



1 **Fate of rice shoot and root residues, rhizodeposits, and microbe-assimilated**
2 **carbon in paddy soil: I. Decomposition and priming effect**

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16



17 **Abstract.** The input of recently photosynthesized C has significant implications on soil organic
18 carbon sequestration, and in paddy soils, both plants and soil microbes contribute to the overall C input.
19 In the present study, we investigated the fate and priming effect of organic C from different sources by
20 conducting a 300-d incubation study with four different ¹³C-labelled substrates: rice shoots (Shoot-C),
21 rice roots (Root-C), rice rhizodeposits (Rhizo-C), and microbe-assimilated C (Micro-C). The efflux of
22 both ¹³CO₂ and ¹³CH₄ indicated that the mineralization of C in Shoot-C-, Root-C-, Rhizo-C-, and
23 Micro-C-treated soils rapidly increased at the beginning of the incubation and then decreased gradually
24 afterwards. In addition, the highest level of C mineralization was observed in Root-C-treated soil
25 (45.4%), followed by Shoot-C- (31.9%), Rhizo-C- (7.9%), and Micro-C-treated (7.7%) soils, which
26 corresponded with mean residence times of 33.4, 46.1, 62.9, and 192 d, respectively. Furthermore, the
27 cumulative mineralization of native soil organic carbon in Shoot-C-treated soils was 1.48- fold higher
28 than in untreated soils, and the priming effect of Shoot-C on CO₂ and CH₄ emission was strongly
29 positive over the entire incubation. However, Root-C failed to exhibit a significant priming effect,
30 which suggests that it could potentially be used to mitigate CH₄ emission. Although the total C contents
31 of Rhizo-C- (1.89%) and Micro-C-treated soils (1.9%) were higher than those of untreated soil (1.8%),
32 no significant differences in total C emissions were observed. However, the ¹³C emissions of Rhizo-C-
33 and Micro-C-treated soils gradually increased over the entire incubation period, which indicated that
34 soil organic C-derived emissions were lower in Rhizo-C- and Micro-C-treated soils than in untreated
35 soil, and that rhizodeposits and microbe-assimilated C could be used to reduce the mineralization of
36 native soil organic carbon and to effectively improve soil C sequestration. The contrasting behaviours
37 of the different photosynthesized C substrates suggests that recycling rice roots in paddies is more



38 beneficial than recycling shoots and reveals the importance of increasing rhizodeposits and

39 microbe-assimilated C in paddy soils *via* nutrient management.

40

41 **Keywords:** Paddy soil; Rice; Plant residues; Rhizodeposits; Microbe-assimilated carbon; CO₂ and

42 CH₄ emission; Priming effect

43



44 1 Introduction

45 The soils of rice paddies, which cover an area of ~165 million ha worldwide, hold great potential for
46 expanded C sequestration (Conrad et al., 2012; Ge et al., 2012; Lal, 2004), and the soil organic carbon
47 (SOC) pools in agricultural systems, of which plant C is the primary substrate, are significantly
48 affected by the input of crop residues (Weintraub et al., 2007). For example, after crops are harvested
49 or die, aboveground biomass, such as straw, stubble, and other surface debris, contribute to annual C
50 inputs (Lu et al., 2003), and photosynthesized C substrates are continuously released by rice plants as
51 rhizodeposits, such as decaying roots, throughout the growing season (Lu et al., 2002, 2003). However,
52 autotrophic soil microbes that assimilate CO₂ contribute to C sequestration in paddy soil, as well (Ge et
53 al., 2013; Yuan et al., 2012a), and since C inputs promote microbial activity and native SOC
54 decomposition (Ye et al., 2015) and the quantity and quality of such inputs influence microbe-mediated
55 decomposition processes (Brant et al., 2006; Creamer et al., 2015), the quantification of different C
56 substrates allocated to paddy soils and their respective effects on native SOC require further
57 investigation.

58 The aboveground biomass and root systems of rice plants represent the only inputs of available
59 organic C to paddy SOC (Johnson et al., 2006), the quantity and quality of which has been reported
60 previously (Chen et al., 2014; Kisselle et al., 2001; Zhang et al., 2015). However, although
61 aboveground biomass has been reported to make significant contributions to SOC sequestration (Lu et
62 al., 2003), rice roots have been reported to contribute 1.5–3-fold more C to SOC than shoots (Hooker et
63 al., 2005), and similarly, Molina et al. (2001) reported that the stalks and leaves of corn contribute 50%
64 less C to SOC than the roots and rhizodeposits. The predominant contribution of crop roots to SOC can
65 partly be explained by the chemical composition of roots, which includes cellulose and lignin, as well
66 as by residue–soil interactions, such as aggregate formation, which physically protect organic C from
67 biodegradation (Baumann et al., 2009; Johnson et al., 2006; Lu et al., 2003).

68 Previous studies have also reported that the rhizodeposits of rice account for ~17% of the
69 photo-assimilates (Nguyen, 2003) that enter paddy soil, and that rice rhizodeposits include soluble
70 exudates, root border cells, dead debris, and insoluble mucilage (Lu et al., 2003). In cereal crops,
71 10–25% of root exudates are incorporated into SOC, and rhizodeposits are thought to play a key role in
72 C cycling and sequestration in plant–soil–microbe systems (Kuzyakov, 2002; Kuzyakov et al., 2003).



73 In addition to the photosynthesized C substrates of plants, soil microbes are also able to assimilate CO₂
74 *via* the Calvin-Benson-Bassham cycle and, thus, can significantly contribute to the net uptake and
75 assimilation of atmospheric CO₂, as well (Ge et al., 2013; Yuan et al., 2012b). In fact, the CO₂ uptake
76 by phototrophic soil microbes has been reported to account for up to 0.36% of the total C fixed in rice
77 paddy soils and 0.19% of the total C fixed in upland soils (Ge et al., 2013; Yuan et al., 2012b).

78 However, the effect of C input from different C sources on the balance and stability of SOC has
79 received limited attention. For example, low-molecular-weight C substrates are protected from
80 mineralization *via* sorption onto soil particles (Jones and Edwards, 1998), which contributes to the
81 stability and sequestration of SOC, whereas the input of fresh organic C, such as green manure, straw,
82 and rhizodeposits, promotes the decomposition of native SOC and results in the emission of CO₂ and
83 CH₄ (Huo et al., 2013; Yuan et al., 2014c). In addition, different C substrates can also have stimulating
84 or restraining effects on the mineralization of native SOC, which are known as positive or negative
85 priming effects (PEs), respectively (Kuzyakov, 2010). Priming is often caused by the addition of
86 substrates with relatively high C availability and nutrient contents, which results in increased microbial
87 activity (Blagodatsky et al., 2010); however, such easily degraded compounds greatly enhance the
88 decomposition of native SOC (Blagodatsky et al., 2007; Qiao, et al., 2014), compared with the effects
89 of ryegrass, cellulose, or wheat straw, which have complex structures that are less available to microbes
90 (Kuzyakov and Bol, 2006; Kuzyakov et al., 2000).

91 Accordingly, the quantity and quality of different C inputs, as well as their fate and PE in paddy
92 soils, are globally important (Bastida et al., 2013; Johnson et al., 2006; Wang et al., 2015). Although
93 numerous studies have estimated the fate of plant residues and rhizodeposits in paddy soils, to our
94 knowledge, there is no comparative information on (1) the decomposition of different organic C
95 sources, such as rice shoots and roots, rhizodeposits, and microbe-assimilated C; or (2) the effects
96 different organic C sources on the mineralization of native SOC. We hypothesized that the
97 decomposition of such material would decrease with the increasing complexity of substrate
98 composition and that the PE of plant residues was stronger than that of rhizodeposits and
99 microbe-assimilated C, owing to their relatively higher quantity and stability in the soil. To investigate
100 these hypotheses by quantifying the contribution of different organic C sources to CO₂ and CH₄



101 emission and by analysing their PE, we conducted a 300-d incubation study using ^{13}C -labelled rice
102 plant residues, rhizodeposits, and microbe-assimilated C in paddy soils.

103

104 **2 Materials and methods**

105 **2.1 Study site and soil sampling**

106 The experimental rice field was located at the Changsha Research Station for Agricultural and
107 Environmental Monitoring, Hunan, China (113°19'52" E, 28°33'04" N; 80 m above sea level), where
108 the soil was a typical stagnic anthrosol, developed from highly weathered granite, and the climate was
109 subtropical, with a mean annual temperature and rainfall of 17.5 °C and 1300 mm, respectively.

110 Moist soil samples were collected from the plough layer (0–20 cm) and sieved (<4 mm) to remove
111 visible plant residues. The soil contained 18.1 g kg⁻¹ organic C, 1.8 g kg⁻¹ total N, and 0.4 g kg⁻¹ total K
112 and had a pH of 5.6 and a soil: water ratio (w/v) of 1: 2.5.

113

114 **2.2 Production of ^{13}C -labelled substrates**

115 Rice cultivation and $^{13}\text{CO}_2$ labelling were performed as described by Ge et al. (2012; 2013), with some
116 modifications. Briefly, 60 pots were filled with 1 kg dry soil, and of these, 40 pots were each planted
117 with three 30-d-old rice seedlings (*Oryza sativa* L. 'Zhongzao 39'), whereas the remaining 20 pots
118 were unplanted. Weeds were removed manually.

119 For ^{13}C labelling, 30 pots (20 planted, 10 unplanted) were transferred to an automatically
120 controlled gas-tight growth chamber (110 cm length, 250 cm width, 180 cm height) and exposed to
121 $^{13}\text{CO}_2$ -fumigation for 18 d (May 14–31, 2013), during the vegetative growth period (including the
122 entire tillering stage). The growth chambers were placed in a rice field to ensure that the environmental
123 conditions of the labelled and control plants would be identical for labelled plants and unlabelled
124 controls, and the remaining 30 pots (20 planted, 10 unplanted), which served as controls for measuring
125 natural ^{13}C abundance, were placed 10–15 m from the growth chambers. The surface of each planted
126 pot was covered with black plastic sheeting, to prevent algal photosynthesis in the floodwater and to



127 ensure that only the rice shoots were exposed to $^{13}\text{CO}_2$ (i.e., not phototrophic microbes in the soil or
128 water), whereas the unplanted pots were left uncovered, so that the soils were directly exposed to $^{13}\text{CO}_2$
129 and so phototrophic soil microbes could assimilate atmospheric $^{13}\text{CO}_2$. All the pots were watered every
130 few days, in order to maintain a water depth of 2–3 cm above the soil surface, until harvest.

131 The CO_2 concentrations of the growth chambers were measured using an infrared analyser
132 (Shsen-QZD, Qingdao, China) and maintained at 360–380 $\mu\text{L L}^{-1}$. The $^{13}\text{CO}_2$ was generated by
133 acidifying $\text{Na}_2^{13}\text{CO}_3$ (1.0 M, 99 atom % ^{13}C ; Cambridge Isotope Laboratories, Tewksbury, MA, USA)
134 with H_2SO_4 (0.5 M) in beakers that were placed inside the growth chambers. During the labelling
135 period, $^{13}\text{CO}_2$ was only released when CO_2 concentrations fell below 360 $\mu\text{L L}^{-1}$, and at CO_2
136 concentrations $>380 \mu\text{L L}^{-1}$, the gas flow was diverted and passed through CO_2 traps (NaOH solution).
137 An air-conditioning system was used to control the temperature inside the chamber within 1 $^\circ\text{C}$ of the
138 ambient temperature in the rice field. Two fans continuously circulated the air in the growth chamber.

139

140 2.3 ^{13}C -labelled substrate collection

141 All the rice plants and soils were sampled destructively after 18 d of $^{13}\text{CO}_2$ labelling. Rice shoots were
142 removed at their bases, whereas rice roots were separated from the soil by washing with deionized
143 water, and both shoots and roots were dried at 60 $^\circ\text{C}$ for 48 h and then cut into <5 mm pieces.
144 ^{13}C -labelled rhizodeposits were obtained by gently shaking moist soil from the roots of rice plants and
145 were prepared for incubation by removing root debris and mixing thoroughly. Meanwhile, to obtain
146 microbe-assimilated ^{13}C , we collected soil from ^{13}C -treated, unplanted pots and mixed it thoroughly.

147

148 2.4 Soil incubation

149 To determine the PEs of different C sources and the effect of different C substrates on CO_2 and CH_4
150 emission, we conducted a 300-d incubation study of paddy soils that had been supplemented with
151 ^{13}C -labelled shoots, roots, rhizodeposits, or microbe-assimilated C. Five treatments were used: (1)
152 unlabelled and unplanted paddy soil supplemented with ^{13}C -labelled shoot residue (Shoot-C), (2)
153 unlabelled and unplanted paddy soil supplemented with ^{13}C -labelled root residue (Root-C), (3)
154 ^{13}C -labelled soil containing ^{13}C -labelled rhizodeposits (Rhizo-C), (4) ^{13}C -labelled soil containing
155 ^{13}C -labelled microbe-assimilated C (Micro-C), and (5) unlabelled and unplanted soil without



156 supplementation (CK). Three additional treatments were used to determine the natural occurrence of
157 ^{13}C : (1) unlabelled and unplanted paddy soil with unlabelled shoot residue, (2) unlabelled and
158 unplanted paddy soil with unlabelled root residue, and (3) unlabelled and unplanted paddy soil with
159 unlabelled rhizodeposits.

160 For the Shoot-C and Root-C treatments, 150 g (100 g dry weight equivalent) unlabelled,
161 unplanted soil with a water content of 50% was homogenized with 0.6 g of labelled and dried shoot and
162 root residue, respectively, with a final residue content of 6 g kg^{-1} . Subsequently, the samples were
163 transferred to 500 ml serum bottles with 100 ml deionized water, to ensure a water layer of >1–2 cm,
164 and the bottles were sealed with butyl rubber stoppers. For the Rhizo-C and Micro-C treatments, 150 g
165 fresh soil containing either ^{13}C -labelled rhizodeposits (from rice roots) or ^{13}C -labelled
166 microbe-assimilated C (from labelled, unplanted pots) were directly weighed into 500 ml serum bottles,
167 respectively. Incubation was conducted at 25 °C in the dark for 300 d, with four replicates for each
168 treatment. CH_4 and CO_2 concentrations of the headspace samples were collected at 1, 3, 5, 10 d and
169 then every 10 d after sealing, the gas was collected using a gas-tight syringe and stored in
170 pre-evacuated Exetainer glass bottles (Labco, High Wycombe, UK). After each sampling point, the
171 serum bottle was ventilated for 10 min, and then sealed with butyl rubber stoppers.

172

173 2.5 Analytical methods

174 The C content of the soil and plant residues (shoots and roots) was determined using dry combustion
175 with an elemental analyser (vario MAX; Elementar Analysensysteme GmbH, Germany), whereas the
176 CH_4 and CO_2 concentrations of the headspace samples were measured using a gas chromatographer
177 (Agilent 7890A, Agilent Technologies, USA) equipped with a thermal conductivity detector for
178 measuring CO_2 and a flame ionization detector for measuring CH_4 . In addition, the stable C isotope
179 composition of soils and plant residues were analysed using an isotope ratio mass spectrometer coupled
180 with an elemental analyser (FLASH 2000; Thermo Fisher Scientific, USA), whereas the stable C
181 isotope composition of CO_2 and CH_4 in the headspace samples were analysed using the isotope ratio
182 mass spectrometer coupled with a GasBench (Thermo Fisher Scientific).

183

184 2.6 Calculations and statistical analysis



185 The $\delta^{13}\text{C}$ values of plant residues, rhizodeposits, microbe-assimilated C, soils, CO_2 , and CH_4 were
 186 calculated as follows:

$$187 \quad \delta^{13}\text{C} (\text{‰}) = \frac{R_s - R_{PDB}}{R_{PDB}} \times 1000 \text{‰}, \quad (1)$$

188 where R_{PDB} is the $^{13}\text{C}/^{12}\text{C}$ ratio of the international Pee Dee Belemnite (PDB) standard ($R_{PDB} =$
 189 0.0112372 ; Lu et al., 2003) and R_s is the sample $^{13}\text{C}/^{12}\text{C}$ ratio. In addition, *Atomic ^{13}C* (%) was
 190 calculated as follows:

$$191 \quad \textit{Atomic } ^{13}\text{C} (\%) = \frac{(\delta^{13}\text{C} + 100) R_{PDB}}{(\delta^{13}\text{C} + 100) R_{PDB} + 1} \times 100\%, \quad (2)$$

192

193 and the incorporation of ^{13}C in plant residues, rhizodeposits, microbe-assimilated C, bulk soils, CO_2 ,
 194 and CH_4 was calculated as follows:

$$195 \quad ^{13}\text{C}_{\text{sample}} (\%) = [(\textit{Atomic } ^{13}\text{C})_L - (\textit{Atomic } ^{13}\text{C})_{UL}] \times \frac{C_{\text{sample}}}{100}, \quad (3)$$

196 where *(Atomic ^{13}C)*, L and *(Atomic ^{13}C)*, UL are the percentages of *Atomic ^{13}C* in labelled and
 197 unlabelled samples, respectively, and $^{13}\text{C}_{\text{sample}}$ and C_{sample} are the total ^{13}C and C content of each
 198 sample.

199 The $^{13}\text{CO}_2$ and $^{13}\text{CH}_4$ efflux (%) were calculated as the increases in $^{13}\text{CO}_2\text{-C}$ and $^{13}\text{CH}_4\text{-C}$,
 200 respectively, as percentages of the ^{13}C input, within each sampling interval, whereas cumulative $^{13}\text{CO}_2$
 201 and $^{13}\text{CH}_4$ emission (%) were calculated as the percentages of the ^{13}C input represented by the sum of
 202 the ^{13}C in $^{13}\text{CO}_2$ and $^{13}\text{CH}_4$, respectively, at each sampling day, and the mineralization percentage of the
 203 input ^{13}C was calculated as the sum of total ^{13}C in CO_2 and CH_4 , at each sampling day, relative to the
 204 initially added total ^{13}C .

205 The temporal dynamics of the cumulative mineralization ratios were described by fitting a first
 206 order single exponential decay curve:

$$207 \quad y = y_0 + a (1 - e^{-bx}), \quad (2)$$

208 where y is the percentage of ^{13}C emission from the labelled-substrate C; y_0 is the pool of
 209 labelled-substrate C remaining in the soil; a is the initial amount of bioavailable labelled-substrate C



210 pool; b is the mineralization rate of substrate C; and x is time (d). Mean residence time ($1/b$) and
 211 half-life ($\ln(2)/b$) were also calculated.

212 The end-member mixing model was used to calculate the fractions of SOC- (C_{SOC}) and plant
 213 residue-derived C (C_{shoot} and C_{root}), as described by Phillips and Gregg (2001) and Phillips et al. (2005).
 214 This model allows the combination of mass spectrometric and efflux measurements. The shoot-derived
 215 $^{13}\text{CO}_2$ emission ($^{13}\text{CO}_{2\text{shoot-derived}}$) was calculated as follows:

$$216 \quad ^{13}\text{CO}_{2\text{shoot-derived}} = \frac{\delta^{13}\text{CO}_{2\text{shoot}} - \delta^{13}\text{CO}_{2\text{CK}}}{\delta^{13}\text{CO}_{2\text{shoot}} - \delta^{13}\text{CO}_{2\text{soil}}} \times \text{CO}_{2\text{shoot}}, \quad (5)$$

217 where $\delta^{13}\text{CO}_{2\text{shoot}}$ and $\delta^{13}\text{CO}_{2\text{CK}}$ are the $\delta^{13}\text{C}$ values of CO_2 derived from C_{shoot} and C_{CK} , respectively;
 218 $\delta^{13}\text{C}_{shoot}$ and $\delta^{13}\text{C}_{soil}$ are the $\delta^{13}\text{C}$ values of C_{shoot} and C_{soil} , respectively; and $\text{CO}_{2\text{shoot}}$ is the total CO_2
 219 derived from C_{shoot} ; and the shoot-derived $^{13}\text{CH}_4$ emission ($^{13}\text{CH}_{4\text{shoot-derived}}$) and the root-derived $^{13}\text{CO}_2$
 220 and $^{13}\text{CH}_4$ emission ($^{13}\text{CO}_{2\text{root-derived}}$ and $^{13}\text{CH}_{4\text{root-derived}}$, respectively) were calculated similarly (Phillips
 221 and Gregg, 2001; Ye et al., 2015).

222 The PE of SOM on CO_2 and CH_4 emission was calculated as follows:

$$223 \quad PE_t (\%) = \frac{Gas - Gas_{CK}}{Gas_{CK}} \times 100\%, \quad (6)$$

224 where PE_t is the PE at time t (d); Gas is the total amount of CO_2 and CH_4 derived from C_{shoot} and C_{root} ;
 225 and Gas_{CK} is the total amount of CO_2 and CH_4 derived from C_{CK} (Ye et al., 2015).

226 Analysis of variance in conjunction with Duncan's multiple range test ($p < 0.05$) and correlation
 227 analysis were conducted using SPSS 17 (SPSS Inc., Chicago, IL, USA), and figures were created using
 228 Origin 8.5 (OriginLab, Northampton, MA, USA).

229

230 3 Results

231 3.1 CO_2 and CH_4 emission of carbon substrate-treated soils

232 The atomic ^{13}C recovered from the CO_2 emission of Shoot-C- and Root-C-treated soils increased
 233 sharply at the beginning of incubation, reached a peak (4.71 and 4.39%) after 10 d, and then slowly
 234 declined until the end of the incubation; and the atomic ^{13}C of CO_2 from Rhizo-C- and Micro-C-treated
 235 soils exhibited a similar pattern, but with lower percentages (Fig. 1a). In addition, both Shoot-C and



236 Root-C had similar effects on the amount of atomic ^{13}C recovered from CH_4 , however, the CH_4 was
237 below the detection limit in Rhizo-C- and Micro-C-treated soils (Fig. 1b).

238 The $^{13}\text{CO}_2$ efflux rates also increased rapidly at the beginning of incubation, peaked after 20 d, and
239 then decreased gradually (Fig. 1c); however, the efflux rates from Shoot-C- (0.71%) and
240 Root-C-treated (0.66%) soils were higher than those of Rhizo-C- (0.11%) and Micro-C-treated (0.06%)
241 soils. The $^{13}\text{CH}_4$ efflux rates exhibited similar patterns (Fig. 1d). Furthermore, the cumulative $^{13}\text{CO}_2$
242 and $^{13}\text{CH}_4$ emissions also increased linearly during the first 60 d of incubation, after which they
243 increase slowly (Fig. 2). The total ^{13}C per 100 g soil was 11.4, 5.75, 1.61, and 0.49 mg in the Shoot-C,
244 Root-C, Rhizo-C, and Micro-C treatments, respectively (Table 1), and the total $^{13}\text{CO}_2$ emissions
245 accounted for 28.6 and 43.8% of the initial ^{13}C from Shoot-C and Root-C, respectively, and 7.9 and
246 7.7% of the initial ^{13}C in Rhizo-C and Micro-C (Fig. 2a). In contrast, the cumulative $^{13}\text{CH}_4$ emissions
247 only accounted for 3.3 and 1.6% of the initial ^{13}C from Shoot-C and Root-C, respectively (Fig. 2b).

248 The cumulative mineralization of substrate-derived ^{13}C was more rapid at the beginning of the
249 incubation and followed a single exponential model (Fig. S1), and at the end of the incubation, we
250 found that the total mineralization percentage was highest in Root-C-treated soils (45.4%), followed by
251 Shoot-C- (31.9%), Rhizo-C- (7.9%), and Micro-C-treated (7.7%) soils. In addition, the bioavailable ^{13}C
252 in the Shoot-C- and Root-C-treated soils was 34.2 and 46.2%, respectively, which was 4–5-fold larger
253 than that of the Micro-C- (9.7%) and Rhizo-C-treated (7.8%) soils, and the mean residence time (MRT)
254 of the Shoot-C-, Root-C-, Rhizo-C-, and Micro-C-treated soils was 33.4, 46.1, 62.9, and 192 d,
255 respectively (Table 2).

256

257 **3.2 Priming effect of Shoot-C and Root-C on CO_2 and CH_4 emission**

258 Over the entire incubation period, the cumulative emissions of CO_2 and CH_4 from the untreated soil
259 was 1692 mg kg^{-1} , and the SOC-derived C emissions from the Shoot-C- and Root-C-treated soils were
260 2519 mg kg^{-1} and 1737 mg kg^{-1} , respectively, which was 1.49- and 1.03-fold that of the untreated soil
261 (Fig. 3). In addition, the end-member mixing model used to partition SOC-derived CO_2 -C and CH_4 -C
262 suggested that the mineralization of native SOC was promoted by the Shoot-C and Root-C treatments.

263 Furthermore, the PE of the Shoot-C treatment peaked at 351% after 20 d of incubation and
264 decreased to 46% by the end of the incubation, whereas the PE of the Root-C treatment peaked at 39%



265 after 50 d of incubation and then decreased to 0.8%. Thus, the positive PE of Shoot-C was clearly
266 stronger than that of Root-C, especially since the PE of Root-C was insignificant (i.e., $p > 0.05$; Fig. 4).

267

268 **3.3 Mineralization of soil organic carbon in Rhizo-C- and Micro-C-treated soils**

269 The total C emissions of Rhizo-C- and Micro-C-treated soils increased significantly from 116 mg kg⁻¹
270 and 81 mg kg⁻¹ after 10 d of incubation, respectively, to 1754 mg kg⁻¹ and 1785 mg kg⁻¹ by the end of
271 the incubation. The total C emission of Rhizo-C-treated soil was significantly higher than that of the
272 Micro-C- and un-treated soil, during the first 200 d of incubation; however, no significant differences
273 were identified at the end of the incubation (Fig. 5a). In addition, the total ¹³C emissions derived from
274 the Rhizo-C and Micro-C treated soils gradually increased over the entire incubation, and the total
275 mineralization of ¹³C in Rhizo-C-treated soils was significantly higher than that in Micro-C-treated
276 soils ($p < 0.05$; Fig. 5b). However, the C-mineralization of neither the Rhizo-C- nor Micro-C-treated
277 soils were significantly different than that of untreated soil, which suggested that the rhizodeposits and
278 microbe-assimilated C had effect on the mineralization of native SOC.

279

280 **4 Discussion**

281 **4.1 Mineralization of carbon substrates in paddy soil**

282 The atomic ¹³C and effluxes of both CO₂ and CH₄ from soils treated with ¹³C-labelled substrates
283 exhibited a rapid increase at the beginning of the incubation, followed by a slow decrease (Fig. 1),
284 which indicated that microbes prefer fresh C substrates over native SOC (Yuan et al., 2012c), as has
285 been reported by previous studies on the decomposition of fresh C substrates in both paddy and upland
286 soils (Lu et al., 2003; Parshotam et al., 2000). In these systems, the initial rapid decomposition is due to
287 the addition of easily degradable organic C, in the form of highly bioavailable compounds with low
288 molecular weight. Then, after the exhaustion of labile C, more recalcitrant components, such as cutin
289 and lignin, and mineral-stabilized SOC are utilized (Baumann et al., 2009). However, the transition
290 could also involve an alteration in species dominance, with rapidly proliferating bacteria using more
291 available compounds during the early stages of decomposition and slower-growing fungi using the
292 more recalcitrant components during later stages (Baumann et al., 2009; Brant et al., 2006).



293 Both CO₂ and CH₄ efflux are important components of the C cycle in paddy soils and represent a
294 major proportion of the C released by microbial decomposition (Yuan et al., 2012c), and the results of
295 the present study suggest that the mineralization of shoot- and root-derived ¹³C was ~3-4 times higher
296 than that of rhizodeposit- and microbe-derived ¹³C (i.e., Root-C > Shoot-C > Rhizo-C > Micro-C; Fig.
297 2). The present study also found that the percentage of Root-C-derived ¹³C recovered from CO₂ was
298 1.6-fold higher than Shoot-C-derived ¹³C, which indicated that root residue was more easily
299 decomposed, a conclusion that was also supported by the higher ¹³CO₂ efflux of Root-C-treated soils.

300 However, the C mineralization rates of Rhizo-C- and Micro-C-treated soils were much slower, and
301 the MRTs of Rhizo-C- and Micro-C-treated soils were 2–4-fold higher than those of Shoot-C- and
302 Root-C-treated soils, likely owing to the formation of mineral-associated organic matter during the
303 labelling period that was well protected from microbial degradation and had a slow turnover rate
304 (Basler et al., 2015; Mikutta et al., 2014; Saidy et al., 2012; Schurig et al., 2013). Furthermore, most of
305 the C in Rhizo-C- and Micro-C-treated soils was not mineralized to CO₂ but, instead, underwent
306 intensive internal recycling (Gunina and Kuzyakov, 2015; Knowles et al., 2010) and were stored as
307 living microbial biomass, and the resulting biomass was either stabilized as occluded particulate
308 organic matter and mineral-associated organic matter (Basler et al., 2015, Schurig et al., 2013) or was
309 incorporated into metabolic products, such as sugars, carboxylic acids, and amino acids, which were
310 incorporated into cell membranes, cell walls, or polymers (Apostel et al., 2015; Gunina et al., 2014).

311

312 **4.2 Effect of carbon substrates on native SOC mineralization**

313 In the present study, the emission of CO₂ and CH₄ by Shoot-C- and Root-C-treated soils during the first
314 50 d were mainly derived from plant residue C, after which the contribution of native SOC increased.
315 However, a positive PE was observed until the end of the incubation, with the exception of
316 Root-C-treated soils (Fig. 4). These results are supported by previous studies that have reported that the
317 initial phase of rapid decomposition was the result of adding easily degraded organic C and other
318 available nutrients that promote both microbial activity and SOC decomposition (Chen et al., 2014;).
319 The compounds decomposed during the slower phase were less available for microbial growth, and as a
320 result of C limitation, most of the available C was likely incorporated into cells and converted to
321 storage compounds, rather than used for growth or respiration (Lu et al., 2003; Brant et al., 2006).



322 However, the extracellular enzymes generated to degrade recalcitrant C substrates might be more
323 effective in decomposing SOC at later stages of incubation, leading to a positive PE (Chen et al., 2014).
324 In addition, the two phases of exogenous C decomposition and the mechanisms of PE simultaneously
325 influence the strength and extent of native SOC mineralization (Chen et al., 2014; Ye et al., 2015).

326 As sources of C that is stabilized by soil minerals, both Rhizo-C and Micro-C augmented the C
327 content of paddy soil (1.89 and 1.9%, respectively) over that of untreated soil (1.8%) and also reduced
328 native SOC decomposition, which suggests that they could be used to protect native SOC, increase the
329 organic carbon storage of paddy soil, and even mitigate global warming (Ge et al., 2012; Li and Yagi,
330 2004, Shen et al., 2014). In the present study, we found that the C emissions of Rhizo-C- and
331 Micro-C-treated soils were similar to those of untreated soil, which suggested that rhizodeposits and
332 microbe-assimilated C input have no effect on native SOC mineralization at any time during the
333 rice-growing season. However, the total Rhizo-C- and Micro-C-derived ^{13}C increased gradually over
334 the incubation period, despite the small initial input during the 18-d labelling period, which implies that
335 the soils' native SOC-derived C were smaller than those of untreated soil and that both Rhizo-C and
336 Micro-C suppressed the mineralization of native SOC. This suppression probably occurred because
337 rhizodeposits and microbe-assimilated C are predominantly composed of highly bioavailable
338 compounds with low molecular weight (Lu et al., 2002) and, in the present study, likely underwent
339 internal recycling *via* microbial metabolism during the incubation, as indicated by their relatively
340 longer MRTs (Table 2; Gunina et al., 2014; Mikutta et al., 2014; Schurig et al., 2013).

341

342 5 Conclusions

343 In the present study, Root-C-treated soils exhibited the highest rate of C mineralization, followed by
344 Shoot-C-, Rhizo-C-, and Micro-C-treated soils, whereas the opposite trend was observed for MRT, and
345 by the end of 300-d incubation, both Shoot-C- and Root-C-treated soils exhibited higher total
346 mineralization and positive PEs. Although plant residues are widely used for improving soil fertility,
347 their contribution to SOC assimilation is inefficient, and their use also contributes to the emission of
348 greenhouse gasses. However, the present study demonstrates that both rhizodeposits and
349 microbe-assimilated C can reduce native SOC decomposition and may more effectively contribute to
350 the stability and sequestration of soil C.



351

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358



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495 rice field in winter season, *Soil Biol. Biochem.*, 84, 75-82, 2015.
- 496

497 **Tables**

498 **Table 1.** The carbon (C) content, atomic ^{13}C , and total ^{13}C in the soil and photosynthesized C substrates
 499 after 18 d of ^{13}C -labelling.

	Bulk soil	Shoot-C	Root-C	Rhizo-C	Micro-C
C content (%)	1.80 ± 0.12	40.50 ± 2.13	28.60 ± 1.15	1.89 ± 0.12	1.90 ± 0.11
Atomic ^{13}C (%)	1.08 ± 0.02	5.78 ± 0.09	4.43 ± 0.07	1.16 ± 0.03	1.11 ± 0.02
Total ^{13}C (mg)	0	11.43 ± 0.52	5.75 ± 0.41	1.61 ± 0.06	0.49 ± 0.05

500 Bulk soil, unplanted and unlabelled soil; Shoot-C, paddy soil supplemented with ^{13}C -labelled shoot
 501 residue; Root-C, paddy soil supplemented with ^{13}C -labelled root residue; Rhizo-C, paddy soil
 502 supplemented with ^{13}C -labelled rhizodeposits; Micro-C, paddy soil supplemented with ^{13}C -labelled
 503 microbe-accumulated C.

504



505 **Table 2.** The size of bioavailable labelled-substrate C pool, mean residence time (MRT), and half-life
506 of cumulative ^{13}C recovery in CO_2 and CH_4 in four different incubation treatments.

Treatment	Size (%)	MRT (d)	Half-life (d)	R ²
Shoot-C	34.2	33.4	23.2	0.99
Root-C	46.2	46.1	31.9	0.99
Rhizo-C	7.8	62.9	43.6	0.98
Micro-C	9.7	192	133	0.98

507 The size of bioavailable labelled-substrate C pool (% initial ^{13}C), MRT, and R² were calculated based
508 on Fig. 1S. Shoot-C, paddy soil supplemented with ^{13}C -labelled shoot residue; Root-C, paddy soil
509 supplemented with ^{13}C -labelled root residue; Rhizo-C, paddy soil supplemented with ^{13}C -labelled
510 rhizodeposits; Micro-C, paddy soil supplemented with ^{13}C -labelled microbe-accumulated C.



511 **Figures captions**

512 **Figure 1.** Atomic ^{13}C (%) recovered from CO_2 (a) and CH_4 (b) emissions and the $^{13}\text{CO}_2$ (c) and $^{13}\text{CH}_4$
513 (d) efflux (% initial ^{13}C) over the 300-d incubation period. The inset in Fig. 1c shows the $^{13}\text{CO}_2$ efflux
514 (% initial ^{13}C) of Rhizo-C and Micro-C over the 300-d incubation period. Values and error bars
515 represent means \pm SE ($n = 4$). Shoot-C, unlabelled paddy soil supplemented with ^{13}C -labelled shoot
516 residue; Root-C, unlabelled paddy soil supplemented with ^{13}C -labelled root residue; Rhizo-C, paddy
517 soil containing ^{13}C -labelled rhizodeposits; Micro-C, paddy soil containing ^{13}C -labelled
518 microbe-accumulated C.

519

520 **Figure 2.** Cumulative $^{13}\text{CO}_2$ (a) and $^{13}\text{CH}_4$ (b) emissions (% of initial ^{13}C) over the 300-d incubation
521 period. Values and error bars represent means \pm SE ($n = 4$). Shoot-C, unlabelled paddy soil
522 supplemented with ^{13}C -labelled shoot residue; Root-C, unlabelled paddy soil supplemented with
523 ^{13}C -labelled root residue; Rhizo-C, paddy soil containing ^{13}C -labelled rhizodeposits; Micro-C, paddy
524 soil containing ^{13}C -labelled microbe-accumulated C.

525

526 **Figure 3.** Cumulative CO_2 and CH_4 emissions by Shoot-C- (a) and Root-C-treated (b) soils over the
527 300-d incubation period. The inset in Fig. 3b shows total C emission derived from SOC of
528 Root-C-treated soils and CK. Values and error bars represent means \pm SE ($n = 4$). Shoot-C, ^{13}C -labelled
529 shoot residue; Root-C, ^{13}C -labelled root residue; SOC, soil organic carbon; CK, unlabelled and
530 unplanted soil without supplementation.

531

532 **Figure 4.** Priming effect (%) of ^{13}C -labelled plant residues over the 300-d incubation period. Values
533 and error bars represent means \pm SE ($n = 4$). Shoot-C, unlabelled paddy soil supplemented with
534 ^{13}C -labelled shoot residue; Root-C, unlabelled paddy soil supplemented with ^{13}C -labelled root residue.

535

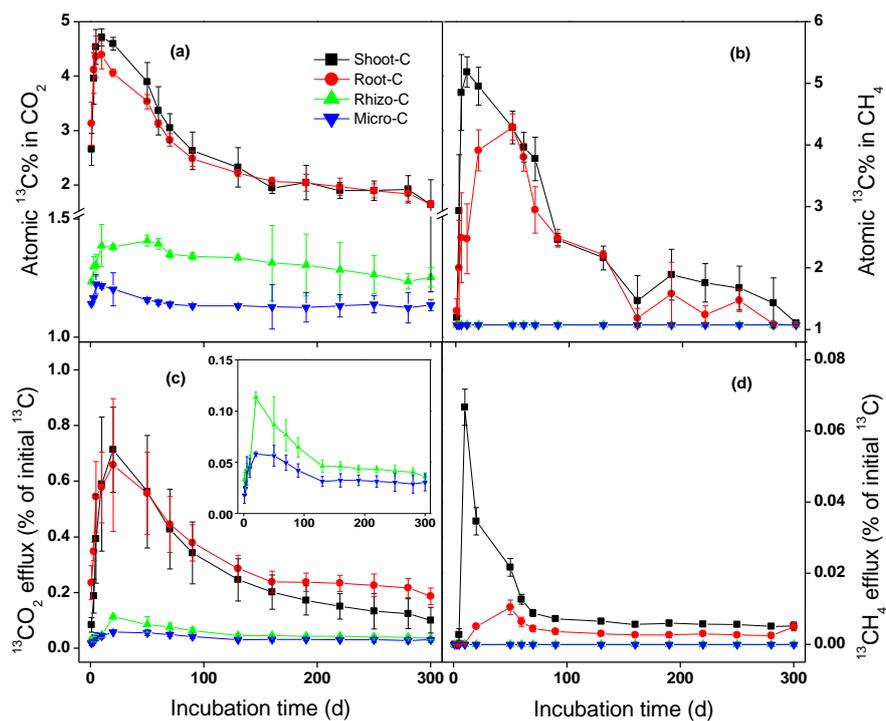
536 **Figure 5.** Total C (a) and ^{13}C (b) emission by ^{13}C -labelled rhizodeposit- and microbe-accumulated
537 C-treated soils over the 300-d incubation period. Values and error bars represent means \pm SE ($n = 4$).
538 Different letters indicate significant differences at $p < 0.05$ (Duncan multiple range test). Rhizo-C,



539 paddy soil containing ^{13}C -labelled rhizodeposits; Micro-C, paddy soil containing ^{13}C -labelled
540 microbe-accumulated C; CK, unlabelled and unplanted soil without supplementation.
541



542 **Figure 1**

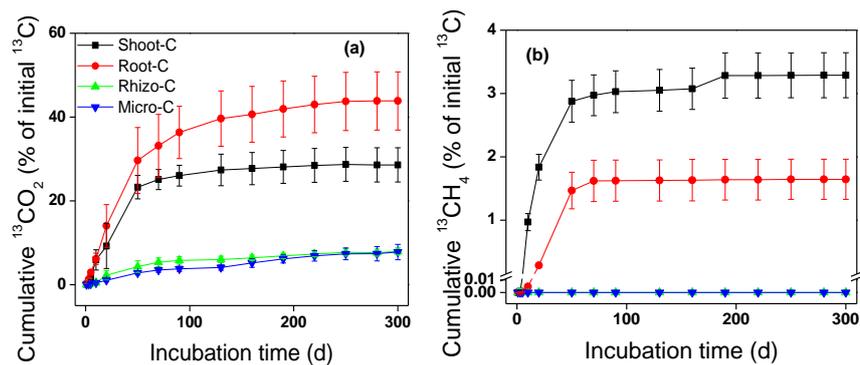


543

544



545 **Figure 2**

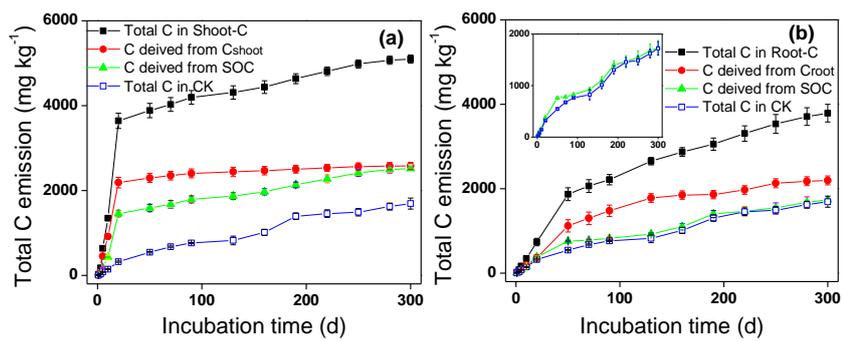


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548 **Figure 3**

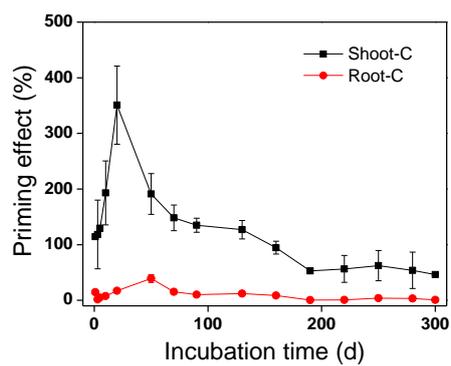


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551 **Figure 4**

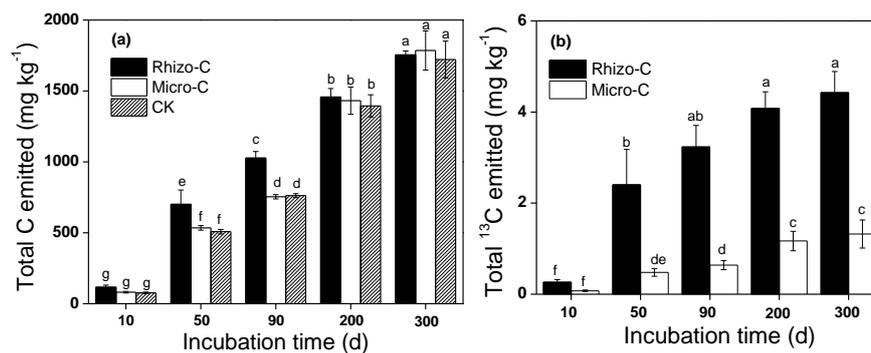


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553



554 **Figure 5**



555