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Interactive priming effect of labile carbon and crop residues on SOM depends on residue decomposition stage: Three-source partitioning to evaluate mechanisms

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ABSTRACT

Inputs of crop residues and labile C (*e.g.* root exudates) can affect the decomposition rate of soil organic matter (SOM) through the priming effect (PE). Most previous priming studies describe the addition of single labile or residue C, ignoring the interactions of labile C and fresh or decaying crop residues commonly present in field conditions. Using a dual $^{13}C/^{14}C$ labelling approach in a 62-day incubation, we investigated the effects of adding labile C (40 μg glucose-C g^{-1} soil) together with wheat shoot or root residues (3.1 mg C g^{-1} soil) on SOM priming at three residue decomposition stages: intensive (day-1), reduced (day-9) and stabilised (day-24). To estimate the PE, total soil CO_2 efflux and microbial biomass were partitioned for three sources: labile C (^{14}C-glucose), plant residues (^{13}C-labelled) and SOM (unlabelled). Without glucose, roots were decomposed less than shoots but induced 1.4-fold stronger cumulative SOM priming (365 μg C g^{-1} soil) than shoots. Addition of glucose increased SOM priming, with a stronger effect in the presence of shoot than root residues. Glucose addition at the intensive stage of shoots decomposition slightly increased SOM priming. However, compared with residues alone PE, the addition of glucose during reduced residue decomposition stage, increased SOM priming by 60% (roots) to 104% (shoots). Remarkably, this SOM priming after glucose addition was followed by a decline in residue decomposition and by an increase (up to 50%) in SOM-derived C in microbial biomass. Hence, following glucose addition, microorganisms utilised more SOM rather than feeding on decaying residues during reduced decomposition stage. During stabilised residue decomposition stage, the impact of glucose on SOM priming declined again, while the residue decomposition rate remained unaffected. Furthermore, a large proportion of added glucose (up to 10%) was retained in microbial biomass and its mineralisation rate declined strongly (compared with intensive and reduced decomposition stage). Therefore, the glucose amount was not sufficient to influence microbial activities determining SOM or stabilised residue decomposition rates. Overall, SOM decomposition increased by 1- to 4-fold more than the amount of added glucose C, which resulted in a negative net soil C balance compared with residues alone. Thus, we demonstrated for the first time that 1) the interactive effects of glucose (trace amount) and residues on SOM priming depend on plant residue type (higher under shoots than roots) and 2) stage of residues decomposition (higher SOM priming when labile C was added after the end of intensive decomposition stage of plant residues).

1. Introduction

Soil organic carbon (C) accrual is controlled by the balance between C input via plants and C output via microbial decomposition of soil organic matter (SOM) (Jastrow et al., 2007). The main sources of C inputs to soil are crop residues (freshly incorporated or partly

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decomposed) and labile C, *e.g.* through rhizodeposition of growing crops (Chen et al., 2014; Datta et al., 2015; Jobbágy and Jackson, 2000). The quality of substrate present alters microbial activities, which in turn can either increase or decrease the decomposition rate of existing SOM (Cheng and Kuzyakov, 2005; Paterson, 2003; Shahbaz et al., 2016). The change in SOM decomposition rate in response to organic C addition to soil is usually termed the priming effect (PE) (Jenkinson et al., 1985; Kuzyakov et al., 2000). Most previous studies on SOM priming have focused on individual effects of labile substrates (glucose or rhizodeposits) or crop residues, ignoring their interactive effects. However, it is critical to understand how SOM priming is affected by labile C input in the presence of crop residues (varying quality and decomposition stages), which is a common situation under natural conditions.

In general, crop residues are added once (*i.e.* before sowing or roots from previous crop), but labile C inputs through root exudation are added over time while residues are decomposing in the soil. After addition, crop residues are processed by microbes, resulting in decomposition stages over time which can be roughly identified as intensive (initial decomposition), reduced (after intensive decomposition) and stabilised (later very slow decomposition) (Shahbaz et al., 2017a). During intensive early decomposition, residues provide enough substrates for microbial activities and therefore they may not need additional energy inputs (Cheng and Kuzyakov, 2005; Wang et al., 2015). However, during later residue decomposition stages microorganisms may become energy-limited due to depletion of easily available compounds from the decaying residues (Fontaine et al., 2007; Wutzler and Reichstein, 2013). Under such conditions, availability of exogenous substrate (*e.g.* labile C) can increase SOM decomposition by mechanisms such as co-metabolism or N-mining if the added substrate does not meet the requirements for balanced microbial growth and activities (Chen et al., 2014; Hamer and Marschner, 2005; Shahbaz et al., 2018). Similarly, plant residue quality is an important determinant of SOM priming, because it represents the availability of labile compounds or the abundance of complex compounds (Bertrand et al., 2006; Schmatz et al., 2017; Wang et al., 2015). For instance, residues such as roots contain higher amounts of complex compounds (*e.g.* acid-insoluble fractions, tannins, lignin) than aboveground plant biomass and therefore provide less labile C to microorganisms (Gentile et al., 2011; Shahbaz et al., 2017a, 2017b). Under low substrate availability, microbes can start mining SOM to meet their nutritional demands, resulting in a positive PE (Fontaine et al., 2003). Under natural conditions, crop residues are usually at various decomposition stages (from intensive to stabilised). However, it is not known whether the quality of decaying residues or their decomposition stage is more important for SOM priming when microorganisms experience a pulse of labile C input (*e.g.* through exudation).

A few studies have examined SOM priming induced by continuous inputs (Paterson and Sim, 2013; Qiao et al., 2014) or repeated inputs (Chigineva et al., 2009; Hamer and Marschner, 2005) of labile C. The reported results are inconsistent, showing strong positive (Hamer and Marschner, 2005), small (Dalenberg and Jager, 1989; Kuzyakov et al., 2007), no (Wu et al., 1993) or negative PE (Blagodatskaya et al., 2007; Kuzyakov and Bol, 2006). The main reasons behind such variations in SOM priming are differences in microbial demand for labile C (*i.e.* microbial activities) and the availability of other competing substrates (*e.g.* residues) in the soil. Due to the difficulty in source partitioning, the mechanisms of SOM priming when labile C becomes available (as a trigger) in the presence of freshly incorporated or decaying residues (varying in type) remain unresolved. Moreover, under varying substrate complexity (*i.e.* labile C, residues and SOM), it is unclear how long the PE persists in soil and whether it is induced every time microbes are activated by added labile C.

Most previous studies on SOM losses have not reported and compared the net soil C balance between primed C and the gain from added organics (Chen et al., 2014; Kuzyakov, 2010). Priming mostly results in SOM losses (Fontaine et al., 2007, 2004a; Sayer et al., 2011), but a fraction of undecomposed added organics remains (*e.g.* residues) in the soil and can compensate for these SOM losses (Fontaine et al., 2004b; Qiao et al., 2014). However, it is unknown whether the final C budget in response to labile C and decaying residues is positive or negative, and whether it is similar at all stages of residue decomposition. Labile C input is only a small fraction of organic inputs, but has a great influence on SOM decomposition (by controlling microbial activities) and strongly influences the net C balance. Therefore, for accurate C budgeting, it is necessary to compare the net soil C balance with and without input of labile C to decomposing plant residues, which is only possible by applying isotopic tracer approach.

This study investigated how SOM priming is affected when labile C is added to a soil containing residues (wheat shoots or roots) at intensive (day-1), reduced (day-9) and stabilised (day-24) decomposition stages. A dual isotope ($^{13}C/^{14}C$) labelling approach was used to quantify three C sources, derived from glucose (^{14}C), plant residues (^{13}C) and SOM (unlabelled), in CO_2 and microbial biomass (MB). We used a low glucose amount (40 μg C g^{-1}, assuming less than 50% of soil MB) so that it stimulates microbial activity, but is not sufficient to induce microbial growth (Blagodatskaya and Kuzyakov, 2008). Specific objectives were: i) to measure the impact of adding shoots compared with roots residues on SOM priming; ii) to determine the combined effects on SOM priming of glucose added during the intensive, reduced and stabilised residue decomposition stages; and iii) to estimate the impact of added glucose C on net soil C balance when residues and glucose are added together.

2. Materials and methods

2.1. Soil sampling and preparation

Soil samples (Ap horizon, 0–25 cm) were taken from an agricultural experimental field located north-west of Göttingen (51°33′36.8″ N, 9°53′46.9″ E) in Germany. The field has been under C3 vegetation (predominantly wheat) for more than 25 years (Kramer et al., 2012). The soil (Haplic Luvisol) has a silt loam texture (87% silt, 7% clay, 6% sand), is carbonate-free and has the following chemical properties: total N 1.3 ± 0.0 g kg^{-1}, organic C 12.6 ± 0.4 g kg^{-1}; $\delta^{13}C$ −27‰ and a pH ($CaCl_2$) 6.0.

Prior to the experiment, the soil was air-dried, sieved (< 2 mm) and fine roots and other visible plant debris were carefully removed. To avoid a temporary respiration flush due to soil disturbance (Blagodatskaya and Anderson, 1999; Datta et al., 2014), the sieved soil was pre-incubated for at least 8 days. For incubation, 25-g portions of soil were weighed into 48 (250-mL) Schott jars, the moisture content was adjusted to 50% of water-holding capacity (WHC) and the jars were pre-incubated at 22 ± 1 °C.

2.2. Wheat residues

Wheat plants were grown to produce homogenously ^{13}C-labelled residues according to the method described by Bromand et al. (2001) with some modifications (Shahbaz et al., 2017a). At maturity, plants were harvested and roots were gently washed to remove sand particles. Shoot (only stem without leaves) and root residues were carefully separated and the uniform distribution of ^{13}C labelled-C within each plant fraction was confirmed: 1) by measuring ^{13}C values at various residue decomposition stages (Shahbaz et al., 2017a) and 2) by measuring ^{13}C in CO_2 efflux derived from residues incubated (in parallel to the planned 62 days soil incubation) in sterilised C− free pure sand, with or without glucose (data not shown). The mean C content of shoots and roots was 39 ± 6.1% (C/N: 17.1) and 28 ± 5.9% (C/N: 15.7), respectively. The atom%^{13}C- value for shoots and roots was 1.36 ± 0.00 and 1.51 ± 0.02, respectively. Isotopic measurements were made using an isotope ratio mass spectrometer coupled to an elemental

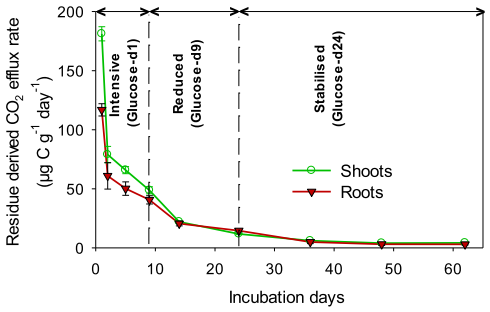

Fig. 1. Dynamics of residues derived CO_2 efflux from soil over 62 days of incubation after addition of wheat shoot and root residues (without glucose). Based on glucose additions (see Material and Methods, and Fig. 4), residues decomposition rate was divided into three phases: 1) intensive (< 9 days, glucose added on 1st day), 2) reduced (9–24 days, glucose added on 9th day) and stabilised (> 24 days, glucose added on 24th day). Error bars represent standard error of means ($n = 4$).

analyser (Delta Plus, EA-IRMS, see details in section 2.6). All residues were chopped and sieved (< 2 mm) to ensure homogeneous mixing with soil.

2.3. Experiment layout and glucose addition

After pre-incubation, the soil was thoroughly mixed with ^{13}C-labelled wheat shoot or root residues at a rate of 3.1 mg C g^{-1}. Thereafter, the soil was amended either with distilled water (control or addition of residues-alone) or with ^{14}C-labelled glucose at a rate of 40 μg C g^{-1}. Before addition, uniformly ^{14}C-labelled glucose (with final activity corresponding to ~1 × 10^5 disintegration per minute (DPM) g^{-1}) was added to unlabelled D(+)-glucose. Glucose was applied to soil in solution to reach a final soil moisture content of 60% WHC. Four sets of Schott jars, each set having 12 vessels for three treatments (soil-alone, soil + shoots and soil + roots) with four replicates per treatment, were prepared: set 1) Control (only distilled water addition) and shoot or root residues addition (no glucose), set 2) ^{14}C-labelled glucose addition at day-1 of incubation, *i.e.* to soil-alone or during intensive decomposition of shoot or root residues (glucose-d1) (Fig. 1), set 3) ^{14}C-labelled glucose addition at day-9 of incubation, *i.e.* to soil-alone or during the reduced decomposition stage of shoot or root residues (glucose-d9), and set 4) ^{14}C-labelled glucose addition at day-24 of incubation, *i.e.* to soil-alone or during the stabilised decomposition stage of shoot or root residues (glucose-d24). Fig. 1 shows that the residue decomposition rate was intensive from one to two days, reduced from two to 14 days and thereafter very reduced or stabilised. However, in the current study we defined these residue decomposition stages on the basis of our glucose additions (as described above). The moisture content of soils without glucose addition was amended similarly to glucose amended soils by using distilled water. The control soils (without glucose or residue addition) were used as reference to estimate the PE due to glucose and/or residue addition to the soil.

2.4. Incubation and sampling

After adding distilled water or glucose solution to the soil, without or with residues, small vials with 3 mL of 1 M NaOH were placed in the incubation vessels to trap released CO_2 (including four controls without soil). The vessels were immediately closed with air-tight seals and incubated at 22 ± 1 °C for 62 days. The vials were replaced with fresh NaOH to measure trapped CO_2 at intervals, allowing measurements at days 1, 2, 5, 9, 14, 24, 36, 48 and 62 of incubation. The treatments glucose-d9 and glucose-d24 were treated similarly to the control in regards to NaOH exchange before glucose addition. However, after glucose addition, the NaOH vials were replaced after 1, 2, 5, 9, 15, 27, 39 and 53 days under glucose-d9 and 1, 2, 5, 9, 15, 24 and 38 days under glucose-d24. The first four sampling dates after glucose addition were kept at similar intervals in all glucose treatment sets. These selected dates showed that the traps never became saturated to more than 60% of their capacity for Na_2CO_3 trapping. Aliquots of sampled NaOH were used to measure ^{14}C, ^{13}C and the total amount of trapped CO_2.

2.5. Microbial biomass

Soil MB was measured by the chloroform fumigation extraction method (modified after Vance et al., 1987). At the end of the experiment, the soil was carefully mixed and 8 g of moist soil were extracted with 32 mL of 0.05M K_2SO_4 for 1 h. Another 8 g of moist soil were first fumigated with ethanol-free $CHCl_3$ for 24 h and then extracted in the same way. The extracts obtained were kept frozen until analysed for total C concentration using a TOC/TIC analyser (Multi N/C 2100, Analytik Jena, Germany). The total amount of extractable C in MB (C_{mic}) was estimated as the difference between extracted C from fumigated and non-fumigated soils, using 0.45 as a K_{ec} factor (Wu et al., 1990).

2.6. Chemical analyses

2.6.1. Total CO_2 efflux

To quantify respiration, the CO_2 trapped in NaOH solution (0.5 mL) was precipitated with 1M $BaCl_2$. The total amount of trapped CO_2 in vials (μg C g^{-1}) was measured by titration of excess NaOH with 0.05 M HCl, using phenolphthalein as an indicator (Zibilske, 1994).

2.6.2. Residue-derived ^{13}C in CO_2 and microbial biomass

Since we used a dual isotopic labelling approach (^{14}C-labelled glucose and ^{13}C-labelled residue), the CO_2-trapping NaOH solution was treated specifically. For ^{13}C measurements, 1.5 mL of CO_2-trapping NaOH solution were precipitated with an equal volume of 1M $SrCl_2$ solution. The solution containing precipitates of $SrCO_3$ was centrifuged at 4000 rpm for 5 min, the pellets obtained were washed with distilled water to remove excess NaOH and the process was repeated unless pellet pH reached 7. The $SrCO_3$ pellets were then dried at 60 °C and stored for ^{13}C analysis. The dried $SrCO_3$ pellets were analysed for ^{13}C by isotope ratio mass spectrometer (Delta Plus, IRMS; Thermo Fisher Scientific, Bremen, Germany) coupled to an elemental analyser (NC 2500; CE Instruments, Milano, Italy), at KOSI, Georg-August University of Göttingen, Germany. For estimation of ^{13}C incorporated in MB, prior to the IRMS analysis both fumigated and non-fumigated K_2SO_4 extracts were freeze-dried and then weighed in tin capsules.

2.6.3. Glucose-derived ^{14}C in CO_2 and microbial biomass

During the incubation period, measurements of ^{14}C activity in CO_2 were performed directly after exchange of the CO_2-trapping NaOH solution with fresh vials. A 1 mL aliquot of the $^{14}CO_2$-enriched NaOH solution was mixed with 3 mL of the scintillation cocktail Rotiszint EcoPlus (Carl Roth Company, Germany) and decay of chemiluminescence in the mixture was measured using a Hidex 300 SL Automatic TDCR Liquid Scintillation Counter (Beckman Coulter Inc., USA). Glucose-derived C (^{14}C) in MB was also measured by scintillation counting, after mixing 5 mL aliquots of fumigated or non-fumigated K_2SO_4 extracts with 15 mL of scintillation cocktail. The efficiency of ^{14}C determination was always above 88% and measurement error never exceeded 2%.

2.7. Calculations

Partitioning into three C sources (^{13}C-residue, ^{14}C-glucose, SOM) of total soil CO_2 or MB was performed step-by-step as described by Shahbaz et al. (2018). The amount of glucose-derived C ($C_{G\text{-derived}}$, μg g^{-1}) in CO_2 or MB was calculated based on ^{14}C radioactivity (in DPM)

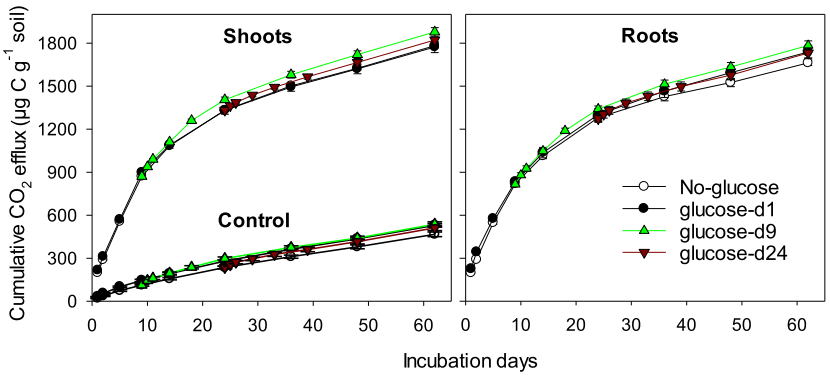

Fig. 2. Cumulative CO_2 production from soil without and with the addition of glucose and plant residues. Glucose was added separately to soil during the intensive (1st day, glucose-d1), reduced (9th day, glucose-d9) or stabilised (24th day, glucose-d24) residues decomposition stage. Error bars represent standard error of means ($n = 4$).

in the measuring pool, the amount of glucose applied (C_G, µg g^{-1}) and the initial radioactivity of the added glucose ($^{14}C_G$, DPM):

$$C_{G-derived} = (C_G \,.^{14}\, C)/\, ^{14}C_G \quad (1)$$

The amount of SOM-derived C ($C_{SOM\text{-}derived}$) in CO_2 or MB was calculated according to the source of C input, *e.g.* under residues ($_R$) or glucose ($_G$) addition alone:

$$C_{SOM-derived\ (R\ or\ G)} = C_{total} - C_{R\ or\ G-derived} \quad (2)$$

And under residues combined with glucose addition:

$$C_{SOM-derived\ (R+G)} = C_{total} - C_{R-derived} - C_{G-derived} \quad (3)$$

where C_{total} is the total amount of C measured in CO_2 efflux (at each sampling time) or in MB, and $C_{R\text{-}derived}$ is the C originating from residues (discussed below).

Since the plant material was ^{13}C-labelled, the fraction of residue-derived C (C_f) in CO_2 or MB was calculated based on atom%^{13}C values according to the mass balance equation (Balesdent et al., 1987):

$$Atom\%^{13}C = [^{13}C\ atoms/(^{12}C + {}^{13}C)\ atoms] \times 100 \quad (4)$$

$$C_f = [(At_{mix} - At_{con})/(At_R - At_{con})] \quad (5)$$

where At_{mix} is the atom%^{13}C value (in evolved CO_2, fumigated or non-fumigated K_2SO_4 extracts) in the residue-amended soils, At_R is the specific atom%^{13}C value of added plant residues (shoots, roots) and At_{con} is the atom%^{13}C value in the unamended control.

The residue-derived C ($C_{R\text{-}derived}$) was then calculated as:

$$C_{R-derived} = C_f \times (TC) \quad (6)$$

where [*TC*] is the total C (µg g^{-1} soil) in each pool (*i.e.* MB or CO_2, as described in section 2.5 and 2.6, respectively).

The SOM PE (µg C g^{-1} soil) was calculated according to the source of C input, *i.e.* under addition of residues alone (PE_R), glucose alone (PE_G) or residues combined with glucose (PE_{R+G}):

$$PE_{R\ or\ G} = C_{SOM-derived\ (R\ or\ G)} - C_{SOM-derived\ (con)} \quad (7)$$

$$PE_{R+G} = C_{SOM-derived\ (R+G)} - C_{SOM-derived\ (con)} \quad (8)$$

where $C_{SOM\text{-}derived\ (con)}$ is the amount of SOM originating from CO_2 in the unamended control. For calculation of residue-derived C in MB, ^{13}C was first calculated separately for fumigated and non-fumigated extracts using Eq. (6), and then following the procedure as discussed in section 2.5.

To estimate the glucose effect on net soil C balance, the individual C balance under addition of residues alone or residues combined with glucose was first calculated as:

$$C_{balance\ (R\ or\ R+G)} = C_{input\ (R\ or\ R+G)} - C_{output\ (SOM,\ R,\ G)} \quad (9)$$

where C_{input} is the C added to the soil through either residues alone or the combination of residues and glucose and C_{output} is the loss of soil C through decomposition of SOM (*i.e.* priming), residues or glucose (by considering the duration of 38 days after each glucose addition). Thereafter, the change in the net soil C balance under residues combined with glucose additions compared with under residues-alone addition was calculated as:

$$Net\ soil\ C\ balance = C_{balance\ (R+G)} - C_{balance\ (R)} \quad (10)$$

2.8. Statistical analysis

To test the effect of residues (shoots vs. roots), glucose C input, and their interactions on the dependent variables, we performed two-way analysis of variance (ANOVA) followed by Duncan's post-hoc test. One-way ANOVA was used to assess the significance of differences between the cumulative effect of treatments when glucose and residues interactive effect was not considered (when comparisons were made with no-glucose). Differences were considered significant at $p < 0.05$. Standard error (SE) was calculated to estimate the precision of the mean (n = 4). Error propagation was calculated when the mean values were used for determining PE (Meyer, 1975).

3. Results

3.1. Total CO_2 efflux

The cumulative CO_2 efflux from the unamended control treatment was 324 ± 19 µg C g^{-1} over the 62-day incubation (Fig. 2). Addition of shoot and root residues increased the cumulative CO_2 efflux to 1782 ± 16 µg C g^{-1} and 1663 ± 18 µg C g^{-1}, respectively (Fig. 2).

Glucose addition alone increased the total CO_2 efflux by 14% compared with the unamended control. With addition of glucose at different residue decomposition stages, the total soil CO_2 efflux under shoots or roots addition still remained fairly similar (Fig. 2). Compared with the CO_2 efflux from soil treated with plant residues, addition of glucose during the reduced residue decomposition stage (glucose-d9) more evidently increased the cumulative soil CO_2 efflux (Fig. 2).

3.2. Residue and glucose decomposition

To quantify the contribution of the different C sources, total soil CO_2 efflux was partitioned into glucose-derived (based on ^{14}C), residue-derived (based on ^{13}C) and SOM-derived (unlabelled C). Similar amounts of residue C were added (3.1 mg C g^{-1} soil), but the cumulative amount of C mineralised from shoots was higher (1048 ± 7 µg C g^{-1} soil) than that mineralised from roots C (876 ± 16 µg C g^{-1}) (insets Fig. 3).

Addition of glucose together with residues decreased the cumulative residue-derived CO_2 efflux by up to 6% compared with that in the residues-only treatment (Fig. 3). This decline in cumulative decomposition was due to a strong short-term (1–5 days) retarding effect of glucose on residue decomposition (inset Fig. 3). Interestingly, this

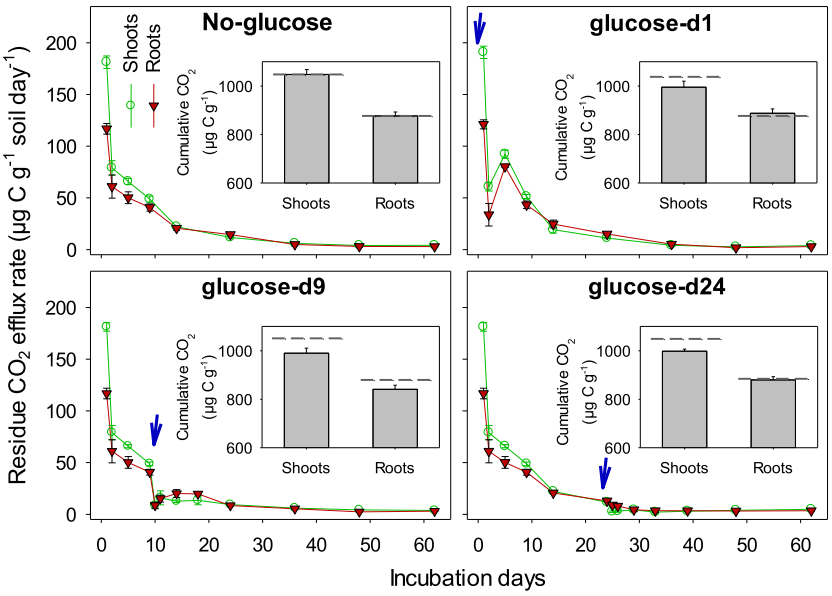

Fig. 3. Residues-derived CO_2 efflux rate with or without glucose addition. The insert diagrams show cumulative residues-derived CO_2 release (µg C g^{-1} soil) over the 62 days of incubation. Glucose was added during the intensive (1st day, glucose-d1), reduced (9th day, glucose-d9) or stabilised (24th day, glucose-d24) residues decomposition stage (as indicated by small arrows). Error bars represent standard error of means ($n = 4$). The dashed lines above bars represent cumulative residues derived C without glucose addition.
The p values from the ANOVA showing the factors effect on cumulative residue decomposed C after addition of glucose combined with residues compared to residues-alone are as: glucose-d1 (Residues < 0.001, Glucose = 0.126, Residues: Glucose = 0.126), glucose-d9 (Residues < 0.001, Glucose = 0.012, Residues: Glucose = 0.482) and glucose-d24 (Residues < 0.001, Glucose = 0.118, Residues: Glucose = 0.074). All pairwise multiple comparisons (Duncan's Method) are presented in Supplementary Material Data. S1.

retarding effect only occurred when glucose was added during the reduced (glucose-d9) or stabilised (glucose-d24) residue decomposition stage. In the short-term (1–5 days after addition), glucose addition decreased the residue decomposition rate by around 13–24% compared with the residues-only treatment (Fig. 3). Although most of the labile parts of residues were already decomposed at the stabilised decomposition stage (*i.e.* up to 30% of total C added had been mineralised to CO_2), adding glucose also resulted in a short-term (1–5 days) decline in shoots decomposition. In contrast, cumulative root residue decomposition remained unaffected by glucose addition during the stabilised decomposition stage (Fig. 3).

Glucose mineralisation, calculated based on ^{14}C activity in total CO_2 efflux (Eq. (1)), mainly occurred during the first 1–5 days and was dependent on the stage of residue decomposition (Fig. 4). Glucose was intensively mineralised (~32 µg C g^{-1}, corresponding to 80% of the total added) when added during intensive residue decomposition (glucose-d1) (Fig. 4). Up to 65% and 44% of added glucose was mineralised when it was added during the reduced (day-9) and stabilised (day-24) residue decomposition stage, respectively. At the intensive residue decomposition stage, mineralisation rate of glucose was highest

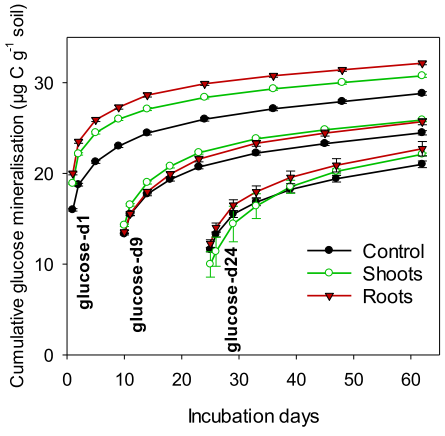

Fig. 4. Cumulative glucose mineralised CO_2 over time after glucose addition during a 62-day incubation. Glucose was added during the intensive (1st day, glucose-d1), reduced (9th day, glucose-d9) or stabilised (24th day, glucose-d24) residues decomposition stage. Error bars represent standard error of means ($n = 4$).

under roots, followed by shoots and glucose alone. However, no such difference appeared when glucose was added during the reduced or stabilised residue decomposition stage (Fig. 4).

3.3. Priming effect

With residue addition, SOM-derived CO_2 contributed to almost half of total CO_2 emissions, indicating a strong positive PE. The cumulative amount of primed SOM-C under root residues addition (365 ± 22 µg C g^{-1}) was much higher than under shoots addition (261 ± 10 µg C g^{-1}) (Fig. 5, left panel).

Addition of glucose at day-1 or day-9 in the soil-alone (without residue) caused up to 76 µg C g^{-1} SOM priming, which was about 17% higher than the PE induced by glucose added at day-24. Glucose addition with residues enhanced cumulative SOM priming (most strongly under reduced residue decomposition, *i.e.* glucose-d9) compared with plant residues alone (Fig. 5). Interestingly, during a strong pulse (1–5 days) of increased SOM decomposition after glucose addition (Fig. 5, right panel), the decomposition rate of residues (mainly shoots) declined (Fig. 3).

To estimate the interactive effect of glucose and residues on SOM priming more precisely, the SOM PE induced by residues amended with glucose (*i.e.* only after glucose additions) was compared with that induced by residues alone (Fig. 6). The contribution of residue-induced PE before glucose addition in glucose-d9 (*i.e.* first 9 days) and in glucose-d24 (*i.e.* first 24 days) was not accounted for.

Compared with residues alone, glucose addition at the intensive residue decomposition stage (glucose-d1) did not affect SOM priming caused by root residues, but it increased the PE induced by shoot residues by 15% (Fig. 6).

Glucose addition during the reduced residue decomposition stage (glucose-d9) strongly increased SOM priming (by up to 160 µg C g^{-1}) compared with residues alone between 9 and 62 days. This increase was higher under shoots (104%) than roots (60%) addition (Fig. 6).

Glucose addition during the stabilised residue decomposition stage (glucose-d24) increased SOM priming by 30–80 µg C g^{-1} soil compared with residues alone in the subsequent period (*i.e.* 24–62 days) (Fig. 6). However, this increase in SOM priming comprised ~50% (root addition) to 240% (shoots addition) of the PE induced by residues alone.

Overall, irrespective of the stage of residue decomposition, SOM priming after glucose addition increased more strongly in the presence of shoot than root residues (Figs. 5 and 6).

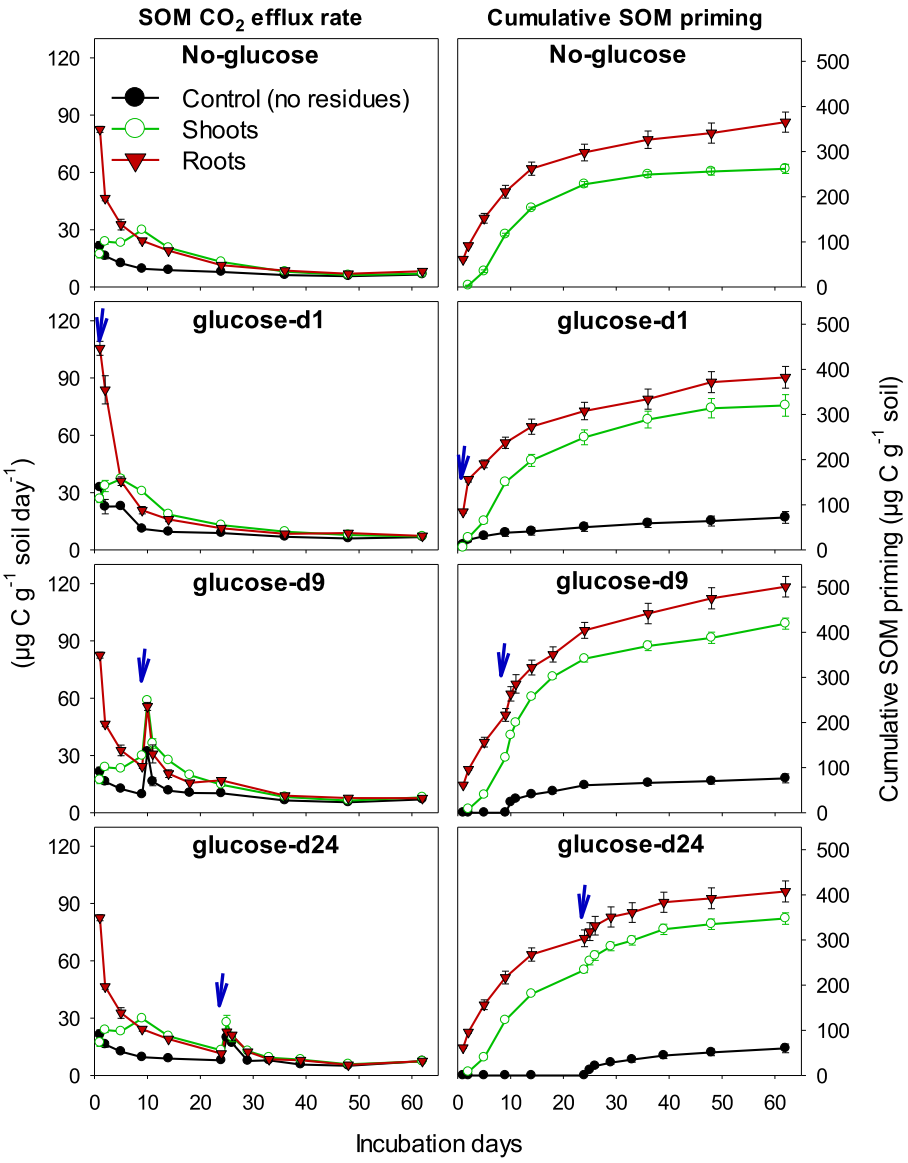

Fig. 5. Soil organic matter (SOM) derived CO_2 efflux rate (left panel) and cumulative SOM priming (right panel) after residues addition with or without glucose over the 62 days of incubation. Glucose was added during the intensive (1st day, glucose-d1), reduced (9th day, glucose-d9) or stabilised (24th day, glucose-d24) residues decomposition stage. Blue arrows indicate glucose addition time during residues incubation. Error bars represent standard error of means ($n = 4$). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

3.4. Microbial biomass

Addition of residues increased total MB (151 ± 6 µg C g^{-1}) compared with the unamended control (93 ± 4 µg C g^{-1}), mainly due to residue-derived C (Fig. 7).

At the end of the 62-day incubation, only about 2–10% of initially added glucose was recovered in MB (depending on the time since glucose addition). More glucose-C was retained in MB when glucose was added during the stabilised (glucose-d24) residue decomposition stage than at the two earlier stages (glucose-d1 and glucose-d9). Glucose addition increased total MB up to 15% stronger (except for roots at glucose-d24), in the presence of shoot than root residues (Fig. 7). However, glucose induced a shift in contribution of residues vs. SOM derived C sources within total MB. Glucose addition increased the SOM-derived C in MB (up to 50%) and this effect was most pronounced when glucose was added during the reduced residue decomposition (glucose-d9) (Fig. 7). In contrast, glucose addition caused a decline in residue-derived C in total MB.

3.5. Net soil C balance

The effect of glucose on net soil C was calculated as described in Eq. (10). In response to glucose addition, the total soil C balance was compared with that under residue-only addition. Since glucose was added at three residue decomposition stages, the comparison of net C balance covered a period of 38 days after all glucose additions (equal to glucose-d24) and a similar corresponding duration under residue-only additions (Table 1). Compared with addition of residues alone, there was a loss in net C remaining in soil with all residues combined with glucose treatments (Table 1). Despite residue decomposition decreasing by 6% after glucose addition (*i.e.* a gain of up to 52 µg residue C g^{-1} soil; Fig. 3), the great loss of SOM (due to priming) resulted in greater overall C losses than under addition of residues alone. The larger loss of net soil C (~90–120 µg C g^{-1}, *i.e.* 3- to 4-fold more than added with glucose) occurred when glucose was added during the reduced residue decomposition stage (glucose-d9) (Table 1).

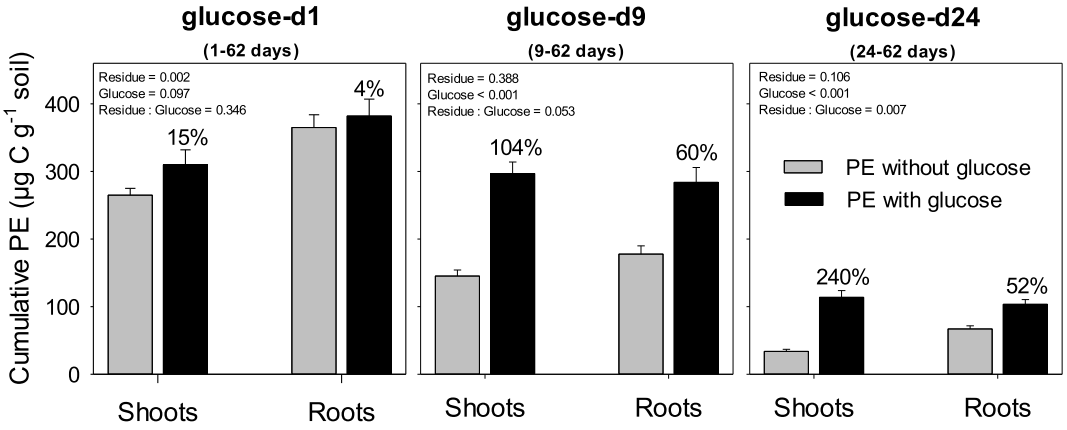

Fig. 6. Cumulative soil organic matter priming effect (PE) after addition of residues-alone or glucose combined with residues. The PE (either with or without glucose) represents the amount of primed SOM after only glucose addition (*i.e.* the PE before glucose addition in glucose-d9 and glucose-d24 was not accounted for). Glucose was added during the intensive (1st day, glucose-d1), reduced (9th day, glucose-d9) or stabilised (24th day, glucose-d24) residues decomposition stage. The numbers above black bars indicate percentage increase (means) in SOM priming after addition of glucose combined with residues compared to residues-alone. Error bars represent standard error of means ($n = 4$).
The presented p values are from the ANOVA of the data (Residues, Glucose, and their interactions). All pairwise multiple comparisons (Duncan's Method) are presented in Supplementary Materials Data. S2.

4. Discussion

4.1. Residue decomposition and priming effect

Addition of both shoot and root residues stimulated SOM decomposition, *i.e.* gave a positive PE. This suggests that the C and energy input with the residues induced microbial mining for nutrients from SOM to balance their growth (Chen et al., 2014; Qiao et al., 2016). Despite addition of the same amount of residue C, root residues decomposed less but induced 1.4-fold higher SOM priming than shoot residues. The relatively small SOM priming under shoot residues could be ascribed to higher availability to microorganisms of shoots C (and nutrients) than root residues C (Shahbaz et al., 2017b). Accordingly, negative SOM priming was observed for a short period (for 1–2 days) after shoots addition, indicating preferential microbial utilisation of shoot residues, which was absent after roots addition. With increasing substrate complexity (or decreasing labile C availability), microbes start SOM mining, resulting in a positive PE (Fontaine et al., 2011; Guenet et al., 2010; Nottingham et al., 2009; Wang et al., 2015). The higher amount of shoots derived-C incorporated in MB and released with CO_2 efflux compared with its root counterpart confirms that shoots-derived compounds were more accessible for microbial uptake (Figs. 3 and 7). Roots had a similar C/N ratio to shoots (see section *2.2*), but the lower decomposition rate of roots can be attributed to other aspects of their biochemical composition (Bertrand et al., 2006). For example, compared with aboveground residues, roots contain higher amounts of recalcitrant compounds such as acid-insoluble fraction, lignin, tannins, suberin *etc*. (Aber and Melillo, 1982; Bertrand et al., 2006). With lower-quality substrates (such as roots), microorganisms switch to SOM to meet their nutrient demands (Dimassi et al., 2014; Fontaine et al., 2003; Nguyen and Marschner, 2016). Under high substrate complexity, microorganisms can change their substrate utilisation pattern by a shift in a fast-to a slow-growing population, which can also feed on SOM (Blagodatsky et al., 2010; Nannipieri et al., 1978). Further, as compared to shoot residues, microorganisms under root additions are more efficient in synthesizing enzymes that can hydrolyze or oxidize SOM

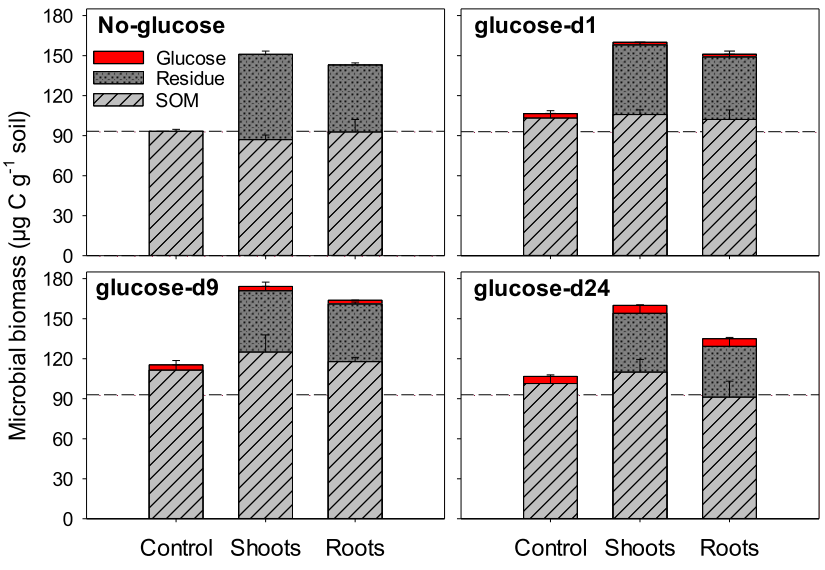

Fig. 7. Contribution of three C sources (soil organic matter (SOM), residues and glucose) to soil microbial biomass C (MBC) after shoot or root residues addition with or without glucose. The soil MBC was measured at the end of incubation (62 days), while glucose was added separately during the intensive (1st day, glucose-d1), reduced (9th day, glucose-d9) or stabilised (24th day, glucose-d24) residues decomposition stage. The dashed line shows microbial biomass C in the control (without residues or glucose). Error bars represent standard error of means ($n = 4$).
The p values from ANOVA show the factors effect on SOM or residues derived MBC after addition of glucose combined with residues compared to residues-alone are as (i) for SOM derived MBC; glucose-d1 (Residues < 0.646, Glucose = 0.004, Residues: Glucose = 0.150), glucose-d9 (Residues < 0.026, Glucose = 0.004, Residues: Glucose = 0.738), glucose-d24 (Residues < 0.553, Glucose = 0.057, Residues: Glucose = 0.047) and (ii) for Residues derived MBC; glucose-d1 (Residues < 0.329, Glucose = 0.028, Residues: Glucose = 0.384), glucose-d9 (Residues < 0.302, Glucose = 0.005, Residues: Glucose = 0.025), glucose-d24 (Residues < 0.659, Glucose = 0.018, Residues: Glucose = 0.442). All pairwise multiple comparisons (Duncan's Method) are presented in Supplementary Materials Data. S3.

Table 1
Impact of glucose (40 μg C g^{-1}) combined with residues addition on net soil C balance compared with the residues-alone. The net soil C balance is based on the difference between C in microbial biomass C (MBC) and CO_2 efflux (of residues, SOM and glucose) after addition of glucose combined with residues compared to residues-alone. At all addition times, the cumulative C in CO_2 efflux was compared after 38 days of glucose addition with the corresponding (38 days) CO_2 efflux of residues-alone. Glucose was added during the intensive (day 1, glucose-d1), reduced (day 9, glucose-d9) or stabilised (day 24, glucose-d24) residues decomposition stage. Values are mean ± SE ($n = 4$).

	C balance under stem + glucose (μg C g^{-1} soil)						
	Residue		SOM		Glucose		Net C balance
	MBC	CO_2–C	MBC	CO_2–C	MBC	CO_2–C	
glucose-d1	−6.1 ± 1.0[a]	+41.0 ± 3.2	+18.1 ± 1.8	−58.2 ± 3.7	+2.1 ± 0.1	−29.3 ± 0.2	**−32.5** ± 2.7
glucose-d9	−18.3 ± 2.1	+51.7 ± 2.9	+38.4 ± 2.8	−140.4 ± 7.9	+3.1 ± 0.1	−24.8 ± 0.2	**−90.3** ± 6.1
glucose-d24	−12.0 ± 1.7	+25.7 ± 2.5	+25.0 ± 1.5	−80.4 ± 4.7	+4.9 ± 0.3	−22.4 ± 0.2	**−59.2** ± 4.0
	C balance under root + glucose (μg C g^{-1} soil)						
	Residue		SOM		Glucose		Net C balance
	MBC	CO_2–C	MBC	CO_2–C	MBC	CO_2–C	
glucose-d1	−4.1 ± 1.0	−27.0 ± 1.9	+9.2 ± 1.1	−17.2 ± 1.3	+2.0 ± 0.0	−31.8 ± 0.4	**−68.9** ± 3.1
glucose-d9	−7.1 ± 0.9	+36.7 ± 3.1	+23.7 ± 2.7	−150.7 ± 10.7	+2.9 ± 0.1	−24.4 ± 0.3	**−119.0** ± 7.2
glucose-d24	−1.4 ± 0.9	−1.5 ± 1.2	−1.8 ± 0.8	−36.5 ± 6.1	+5.6 ± 0.2	−22.7 ± 0.9	**−58.3** ± 5.4

[a] Positive (+) or negative (−) sign before mean values represents gain or loss of C, respectively, from soil organic matter (SOM) or plant residues (under residue and SOM columns) after glucose addition compared with residues-alone addition.

compounds and thus resulting in the PE (Shahbaz et al., 2017a). Therefore, although both residue types induced PE, the greater intensity of SOM priming under roots than shoots can be linked to resource limitation with roots and thus more nutrient mining from SOM.

4.2. Three-source partitioning and glucose-induced priming patterns during residue decomposition

We used a low level of added glucose (40 μg C g^{-1}, < 50% C of MB and corresponding to 1.3% of added residue-C) in order to activate existing microorganisms without providing substrate for their growth (Blagodatskaya and Kuzyakov, 2008; De Nobili et al., 2001). The glucose-mediated increase in MB and PE was in agreement with that reported in other studies (De Nobili et al., 2001; Mondini et al., 2006). However, adding the same glucose amount at three stages of residue decomposition gave differing SOM priming that strongly depended on the type and stage of residue decomposition (Fig. 8). Therefore, mechanisms previously cited to explain SOM priming, *e.g.* microbial activation (Blagodatskaya et al., 2007), preferential utilisation (Kuzyakov et al., 2000), microbial growth strategy (Fontaine et al., 2003) and C starvation/N mining (Craine et al., 2007; Hobbie and Hobbie, 2013), contributed differently after labile C input at different stages of residue decomposition (see below).

4.2.1. Glucose-induced PE at the intensive residue decomposition stage

Most soil microorganisms are considered energy and/or easily available substrate limited (Hobbie and Hobbie, 2013), so the availability of labile substrate can stimulate SOM decomposition (Hamer and Marschner, 2005; Shahbaz et al., 2018; Stenström et al., 2001). Addition of glucose at the intensive residue decomposition stage (glucose-d1) increased SOM priming by up to 15% compared with under shoot residues alone (Fig. 6). Since the residues were freshly incorporated, the available C from residues was sufficient to activate microbial growth (Cheng and Kuzyakov, 2005). Accordingly, residue decomposition rate remained unaffected after glucose addition and most of the assimilated glucose C (up to 70%) was respired immediately by the microorganisms growing on the decomposing residues. Moreover, the mineralisation rate of glucose was higher in the presence of residues (higher under roots than shoots) than with addition of glucose alone (*i.e.* control, where glucose was utilised by SOM decomposers) (Fig. 4). This indicates that residue decomposers have a low demand for exogenous labile C, which lowers the C use efficiency of added glucose (Geyer et al., 2016). This indicates in turn that the amount of added glucose C may not have been enough to strongly influence microbial growth, which could have affected SOM priming at the intensive residue decomposition stage. Therefore, glucose addition alone (without other nutrients) during a period of high C availability from residues did not further increase SOM priming compared with residues alone.

4.2.2. Glucose-induced PE during the reduced residue decomposition stage

Addition of glucose during the reduced residue decomposition stage (glucose-d9) strongly enhanced the pulse in SOM decomposition rate. During the first 9 days, residues were already intensively decomposed, making soil microorganisms resource-limited due to increasing recalcitrance of remaining residues (*i.e.* depletion of labile resources). Therefore, glucose addition during the reduced residue decomposition could have activated a more diverse microbial population consisting of both SOM and residue decomposers (Mau et al., 2015). In the presence of several levels of substrate complexity (*i.e.* more labile-glucose to partly decomposed residues, SOM) microbial communities can be dominated by slow growers (K-strategists), which better decompose SOM (Chen et al., 2014; Fontaine et al., 2003; Geyer et al., 2016; Shahbaz et al., 2018). Therefore, due to the heterogeneous nature of SOM (with C/N ratio 9.6, much lower than for residues), glucose addition shifted the active microorganisms from residues towards SOM utilisation (Blagodatskaya and Kuzyakov, 2008; Fontaine et al., 2003). This was confirmed by a substantial increase in SOM-derived CO_2 and a decrease in residue decomposition immediately after glucose addition. This indicated strong nutrient limitation for microorganisms during long-term decomposition of plant residues. The decomposition rate of shoots was still higher than that of roots, indicating higher microbial activity (thus nutrients demand) under shoots than roots (Fig. 4). Indeed, a higher amount of total MB C was recovered under shoots than roots addition. Accordingly, in response to glucose addition the SOM was more intensively primed under shoots (104% increase) than under roots addition (60% increase) than residue alone (Figs. 6 and 8). This intensive SOM priming showed that, during the reduced residue decomposition stage, the amount of glucose-C was sufficient to accelerate microbial activities which induce SOM priming (*e.g.* for N mining) (Dijkstra et al., 2013; Fontaine et al., 2004b; Paterson and Sim, 2013). Contrary to expectations, total MB under glucose addition increased compared with under residue-only addition (Fig. 7). However, this increase was due solely to the increase in SOM-derived C in MB, which confirms the shift in microbial metabolism towards SOM utilisation after glucose addition. Such glucose-induced SOM priming followed by an increase in SOM-derived C in MB is characterised as real PE, *i.e.* due to increased turnover of SOM by microorganisms (Blagodatskaya and Kuzyakov, 2008; Kuzyakov et al., 2000).

4.2.3. Glucose-induced PE during the stabilised residue decomposition stage

In terms of absolute amount, glucose addition during the stabilised residue decomposition stage (glucose-d24) surprisingly resulted in a slow increase in SOM priming (30–80 μg C g^{-1}), compared with glucose-d9. However, the relative increase in SOM priming compared with under residues only (in the same period) was up to 52% (roots) to 240% (shoots) higher for glucose-d24 (Fig. 5). The residue and SOM decomposition rate was lowest/or stabilised at the time of glucose addition (*i.e.* glucose-d24), and thus microbial activity (both SOM and residue decomposers) was also presumably lowest. Compared with other additions, the contribution of glucose-C in the respired CO_2 strongly declined and up to 10% of added glucose was retained in MB (Figs. 4 and 7). Thus, even during re-utilisation of glucose-C the C use efficiency was higher, which indicates relative domination of slow-growing microorganisms (Blagodatskaya et al., 2014; Geyer et al., 2016). This means that the added glucose amount (40 μg C g^{-1}) was not sufficient to strongly increase microbial activities (and thus PE) during the stabilised residue decomposition stage (Blagodatskaya and Kuzyakov, 2008; De Graaff et al., 2010). Therefore, in response to a low glucose amount (< 50% of MB), only a small microbial fraction was presumably able to react (Hobbie and Hobbie, 2013; Mondini et al., 2006; Morita, 1988). However, a relatively large increase in SOM priming with shoots indicated that this reactive microbial fraction was still higher (more abundant) under shoot than under root residues addition.

4.3. Effects of glucose addition on net soil carbon balance

Incorporation of residues alone had an obvious net positive effect on SOM content after accounting for both residue decomposition and residue-induced SOM priming. However, the effects of glucose addition on SOM decomposition were dependent on residue type (higher under shoots than under roots) and decomposition stage (Fig. 8), and thus need to be evaluated in the context of net C balance. To calculate changes in net soil C balance after glucose addition, we compared net C balance under glucose plus residue addition with that under residue-only addition in a fixed period (see section 3.5).

Under addition of single substrates, SOM priming has been accompanied by a loss in SOM (Blagodatskaya et al., 2007; Brant et al., 2006; Fontaine et al., 2004b; Qiao et al., 2016). Although priming may lead to SOM loss, the net soil C balance is usually positive when the remaining substrate-C is accounted for (Hamer and Marschner, 2005; Fontaine et al., 2007; Qiao et al., 2014). In our case, irrespective of residue type, the net C balance due to glucose addition remained negative (1- to 3-

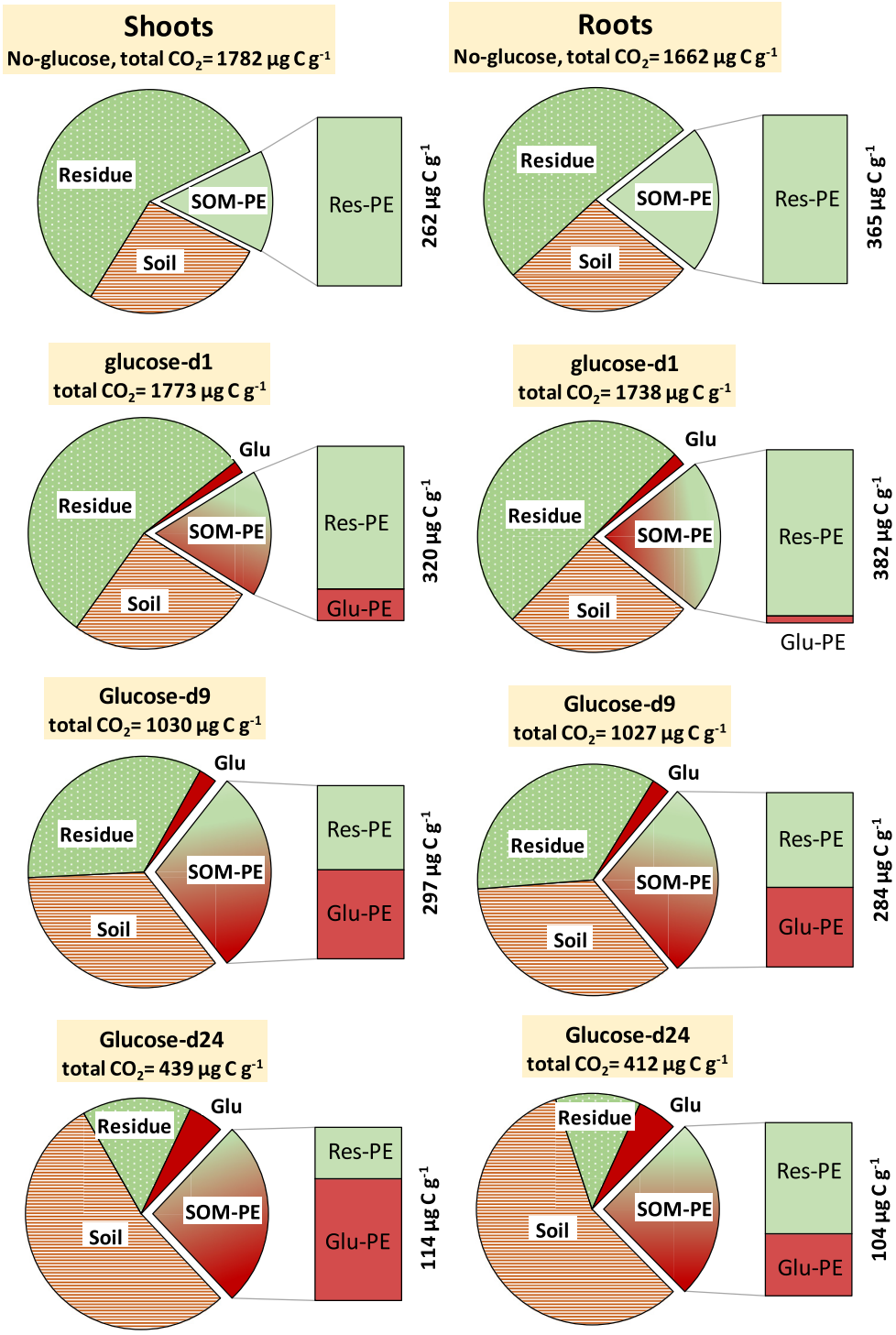

Fig. 8. Contribution of three C sources (soil organic matter (Soil), residues (Res) and glucose (Glu)) to cumulative CO_2 efflux after addition of shoot residues (left panel) or root residues (right panel) with or without glucose. Glucose was added during the intensive (1st day, glucose-d1), reduced (9th day, glucose-d9) or stabilised (24th day, glucose-d24) residues decomposition stage. The priming effect (PE) is only for the period after glucose addition either with or without glucose. The contribution of the residues-alone and residues combined with glucose to total PE is shown as stacked columns. The glucose-induced PE is the difference between total PE of residues combined with glucose and of residues-alone. Values next to stacked columns show total amount of primed SOM. The PE partitioning clearly shows that the increase in total PE after glucose addition was much higher when glucose was added at day 9 of soil residues incubation.

fold the added glucose C amount) at all residue decomposition stages compared with that due to input of residues alone (Table 1). Although residue decomposition declined after glucose addition (*i.e.* gain in residue C), the strong acceleration in SOM decomposition (compared with added glucose C) caused a net loss of soil C compared with under residue-only addition. However, the highest net C loss (absolute amount) occurred when glucose was added during the reduced residue decomposition stage (glucose-d9) (Table 1). This suggests that labile C inputs such as root exudates (*e.g.* under field conditions) can increase SOM turnover strongly after intensive decomposition of residues (*e.g.* in early spring or in organic farming). Therefore, they could contribute greatly to the rhizosphere priming frequently discussed in the literature (Adl, 2016; Cheng and Kzyakov, 2005; Kumar et al., 2016; Oburger and Jones, 2018; Paterson, 2003). Priming studies should thus consider the net C balance between primed SOM and the gain or loss of C from added substrates for accurate assessment of the C budget. This would increase knowledge about the short- and long-term response of SOM priming and its sources, after microbial activation by *e.g.* labile C input in the presence of plant residues (fresh or decaying), a common situation in the rhizosphere.

5. Conclusions

Despite lower decomposition rate, the addition of root residues to soil caused 1.4-fold higher SOM priming than the addition of shoot residues. Addition of glucose (trace amount, *i.e.* 40 μg C g^{-1} soil) together with residues increased SOM priming, but the interactive effect on SOM decomposition depended both on type and stage of residue decomposition. Glucose induced stronger SOM priming when added with shoots compared with root residues. At the intensive or stabilised residue decomposition stage, glucose addition resulted in no or little increase in SOM priming compared with residues alone. This was either due to limited microbial demand for exogenous C (*e.g.* during intensive decomposition) or to the amount of added C being insufficient to strongly influence microbial activities that determine SOM decomposition. However, glucose addition during the reduced residue decomposition stage (day-9) increased SOM priming by 60–104% compared with residues only. This SOM priming was followed by a decline in residue-derived C and an increase in SOM-derived C in microbial biomass. Thus during the reduced residue decomposition stage, the activities of both residue and SOM decomposers were greatly affected by added glucose, which resulted in preferential microbial utilisation of SOM (to meet their nutritional demands) rather than residues. The interactive effect of glucose and residues on SOM priming was mainly prominent for a short period (1–5 days), but glucose alone increased SOM decomposition by 1- to 4-fold of the amount of added glucose-C. This resulted in an overall decrease in the net soil C balance under glucose plus residue addition compared with the addition of residues alone. Such critical evaluation of SOM priming was the only possible using a dual ($^{13}C/^{14}C$) labelling approach, which is crucial for a better understanding of SOM stabilisation mechanisms and C budgeting in response to labile C inputs during residue decomposition. Altogether, our findings are important for evaluating the impact of labile C inputs, such as root or microbial exudates (*e.g.* under field conditions), for both short- and long-term on SOM turnover during crop residue decomposition, a common situation in the rhizosphere.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.soilbio.2018.08.023.

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