Soil Biology and Biochemistry 121 (2018) 138–146

Contents lists available at ScienceDirect

Soil Biology and Biochemistry

journal homepage: www.elsevier.com/locate/soilbio

Priming effects induced by glucose and decaying plant residues on SOM decomposition: A three-source $^{13}C/^{14}C$ partitioning study

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ARTICLE INFO

Keywords:
Dual isotopic labeling
Glucose
Residue quality
SOM mineralisation
Microbial activation

ABSTRACT

Decomposition of soil organic matter (SOM) may either increase or decrease after fresh organic inputs, the phenomena which are termed as "priming effect". Crop residues and labile C additions can prime SOM decomposition, but it is not known how labile C inputs affect SOM in the presence of decaying plant residues varying in quality (*e.g.* from previous crops, a common situation in arable soils). We used a dual $^{13}C/^{14}C$ isotopic labelling to partition soil CO_2 efflux and microbial biomass for three C sources: labile C (glucose), partly decomposed wheat residues (leaves and roots) and SOM. ^{14}C-labelled glucose was added to the soil after 30 days of pre-incubation with ^{13}C-labelled residues (separately leaves or roots). After glucose addition, the leaf residue decomposition rate declined by up to 65%, while roots remained unaffected. Despite the differences between residue decomposition rates, the quantity of primed SOM remained similar between leaf and root residue treatments after the addition of glucose. Glucose alone caused cumulative positive SOM priming of 193 μg C g^{-1} soil over 90 days, corresponding to 60% of SOM decomposition without addition. Addition of glucose to soil together with partly decomposed plant residues induced up to 45% higher SOM priming than single residues priming effect (~250 μg C g^{-1}). Remarkably, this priming effect induced by glucose and residues was only due to intensive SOM decomposition during the first 18 days. On the subsequent period (after 18 days of glucose), decline in SOM priming and increase in residue decomposition indicate a shift in microbial activity *i.e.* from active-to slow-growing microbes. Glucose addition strongly increased the proportion of microbial biomass from SOM but decreased the proportion from residue C, suggesting a preferential use of SOM over plant residues following glucose exhaustion. These results are consistent with the view that labile C inputs induce SOM priming and suggest for the first time, that labile C controls the intensity and decomposition rate of both SOM and decaying plant residues. Concluding, irrespective of the quality of partly decomposed residues, input of labile C (*e.g.* through rhizodeposition) has overall an additive effect in increasing decomposition of SOM. Such studies of interactions between pools and identification of three C sources were only possible by the application of an innovative dual $^{13}C/^{14}C$ labelling approach.

1. Introduction

Soil organic matter (SOM) decomposition is an important regulator of global climate change and soil fertility. A holistic approach to studying the processes and mechanisms involved in SOM stabilisation in response to organic inputs may help to improve strategies for sustainable agricultural production (Campbell and Paustian, 2015). The amount of C stored in SOM depends on the balance between SOM inputs from organic sources and losses via decomposition to CO_2. The SOM decomposition is controlled by several factors, including type and time of organic inputs, and interdependence of various SOM components (Eskelinen et al., 2009; Schmidt et al., 2011), but little is known how these factors eventually affect SOM stabilisation.

The SOM mainly consist of decomposed and transformed organics, undecomposed fresh or decaying crop residues and labile C *e.g.* released through rhizodeposits (Dennis et al., 2010; Rossell et al., 2001; Schmidt

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https://doi.org/10.1016/j.soilbio.2018.03.004
Received 25 October 2017; Received in revised form 2 March 2018; Accepted 4 March 2018

et al., 2011). Evidence suggests that recently added SOM components, such as from rhizodeposition or crop residues, can modulate the decomposition rate of existing SOM (Mwafulirwa et al., 2017; Shahzad et al., 2015; Wang et al., 2015). The change in SOM decomposition rates due to additional C inputs is often defined as the priming effect (PE) (Jenkinson et al., 1985; Kuzyakov et al., 2000). Thus, added organics influence the microbial activity which can decrease or promote the decomposition of SOM, an effect which may persist long after exhaustion of the added substrate, ultimately may result in net soil C loss (Fontaine et al., 2011; Guenet et al., 2010). However, the question is whether and to what extent exogenously added SOM components influence the decomposition rates of each other, and ultimately affect SOM stabilisation.

The organic inputs mainly include aboveground residues, dead roots and labile C. The labile C substrates are generally released into the soil through rhizodeposition and crop root death (De Graaff et al., 2010; Kumar et al., 2016). The nature (*i.e.* quality, fresh or decomposed) and timing of organics input is also crucial because it controls microbial activity which affects the decomposition of both added organics and SOM priming (Kuzyakov, 2010; Wang et al., 2015). Since cropped soils frequently contain partly decomposed residues or dead roots from previous crops (*e.g.* in autumn), the mechanisms of residue decomposition and SOM priming are likely to be complex when labile C becomes available from the growing crop.

Most previous studies investigating the impact of labile C on SOM decomposition have used glucose as a substrate. Glucose is a component of root exudates and in addition, it can be released during cellulose decomposition (Derrien et al., 2004; Dorodnikov et al., 2009). Since the priming of SOM is facilitated by increased microbial activity, the availability of such labile C may, therefore, changes the decomposition rate of SOM and that of already decomposing crop residues (Blagodatskaya et al., 2011; Nottingham et al., 2009). However, decomposing crop residues (depending on quality) themselves can also prime the decomposition of SOM (Qiu et al., 2016; Shahbaz et al., 2017a, 2017b; Wang et al., 2015). The effects of glucose on SOM versus crop residues decomposition (or the combined effect of glucose and decaying residues on SOM) has not been clearly identified, because of the difficulty in partitioning the C sources (glucose, SOM and residues) (Blagodatskaya et al., 2011; Whitman and Lehmann, 2015). Most studies have only accounted for the individual role of labile C or crop residues (contrasting type) on SOM priming, despite the likelihood of complicated interactions between the decomposition processes of glucose and crop residues on SOM decomposition.

The aim was to examine, how labile C input affect SOM decomposition in the presence of partly decomposed wheat residues (leaves and roots). A three-source partitioning approach (Blagodatskaya et al., 2011), was modified using dual isotope labelling to partition the decomposition of glucose (^{14}C), decaying plant residues (^{13}C) and unlabelled SOM. Specific objectives of the study were: (1) to see the PE induced by single residues on SOM decomposition with or without glucose, (2) to differentiate the effects of glucose on SOM versus residues decomposition, when added in combination with partly decomposed residues, (3) to examine the combined/interactive effects of glucose and decaying residues on SOM decomposition. To reach a stabilised level both for residue decomposition rate and decomposers activity, the residues were partly decomposed (*i.e.* for 30 days pre-incubation) before glucose addition. Therefore, we hypothesised that: regardless of the type of decaying residues (leaves or roots), glucose is mineralised at the same rate (among residues), and thus the intensity of SOM priming increases at the same rate for glucose + leaves and glucose + roots added to the soil.

2. Materials and methods

2.1. Soil sampling

The soil was sampled from the Ap horizon (0–25 cm) of an experimental field located on a terrace plain of the river Leine northwest of Göttingen, Germany (51°33′36.8″N, 9°53′46.9″E). The soil is classified as a Luvisol (87% silt, 7% clay, 6% sand), is carbonate free (tested with 10% HCl) and had the following characteristics at the time of sampling: organic C 12.8 ± 0.4 g kg^{-1}; total N 1.3 ± 0.0 g kg^{-1}, $\delta^{13}C$ −26.8‰ and pH ($CaCl_2$) 6.0. The field has only had C3 vegetation (predominantly wheat) over its whole farming history (Kramer et al., 2012). After the sampling, the soil was air-dried, sieved (< 2 mm) and fine roots and other visible plant debris were carefully removed.

2.2. Wheat residue and chemical analysis

Wheat plants were grown to produce homogenously ^{13}C-labelled residues according to the method described by Bromand et al. (2001) with some modifications (*see* Shahbaz et al., 2017b). The wheat plants were grown in a controlled chamber until maturity (120 days of growth). In order to achieve an even labelling, the plants were pulse-labelled with 99% $^{13}CO_2$ at regular intervals over the course of their growth. Homogeneous labelling of plant material was confirmed by measuring ^{13}C values at various residue degradation stages (Shahbaz et al., 2017b). At maturity, the entire plants were harvested and the roots were gently washed to remove sand particles. Leaf and root parts of wheat residues were then carefully separated, to obtain residues of contrasting quality. For homogeneous mixing with soil, leaf and root residues were chopped and sieved (< 2 mm). Mean C contents in leaves and roots were 391.9 ± 6.1 (C/N: 17.2) and 298.3 ± 5.9 (C/N: 15.5) g kg^{-1}, respectively. ^{13}C analyses were performed using an isotope ratio mass spectrometer coupled to an elemental analyser (Delta Plus, EA-IRMS, *see* section Isotopic and chemical analyses). The ^{13}C atom% values for leaves and roots were 1.53 ± 0.00 and 1.51 ± 0.02, respectively.

2.3. Experiment layout and incubation conditions

Portions of 50 g of air-dried and sieved (< 2 mm) soil were weighed into 350-mL incubation bottles and pre-incubated with distilled water at 50% of water-holding capacity (WHC) for seven days. Thereafter, to obtain partly decomposed residues, ^{13}C labelled wheat residues (leaves and roots separately, at a rate of 11 g DM kg^{-1} soil) were pre-incubated in the soil, with six replicates per treatment. The added residues were thoroughly mixed into the soil and water content was adjusted to 60% of soil WHC. The residue pre-incubation period was set to 30 days, to reach a constant residue decomposition rate (Fig. 1). This was intended to resemble the situation in the field when residues and dead roots from the previous crop are partly degraded and labile C substrate is released into the soil.

After 30-days plant residues pre-incubation in the soil, the amount of microbial biomass was determined in order to observe changes in its composition after glucose addition. Before glucose addition, the amounts of SOM- and residue-derived C in microbial biomass were calculated (*see* section Microbial biomass.

Soil without or with residue addition was amended with ^{14}C-labelled glucose solution (170 μg C g^{-1}, corresponding to 100% microbial C in the without addition control) and incubated over a period of 3 months (Fig. 1). Six treatments were established (soil alone without addition, soil + glucose, soil + leaf, soil + leaf + glucose, soil + root and soil + root + glucose), each with three replicates. Before addition to soil, uniformly ^{14}C-labelled glucose with a final activity of 2.9×10^6 disintegrations per minute (DPM) activity per mL was applied to unlabelled glucose. The labelled glucose was then applied on the soil surface as a 1 mL aqueous solution to reach a final moisture content of 70% WHC. The moisture content of without addition control soil samples (*i.e.* without glucose/residues) was maintained with distilled water and they were used as a reference to estimate the PE due to glucose and/or residue addition to the soil.

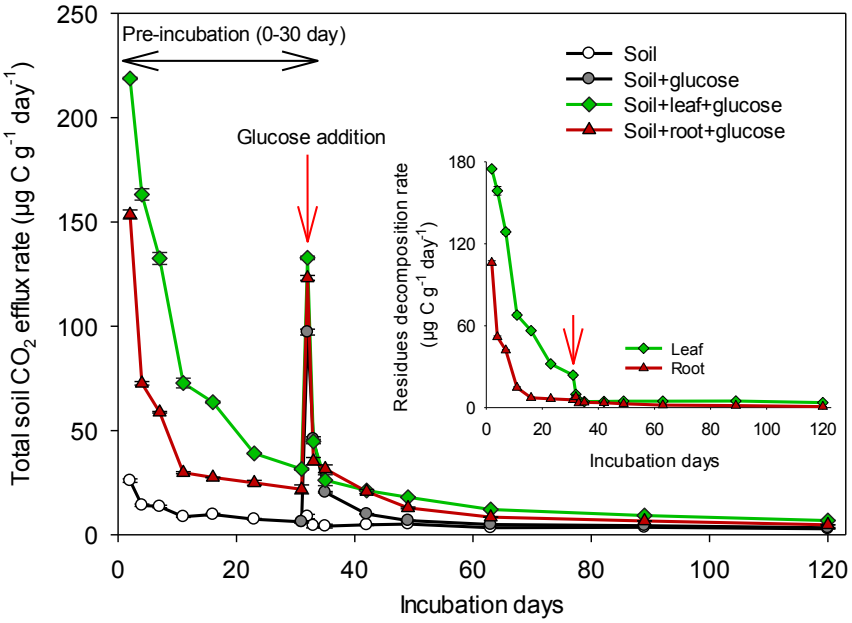

Fig. 1. Rates of total CO_2 efflux from soil, before (during 30 day pre-incubation period) and after glucose addition depending on the residue type and glucose input. The inset represents the decomposition rates of wheat residues (leaves and roots). Errors bar represent standard error of mean ($n = 3$).

2.4. Sampling

After addition of glucose or distilled water to 30-day residue pre-incubated soils, small vials with 5 mL of 1 M NaOH were placed in the incubation bottles (including four null control bottles *i.e.* without soil) to trap released CO_2. The bottles were immediately closed air-tight and incubated at 22 ± 1 °C for 90 days. The vials were replaced at intervals with fresh NaOH vials to measure trapped CO_2, allowing measurements at 1, 2, 4, 11, 18, 32, 59 and 90 days of incubation. These dates were selected to prevent the traps being saturated with more Na_2CO_3 than 60% of their capacity. Aliquots of sampled NaOH were used to measure ^{14}C, ^{13}C and the total amount of trapped CO_2. A negligible amount of atmospheric CO_2 was trapped in null control NaOH solution, which was considered for correcting the total CO_2 flux. Since we used labelled residues for the incubation, therefore, we did not expect any effect of trapped CO_2 (in null-control) on ^{13}C data/calculations. Note that during the residue pre-incubation period, vials with fresh NaOH were also replaced regularly to avoid anoxic conditions and to measure CO_2 efflux.

2.5. Microbial biomass

The microbial biomass C was determined using the chloroform fumigation-extraction method described by Vance et al. (1987). Before analysis, the soil was carefully mixed and 6 g (moist) soil were extracted with 24 mL 0.05 M K_2SO_4 at 22 °C for 1 h. Another 6 g (moist) soil were first fumigated with ethanol-free $CHCl_3$ for 24 h and then extracted in the same way. The obtained extracts were kept cold (< 4 °C) and analysed for total C concentration using a TOC/TIC analyser (Multi N/C 2100, Analytik Jena, Germany). The total amount of microbial biomass C (extractable) was calculated as the difference between K_2SO_4 extracted C in fumigated and non-fumigated soils, using 0.45 as the conversion factor (K_{ec}) (Wu et al., 1990). Glucose-derived C in microbial biomass was determined on the base of ^{14}C activity in fumigated or non-fumigated K_2SO_4 extracts (*see detail* section Isotopic and chemical analyses and Calculations and statistics).

2.6. Isotopic and chemical analyses

To quantify respired CO_2, NaOH solution was precipitated with 1 M $BaCl_2$. The total amount of trapped CO_2 was then measured (µg C g^{-1}) by titration of excess NaOH with 0.05 M HCl using phenolphthalein as an indicator.

Since a dual labelling approach (^{13}C-labelled residues and ^{14}C-labelled glucose) was used, the NaOH-trapped CO_2 samples were specifically prepared. For ^{13}C measurements, 3 mL of trapped CO_2 as Na_2CO_3 in NaOH was precipitated with an equal volume of 1 M $SrCl_2$ solution. The NaOH solution, containing $SrCO_3$ precipitates, was centrifuged for 5 min at 4000 rpm. The process was repeated with distilled water to remove excess NaOH and to bring the pH to 7. After removing water, the $SrCO_3$ pellets were dried at 60 °C and stored for ^{13}C analysis. The pellets were analysed for ^{13}C values using an isotope ratio mass spectrometer (Delta Plus, IRMS; Thermo Fisher Scientific, Bremen, Germany) coupled to an elemental analyser (NC 2500; CE Instruments, Milano, Italy) at the Centre for Stable Isotope Research and Analysis (KOSI), Georg-August University of Göttingen, Germany. For ^{13}C measurement in microbial biomass, aliquots of K_2SO_4 extract from both fumigated and non-fumigated samples were freeze-dried and then weighed into capsules for analysis.

The measurements of ^{14}C activity were performed directly after replacement of CO_2-trapped NaOH vials with fresh vials during the course of incubation. The NaOH activity of ^{14}C trapped with CO_2 was measured after the decay of chemiluminescence in the scintillation cocktail Rotiszint Eco Plus (Carl Roth, Germany) using a 1450 LSC & Luminescence Counter MicroBeta TriLux (Perkin Elmer Inc., USA). Similarly, glucose-derived C (^{14}C activity) in microbial biomass was measured by scintillation counter after mixing fumigated or non-fumigated K_2SO_4 extracts with the scintillation cocktail. The ^{14}C activity measurement error never exceeded 2% and the efficiency of ^{14}C counting values was always above 85%.

2.7. Calculations and statistics

To partition the three C sources (^{13}C-residues, ^{14}C-glucose, unlabelled-SOM) in total CO_2 efflux and microbial biomass, calculations were carried out step-by-step as described by Blagodatskaya et al. (2011). First, the amount of glucose-derived C ($C_{G\text{-derived}}$, µg g^{-1}) in CO_2 and microbial biomass was determined, based on amount of applied glucose (C_G, µg g^{-1}), initial radioactivity of added glucose ($^{14}C_G$) and current ^{14}C radioactivity (C_{curr} in DPM) of the corresponding pool

(*i.e.* CO_2 and fumigated or non-fumigated K_2SO_4 extracts):

$$C_{G\text{-derived}} = C_G \times {}^{14}C_{curr}/{}^{14}C_G \quad (1)$$

The amount of SOM-derived C ($C_{SOM\text{-derived}}$) in glucose-amended soil without or with residues in CO_2 or microbial biomass was then calculated as:

$$\text{Without residues in soils: } C_{SOM\text{-derived}} = C_{total} - C_{G\text{-derived}} \quad (2)$$

$$\text{With residues in soils: } C_{SOM\text{-derived}} = C_{total} - C_{G\text{-derived}} - C_{res\text{-derived}} \quad (3)$$

where C_{total} is the total amount of C in CO_2 efflux (at each sampling point) and microbial biomass in soils with or without residue addition; $C_{G\text{-derived}}$ is the amount of glucose-derived C and $C_{res\text{-derived}}$ is residue-derived C (see below).

In the second step, we calculated residue-derived C in each pool. As the plant material was ^{13}C-labelled, residue-C in CO_2 and microbial biomass was calculated from the ^{13}C atom% values (Poirier et al., 2014) given by IRMS and calculated according to:

$$At\%{}^{13}C = [\text{number of } {}^{13}C \text{ atoms} / (\text{number of } ({}^{12}C + {}^{13}C) \text{ atoms})] * 100 \quad (4)$$

The fraction of C (*f* C) from residues in CO_2 or microbial biomass was calculated as:

$$f\,C = [(At_{mix} - At_{con}) / (At_s - At_{con})] \quad (5)$$

where At_{mix} is atom% ^{13}C values (CO_2 trapped in NaOH, fumigated and non-fumigated K_2SO_4 extracts) for residue-amended soil; At_s is specific atom% ^{13}C value of incorporated residue (leaves or roots); and At_{con} is atom% ^{13}C value of the without addition control soil.

The amount of residue-derived C ($C_{res\text{-derived}}$), was computed as:

$$C_{res\text{-derived}} = f\,C \times [TC] \quad (6)$$

where [*TC*] represents total C (μg g^{-1}) in CO_2 and microbial biomass (as calculated in section Microbial biomass and Isotopic and chemical analyses, respectively).

Similarly, the amount of SOM-derived C ($C_{SOM\text{-derived}}$) was calculated by subtracting $C_{res\text{-derived}}$ and $C_{G\text{-derived}}$ (where glucose added) from the total C.

The PE (μg C g^{-1}) was calculated according to Blagodatskaya et al. (2011). The PE of alone glucose or residue additions on SOM decomposition was calculated as:

$$PE = {}^{amended}C_{SOM\text{-derived}} - {}^{CK}C_{SOM\text{-derived}} \quad (7)$$

where ${}^{amended}C_{SOM\text{-derived}}$ is the amount of SOM-derived CO_2–C (μg C g^{-1} soil) in soil amended only with glucose or residues and ${}^{CK}C_{SOM\text{-derived}}$ is the amount of CO_2–C in the without addition control.

The PE of glucose addition on residue decomposition was calculated as:

$$PE = {}^{res+G}C_{res\text{-derived}} - {}^{res}C_{res\text{-derived}} \quad (8)$$

where ${}^{res+G}C_{res\text{-derived}}$ and ${}^{res}C_{res\text{-derived}}$ represent the amount of residue-derived CO_2-C (μg C g^{-1}) in the soil + residue + glucose and soil + residue treatments, respectively.

For treatment soil + residue + glucose, the PE was calculated in order to examine the simultaneous effects of glucose addition on SOM compared with residue decomposition:

$$\text{PE on residues} = {}^{res+G}C_{G\text{-derived}} - {}^{res}C_{res\text{-derived}} \quad (9)$$

$$\text{PE on SOM} = {}^{res+G}C_{SOM\text{-derived}} - {}^{res}C_{SOM\text{-derived}} \quad (10)$$

where ${}^{res+G}C_{SOM\text{-derived}}$ and ${}^{res}C_{SOM\text{-derived}}$ represent the amount of SOM-derived C in the soil + residue + glucose and soil + residue treatments, respectively.

For the estimation of residue-derived C in microbial biomass, residue-derived C was first calculated separately for fumigated and non-fumigated samples using Eq. (6) and then the value for the non-fumigated sample was subtracted from that for the fumigated sample. The cumulative amount of PE or C efflux (derived from residue, SOM, glucose) was calculated by adding up the calculated values of single sampling point to the next sampling over the entire experiment.

One-way ANOVA was used to assess the significance of differences in C fluxes between treatments, followed by Duncan's post-hoc test. Standard error (SE) of CO_2 and microbial biomass values was calculated to estimate the precision of mean values. The error propagation was calculated when the mean values were used for determining PE (Meyer, 1975). The significance of effects of glucose and residues addition was assessed by two-way ANOVA at $p < 0.05$.

3. Results

3.1. CO_2 release during pre-incubation

Up to 45% of leaf residues and 27% of added root residues were decomposed during the 30-day residue pre-incubation period (data not shown). Although residues were already intensively decomposed, the decomposition rate of leaf residues was still higher than that of root residues (Fig. 1). However, after pre-incubation, the decomposition rate for residues reached a stable level, which was assumed to be relatively constant for the rest of the incubation period. A considerable amount of SOM-derived C (~300 μg C g^{-1}) was released from the without addition control during pre-incubation.

3.2. Total CO_2 efflux

Over 90 days of incubation (after 30 days of pre-incubation), the cumulative amount of CO_2 released from without addition (control) soil was 324 ± 19 μg C g^{-1} (Fig. 2a). Addition of single leaf and root residues to soil increased cumulative soil CO_2 release to 733.2 ± 25 μg C g^{-1} and 652.7 ± 19 μg C g^{-1}, respectively.

Single glucose addition (*i.e.* without residues) increased the total soil CO_2 release to 82% compared to without additions control (Fig. 2a). Similarly, the cumulative amount of soil CO_2 released under glucose + residue addition was 55% and 39% higher than with only leaf or root residue additions, respectively (Figs. 2a and 6).

3.3. Glucose and residue decomposition

To determine the contribution of various pools, the total soil CO_2 efflux was partitioned into glucose-, residue- and SOM-derived C sources. Glucose decomposition was calculated based on ^{14}C activity in total CO_2 efflux (Eq. (1)). Although glucose was intensively mineralised after addition, two distinct mineralisation phases were observed: 1) strong mineralisation of the applied glucose and its labile transformation products in the first 18 days and 2) slow mineralisation of stable glucose-derived metabolites thereafter (Fig. 2c). During the first of these phases, a large proportion of initially added ^{14}C labelled CO_2 was respired (47% of that added to leaf residue-treated soil and 42% of that to root residue-treated soil). After this period, the respired $^{14}CO_2$ made up only 5% of the initially added glucose amount until 90 days. The cumulative amount of glucose-derived CO_2 from leaf residue-treated soil was 17% greater than the glucose respired amount obtained from glucose alone or glucose + root treatments (Fig. 2c).

Despite the same level of residue additions, the CO_2 derived from leaf residues showed a much greater cumulative amount (361 ± 9 μg C g^{-1}) than root-residue derived CO_2 (167 ± 6 μg C g^{-1}) under without glucose addition. This difference was proportionally similar to that in the pre-incubation period before glucose addition (data not shown; cf. Fig. 1). After glucose addition, the leaf residue decomposition rate was declined to 65% of the leaf-residue decomposition rate under without glucose for around 1–2 days (Figs. 1 and 2b). Despite this decrease in decomposition rate, the cumulative amount of leaf residue-derived CO_2

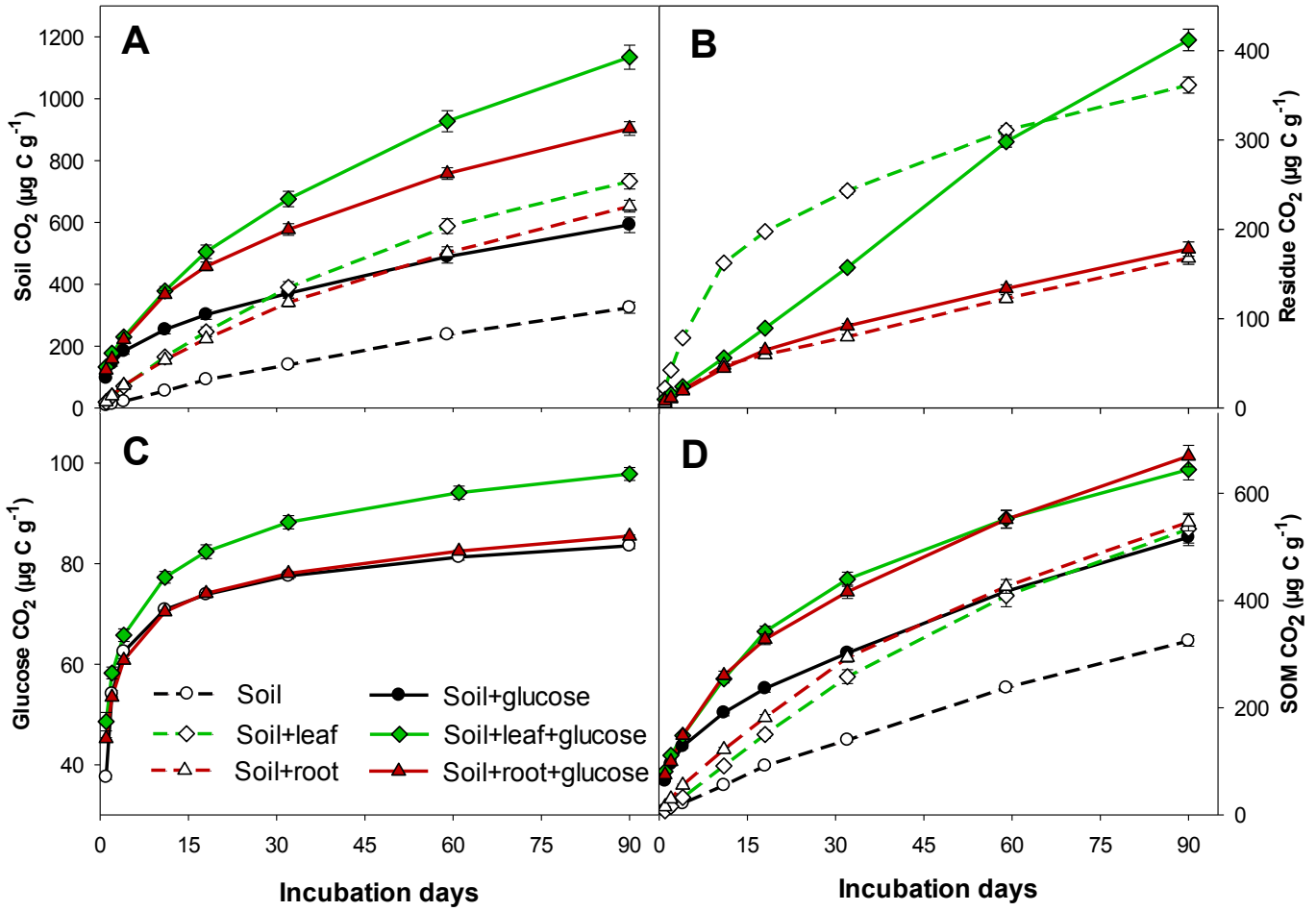

Fig. 2. Cumulative CO_2 release from soils amended with or without residues combined with or without glucose (A) and contribution of three C sources (B, C and D) to total soil CO_2 efflux. The three C sources include: 1) partly decomposed residues derived CO_2 (B) with or without glucose addition, 2) glucose derived CO_2 (C) in glucose amendments and, 3) soil organic matter (SOM) derived CO_2 (D) with or without glucose addition over the incubation period of 90 days. Error bars represent standard error of mean ($n = 3$).

in the glucose + leaf treatment was slightly higher (412 ± 18 µg C g^{-1}) than in the alone leaf residues treatment at the end of the experiment (Fig. 2b). The cumulative amount of root-derived CO_2 was 1.3-fold lower than found for leaf residues (with or without glucose). The root decomposition rate remained unaffected after glucose addition (Fig. 2b).

3.4. Priming effect

The increase in CO_2 efflux originating from SOM after residue addition contributed almost half of the total CO_2 emissions (Fig. 2d). This suggested a large contribution of primed CO_2 from SOM to total CO_2 efflux. Over the course of incubation, alone partly decomposed leaf and root residues induced cumulative SOM priming up to 220–250 µg C g^{-1}, respectively (Fig. 3).

Separating the 90-day incubation into two phases, before and 18 days after glucose addition, during the first phase single glucose primed up to 145 µg C (out of total SOM-primed 193 µg C), which was around 3-fold higher than the amount of glucose-primed C during the rest of the incubation period (*i.e.* 18–90 days) (Fig. 3).

Glucose addition together with residues interacted differently to induce short-term and long-term PE on SOM. To assess the PE of glucose on residues (*i.e.* leaf and root) versus SOM in the residues + glucose

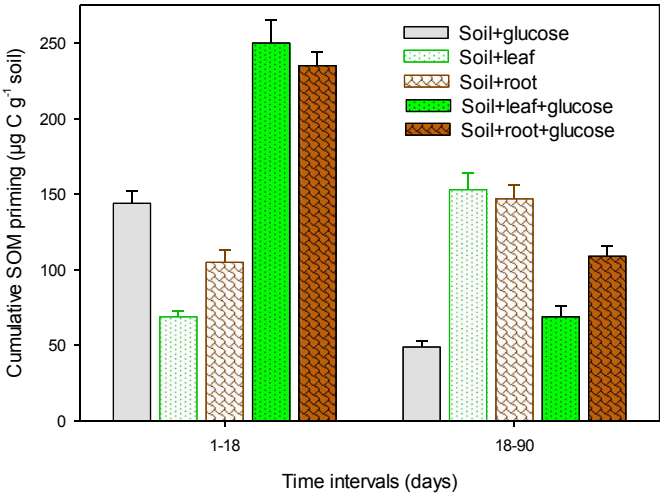

Fig. 3. Cumulative soil organic matter (SOM) priming induced by, single residue or glucose additions and by the combination of glucose + residues, during 1–18 and 18–90 days. The SOM priming is the difference of SOM decomposition between the soils amended by residues, glucose or glucose + residues with the no-addition control (calculated according to equation (7)). Error bar represents standard error of mean ($n = 3$).

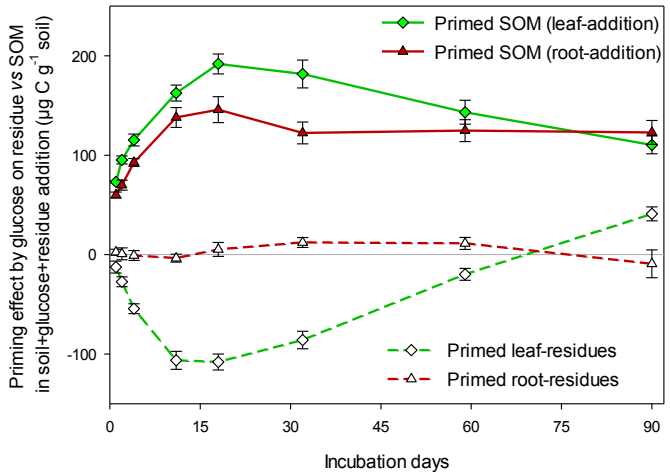

Fig. 4. Priming effects of added glucose on the decomposition of partly decomposed residues (leaves and roots) and of soil organic matter (SOM). The priming effects are the differences in SOM/or residue decomposition between the soil + residue + glucose and soil + residue amendments. Error bars represent standard error of mean ($n = 3$).

additions, the residue-derived and SOM-derived CO_2 effluxes from residues + glucose were compared with those from single residue additions. Compared with only residue addition, the glucose + residues treatments increased SOM priming by 37 (under root) to 45% (under leaf) (Figs. 3 and 6). This increase in PE was solely due to the great contribution of primed SOM during first 18 days after glucose addition (*i.e.* during first glucose mineralisation phase) (Figs. 3 and 4). After this glucose mineralisation phase, the contribution of primed C to total PE in the glucose + residue treatments was lower than that in the residue alone treatments (*i.e.* with no glucose added).

This partitioning of residue-derived and SOM-derived C in glucose + residue additions revealed that glucose had an opposing PE on residues (especially leaves) and SOM decomposition (Fig. 4). Although glucose addition initially induced stronger SOM priming in leaf + glucose, the cumulative PE (~120 µg C g^{-1} soil) of glucose remained similar in soils with leaf and root residue addition (Fig. 4). In contrast, the PE caused by glucose on residue decomposition was negative (slightly for roots and strongly for leaf residues) during the first glucose mineralisation phase (*i.e.* 1–18 days) (Fig. 4). However, in the latter period, cumulative decomposition of both leaf and root residues in treatments with glucose addition gradually reached the level of residue decomposition in soils without glucose addition (Figs. 2b and 4).

Please note, the C efflux rates (total CO_2, SOM, residue, glucose) after pre-incubation and all the $^{13}C/^{14}C$ isotopic data is provided as supplementary information.

3.5. Microbial biomass

To measure the changes in SOM- and residue-derived C in microbial biomass, the amount of microbial biomass C was determined at the time of glucose addition and at the end of incubation. After the 30-day residue pre-incubation, a greater amount of both SOM-derived (~220 µg C g^{-1}) and residue-derived (~150 µg C g^{-1}) microbial biomass was recovered with leaf residue addition than with root residue addition to the soil (Fig. 5, left). Microbial biomass in the control soil was ~170 µg C g^{-1}. Similarly to the initial pattern, a higher amount of total microbial biomass (~250 µg C g^{-1}) was recorded for leaf residue addition, followed by root residue addition (~175 µg C g^{-1}), at the end of incubation (Fig. 5, right). Partitioning of C sources in microbial biomass revealed that a remarkable amount of SOM-derived C caused an increase in total microbial biomass (compared with controls), added either as only residues or in the combined glucose + residue treatments (Fig. 5).

Following the 90 days of incubation, only 2% of glucose-derived C was detected in total microbial biomass (Fig. 5, right). The addition of glucose alone (to non-residue treated soil) significantly increased the amount of total microbial biomass (by up to 18%), which was mainly due to SOM-utilising microorganisms. However, although glucose had a non-significant effect on total soil microbial biomass C as compared with that in residue-alone treatments, glucose addition caused a great

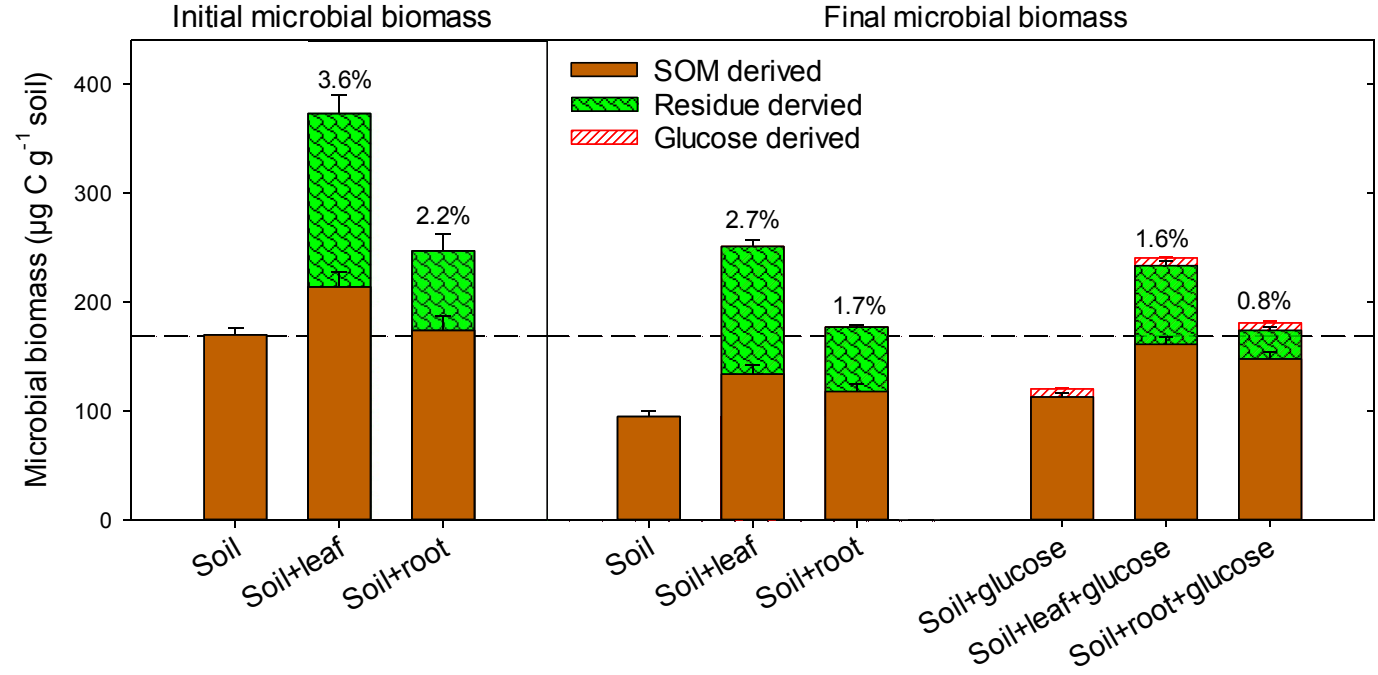

Fig. 5. Contribution of soil organic matter (SOM), residues and glucose derived carbon (C) to total microbial biomass C. The left panel represents the soil microbial biomass C at the start of the experiment (*i.e.* after 30 days of residue pre-incubation). The right panel shows the final microbial biomass C (at the end of experiment) with or without glucose additions. Error bars represent standard error of mean ($n = 3$). Numbers on the green bars show the percentage of initially added residues C incorporated into microbial biomass. Dashed line is the initial amount of microbial biomass C in no-addition control *i.e.* after pre-incubation.

shift in C sources, with *e.g.* the contribution of the residue-derived microbial fraction decreasing strongly (by 55–65%) after glucose addition (Fig. 5, right). In contrast, glucose addition caused a strong increase in the proportion of SOM-derived C in microbial biomass compared with in control soil without glucose (Fig. 5, right).

4. Discussion

4.1. Effect of glucose on SOM priming

For the first time, we demonstrated how labile C controls the intensity and decomposition rate of both SOM and decomposing plant residues by modified dual $^{13}C/^{14}C$ labelling approach. Glucose addition and its interaction with added residues induced up to 45% higher positive SOM priming than alone residue PE, which agrees to previous work (Mwafulirwa et al., 2017). Remarkably, this increase in glucose and residue PE was only due to intensive SOM decomposition during the first 18 days after glucose addition. When the sources of SOM priming were partitioned separately into residue- and glucose-induced SOM priming in the glucose + residue additions, it became apparent that the PE during the first 18 days was mainly caused by glucose *i.e.* residues played no role in priming (Figs. 3 and 4). Later (18–90 days), residues were solely responsible for SOM priming, while glucose did not contribute to PE. However, the SOM priming under single glucose addition lasted over the whole incubation period. The strong pulse of SOM priming caused by glucose addition was most likely due to increased microbial activity, supporting the microbial activation hypothesis (De Graaff et al., 2010; Cheng and Kuzyakov, 2005; Mondini et al., 2006). A comparable SOM priming between decaying leaf and root residues after glucose addition suggested that SOM-decomposing microorganisms responded similarly to added labile C (Cui et al., 2017; Paterson and Sim, 2013). This direct coupling of glucose-induced SOM decomposition with increased microbial activity was supported by the direct relationship between glucose mineralisation and SOM priming (Figs. 2c and 3).

A current conceptual view on priming is that SOM decomposability depends on the ability for microbial investment (*e.g.* release of exoenzymes), with sufficient C resources needed to initiate SOM decomposition (Blagodatskaya et al., 2014a; Derrien et al., 2014; Dorodnikov et al., 2009; Paterson and Sim, 2013). The presence of labile C stimulates microbial growth by triggering metabolic activity, primarily for utilisation of easily available substrates, which may trigger co-metabolism of SOM (Blagodatskaya and Kuzyakov, 2008; Chen et al., 2014; De Graaff et al., 2010). Strong SOM priming during the first 18 days after glucose addition to gather with residues apparently supports this priming concept. However, the conceptual view on SOM priming has been extended by considering that only the active fraction of the microbial community has the capacity to utilise SOM (Shahbaz et al., 2017b). The substrate availability to that SOM-utilising microbial fraction determines the intensity of PE, due to its strong dominance over non-active microorganisms (*i.e.* non/less SOM-utilising) (Blagodatskaya et al., 2011; Fontaine et al., 2003). In this study, we had several levels of substrate complexity from labile glucose to partly decomposed plant residues and SOM. Therefore, we assumed that glucose addition would activate the microbial fraction which may consist of both r- (fast) and k-strategists (slow) to be involved in SOM priming (Chen et al., 2014; Fontaine et al., 2003). Glucose addition decreased the decomposition of partly decomposed residues (mainly leaf, discussed below), but strongly increased SOM decomposition, suggesting preferential microbial utilisation of SOM over residues (Cui et al., 2017). This suggestion is supported by the higher contribution of SOM-compared with residue-derived C to total microbial biomass. Indeed, glucose addition increased SOM-derived C in microbial biomass by up to 60% compared with residue addition alone (Fig. 5, right panel). This indicates that the SOM priming is not a ubiquitous function of all microbial community members and that labile C increases nutrient demand by active microbes (Derrien et al., 2014; Fontaine et al., 2003). Since no extra nutrients were supplied, we assume that to balance their growth, microorganisms started SOM mining (*e.g.* for N, due to its heterogeneous nature) after glucose addition (Blagodatskaya and Kuzyakov, 2008; Fontaine et al., 2011; He and Yu, 2016), instead of feeding on 30 days decomposed residues. This could further explain the increase in positive SOM priming when glucose was added in combination with residues (during first 18 days), compared with adding residues alone. The decline in glucose induced positive SOM priming on subsequent days (after 18 days) suggests that the depletion of labile

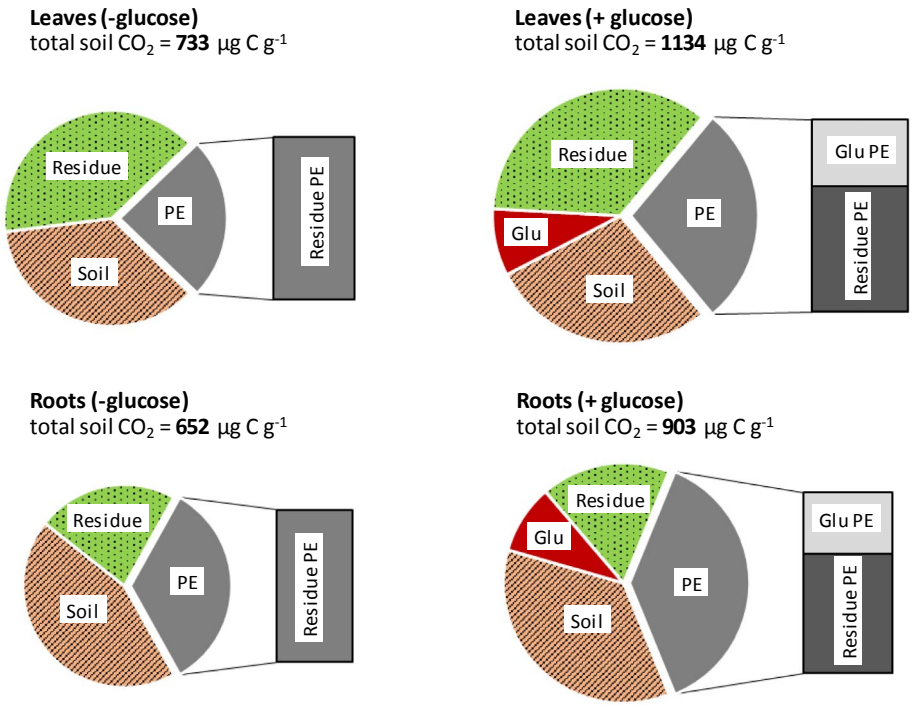

Fig. 6. Contribution (%) of three C sources to cumulative CO_2 efflux from partly decomposed residue treated soils without (left panel) or with glucose additions (right panel). The three sources include: 1) C of partly decomposed residues (leaves or roots), 2) Soil-derived C from without addition control, and 3) the priming effect induced by either residues or the combination of residues + glucose. The right segment of pie-plots represent the contribution of glucose or residues induced PE in total SOM priming.

SOM compounds and a shift in microbial activity, *i.e.* from fast-to slow-growing microbes.

4.2. Effect of glucose on residue decomposition

We added glucose 30 days after residue decomposition in order to simulate labile C inputs in the field (*e.g.* through rhizodeposition), when residues from the previous crop had been partly degraded. This is the common situation in spring, when the root exudates (rhizodeposits) from growing crops are released into rhizosphere soil containing residues from the crop harvested *e.g.* in the previous autumn. In contrast to SOM decomposition glucose addition decreased residue decomposition. This contrasting relationship was mainly evident during the first 18 days after glucose addition, reflecting the importance of labile C availability for microorganisms and changes in their substrate preference for decomposition (Fontaine et al., 2003). This means that after the activation of microorganisms by labile C input, the partly degraded residues (*i.e.* remaining 55%–77%, Shahbaz et al., 2017b), as compared to heterogeneous SOM, were unable to meet increased nutritional demand (Fontaine et al., 2003, 2011; Qiu et al., 2016). This low vulnerability of partly degraded residue decomposition compared with SOM was confirmed by a decrease of residue-derived C but not SOM-derived C proportion in microbial biomass. Accordingly, the C from residues in microbial biomass was presumably turned over and decomposed faster than the C from SOM. Therefore, after glucose addition microorganisms mainly mined SOM as it probably contained higher amounts of easily accessible N and P compounds (C/N = 9.6) (Chen et al., 2014; He and Yu, 2016) than the partly degraded residues (C/N = above 20 both for leaves and roots, data not shown). The leaf residue decomposition rate was immediately reduced (by up to 65%) following glucose addition, while root residue decomposition remained unaffected (Fig. 1). In contradiction to our hypothesis, the cumulative amount of glucose-mineralised C in the presence of leaf residues was 17% higher than with root residues. This reflects either faster microbial turnover or activity of leaf residue-feeding microorganisms or/and higher C use efficiency than for root residues (Blagodatskaya et al., 2014b; Manzoni et al., 2012). Roots are decomposed more slowly than shoots because of the relatively high amount of recalcitrant compounds (*e.g.* lignin, suberin, tannin) in roots, which is not affected by glucose addition (Bertrand et al., 2006; Shahbaz et al., 2017a, 2017b). However, despite the decline of residues decomposition (mainly leaf) after glucose addition, the initial deceleration was reversed (by fast-to slow growing microbes) after 3 weeks residue decomposition greatly increased as the glucose-induced SOM priming declined (Fig. 4).

4.3. Priming effects of residues on SOM

Adding residues alone to soil increased total CO_2 emissions and induced consistent net positive priming of SOM decomposition in the long-term. The intensity and causes of the short-term SOM priming (during pre-incubation) induced by leaf and root residue addition have been described previously (see Shahbaz et al., 2017b). A low amount of residue-derived CO_2 over time was expected, considering that addition of residues is usually followed by depletion of easily decomposable compounds (Majumder and Kuzyakov, 2010; Stewart et al., 2015). The stage of preferential utilisation of labile substrates from the residues ended already during the 30-day pre-incubation and thus residue labile C could not induce SOM decomposition. Over the next three months (following the 30-day pre-incubation), there was a slow but consistent residue-induced positive PE on SOM, which may be explained mostly by co-metabolism of slow growing (k-strategist) microbes (Horvath, 1972; Kuzyakov et al., 2000). As compared to glucose and residues induced PE, greater long-term SOM priming (after 18 days) under single residue addition could mainly be attributed to the availability of relatively high amounts of decomposable SOM. Glucose addition accelerated and intensified the PE (*i.e.* utilised most of the decomposable SOM), but without glucose the PE was smaller and slower, but consistent in the longer term. Thus residue-induced priming was most likely based on more lasting alterations in microbial activity (*i.e.* successional changes in microbial community), which may have remained stable even after depletion of labile residue compounds (De Graaff et al., 2010; Mondini et al., 2006; Shahbaz et al., 21017b). Accordingly, residue-mediated changes in microbiological activities and nutrient contents could profoundly affect SOM decomposition.

5. Conclusions

Glucose addition to soil together with partly decomposed (*i.e.* for 30 days) plant residues (a common situation under rhizodeposition and detritusphere) resulted in greater positive SOM priming (up to 45%) than the incorporation of residues alone. This additive PE was only due to strong increased SOM decomposition during the first 18 days after glucose addition. Irrespective to residue quality (leaves or roots), glucose accelerated and intensified the SOM priming (*i.e.* by activating both fast- and slow growers), while the priming induced by plant residues without glucose was smaller but consistent in the long term. The increase in SOM-derived, but not residue-derived C incorporation into microbial biomass, suggested that the large SOM pool was preferentially utilised over small decaying plant residues pool after the depletion of glucose. Though the decomposition rate of residues declined to 65% (*e.g.* leaves) immediately after glucose addition, the initial deceleration was reversed after 3 weeks residue decomposition greatly increased as the glucose-induced SOM priming declined. Despite differences in the decomposition rate of leaf and root residues, SOM priming remained comparable between both residues after glucose addition. These results reveal the importance of labile C (*e.g.* in the rhizosphere) for decomposition of SOM and decaying plant residues, such as dead roots or leaves (as a proxy for previous crop residues under field conditions). The insight into the decomposition dynamics of SOM and decaying crop residues in the presence of labile C is important element for SOM budgeting studies and for understanding microbial competition with living roots *e.g.* for soil nutrients (like N, P).

Acknowledgements

We are thankful to the German Academic Exchange Service (DAAD) by providing financial support to MS and AK. We acknowledge the help of Klaus Schützenmeister in isotopic labelling of the plant material and Karin Schmidt in measuring microbial C. The isotopic analysis was performed by Kompetenzzentrum Stabile Isotope at Göttingen (KOSI). This study was funded by DFG (Deutsche Forschungsgemeinschaft, projects KU 1184/29 and HE 6726/6). EB's participation was supported by the Russian Science Foundation (project N 14-14-00625). The publication was supported by the Russian Government Program of Competitive Growth of Kazan Federal University and with the support of the “RUDN University program 5–100”.

Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.soilbio.2018.03.004.

References

Bertrand, I., Chabbert, B., Kurek, B., Recous, S., 2006. Can the biochemical features and histology of wheat residues explain their decomposition in soil? Plant and Soil 281, 291–307. http://dx.doi.org/10.1007/s11104-005-4628-7.

Blagodatskaya, E., Kuzyakov, Y., 2008. Mechanisms of real and apparent priming effects and their dependence on soil microbial biomass and community structure: critical review. Biology and Fertility of Soils 45, 115–131. http://dx.doi.org/10.1007/s00374-008-0334-y.

Blagodatskaya, E., Yuyukina, T., Blagodatsky, S., Kuzyakov, Y., 2011. Three-source-partitioning of microbial biomass and of CO_2 efflux from soil to evaluate mechanisms of priming effects. Soil Biology and Biochemistry 43, 778–786. http://dx.doi.org/10.

1016/j.soilbio.2010.12.011.
Blagodatskaya, E., Khomyakov, N., Myachina, O., Bogomolova, I., Blagodatsky, S., Kuzyakov, Y., 2014a. Microbial interactions affect sources of priming induced by cellulose. Soil Biology and Biochemistry 74, 39–49. http://dx.doi.org/10.1016/j.soilbio.2014.02.017.
Blagodatskaya, E., Blagodatsky, S., Anderson, T.-H., Kuzyakov, Y., 2014b. Microbial growth and carbon use efficiency in the rhizosphere and root-free soil. PLoS One 9 (4), e93282. http://dx.doi.org/10.1371/journal.pone.0093282.
Bromand, S., Whalen, J.K., Janzen, H.H., Schjoerring, J.K., Ellert, B.H., 2001. A pulse-labelling method to generate 13C- enriched plant materials. Plant and Soil 235, 253–257. http://dx.doi.org/10.1023/A:1011922103323.
Campbell, E.E., Paustian, K., 2015. Current developments in soil organic matter modeling and the expansion of model applications: a review. Environental Research Letters 10, 123004. http://dx.doi.org/10.1088/1748-9326/10/12/123004.
Chen, R., Senbayram, M., Blagodatsky, S., Myachina, O., Dittert, K., Lin, X., Blagodatskaya, E., Kuzyakov, Y., 2014. Soil C and N availability determine the priming effect: microbial N mining and stoichiometric decomposition theories. Global Change Biology 20, 2356–2363. http://dx.doi.org/10.1111/gcb.12475.
Cheng, W., Kuzyakov, Y., 2005. Root effects on soil organic matter decomposition. In: Wright, S., Zobel, R. (Eds.), Roots and Soil Management: Interactions between Roots and the Soil. Agronomy Monograph No. 48. American Society of Agronomy, Madison, Wisconsin, USA, pp. 119–143.
Cui, J., Ge, T., Kuzyakov, Y., Nie, M., Fang, C., Tang, B., Zhou, C., 2017. Interactions between biochar and litter priming: a three-source 14C and δ13C partitioning study. Soil Biology and Biochemistry 104, 49–58. http://dx.doi.org/10.1016/j.soilbio.2016.10.014.
De Graaff, M.A., Classen, A.T., Castro, H.F., Schadt, C.W., 2010. Labile soil carbon inputs mediate the soil microbial community composition and plant residue decomposition rates. New Phytologist 188, 1055–1064. http://dx.doi.org/10.1111/j.1469-8137.2010.03427.x.
Dennis, P.G., Miller, A.J., Hirsch, P.R., 2010. Are root exudates more important than other sources of rhizodeposits in structuring rhizosphere bacterial communities? FEMS Microbiology Ecology 72, 313–327. http://dx.doi.org/10.1111/j.1574-6941.2010.00860.x.
Derrien, D., Marol, C., Balesdent, J., 2004. The dynamics of neutral sugars in the rhizosphere of wheat. An approach by13C pulse-labelling and GC/C/IRMS. Plant and Soil 267, 243–253. http://dx.doi.org/10.1007/s11104-005-5348-8.
Derrien, D., Plain, C., Courty, P.-E., Gelhaye, L., Moerdijk-Poortvliet, T.C.W., Thomas, F., Versini, A., Zeller, B., Koutika, L.-S., Boschker, H.T.S., Epron, D., 2014. Does the addition of labile substrate destabilise old soil organic matter? Soil Biology and Biochemistry 76, 149–160. http://dx.doi.org/10.1016/j.soilbio.2014.04.030.
Dorodnikov, M., Blagodatskaya, E., Blagodatsky, S., Marhan, S., Fangmeier, A., Kuzyakov, Y., 2009. Stimulation of microbial extracellular enzyme activities by elevated CO_2 depends on soil aggregate size. Global Change Biology 15, 1603–1614. http://dx.doi.org/10.1111/j.1365-2486.2009.01844.x.
Eskelinen, A., Stark, S., Männistö, M., 2009. Links between plant community composition, soil organic matter quality and microbial communities in contrasting tundra habitats. Oecologia 161, 113–123. http://dx.doi.org/10.1007/s00442-009-1362-5.
Fontaine, S., Henault, C., Aamor, A., Bdioui, N., Bloor, J.M.G., Maire, V., Mary, B., Revaillot, S., Maron, P.A., 2011. Fungi mediate long term sequestration of carbon and nitrogen in soil through their priming effect. Soil Biology and Biochemistry 43, 86–96. http://dx.doi.org/10.1016/j.soilbio.2010.09.017.
Fontaine, S., Mariotti, A., Abbadie, L., 2003. The priming effect of organic matter: a question of microbial competition? Soil Biology and Biochemistry 35, 837–843. http://dx.doi.org/10.1016/S0038-0717(03)00123-8.
Guenet, B., Neill, C., Bardoux, G., Abbadie, L., 2010. Is there a linear relationship between priming effect intensity and the amount of organic matter input? Applied Soil Ecology 46, 436–442. http://dx.doi.org/10.1016/j.apsoil.2010.09.006.
He, N.P., Yu, G.R., 2016. Stoichiometrical regulation of soil organic matter decomposition and its temperature sensitivity. Ecology and Evolution 6, 620–627. http://dx.doi.org/10.1002/ece3.1927.
Horvath, R.S., 1972. Microbial co-metabolism and the degradation of organic compounds in nature. Bacteriological Reviews 36, 146–155.
Jenkinson, D.S., Fox, R.H., Rayner, J.H., 1985. Interactions between fertilizer nitrogen and soil nitrogen—the so-called 'priming' effect. European Journal of Soil Science 36, 425–444. http://dx.doi.org/10.1111/j.1365-2389.1985.tb00348.x.
Kramer, S., Marhan, S., Ruess, L., Armbruster, W., Butenschoen, O., Haslwimmer, H., Kuzyakov, Y., Pausch, J., Scheunemann, N., Schoene, J., Schmalwasser, A., Totsche, K.U., Walker, F., Scheu, S., Kandeler, E., 2012. Carbon flow into microbial and fungal biomass as a basis for the belowground food web of agroecosystems. Pedobiologia 55, 111–119. http://dx.doi.org/10.1016/j.pedobi.2011.12.001.
Kumar, A., Kuzyakov, Y., Pausch, J., 2016. Maize rhizosphere priming: field estimates using 13C natural abundance. Plant and Soil 409, 87–97. http://dx.doi.org/10.1007/s11104-016-2958-2.
Kuzyakov, Y., 2010. Priming effects: interactions between living and dead organic matter. Soil Biology and Biochemistry 42, 1363–1371. http://dx.doi.org/10.1016/j.soilbio.2010.04.003.
Kuzyakov, Y., Friedel, J.K., Stahr, K., 2000. Review of mechanisms and quantification of priming effects. Soil Biology and Biochemistry 32, 1485–1498. http://dx.doi.org/10.1016/S0038-0717(00)00084-5.
Majumder, B., Kuzyakov, Y., 2010. Effect of fertilization on decomposition of 14 C labelled plant residues and their incorporation into soil aggregates. Soil and Tillage Research 109, 94–102. http://dx.doi.org/10.1016/j.still.2010.05.003.
Manzoni, S., Taylor, P., Richter, A., Porporato, A., Ågren, G.I., 2012. Environmental and stoichiometric controls on microbial carbon-use efficiency in soils. New Phytologist 196, 79–91. http://dx.doi.org/10.1111/j.1469-8137.2012.04225.x.
Meyer, S.L., 1975. Data Analysis for Scientists and Engineers. Wiley, New York.
Mondini, C., Cayuela, M.L., Sanchez-Monedero, M.A., Roig, A., Brookes, P.C., 2006. Soil microbial biomass activation by trace amounts of readily available substrate. Biology and Fertility of Soils 42, 542–549. http://dx.doi.org/10.1007/s00374-005-0049-2.
Mwafulirwa, L.D., Baggs, E.M., Russell, J., Morley, N., Sim, A., Paterson, E., 2017. Combined effects of rhizodeposit C and crop residues on SOM priming, residue mineralization and N supply in soil. Soil Biology and Biochemistry 113, 35–44. http://dx.doi.org/10.1016/j.soilbio.2017.05.026.
Nottingham, A.T., Griffiths, H., Chamberlain, P.M., Stott, A.W., Tanner, E.V.J., 2009. Soil priming by sugar and leaf-litter substrates: a link to microbial groups. Applied Soil Ecology 42, 183–190. http://dx.doi.org/10.1016/j.apsoil.2009.03.003.
Paterson, E., Sim, A., 2013. Soil-specific response functions of organic matter mineralization to the availability of labile carbon. Global Change Biology 19, 1562–1571. http://dx.doi.org/10.1111/gcb.12140.
Poirier, V., Angers, D.A., Whalen, J.K., 2014. Formation of millimetric-scale aggregates and associated retention of 13C-15N-labelled residues are greater in subsoil than topsoil. Soil Biology and Biochemistry 75http://dx.doi.org/10.1016/j.soilbio.2014.03.020. 45–33.
Qiu, Q., Wu, L., Ouyang, Z., Li, B., Xu, Y., Wu, S., Gregorich, E.G., 2016. Priming effect of maize residue and urea N on soil organic matter changes with time. Applied Soil Ecology 100, 65–74. http://dx.doi.org/10.1016/j.apsoil.2015.11.016.
Rossell, R.A., Gasparoni, J.C., Galantini, J.A., 2001. Soil Organic Matter Evaluation. In: Lal, R., Kimble, J.M., Follett, R.F., Stewart, B.A. (Eds.), Assessments Methods for Soil Carbon. Lewis Publishers, USA, pp. 676.
Schmidt, M.W.I., Torn, M.S., Abiven, S., Dittmar, T., Guggenberger, G., Janssens, I.A., Kleber, M., Kögel-Knabner, I., Lehmann, J., Manning, D.A.C., Nannipieri, P., Rasse, D.P., Weiner, S., Trumbore, S.E., 2011. Persistence of soil organic matter as an ecosystem property. Nature 478, 49–56. http://dx.doi.org/10.1038/nature10386.
Shahbaz, M., Kuzyakov, Y., Heitkamp, F., 2017a. Decrease of soil organic matter stabilization with increasing inputs: mechanisms and controls. Geoderma 304, 76–82. http://dx.doi.org/10.1016/j.geoderma.2016.05.019.
Shahbaz, M., Kuzyakov, Y., Sanaullah, M., Heitkamp, F., Zelenev, V., Kumar, A., Blagodatskaya, E., 2017b. Microbial decomposition of soil organic matter is mediated by quality and quantity of crop residues: mechanisms and thresholds. Biology and Fertility of Soils 53, 287–301. http://dx.doi.org/10.1007/s00374-016-1174-9.
Shahzad, T., Chenu, C., Genet, P., Barot, S., Perveen, N., Mougin, C., Fontaine, S., 2015. Contribution of exudates, arbuscular mycorrhizal fungi and litter depositions to the rhizosphere priming effect induced by grassland species. Soil Biology and Biochemistry 80, 146–155. http://dx.doi.org/10.1016/j.soilbio.2014.09.023.
Stewart, C.E., Moturi, P., Follett, R.F., Halvorson, A.D., 2015. Lignin biochemistry and soil N determine crop residue decomposition and soil priming. Biogeochemistry 124, 335–351. http://dx.doi.org/10.1007/s10533-015-0101-8.
Vance, E., Brookes, P., Jenkinson, D., 1987. An extraction method for measuring soil microbial biomass C. Soil Biology and Biochemistry 19, 703–707. http://dx.doi.org/10.1016/0038-0717(87)90052-6.
Wang, H., Boutton, T.W., Xu, W., Hu, G., Jiang, P., Bai, E., 2015. Quality of fresh organic matter affects priming of soil organic matter and substrate utilization patterns of microbes. Scientific Reports 5, 10102. http://dx.doi.org/10.1038/srep10102.
Whitman, T., Lehmann, J., 2015. A dual-isotope approach to allow conclusive partitioning between three sources. Nature Communications 6, 8708. http://dx.doi.org/10.1038/ncomms9708.
Wu, J., Joergensen, R., Pommerening, B., Chaussod, R., Brookes, P.C., 1990. Measurement of soil microbial biomass C by fumigation-extraction—an automated procedure. Soil Biology and Biochemistry 22, 1167–1169. http://dx.doi.org/10.1016/0038-0717(90)90046-3.