Answer to reviewers

We would like to thank the reviewers for their helpful comments and suggestions, which have greatly improved our manuscript. We hope that our response answers all their concerns. We considered each reviewer individually, with the reviewer's comments in normal font, our answers in italics.

Anonymous Referee #1

Received and published: 8 July 2015

The paper by Basler et al. investigates on the relative prominence of recycling versus stabilization processes of soil sugars, a relevant component soil organic matter (SOM). The authors have addressed the problem by performing a three year incubation of a silty loam soil, under different types of land use (i.e. respectively: arable land, grassland and forest) and by adding 13C-labelled glucose in order to track the possible incorporation patterns. Their main observations are that two main tracer dynamics take place for different sugars and these are all dominated by a pool which persists (i.e. high mean residence time, MRT), independently of soil C content. Higher labelled C incorporation is measured in the microbial biomass than in the CO2 produced. The authors consequently suggest that all together these things point at the predominance of recycling over stabilization as main sugar dynamic occurring into soils. Understanding the fate of carbon in soils is of great relevance for the consequences it implies for soil management and more in general for the global carbon cycle. This study gives insights on the possible degradation patterns of soil sugars, which are important contributors in these dynamics. However, as a general comment I would have expected that the authors had put more emphasis on the relevance and the contribution that this study may represent for the soil (and global) carbon cycle understanding. A statement or even a paragraph in the Abstract and/or in the Introduction sections which highlight these aspects would be beneficial for the paper.

→*A sentence to highlight this aspect was included in the abstract.*

I also have some specific request for revisions that may improve the paper. However, I recommend publication in Biogeosciences after the authors consider them.

1. Introduction:

1) page 3, lines 2 to 3: Please add references to this sentence.

2) page 3, line 3: Please define the acronym SOM before you start using it in the text.

3) page 3, line 6: Although you introduce the concept of "mean residence times" already in the Abstract, I would suggest you to re-define it here and add again its acronym, i.e. MRT, because you are using it later in the text.

4) page 3, line 14: There is a typo after the colon, the sentence "their high degradability. . ." starts with an uppercase instead than with a lowercase letter.

→ *Thank you for your comments, we have implemented all these recommendations.*

5) page 3, lines 23 to 24: Please add references to this sentence. Besides, I would develop a bit this sentence by explaining which kind of effects you intend here.

→ *We rephrased this sentence because we did not intend to relate to the effects of recycling and stabilization but their importance for C turnover*

6) page 4, lines 2 to 4: Please refer to the Figure/Table which show the experimental set-up reported here.

→ *We improved section 2.2 (Soil incubation) to clarify that soil samples were incubated individually We therefore believe that a diagram of the experimental setup is now not necessary.*

2. Material/Methods:

2.1 Study Site: It might be helpful to clarify the set-up of the experiment if you could draw a diagram showing the vertical section of the different soils and horizons employed in the experiment.

→ *We improved section 2.2 (Soil incubation) clarify that soil samples were incubated individually We therefore believe that a diagram of the experimental setup is now not necessary.*

2.2 Soil incubation:

1) page 4, line 27: Please define "Corg", before using this abbreviation in the text.

2.4 13C analysis of individual sugars:

1) page 5, line 19: Please correct the typo "13C" to "13C".

2.4.1 Extraction procedure:

1) page 5, line 23: Please define TFA before using the acronym in the text.

→ *We have revised the text as suggested.*

2.4.2 Analysis:

1) page 6, line 7: I believe the title of this section is too generic. Please rename it as "Isotopic Analysis" for instance.

→ *We renamed this section to "sugar analysis" as this section now comprises both the isotopic analysis and the determination of sugar amounts.*

2.6 Calculation and statistics:

1) page 8, line 7: The number assigned to the equation should be (5), instead of (6) and consequently the numbers assigned to the following formulas need to be corrected as well.

→*The section 2.6 was restructured. However, we took this point into consideration in the final version.*

3. Results:

3.1 Carbon concentrations and incorporation of the labelled C into soil organic matter fractions and the respired CO2:

1) page 9, lines 4 to 5: Please add the corresponding acronym after "microbial biomass" and re-define "ex-C" before using this abbreviation in the text.

→ *exC stands for extractable carbon and was first mentioned and explained in the method part/chloroform fumigation (2.5). Microbial biomass was removed and replaced by the acronym Cmic, which was also introduced in the method section.*

3.3 Dynamics of label-derived C of the individual sugars:

1) page 11, line 1: I am not sure I understand what the letter "a" stands for, when you report the MRT for gal (5957a) and for rha (1-365a), calculated from the nonlinear regression analysis: it is not reported either in the text or in Table 3. Is it referring to Figure 3, panel a? Also please correct the extra space after 1-365.

→ *The "a" referred to years. To avoid misunderstanding we replaced a by yr.*

4. Discussion: My main suggestion here is to add the references to Tables and Figures

in the text while you discuss them in this section; it would make easier to follow your

argumentation. Figure 1. and 2.

1) page 27, lines 6 to 7 and page 28, lines 5 to 6: I am not sure I understand the different letters notation you use in this figures and how you explain it in the captions. Please rephrase this.

Figure 3.

1) page 29. Please correct the typo in panel c): the x axis label says [month] instead of [months] as for the other panels.

→ *Thank you for these comments; we have changed the points as suggested.*

Anonymous Referee #2

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General Comments.

In the present investigation, the authors address the fate of neutral sugars as an important part of SOM in a three year incubation study. Hereby, the main aim is to disentangle the importance of stabilization vs. recycling for the sugar dynamics in soil. This is done by means of application of 13C enriched

glucose to three different soil and land use types followed by extraction and compound specific isotope analysis of microbial sugars at various time steps together with CO2 fluxes and measurements of microbial biomass. The authors found evidence, that after an initial phase of high metabolization rates and thus sugar derived C losses in the form of CO2, recycling by the microbial community of sugar-derived C becomes very effective. Though in general sugar dynamics in the long term were dominated by a pool showing high mean residence times, there were differences between two groups of microbial sugars in the incorporation dynamic of glucose derived 13C. These findings were not affected by the C content of the investigated soils. The study gives valuable information about the importance of recycling of SOM via the sugar pool in soil. My main points of criticism are that the authors use the term MRT though the unknown rate of sugar synthesis is not known and thus the criteria for MRT calculation are not met.

→ *We agree with this comment. However, we are referring to the MRT of the carbon allocated to sugars, but not the sugars themselves, as this is the only information we can derive from our measurements. This was clarified in the introduction (second paragraph).*

Second, while there are really strong arguments that sugar dynamics are dominated by recycling, the authors do not discuss that they cannot rule out that the differentiation into a fast and a slow reacting sugar pool could also be caused by stabilization mechanisms.

→ *We agree with the reviewer that we cannot present a final proof to exclude stabilization as underlying mechanism, although we believe that the basis for our argumentation is strong enough.*

*To finally prove the recycling the application of position-specifically labelled substances followed by a position-specific isotope detection would be necessary. However, the measurement techniques for this kind of studies does not (yet) exist.*Finally the authors fail to draw more implications of their finding e.g. on the interpretation of data from foregoing investigations on the persistence of SOM compounds, where high MRT was found, irrespective of the chemical structure.

→*We fully agree here and added a respective comment in the conclusion.*

Nevertheless, after these points and a number of more detailed suggestions have been implemented into the recent manuscript, I suggest to resubmit and publish the manuscript.

Specific Comments:

p.3 l. 4: While in this paragraph it is stressed that recalzitrance is an inadequate model to explain decomposition dynamics, you later on (p. 3 l. 15) define sugars as an easy to degrade compound. This perfectly shows that neither recalcitrance, nor other stabilizing factors can completely explain or predict the fate of certain compounds or compound classes in soil. I would suggest to reorganize these first two paragraphs in a way that shows these contradicting views and thus makes clear the importance of disentangling stabilization vs. recycling.

→*We changed this section to more clearly focus on the main points here.*

p.3 l.16: how is the term "apparent" defined? If you want to express, that the turnover times have been determined by means of 14C dating and could thus by biased by the synthesis of sugars from old

carbon sources, you should explicitly say so. However, in this case stabilization mechanisms like sorption or inclusion (p.3 l.18) would include truly old sugars, thus not contributing to apparent high mean residence times as you write.

→*"apparent MRT" here means that these are the MRT that one would get if recycling would be excluded. The term has been used before (e.g. Flessa et al., 2008) exactly due the necessary distinction between "true" MRT of sugars (which to our knowledge have not been measured yet in soils) and MRT of carbon in sugars. We also added an explanation in the introduction.*

p.4 l.3: Beside the differing concentrations, the more important thing would be differences in the chemical quality or overall usability of C in these systems. This is discussed later on, but actually it should already be stated here.

→*We have taken this into account by mentioning the different C qualities of the investigated soils in the introduction.*

p.4 l.26: clarify, if the glucose was equally labeled or if the 99 at% are only valid for a certain C-position.

→ *This was clarified by stating U-13C.*

p.5 l.4: How do the 4 g fit to the time steps when CFE has been performed or how was the whole incubation system treated after sampling for CFE? In the same way as for 4 g?

→ *A sentence was introduced in the "soil incubation" section to clarify that soil for Cmic analysis was sampled together with the soil for sugar analysis*

p.5 l.17-18: 13C signature of soil derived CO2 is not measured by the simple difference between the two samplings, but rather by plotting the isotopic composition vs. the reciprocal of the sampling time an then prolonging the linear equation to the cutting point with the y-axis (Keeling Plot).

→ *Although a Keeling plot of our data would lead to the same results, we applied a mass and isotopic balance calculation. This was clarified in the text "*from the difference in concentration and isotopic composition of the two samplings"

p.6 l.16: The equation uses data from an unlabeled treatment. It was not specified how this treatment was set up; please specify.

→ *A sentence to clarify this was added in the "Soil incubation" section: "*Controls under natural abundance conditions were treated identically."

p.6 l.17: It is rather unclear what you want to state by saying the analysis pattern differed - do you mean a difference in the sampling frequency*?*

→ *This sentence was rephrased: "*The analysis frequency differed among the different soils: To check if short sampling intervals will reveal additional sugar dynamics…"

p.8 l.2: In the equation S(t) is defined as the level of isotopic enrichment. However, in figure 3, where this formula is used, it is not fitted to S(t) but to RSA. Please clarify.

→ *The section 2.6 was modified. The parameter S of the decay functions was changed to y, were y represents the RSA values of the individual sugar.*

p.8 l.19: How can you identify newly synthesized sugars? While it is clear that the amount of label incorporated into microbial sugars represents newly synthesized sugars, it does on the other hand not mean that these are the only freshly synthesized sugars; i.e. you would underestimate the amount of freshly synthesized sugars because whenever old unlabeled carbon is used to synthesize sugars, you would not see, or you would even interpret the following drop of enrichment as a drop in synthesized sugar amount. Though I am aware of the fact, that all tracer studies and especially those that are ran over a longer time period, face this problem and that solutions to overcome this problem are scarce I would suggest to comment on this problem in the text: First of all it should be considered by clearly stating, that newly synthesized sugars are defined as the part of the sugar pool showing incorporation of the label. Second, at some point in your discussion section you should discuss the implications of this problem for your data interpretation.

→ *We absolutely agree here and consequently rephrased this to "labelled sugar" instead of "newly synthesized sugar"*

p.9 l.6: what about RSA in bulk soil?

→ *We rephrased this, the RSA value of bulk soil is ranked in the arrangement.*

p.9 l.8: In the method section it was stated, that the incubation was done for 30 months. Here you say that it was 34 months; please clarify

→*We clarified this. The incubation was done for 34months, but sugar analysis was only made for the first 30 months.*

p.11 l.1: It is not stated that MRT could frequently not be calculated for a number of sugars, due to positive k values. Please also note, that for these sugars it is not even correct to define the function as a decay function. Though this fact is already part of the discussion it should also be clearly stated at this point. At this point I would like to stress that the setup of the experiment does not really justify the term MRT. Though the equations are used in the right way, you also have to check if the processes defining e.g. the form of your kinetic functions, are really pure decay processes. Only for this situation it makes sense to speak of MRT. If there is resynthesis of the substance of interest, you would need to correct for the rate of synthesis. However, in your case I see no possibility to get these data. The fact that the recycling of label, i.e. the reincorporation of 13C into newly synthesized sugars impeded the differentiation of several pools (based on the calculated MRT?) is discussed in section 4.3. However, it needs to be stressed, that the calculation of MRT is not just impeded, but that the use of MRT is simply not possibly at this point as the settings simply do not meet the definition of MRT. The actual data set only allows to calculate something that might be defined as a MRT for the label being recycled / circulated through the specific sugars. I feel that this does not really hamper the interpretation of the data - it still enables you to show the importance of recycling of freshly incorporated C into the SOM pool vial sugars and differentiate between different sugars. At this point it might also be usefulto skip the calculation of any residence times and only differentiate by means of

the calculated k-values (the smaller the value, the more recycling takes place) - this would enable you to also discuss the role of those sugars having a negative k-value.

→We agree here. However, we wanted to show MRT (where possible) as this is the most commonly used value in soil carbon dynamics. For clarification, we added sentences in the Results and the Discussion sections that decay was not always observed (the implications here of are part of the discussion anyway).

p.12 l.6: It would probably give a more complete picture, if the partitioning of label between the different soil pools would be shown and discussed. Please note that the RSA only gives the proportion of a pool that is made up from incorporated label. However, it does not show, were most of your label was incorporated.

→We added this information in a new Figure to draw a more complete picture of the dynamics during the incubation.

p.13 l.18: If glucose (i.e. also labeled glucose) is bound to SOM and is accessible for microorganisms, one should expect significant enrichments in the exC pool. Please discuss this a bit more into depth.

→ The first time we measured the exC is after 6 month, at this time the proportion of e glucose derived C is negligible (a high contribution would only be expected immediately after addition. We included this data now in a new figure

p.14 l.13-15: Please also discuss the sinus like fluctuations for instance in the case of manose - this could be an interesting point in showing that there are also short time dynamics present. Probably this could also be the starting point to investigate the short term dynamics of the microbial community in a long term experiment - i.e. the switching between times of degradation of old SOM and the recycling of C from dead and rel.young microbial biomass. I would encourage you to at least discuss this aspect, as these fluctuations are really striking.

→ Some sentence about this aspect was included in the section 4.3.

p.14 l.15-18: You note, that due to a de novo synthesis of plant derived sugars by microbes, it was not possible to differentiate between a sugar pool that is only affected by stabilization (plant derived sugars) and another one that is also affected by recycling.While this is true, I do not understand, how it could have helped you, if there was no de novo synthesis of Ara and Xyl. In that case both would have not been labeled and thus it would not have been possible to calculated degradation kinetics. To be able to do so, you would have needed to add labeled Ara and Xyl to the same or a parallel experiment. Thus, this part is confusing and you should clarify this, because I do not really understand, how you were going to disentangle stabilization vs. recycling based on this approach even if you would not have synthesis of plant derived sugars – please clarify.

→Although the original idea of the study was to find different dynamics for sugars of microbial origin vs. sugars of plant origin we had to acknowledge that all sugar dynamics were dominated by microbial production (and not only influenced in case of the "plant derived sugars", as we hypothesised). This is why the original idea did not work out.

p.16 l.5-8: It is stated that the high MRT indicate that recycling dominates sugar dynamics. However, from a mechanistic point of view this straightforward interpretation is not justified as it is not considering, that the stabilization of microbial sugars would also lead to high MRT and would also end in a steady state in the end of the experiment. Though I agree that due to a bundle of reasons it is much more likely that recycling plays the dominant role, this is not discussed enough in detail in the discussion section. Clearly speaking, the pros and cons for recycling or stabilization are not always clearly named and are not weighed up against each other. However, this is very important, as the experiment itself does not investigate stabilization, e.g. there are no data on the desorption of sugars or other stabilizing mechanisms that are named in the introduction; even if there are few / no studies on stabilization of sugars in soil, the possibility of e.g. sorption to different surfaces in soil should be considered and discussed, based on the chemical characteristics of sugars.

→We do agree here, this why we added further arguments considering recent literature in (on sorption). However, we do not conclude that recycling dominates the dynamics solely on the long calculated MRT. More important is the microbial biomass, especially the high labelling after the long time and the pronounced difference to the produced CO2

Technical Comments:

p.3 l.25: missing space between Derrien et al. and following brackets

p.5 l.19: Superscribe 13 in the word 13C

p.5 l.25: Use a small "a" in hPa

p.6 l.12: space between author and year

p.6 l.16: leave space before and after the mathematical operators

p.7 l.7: space between mL and 0.05

p.7 l.11: use "filtrates" rather than "salts"

→ *We apologize for these errors, and we have corrected the text as suggested.*

p.7 l.11: please at least give the brand of your instrument and the temperature/reactor filling at which the analysis in the EA has been done

→The reactor is filled with tungsten oxide and silvered cobaltous oxide. This information was added in the Materials/Methods section.

p.7 l.15-16: use the presence instead of the past as you define the variable of a mathematical function

→We changed this as suggested.

p.7 l.18: kec factor is not defined - it is under discussion, whether this factor is really applicable for all ecosystems, i.e. if it stays constant. As it would anyway not alter the rel. differences between your different soils, I would rather suggest to leave away the factor and define the value as the "extractable microbial biomass".

→ *We are aware of this discussion concerning the kec factor. However, we decided to provide these data due to the comparableness with other studies.*

p.8 l.7: enumeration of this equation and the following ones is incorrect.

→*The section 2.6 was modified. We kept this point in mind during the new structuring.*

p.9 l.12: missing space between µg and C p.10 l.24: kinetics describe reactions but not a soil pool; thus you should rather say kinetics for soil sugar turnover. Please rephrase. p.13 l.31-32: use "incorporation" instead of "input" and "especially for easily" instead of "especially in easily" Table 3: move "wheat Ap to the top of the first section so that the structure is the same for all sections. Also you should increase the distance between the section to get the separation more clear.

Table1: The spacing between the different rows in "Distribution of sugars [%]" is too small and makes the table difficult to read.

→*Thank you, we have followed these recommendations.*

Figure 1: it is not clear, whether the significant differences were found between the different systems but within one time step or throughout the three time steps – please clarify. Also there is an error in the block setting of the figure capture (last line).

→ *For clarification we rephrased the capture.*

Figure 2: Please explain why there is no data for CO2 fluxes for grassland and forest at time step 0.

→ *We cannot provide data for the CO_2 for forest and grassland, as we still had some trouble at the beginning with the experiment. Leaky microcosms and high inaccuracies in the measurements due to required dilution of the samples forced us to neglected these values*

References

Flessa, H., Amelung, W., Helfrich, M., Wiesenberg, G. L., Gleixner, G., Brodowski, S., Rethemeyer, J., Kramer, C., and Grootes, P. M.: Storage and stability of organic matter and fossil carbon in a Luvisol and Phaeozem with continuous maize cropping: A synthesis, J. Plant Nutr. Soil Sc., 171, 36–51, 2008.

Microbial carbon recycling - an underestimated process controlling soil carbon dynamics. Part I: A long-term laboratory incubation experiment

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Abstract

Independent of its chemical structure carbon (C) persists in soil for several decades, controlled by stabilisation and recycling. To disentangle the importance of the two factors on the turnover dynamics of soil sugars, an important compound of soil organic matter (SOM), a three year incubation experiment was conducted on a silty loam soil under different types of land use (arable land, grassland and forest) by adding ^{13}C-labeled glucose. The compound specific isotope analysis of soil sugars was used to examine the dynamics of different sugars during incubation.

Sugar dynamics were dominated by a pool of high mean residence times (MRT) indicating that recycling plays an important role for sugars. However, this was not substantially affected by soil C content. Six months after label addition the contribution of the label was much higher for microbial biomass than for CO_2 production for all examined ~~soils~~land use types, corroborating that substrate recycling was very effective within the microbial biomass. Two different patterns of tracer dynamics could be identified for different sugars: while fucose

~~(fuc)~~ and mannose ~~(man)~~ showed highest label contribution at the beginning of the incubation with a subsequent slow decline, galactose ~~(gal)~~ and rhamnose ~~(rha)~~ were characterised by slow label incorporation with subsequently constant levels, which indicates that recycling is dominating the dynamics of these sugars. This may correspond to a) different microbial growing strategies (r and K-strategist) or b) location within or outside the cell membrane (lipopolysaccharides vs. exopolysaccharides) and thus be subject of different re-use within the microbial food web. Our results show how the microbial community recycles substrate very effectively and that high losses of substrate only occur during initial stages after substrate addition. This study indicates that recycling is one of the major processes explaining the high MRT observed for many SOM fractions and thus is crucial for understanding the global soil C cycle.

1 Introduction

Organic matter that enters the soil is immediately subject to microbial degradation (Fontaine et al., 2003). It has long been assumed that the chemical structure of soil organic matter (SOM) compounds is a key factor controlling decomposition dynamics (Stevenson, 1994). However, in recent years, several studies have shown that carbon (C) compounds are persistent in soil independent of their chemical structure and that mean residence times (MRT) of many compound classes are in the same range (Derrien et al., 2006; Amelung et al., 2008; Gleixner et al., 2002; Kiem and Kögel-Knabner, 2003; Derrien et al., 2007; Schmidt et al., 2011). Two main mechanisms have been discussed to control the C dynamics in soil: on the one hand preservation of ~~soil organic matter~~SOM due to stabilisation and on the other hand recycling, i.e. the synthesis of C compounds from old C sources (Gleixner et al., 2002; Sauheitl et al., 2005~~). The main stabilisation mechanisms are organo-mineral association to minerals and protection within soil structures like aggregates (~~; Six et al., 2002; von Luetzow et al., 2006;~~(~~Sollins et al., 1996~~)~~).

The question of stabilisation vs. recycling is particularly imminent for sugars: ~~Their~~ their high degradability and usability suggest a rapid turnover in soils. In contrast, sugars are characterized by high ~~apparent~~ turnover times, similar to bulk soil C (Gleixner et al., 2002; Derrien et al., 2007). While chemical recalcitrance can be ruled out, it is unknown whether spatial inaccessibility and interactions with surfaces and metal ions on the one hand or recycling on the other hand are predominant for the observed high apparent ~~mean residence times~~MRT (where "apparent MRT" refers to the MRT of the compound as opposed to the MRT of the underlying C). Vascular plant-derived carbohydrates are mainly characterised by the pentose sugars arabinose (ara) and xylose (xyl), whereas hexoses (galactose (gal) and manose (man)) and desoxyhexoses (fucose (fuc), ~~rha~~rhamnose(rha)~~-~~ are primarily produced by microorganisms (Moers et al., 1990).

Studies that aim to disentangle ~~the effects~~contribution of recycling and stabilisation to the fate of carbohydrates are rare. Based on exponential decay functions, several studies suggest the existence of different sugar pools in soils (Cheshire et al., 1988; Derrien et al., 2007; Muramaya, 1984). Derrien et al. (2007) and Muramaya (1988) performed glucose incubation experiments with incubation periods up to 1 year, but conclusion about factors controlling the long-~~-~~term decay kinetics of soil sugars were not possible, presumably due to the short

duration of the experiment and a low number of sampling times. The aim of the present study was to investigate the long-term decay of different (plant and microbial derived) sugars in soil. Therefore, a three year incubation experiment combined with short sampling intervals was set up to evaluate whether sugar pools with different turnover dynamics can be identified in soil during long-term incubation. The incubation was performed on ~~soils~~ a silty loam ~~with~~ under different land use types (and hence soil C concentrations and chemical qualities) ~~on the same soil type~~ to assess the influence of soil C content on microbial recycling. We hypothesize (i) that the high MRT of soil sugars that have often been observed results mainly from microbial recycling and not from stabilisation processes and (ii) that the importance of microbial recycling increases with decreasing soil C content.

2 Material/Methods

2.1 Study Site

Soil samples were collected from the long-term field experiment at "Höhere Landbauschule" Rotthalmünster, Bavaria, Germany (N 48° 21' 47'', E 13° 11' 46''). The mean annual temperature is 9.2 °C and the mean annual precipitation is 757 mm. Soil samples were taken in April 2011 from the following sites and soil depths: (i) the Ap horizon (0-30 cm) and (ii) the E horizon (30-45 cm) of a continuous wheat plot (*Triticum aestivum L.*) established in 1969. Previous vegetation on the wheat plot was grassland. (iii) The Ah horizon (0-10 cm) of a grassland established in 1961 and (iv) the Ah horizon (0-10 cm) of a nearby spruce stand. The soil was classified as a stagnic Luvisol derived from loess (IUSS Working Group WRB, 2014). The soil texture is silty loam. Field moist soil was carefully sieved to 2 mm and stored at 10 °C until use. The soils are described in detail by John et al. (2005) and Helfrich et al.(2006).

2.2 Soil Incubation

For incubation, 1000 g dry weight (dw) soil of the wheat Ap and E horizon and 700 g dw soil of the grassland and forest Ah horizon were placed individually in microcosms, with 3 replicates for each ~~soil~~site and depth. The soil was not compacted and equal filling levels of

the microcosms resulted for all soils. The soil was amended with 400 mg 99% uniformly-labelled [U-^{13}C] glucose ~~U-^{13}Clabelled glucose~~ (Euroisotrop, Saint-Aubin, France) equivalent to a C addition of 3, 5, 2 and 1 % of total organic C (C_{org}) in the wheat Ap, E, grassland and forest soil, respectively. The glucose was applied in solution to the soil while adjusting the water holding capacity of 50%, thoroughly mixed and filled in the microcosms. The microcosms were incubated for ~~30~~ 34 months at a constant temperature of 10 °C, representing the mean annual soil temperature in Rotthalmünster. The microcosms were kept semi-closed to enable aeration and to reduce drying-out at the same time. Every two weeks approximately 4 g of soil was removed from each microcosm and additionally 20 g after 6, 20 and 34 months of incubation for soil microbial biomass analysis. On these occasions, the complete soil was taken out of the microcosms, thoroughly mixed and carefully rewetted by sprinkling with deionised water to keep fluctuations of soil water content below 10%. The soil samples were stored at -18 °C until extraction. Controls under natural abundance conditions were treated identically.

2.3 CO_2 respiration

The CO_2 respiration was measured biweekly before soil sampling. At first, microcosms were closed and a headspace sample was taken after approximately 30 minutes of equilibration. With an air tight syringe, 50 mL of synthetic air was pushed into the vessel and the headspace was mixed by pumping the syringe 3 to 4 times. Afterwards 50 mL of the headspace air was taken and transferred to pre-evacuated Exetainers (Labco Limited, Buckinghamshire, UK). A second headspace sample was taken identically after 24 h of CO_2 accumulation in the closed microcosms. The CO_2 concentrations and isotopic values were measured by an IRMS Delta Plus with GP interface and GC-Box (ThermoFisher, Bremen, Germany) and the amount ~~and isotopic composition~~ of the produced CO_2 was calculated from the difference in concentration and isotopic composition of the two samplings.

2.4 ^{13}C analysis of individual sugars

2.4.1 Extraction procedure

Carbohydrates were extracted and purified using a modified procedure based on Amelung et al. (1996) as described by Basler and Dyckmans (2013). The sugars were extracted from

500 mg wet soil by hydrolysis with 10 mL 4 M trifluoroacetic acid (TFA) and at 105 °C for four hours. Afterwards, the samples were filtered through a glass fibre filter (Minisart GF, Sartorius, Göttingen, Germany) and dried by rotary evaporation (40 °C, 50 ~~hPA~~hPa). The samples were re-dissolved with 0.5 mL water and evaporated to dryness 3 times to remove all traces of TFA. After the evaporation process the samples were re-dissolved in approximately 3 mL water and passed through 4 g Dowex X8 cation exchange resin (Sigma Aldrich, Steinheim, Germany) and 5 g Serdolit PAD IV adsorption resin (Serva Electrophoresis GmbH, Heidelberg, Germany) for purification. Carbohydrates were eluted from the resin by adding 8 times 2 mL water. The eluate was freeze-dried and stored at -18 °C until analysis. For HPLC/o/IRMS analysis the samples were dissolved in 3 mL water.

The TFA extraction method is known to effectively extract hemi-cellulosic sugars but cellulose is not cleaved by this method (Amelung et al., 1996). The results presented here thus only refer to non-cellulosic sugars.

2.4.2 Sugare ~~A~~analysis

The compound specific ~~isotope~~ analysis of amounts and isotope ratios were ~~was~~ performed using a high-pressure liquid chromatography system (Sykam, Fürstenfeldbruck, Germany) coupled to an isotope ratio mass spectrometer (Delta V Advantage, Thermo Scientific, Bremen, Germany) via an LC-Isolink interface (Thermo Scientific, Bremen, Germany) as described by Basler and Dyckmans (2013). Shortly, the chromatographic column (Carbo Pac 20, Dionex, Germering, Germany) was held at 10 °C and a 0.25 mM NaOH solution was used as mobile phase at a flow rate of 250 µL min $^{-1}$.

The isotopic values are reported in atm%excess notation:

$$atm\%excess = atm\%_{labelled} - atm\%_{unlabelled} \quad (1)$$

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The analysis frequency ~~pattern~~ differed among the different ~~soils~~types of land use: To check if ~~a frequent~~ short sampling intervals ~~pattern~~ will reveal additional sugar dynamics, all samples (i.e. two-week intervals) from the incubation of the wheat Ap horizon were analysed for the 30 month sampling period. However, as the results did not indicate a multi-pool dynamic, (see Results, Fig.~~3~~4), the frequency of analysis was reduced for the other ~~soils~~sites. From the forest and grassland incubations, samples were analysed in four week intervals over a 24

month period, and from the wheat E horizon, samples were analysed in 8 week intervals for a period of 30 months. Sugar analysis was made from only one microcosm to account for time-dependent dynamics rather than differences among different incubations. To assess the variability among different microcosms, after 6 and 24 month, all incubation microcosms were analysed for sugar content and isotopic composition. The mean coefficient of variation among the replicates was below 5%, therefore the results of the incubations presented here are taken as representative.

2.5 Chloroform-Fumigation-Extraction

The soil microbial biomass (C_{mic}) was measured before and after 6, 20 and 34 months of incubation by the chloroform-fumigation extraction method (Brookes et al., 1985; Vance et al., 1987). In brief, each sample was divided into two sub-samples of 10 g moist soil. One soil sub-sample was directly extracted as described below. The other sub-sample was placed in a desiccator together with 80 mL of ethanol free CH_3Cl. Desiccators were evacuated and the samples were left at 25 °C for 24 h (fumigation). All samples were extracted by shaking with 60 mL 0.05 M K_2SO_4 (Engelking et al. 2008) for one hour and subsequently filtered (Whatman 595 ½, Maidstone, UK)). The soil extracts were analysed for their C content using a TOC analyser multi C/N® 2000 (Analytik Jena, Jena, Germany). For stable isotope measurements, around 50 mg of the freeze-dried ~~salts~~ filtrates were filled in tin capsules and analysed by elemental analyser/isotope ratio mass spectrometry (EA/IRMS) using an EuroVector elemental analyser (HEKAtech GmbH, Wegberg, Germany) coupled to a Delta Plus XP isotope ratio mass spectrometer (Thermo Scientific, Bremen, Germany). Samples are combusted in a reactor filled with tungsten oxide and silvered cobaltous oxide at 1020 °C.

The isotopic signature of the microbial biomass C ~~(C_{mic})~~ was calculated as follows:

$$atm\%excess C_{mic} = \frac{(atm\%excess\,C_F \times C_F) - (atm\%excess\,C_{nF} \times C_{nF})}{(C_F - C_{nF})} \quad (2)$$

Where $atm\%excess\,C_F$ and $atm\%excess\,C_{nF}$ ~~were~~ are the isotopic composition of the fumigated and non-fumigated extracts and C_F and C_{nF} ~~were~~ are the C concentrations in the extracts of the fumigated and non-fumigated soil samples, respectively. For calculation of

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total microbial biomass-C, a kec factor of 0.45 was used ~~to calculate the total microbial biomass C~~ (Joergensen, 1996). Carbon extracted from non-fumigated samples represents the K_2SO_4 extractable C fraction (exC).

2.6 Calculation and statistics

All statistical analyses and modelling ~~was~~ were performed with R 3.0.2 (R Core Team, 2013).

The relative specific allocation (RSA) describes the fraction of labelled C relative to total C in a given compartment (Deleens et al., 1994; Dyckmans and Flessa, 2002) and is calculated as follows:

$$RSA = \frac{atom\%_{sample} - atom\%_{control}}{atom\%_{label} - atom\%_{control}} \quad (3)$$

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The partitioning (P) describes the proportion of the labelled element in a given soil C compartment relative to the total labelled element in the whole (Deleens et al., 1994; Dyckmans and Flessa, 2002).The partitioning of labelled C was calculated from:

$$P[\%] = \frac{RSA_{fraction} \times A_{fraction}}{RSA_{bulksoil} \times A_{bulksoil}} \quad (4)$$

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where A is the amount of the respective fraction.

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The following exponential functions were used to analyse decay kinetics for each individual sugar:

mono exponential ~~decay~~ function

$$y = a \times e^{(-k_1 t)} \quad (~~3~~5)$$

bi-exponential ~~decay~~ function

$$y = a \times e^{(-k_1 \times t)} + b \times e^{(-k_2 \times t)} \quad (~~4~~6)$$

In the equations, y represents the ~~level of isotopic enrichment~~RSA value of individual sugar; k the decay constant of the sugar pool, and a and b represent initial pool sizes.

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The MRT of C in the respective sugar pool was calculated according to Derrien and Amelung (2011):

$$MRT = 1/k \quad (6\,7)$$

where k is the decay constant estimated by fitting Eqs. (3 5) or (4 6) to the measured values.

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Equations (3 5) and (4 6) were fitted to the data using R. The best model for each sugar and soil was identified using the Akaike information criterion (AIC;(Akaike)). The AIC is defined as:

$$AIC = 2z - 2\ln(L) \quad (7\,8)$$

where z is the number of parameters in the model and L the maximized value of the likelihood function for the model.

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~~The relative specific allocation (RSA) describes the fraction of labelled C relative to total C in a given compartment (Deleens et al., 1994; Dyckmans and Flessa, 2002) and is calculated as follows:~~

$$RSA = \frac{atom\%_{sample} - atom\%_{control}}{atom\%_{label} - atom\%_{control}} \quad (8)$$

A Pearson correlation test was conducted to determine the relationship between distributions of ~~newly synthesized~~labelled sugar and total sugar of the organic matter and to test the model efficiency. The statistical significance of the sugar composition, ratios and label derived proportions among different sugars, sampling times were tested by Kruskal–Wallis one-way analysis of variance.

3 Results

3.1 Carbon concentrations and incorporation of the labelled C into soil organic matter fractions and the respired CO_2

Dynamics of added label were monitored in bulk soil, microbial biomass, CO_2 respiration and exC. In general, ~~the proportions of label derived C (RSA) were highest in~~ C_{mic}, showed the highest proportions of label derived C (RSA) followed by CO_2, the lowest RSA were found in exC (Fig. 1).

After 6 months of incubation 1.1, 1.2, 0.9 and 0.3% of the bulk C pool of the wheat Ap, wheat E, grassland Ah and forest Ah, respectively, were derived from labelled C. Between 6 and 34

month of incubation about 30, 20 and 40% of label derived C was lost from the bulk soil C pool in wheat, grassland and forest incubations respectively, while total C concentrations did not change significantly (Fig. 1). The C_{mic} of the wheat Ap, ~~Al,~~E grassland Ah and forest Ah were 230, 140, 851 and 622 µgC g^{-1}dw soil after 6 months of incubation (Fig. 2). This corresponds to an increase of 8%, 40% and 35% of C_{mic} compared to the initial content before glucose addition in wheat Ap, wheat E and forest Ah, respectively. The grassland Ah lost 8% of C_{mic} after incubation started (Fig. 2) After 6 months, 23, 19, 15 and 21% of the C_{mic} in the wheat Ap, E, grassland and forest incubations were derived from the added label and label contribution decreased during further incubation. Also, total C_{mic} decreased during incubation, with the exception of the forest Ah soil (Fig. 1). The CO_2 emitted from the incubated soils showed similar behaviour, i.e. decreasing production of CO_2 accompanied with decreasing label contribution. However, the contribution of added label to CO_2 production (4–8 %) was much lower than for microbial biomass (15-25%; Fig. 1). The exC only showed marginal proportions of label-derived C (0.03-0.14%), which also decreased with increasing incubation time.

When regarding the partitioning of labelled C into the different investigated soil fractions (Fig. 3), the bulk soil contained between 26.5 and 42.8% of the added label after 6 months of incubation. The label continually decreased in all treatments with incubation time due to CO_2 losses). The partitioning of labelled C to the sugar pool and Cmic was of comparable size but showed a more pronounced decreased ~~more pronouncedly~~ with ongoing incubation time in the C_{mic} pool as compared to sugars. ~~Partitioning~~Less than 1% of the added label was found in the ~~to~~ Cex ~~was always below 1 % and showed a decreasing trend in all incubations with time~~.

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3.2 Incorporation of added label into sugars

Around 9% of bulk soil C in the wheat Ap, E and grassland Ah incubations and 5% in forest Ah were attributed to sugars. The relative proportions of the individual sugars were quite similar among the investigated soil horizons (Table 1). The dominant sugar in all ~~soils~~ types of land use was glucose (glc), followed by the hexoses gal and man and the pentoses ara and xyl. The desoxyhexoses (fuc, rha) showed smallest contributions, with the exception of fuc in forest soil, which occurred in similar proportions as ara. After 6 months of incubation, label-

derived C incorporated into all sugars (with the exception of glucose) was 1.9 and 1% in the incubated wheat Ap and E horizons, respectively and this proportion decreased during further incubation (data not shown). In contrast, in the grassland and forest soils, label derived C increased during incubation from 1.2 and 0.6% after 6 months to 1.4 and 0.8%. Apart from glc, ~~newly synthesised m~~label derived microbial sugars were mainly composed of man (~12%) and gal (~9%) and smaller proportions of rha (~6%), fuc, ara and xyl (~3%) (Table 2).

3.3 Dynamics of label-derived C of the individual sugars

Glucose showed highest contribution of labelled C throughout the experiment. Values decreased from 6.4, 6.2, 6.2, and 2.3% after 6 months to 4.2, 3.5, 3.1 and 1.4% in wheat Ap, E, grassland Ah and forest Ah, respectively (data not shown). The trends for the other sugars were quite similar in the different incubated soils (Fig. ~~3a~~4a-d): Man and fuc showed a decreasing trend in label contribution, whereas the label contribution increased in rha and gal during the first weeks of incubation, but did not change afterwards. Mannose and rha showed contributions of labelled C between 0.3 and 1.9% for the different incubations after 6 months, followed by gal and fuc (0.3-1.5%, Fig. ~~3~~4). The mainly plant-derived sugars ara and xyl showed considerable contribution of label-derived C of about 0.2 and 0.6% after 6 months, although to a lesser extent than the "microbial sugars" (man, gal, rha). The contribution of labelled C to ara slightly increased during the whole incubation time in all but the forest soil, where an initial increase was followed by a decrease. The contributions of labelled C to xyl increased weakly in both wheat soil horizons, whereas it was constant in the grassland and forest soil. Non-linear regression analysis was performed on RSA values to analyse the kinetics of soil sugar turnover~~s~~. Mono-exponential (Eq.~~3~~5) as well as bi-exponential (Eq. ~~4~~6) ~~decay~~ functions were tested to describe the dynamics of soil sugars. AIC values were used to identify the best fit (Table S1). No clear pattern was observed whether dynamics of individual sugars or of different soils were characterized by mono or bi exponential models (Table S2). Best fits for each sugar and ~~soil~~ land use are shown in Fig. ~~3~~4. In the cases where a decaying label contribution was observed, ~~T~~the MRT of the sugar C~~–~~, calculated from the nonlinear regression analysis with Eqs. (~~3~~5) and (~~4~~6), ~~of the different sugars~~ ranged from a few months

for the labile pool over several years (1-365 ~~a~~yr), representing an intermediate pool (Table 3). The highest (~~5957a~~5957 yr) was calculated for gal in the wheat Ap.

4 Discussion

4.1 Glucose incorporation into soil C and microbial biomass C

Our aim was to investigate the transformation and stabilisation processes of the added labelled C during the first three years after substrate addition. After 6 months of incubation, the bulk soil C pool still contained 25 to 42% of the added label, which is in line with findings of previous studies, where less than 50% of added glucose were recovered after one or two months of incubation (Saggar 1999, Murayama 1988). As an easily accessible C source, glucose stimulates microbial growth in soil and leads to increased initial respiration, especially of newly added C (Schneckenberger et al., 2008). After 6 months, between 15 and 23% of the C_{mic} was derived from the added label and the proportion decreased during further incubation (Fig. 1). As the living microbial biomass actively takes up and incorporates the added glucose, it is expected to have a higher C turnover than the bulk soil C pool. However, the contribution of added label to microbial biomass C was quite high and remained at a high level during the whole incubation (resulting in label contribution of up to 15 % after 30 month, Fig. 1). This could be related to the fact, that some microorganisms, especially K-strategists, are able to store glucose as an intracellular reservoir (as glycogen) (Blagodatskaya et al., 2007, Wilson et al., 2010). This is contradicted by the fact that label partitioning into the sugar pool decreases more slowly than to the C_{mic} pool and that the relative importance of glc as compared to the other sugars remains fairly constant (Fig. 3). Moreover our data on decreasing microbial biomass and decreasing C mineralization over time indicate substrate limitation. It seems unlikely, that high amounts of glucose are stored within the microbial biomass under these conditions. It is more likely that the microbial community maintained their metabolic capacity by feeding on dead microbial biomass as was also shown by Kindler et al. (2006) or Guenet et al. (2011). This would be in line with the slow decline of glucose-derived label contribution in the microbial biomass, which was similarly shown by Gunina et al. (2014). Their data indicate that substrates entering citric acid cycle are preferentially respired whereas substrates, like glucose, entering glycolysis are preferentially incorporated

into microbial biomass, i.e. recycled.~~.~~ Corroborating this, ~~Further,~~ our data indicate that considerable amounts of "old" SOM are used for energy gain (mineralization) rather than recent microbial necromass as the RSA of CO_2 is much lower than that of the microbial biomass throughout the experiment. Probably, the constant mixing of the soil during the biweekly sampling events increased the accessibility also of "old" soil C sources. This is in line with Lamparter et al. (2009) and Joergensen and Raubuch (2003) who showed that mixing and rewetting improve the C availability for microbial uptake.

Together with the observed long MRT of sugar C~~s~~ our data indicate that after high initial losses of added C substrate that has often been observed after glucose (Schneckenberger et al., 2008; Saggar et al., 1999), or microbial necromass addition (Miltner et al., 2012; Kindler et al., 2006) the microbial biomass recycled C substrates efficiently and with only minimal C losses.

4.2 Effect of incubation on sugar composition

The relative amounts of the investigated sugars did not differ substantially among the different soils investigated here. Sugars made up around ~~9~~8% of the C in arable and grassland soils, in the forest soil the proportion was smaller with ~~5~~6%, corroborating earlier findings (Lowe and Brown, 1975; Rumpel and Dignac, 2006; Guggenberger et al., 1994; Cheshire, 1979). Furthermore, the general sugar distribution pattern did not differ significantly among the ~~soils~~investigated types of land use: the dominant sugar was glc, followed by man and gal. The contribution of the plant-derived sugars xyl and ara was somewhat smaller and only minimum proportions of rha and fuc were found. The only variation was observed in the forest soil, where ara was half and fuc was twice of the proportion observed in the other soils. The general distribution of sugars in the arable and grassland soils were concordant with studies by Muramaya (1988), Derrien et al. (2007), Creamer et al. (2012).

There was a close correlation between total and labelled sugar content for the microbial sugars (R =0.69, Data not shown, no correlation for ara and xyl), indicating that the dynamics before and during incubation were basically the same with the exception of plant input. During the incubation highest synthesis rates were observed for man and gal, followed by rha and fuc, whereas new synthesis of xyl and ara was less. These findings are similar to those of

Muramaya (1988) and Derrien et al. (2007). The (small) new synthesis of ara and xyl can probably be traced back to fungi and yeast, as shown by Coelho et al. (1988) and Cheshire et al. (1976). As supply by plant debris or root exudates was missing the dynamics of ara and xyl were obviously controlled by the microbial community during the incubation.

Proportions of labelled C ranged between 0.6 to 1.9% of the individual sugars (without glucose) after 6 months of incubation. During further incubation, the proportion of the added label in the sugar pool of both wheat soil incubations decreased very slightly by 5%, whereas it increased in the grassland and forest soil incubations. Additionally, an increase of total sugar amounts occurred in grassland and forest soil incubations, whereas in the wheat soil the amounts decreased by 20% (Data not shown). This suggests that in both wheat soil incubations, due to limited C supply, recycling dominated the sugar C dynamics as the microbial community used all available C-sources. Thus, the contributions of labelled C decreased, as greater amounts of soil organic C (and not only the recently added glucose) were used in microbial metabolism. This showed how effectively the microbial community converts C compounds and responds to changing conditions. This corresponds with studies by Salomé et al. (2010), Kramer and Gleixner (2006; 2008), Creamer et al. (2014) who showed that microorganisms change their feeding strategies from recent to more old SOM compounds depending on C availability and quality.

The increasing contribution of label C to the sugar pool in the SOM-rich grassland soil can be related to the fact that a considerably larger soil C-pool was initially accessible for microbial metabolism. In the grassland soil, this corresponds with less label-derived C in microbial biomass and CO_2 as compared to the soils under other ~~soils~~land use. However, with increasing incubation time more labelled C was incorporated into the sugar pool because the amount of accessible “old” C decreased continuously and thus glucose, bound to SOM is successively used. In the forest soil, microbial biomass and CO_2 contained more label derived C as compared to the grassland soil. This suggests that the added labelled C source was predominantly used by the microbial biomass because most of the “old” C was not accessible for metabolism, i.e. was stabilised. Waldrop and Firestone (2004) found that the microbial community preferentially incorporated added easily degradable C compounds in low quality SOM soils. Forest litter is enriched in aromatic, phenolic and alkyl-C, which might be less attractive for microorganisms (Kögel-Knabner, 2002; Nierop et al., 2001; Helfrich et al.,

2006). Therefore, the added glucose provided an easily utilisable C source compared to the SOM in the forest soil and was preferentially used by the microbial community as reflected by the high label contribution to C_{mic} and CO_2 in relation to the bulk soil label contribution (Fig.1 and Fig.3). Additionally, in the acid forest soil, decomposition occurred mainly in the humus layer, whereas in arable or grassland, decomposition occurred directly in mineral soil (Kögel-Knabner et al., 1988; Helfrich et al., 2006; Guggenberger and Zech, 1994). Therefore, the C ~~input~~incorporation seems to be lower than in arable and grassland soils, especially ~~in~~ for easily utilisable compounds. Together with litter quality the reduced microbial activity promote the effect of SOM stabilisation in forest soils. Summing up, the accessibility of C compounds control the effect of recycling and stabilisation: Both recycling and stabilisation are important processes in forest soils. However, for arable soils and grassland, recycling seems to dominate the C dynamics.

4.3 Sugar dynamics

Several studies aimed at differentiating different sugar pools, based on incubations for up to 1 year (Muramaya, 1988; Derrien et al., 2007), but conclusions about factors controlling the long term decay kinetics of soil sugars were not possible, presumably due to the short duration of the experiment and a low number of sampling times. Hence, the intended target of our study was to investigate the long-~~-~~term dynamics of sugars, based on highly frequent sampling during 3 years of incubation to identify multiple decay pools. However, the apparent high importance of recycling, which was shown by increasing label incorporation (Fig.4) and as a consequence positive k-values (Table S2), impeded the differentiation of several pools of the investigated sugars. This displays the drawback of the experiment, as recycling of the added C substrate influenced the decay dynamics. Ara and xyl, as supposedly plant-derived sugars, showed a considerable de-novo synthesis by microorganisms and thus the differentiation into plant derived sugars subject only to stabilisation and microbial sugars, subject to stabilisation and recycling was difficult. In our study the sugar dynamics were described by mono and bi-exponential functions. An incubation study by Derrien et al. (2007), however, used bi-exponential decay functions to describe sugar decay dynamics with a constant pool (k=0) as it apparently remained undecomposed throughout the incubation. However, in our experiment, the contribution of labelled C to the individual sugars changed throughout the incubation even ~~if~~ though very slightly, thus the assumption of a constant pool

would not correspond to our data. A labile pool could be determined for rha and gal in the wheat Ap; for xyl, fuc and man in wheat E and for ara, xyl, fuc and gal in the forest Ah (Table 3). The MRT ranged between a few days and up to two months, depending on the different investigated soils (Table 3). These data agree well with the study by Derrien et al.(2007). They reported MRT of 17 days for the labile sugar pool. The MRT of the stable microbial-derived sugars ranged up to 365 years. The highest MRT was estimated for gal in the wheat Ap with 5957 years. This is even more surprising because interactions of sugars with the soil matrix are reported as less important for their fate (Gunina and Kuzyakov, 2015) supporting the idea of recycling and not stabilization as dominant ~~process.~~process. Therefore, ~~S~~such high values can only be explained by a high contribution of substrate recycling and corresponds with the observed high proportions of labelled C in the microbial biomass throughout the experiment. ~~-~~From pure culture studies it is known that 5% of the dry weight of prokaryotic cells consist of polysaccharides (Madigan et al., 2003). Thus, the label contribution of the soil sugars to microbial biomass is relatively low and turnover of microbial biomass thus masks changes in sugars over time. Additionally, with chloroform-fumigation extraction mainly C of the cytoplasm is determined, whereas more complex structures in cell walls are probably hardly extracted (Joergensen, 1996; Apostel et al., 2015). This may lead to an overestimation of the dynamics of labelled C in microbial biomass as cell walls probably are neither strongly labelled at the beginning of the experiment, nor do they cycle as fast as the other pools of the microbial biomass (Glaser and Gross, 2005; Miltner et al., 2009; Malik et al., 2013).

Apart from long term label incorporation trends (discussed below), all sugars show small sinus like fluctuations (Fig. 4, most pronounced for man). One could speculate that this phenomenon might be related to shifts in the microbial community, which in turn increased resource availability, in which extracellular enzymes metabolites or lysed cells of one functional group increase substrates for another (Blagodatskaya and Kuzyakov, 2008; Mau et al., 2015).

~~Further, t~~More importantly, the similar behaviour of fuc and man on the one hand and gal and rha on the other is of interest (Fig. 4). While fuc and man showed highest label contribution directly at the beginning of the experiment and exhibited remarkable decline afterwards, label contribution in rha and gal increased during the first weeks of the experiment and reached steady state after 4 months. These different dynamics could be related with different strategies

of microbial groups: fuc and man could be representative for ~~r~~ r-strategist that quickly acquire new substrates but are forced into dormancy if nutrient supply becomes limited, whereas K-strategists could be represented by the dynamics of gal and rha: These groups only slowly profit from the added labelled nutrients, but are able to live on these resources for very long times. One could speculate whether the slow increase in gal and rha is due to recycling of starving r-strategist or results from the use of stored glucose (Blagodatskaya et al., 2007) acquired at the beginning of the experiment.

Another explanation for the different dynamics could be different provinces of the two pools. For example exopolysaccharides are part of microbial biofilms and are composed mainly of fuc, gal, man and glc (Freitas et al., 2011; Neu and Lawrence, 1997). On the other hand, lipopolysaccharides (LPS) are part of the outer cell membrane and are composed of gal, rha and man monosaccharide units (Lengeler et al., 1999). If the dynamics of fuc and man would be representative for the dynamics of exopolysaccharides of microbial biofilms, this would indicate that they quickly incorporate available substrate but rely on "old" SOM-derived C when the added substrate is no longer available. Likewise, the gal and rha dynamics could be characteristic for LPS, indicating that these underlie a repeated recycling within the microbial biomass pool: the labelled substrate is only slowly incorporated into the LPS pool but is then retained there for long times.

5 Conclusion

The observed high MRT for sugars indicate that recycling dominates sugar dynamics in soil and that the high importance of recycling is not substantially affected by soil C content. Thus, MRT of substance classes, as stated in many previous studies, has to be taken with care, as they do not necessarily reflect the MRT of these substances but rather the MRT of the pool-derived C, which may be frequently recycled within or outside of this pool.

Further, the persistently higher contribution of added label to microbial biomass as compared to CO_2 production indicates that substrate recycling is very effective in the long term. Two different patterns of tracer dynamics could be identified for different sugars: fuc and man showed highest label contribution at the beginning of the incubation with a subsequent slow decline. Galactose and rha, on the other hand were characterised by slow label incorporation with subsequently constant levels, indicating that the dynamics of these sugars are dominated by substrate recycling.

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Table 1.Sugar composition of the organic matter in the wheat Ap, wheat E, grassland Ah and forest Ah soils before incubation. Means ± standard error, n= 3.

	Depth [cm]	SugarC [%]	Distribution of sugars[%]						
			ara	xyl	fuc	rha	gal	man	glc
wheat Ap	0-30	8±0.1	14±0.9	15±0.3	4±0.2	7±0.1	17±0.1	15±0.2	29±0.6
wheat E	30-45	7±0.8	13±0.2	13±0.5	4±0.3	8±0.1	17±0.0	15±0.1	31±0.5
grassland Ah	0-10	8±0.6	14±0.2	13±0.2	5±0.1	9±0.1	16±0.2	14±0.5	29±0.6
forest Ah	0-10	6±0.3	7±0.2	12±0.2	7±0.3	5±0.2	14±0.7	18±0.3	36±0.6

Table 2. Relative distribution of total label derived sugar C [wt%] among different sugars after 6 and 24 months of incubation (means ± standard error; n=3). Significant differences ($p<0.05$) between the two sampling times are indicated by an asterisk.

	wheat Ap					wheat E					grassland Ah					forest Ah				
Sugar	6m		24m			6m		24m			6m		24m			6m		24m		
fuc	4.0	± 1.1	3.7	± 1.9		2.7	± 0.7	3.0	± 0.4		1.3	± 0.0	1.4	± 0.1		2.1	± 0.1	3.0	± 0.2	*
ara	2.7	± 0.1	3.4	± 0.1	*	3.3	± 0.1	4.2	± 0.0	*	2.5	± 0.2	2.8	± 0.2		0.9	± 0.0	1.4	± 0.0	*
rha	8.7	± 1.2	9.7	± 2.6		7.9	± 1.0	9.8	± 0.6		4.6	± 0.1	5.6	± 0.1	*	1.5	± 0.1	2.3	± 0.1	*
gal	9.9	± 0.1	12.6	± 0.2	*	10.1	± 0.6	13.2	± 0.5	*	6.0	± 0.1	7.6	± 0.0	*	5.1	± 0.3	8.0	± 0.2	*
glc	60.7	± 2.9	54.6	± 5.6		61.0	± 2.8	52.8	± 1.4	*	75.1	± 0.3	70.3	± 1.0	*	78.5	± 1.1	66.8	± 1.3	*
xyl	2.2	± 0.2	2.7	± 0.2	*	2.8	± 0.3	3.1	± 0.1		1.9	± 0.1	2.0	± 0.4		2.5	± 0.2	4.0	± 0.3	*
man	11.8	± 0.7	13.3	± 0.6	*	12.1	± 0.4	14.0	± 0.3	*	8.8	± 0.2	10.3	± 0.3	*	9.5	± 0.5	14.3	± 0.4	*

Table 3. Estimated apparent MRT and pool size of sugars in the ~~Wheat~~ wheat Ap, wheat E, grassland Ah and forest Ah incubations. * reflects initial exponential growing pools.

		labile pool		intermediate/stable pool	
		years	pool size [mg g^{-1}]	years	pool size [mg g^{-1}]
wheat Ap	fuc	\	\	44	0.30
~~wheat Ap~~	rha	0.02	0.84*	\	\
	gal	0.07	0.17*	5957	0.67
	man	\	\	21	0.82
wheat E	ara	\	\	82	0.16
	xyl	0.2	0.07	\	\
	fuc	0.2	0.11	71	0.07
	man	0.6	0.17	79	0.50
grassland Ah	ara	0.1	0.15*		
	fuc	\	\	79	0.15
	rha	\	\	231	0.54
	gal	0.1	0.32	\	\
	man	0.04	0.25*	15	1.03
forest Ah	ara	1.20	0.26	3	0.37
	xyl	0.05	0.45*	34	0.34
	fuc	0.6	0.24	82	0.06
	rha	\	\	365	0.19
	gal	0.06	0.44*	54	0.66
	man	\	\	45	1.25

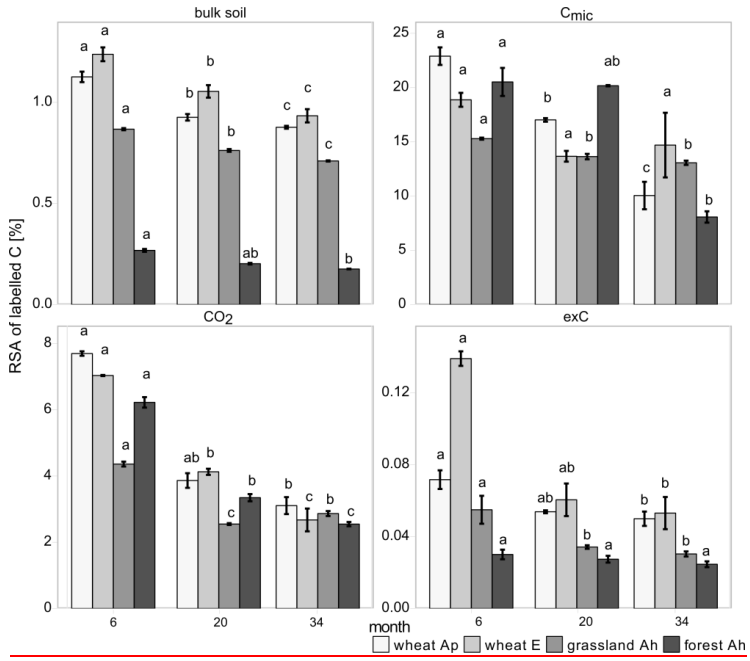

Figure 1. Fraction of labelled C ~~on~~ in total C of bulk soil C, microbial biomass (C_{mic}), respired CO_2,and ~~-~~K_2SO_4-extractable carbon (exC) ~~in~~ of the wheat Ap and E, grassland Ah and forest Ah after 6, 20 and 34 months of incubation. Different letters indicate significant differences ($p<0.05$) within one treatment over time. Means ± standard error (n=3).

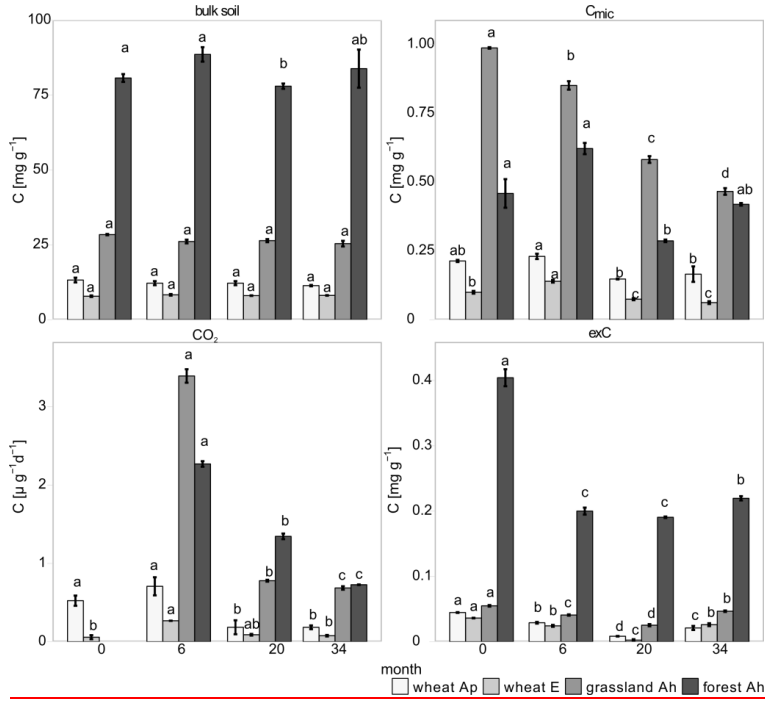

Figure 2. Concentrations of bulk soil C, microbial biomass C (C_{mic}), respired CO_2 and K_2SO_4-extractable carbon (exC) in -wheat Ap and E, grassland Ah and forest Ah before (0) and after 6, 20 and 34 months of incubation. Different letters indicate significant differences ($p<0.05$) within one treatment over time. Mean and standard error (n=3).

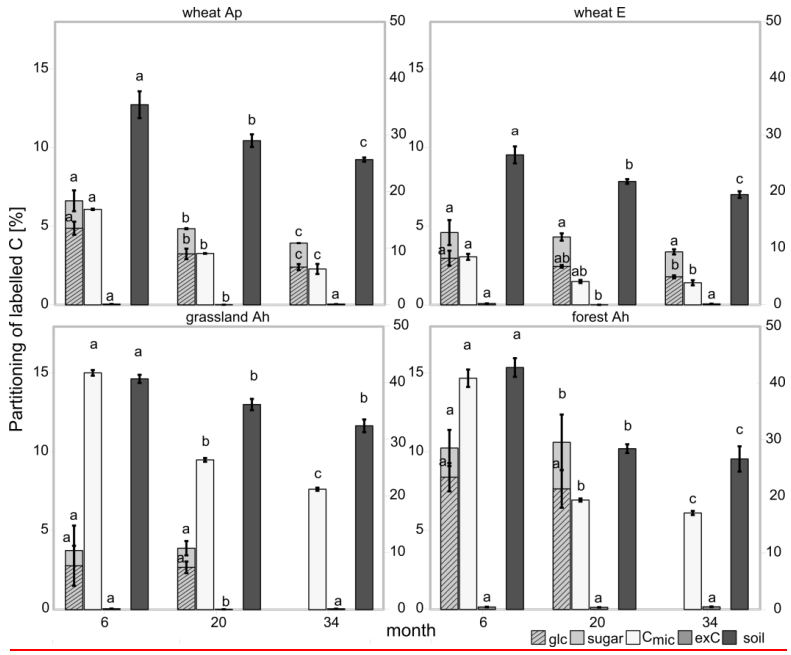

Figure 3. Partitioning of the labelled C into microbial biomass (Cmic), K_2SO_4-extractable carbon (exC), glc and sum of all sugars (left axis) and bulk soil (right axis) in wheat Ap and E, grassland Ah and forest Ah after 6, 20 and 34 months of incubation. Different letters indicate significant differences ($p<0.05$) within one treatment over time. Means ± standard error (n=3).

Formatiert: Seitenumbruch oberhalb

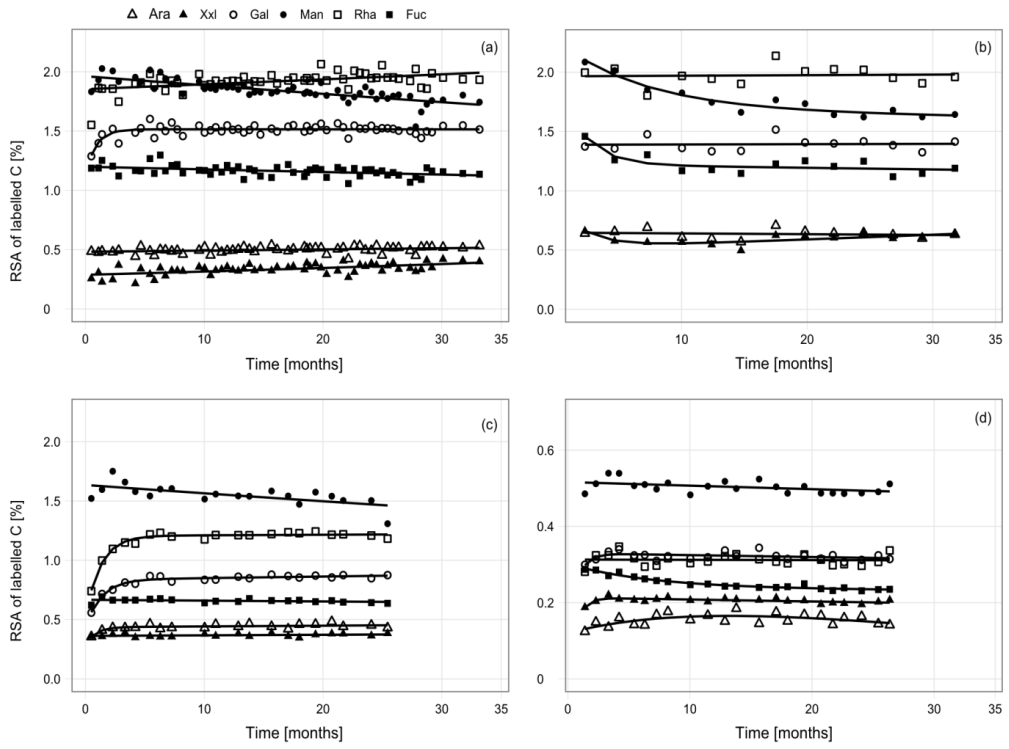

Figure 3. RSA of labelled C of individual sugars in the incubated soil samples. Lines show the fit of the observed data. a) wheat Ap ,b) wheat E horizon of c) grassland and d) forest soil. The parameters of the exponential equations are given in Table S2.