rates determined for C_{org}, total lipids and FA fractions and shown separately for rhizosphere and root-free loess derived from the ^{14}C isotopic labels and given in k [day^{-1}]. Standard errors of the mean of triplicate ^{14}C measurements are always smaller than symbol size.

In our experiments, the ^{14}C activity of initial loess and plant samples is 0. After the calculation, the incorporated fraction can be related to the period after the first isotopic pulse to calculate the incorporation rate k [days^{-1}]:

$$k\ [\text{days}^{-1}] = \ln(1 - f_{\text{incorporated}}) \times (\text{days after first isotopic pulse})^{-1} \quad (2)$$

The incorporation rates were almost twice as high for C_{org} in rhizosphere than in root-free loess and decreased with ongoing duration of the experiment (Fig. 2). The larger contribution of rhizodeposits in the rhizosphere and the higher microbial activity therein results in the higher incorporation rates within the rhizosphere (Blagodatskaya and Kuzyakov, 2008). The decrease during the experiment is a result of the fast incorporation of the ^{14}C signal observed in the beginning, whereas with ongoing duration part of the C_{org} incorporated during the experiment was already decomposed. For total lipids and FAs, initial incorporation rates were significantly slower than for C_{org} in a range of more than one order of magnitude because of the fact that <10% of the incorporated C in loess corresponds to lipid components. Incorporation rates of total lipids and FAs show similar tendencies as those of C_{org}. The incorporation rates of lipids were always higher than those of FAs due to the fact that FAs are a component of the total lipids, whereby a uniform incorporation of total lipids and FAs into rhizosphere and root-free loess was observed.

The calculated incorporation rates can be extrapolated to annual scale by multiplying the rates with 365 days, when assuming uniform plant growth throughout 1 year. This resulted in incorporation rates for lipids (k_{Lip}) and FAs (k_{FA}) for the rhizosphere in the range: k_{Lip} 0.82 year^{-1} and k_{FA} 0.31 year^{-1}, as well as for root-free loess: k_{Lip} 0.70 year^{-1} and k_{FA} 0.48 year^{-1} after the first isotopic pulse for young plants. Thereafter, incorporation rates decreased until the end of the experiment until k_{Lip} 0.17 year^{-1} and k_{FA} 0.03 year^{-1} for rhizosphere as well as k_{Lip} 0.11 year^{-1} and k_{FA} 0.05 year^{-1} for root-free loess. This enables us to differentiate a fast incorporation and turnover of root-derived lipids after the first isotopic pulse with high incorporation rates and an intermediate turnover of root-derived lipids in loess as determined after 20–25 days. Particularly for FAs, no significant changes in the incorporation rates were observed after 15 days, indicating almost uniform conditions of incorporation of fresh root-derived components and turnover of already incorporated components.

The extrapolated annual incorporation rates are in the same order of magnitude as turnover rates of FAs and alkanes as other representatives for lipids, as derived from long term field experiments: 0.002–0.031 year^{-1} (Cayet and Lichtfouse, 2001; Wiesenberg et al., 2004, 2008a; Quénéa et al., 2006). In our experiment we could not take into account the seasonality effect present under field conditions, i.e. incorporation of fresh root-derived C during the growing season and a variation in mineralization during the seasons. The transferability of the data obtained in this study to soils under field conditions in general is possible for short term effects. The lower amount of organic carbon and microbial biomass in loess vs. soil might result in lower incorporation rates in soil because of stronger mineralization of soil organic carbon. Therefore, the results from the laboratory experiment reveal an upper limit for the incorporation rates of root-derived lipids, with a strong incorporation and turnover dynamics of root-derived lipids in the short term on a day to week scale. Hence, a contribution from root-derived lipids is an important part of soil lipids, which is responsible for short term lipid dynamics in soil. This is of major importance in soils where almost no litter is incorporated, as in many arable soils (Wiesenberg et al., 2004).

4. Conclusions

The main objectives of the study were to trace short term changes in the soil lipid pool derived from the incorporation of exclusively root-derived biomass.

Over 3 months plant growth, the lipid composition changed in loess and facilitated the differentiation of rhizosphere and root-free loess on a molecular level. While the rhizosphere contained FAs indicative of the presence of fresh root biomass and microorganisms, root-free loess comprised dead root fragments, which were not part of the intact rhizosphere any more. Additionally, root-free loess did not contain notable amounts of microbial markers, supporting the microbial hotspot theory, with most microorganisms living in the rhizosphere.

The ^{14}C activity of lipids and FAs resulting from multiple isotopic pulse labels indicated a homogeneous ^{14}C distribution in plant lipids throughout the experiment. In contrast, the total ^{14}C activity did not increase linearly with growth stage and thus different utilization of ^{14}C. Short term high incorporation rates reflect a strong contribution of root-derived lipids in soil. At the end of the experiment, incorporation rates decreased and were indicative of intermediate turnover of lipids in soil, in agreement with rates derived from long term field experiments.

Estimation of the dynamics of root-derived lipids in soil on an hour to day scale, as well as their contribution to the total soil lipid pool on an annual scale, remains unknown and should be obtained in future studies in order to improve knowledge concerning the incorporation and turnover of soil lipids on different time scales.

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