Soil Biology and Biochemistry 144 (2020) 107787

Contents lists available at ScienceDirect

Soil Biology and Biochemistry

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

Soil DOC release and aggregate disruption mediate rhizosphere priming effect on soil C decomposition

Yanghui He [a,b], Weixin Cheng [b], Lingyan Zhou [a], Junjiong Shao [a], Huiying Liu [a], Huimin Zhou [a], Kai Zhu [b], Xuhui Zhou [a,c,*]

[a] Center for Global Change and Ecological Forecasting, Zhejiang Tiantong Forest Ecosystem National Observation and Research Station, Shanghai Key Lab for Urban Ecological Processes and Eco-Restoration, School of Ecological and Environmental Sciences, East China Normal University, Shanghai, 200241, China
[b] Environmental Studies Department, University of California, Santa Cruz, CA, 95064, USA
[c] Shanghai Institute of Pollution Control and Ecological Security, 1515 North Zhongshan Rd, Shanghai, 200437, China

ARTICLE INFO

Keywords:
Photosynthesis
Rhizosphere processes
Soil carbon decomposition
Soil aggregation
Dissolved organic carbon
Plant–soil interactions

ABSTRACT

Roots and the associated rhizospheric activities regulate the mineralization of native soil organic matter (SOM), which is referred to as the rhizosphere priming effect (RPE). Although the importance of RPE for carbon cycle has increasingly been recognized, experimental evidence for how soil structural changes modulate the RPE is still unavailable. We addressed this issue by growing soybean plants (C_3) in a C_4-derived soil in a continuous ^{13}C-labeling greenhouse. We hypothesized that root-induced soil structural change regulated the RPE by destabilizing soil matrix-protected organic carbon. Our results showed that the RPE was tightly coupled with plant photosynthetic activity, the disruption of coarse macro-aggregates, and the increased release of dissolved organic carbon (DOC) from the soil matrix. These findings indicate that living roots together with rhizodeposits not only can directly stimulate rhizospheric microbial activities, but also can make soil matrix-protected organic carbon available to microbial attacks and further enhance the RPE. This study suggests that the RPE on SOM mineralization is intimately linked with the dynamics of soil structures and DOC, which should be considered in future studies on mechanistic understanding and modeling of the RPE.

1. Introduction

Globally, the amount of soil organic carbon (SOC) stored in the upper 1 m is estimated to be 1500 Pg, which is approximately twice as large as that in the atmosphere and three times in plant biomass (Schlesinger, 1997; Jobbágy and Jackson, 2000). Small changes in SOC can lead to a significant impact on atmospheric CO_2 concentration (Smith et al., 2008), highlighting the importance of SOC in global climate change. A consensus is emerging that root activities can either inhibit or stimulate the decomposition rate of native SOC, which is known as the 'rhizosphere priming effect' (RPE, Cheng and Kuzyakov, 2005; Finzi et al., 2015). Recent analyses suggested that the magnitude of the RPE could range from 50% reduction to 400% increase in SOC decomposition rates as compared to the decomposition rate in the unplanted control soil under the same environmental conditions (Cheng et al., 2014; Huo et al., 2017). Although the RPE can play a critical role in the C cycle, the underlying mechanisms behind the RPE have not been completely understood (Kuzyakov, 2010; Cheng et al., 2014).

Several hypotheses have been proposed as the mechanisms causing the RPE. The microbial activation hypothesis states that root exudates provide readily bioavailable substrates for rhizosphere microorganisms (Fontaine et al., 2003; Bais et al., 2006; McCormack et al., 2017), which may stimulate the production of extracellular enzymes, thus resulting in an increase in co-metabolic mineralization of native soil C and a positive RPE (Hamer and Marschner, 2005; Brzostek et al., 2013; Zhu et al., 2014). However, the so-called negative RPE can be attributed to the nutrient competition hypothesis, suggesting that plants inhibit microbial growth and metabolism by competing with microorganisms for mineral nutrients (Cheng and Kuzyakov, 2005; van der Heijden et al., 2008; Kuzyakov and Xu, 2013). Moreover, the preferential substrate utilization hypothesis states that soil microbes prefer root exudates to native soil organic matter (SOM) when mineral nutrients are abundant (Cheng, 1999), causing a decrease in native SOC decomposition and thus the negative RPE.

The above-mentioned hypothetical mechanisms underlying the RPE mainly focus on the biotic interactions between plants and microbial

* Corresponding author. School of Ecological and Environmental Sciences, East China Normal University, Shanghai, China.
E-mail address: xhzhou@des.ecnu.edu.cn (X. Zhou).

https://doi.org/10.1016/j.soilbio.2020.107787
Received 31 January 2019; Received in revised form 1 February 2020; Accepted 15 March 2020
Available online 16 March 2020
0038-0717/

activities. However, these mechanisms alone cannot fully explain the RPE, because microbial and enzymatic access to substrate C is severely limited by protective associations. For example, soil aggregation has a strong impact on SOM turnover (Six et al., 2004; Rasse et al., 2005; Schmidt et al., 2011). The inaccessibility of SOM to microbial decomposers within soil macro- and micro-aggregates and their anoxic conditions reduce the activity of soil micro-organisms, leading to physical protection of native SOM (Six et al., 2002). Previous studies propose that living roots profoundly affect the destruction and formation of soil aggregates, which may facilitate the release of aggregate-protected C into more accessible pools (Magid et al., 1999; Kuzyakov, 2010). Another mechanism underlying SOC stability is the interaction of SOM with clay minerals, which protects SOC from being immediately accessed and decomposed by microbes (Schulten and Leinweber, 2000; Mikutta et al., 2006; Kleber et al., 2015). This clay protection mechanism is particularly relevant to the RPE because root exudates (e.g., organic acids) can facilitate the release of mineral-protected C (Keiluweit et al., 2015). Despite the crucial role that changes in soil physical structures induced by roots (including destruction and formation) may play in the RPE, direct experimental evidence is still absent.

Here we tested whether the RPE was modulated by root-induced changes in soil structure. We intended to manipulate the levels of the RPE by changing light intensity, since plant photosynthesis has been considered as a determinant of root exudation and rhizosphere processes (Badri and Vivanco, 2009; Shahzad et al., 2012). In a well temperature-controlled greenhouse, soybeans (*Glycine max* (L.) Merr., a C_3 plant) were grown in a C_4-derived soil (which was from Kansas grassland dominated by C_4 plants), and subjected to two light intensities (100% and 54% of full light). By combining the natural ^{13}C abundance and continuous ^{13}C-depleted CO_2-labeling approaches, we augmented the ^{13}C-labeling signal strength to partition root-derived carbon from soil-derived carbon more precisely. In this study, we quantified the RPE by measuring the rate of SOM-derived CO_2 release in planted treatments minus the rate from the bare soil treatment. Changes in the aggregate fractions and the $\delta^{13}C$ values of aggregate-associated C, as well as DOC dynamics and their $\delta^{13}C$ values, were measured to investigate the changes in the soil protective associations. We hypothesized that the RPE in the shading treatment would be lower than those in the full light treatment because microbial activities increased in the presence of root exudates from photosynthesis (Nagel et al., 2006). We also hypothesized that the disruption of the protective associations could be intensified by roots, thereby stimulating native SOM mineralization.

2. Materials and methods

2.1. Experimental setup

The experiment was conducted in a temperature-controlled greenhouse equipped with continuous labeling with ^{13}C-depleted CO_2 (−37.5‰) at the University of California, Santa Cruz. A constant CO_2 concentration (400 ± 5 ppm) and $\delta^{13}C$ value (−18 ± 0.5‰) inside the greenhouse were maintained by automatically adjusting the flow rate of CO_2-free air and pure CO_2 into the greenhouse throughout the experiment. When the CO_2 concentration inside the greenhouse declined to 390 ppm, a pulse of ^{13}C-depleted pure CO_2 from a gas tank was injected into the greenhouse. This labeling method has been conducted successfully before (Dijkstra and Cheng, 2007a; Zhu and Cheng, 2011), and more details can be found in Dijkstra and Cheng (2007b) and Pausch et al. (2013).

We filled 30 bottom-capped PVC pots (diameter 15 cm, height 40 cm, equipped with an inlet tube at the bottom for aeration and CO_2 trapping) with soil taken from a C_4-grass dominated area at Konza Prairie Biological Station, Kansas, USA. The soil is a clay loam Mollisol, collected from the Ah horizon (0–30 cm). The soil contained 20.5 mg organic C g^{-1} soil and 2.1 mg N g^{-1} soil, with a pH value of 7.1. Vegetation at this site was dominated by C_4 grasses, and the $\delta^{13}C$ value of the SOC was −15.4‰. A nylon bag filled with 5.5 kg washed sand was placed at the bottom of each PVC pot. Four kilograms of air-dried, sieved (passing a 4-mm screen) Kansas soil was packed into each pot. After adjusting the soil moisture to 60% water-holding capacity (0.3 mL deionized water per g dry soil), we pre-incubated these 30 pots inside the greenhouse for 1 week. Ten pre-soaked seeds of soybean were sown in each pot (10 shading pots and 10 full light pots) and 10 pots were kept unplanted as a control. After 7 days of germination, seedlings were thinned to three plants per pot.

The shading cloth (hard plastic cradle 170 cm long, 100 cm wide and 150 cm high, wrapped with a black porous nylon net) was placed after the early vegetative growth stage (35 days after planting) and moved inside the greenhouse every week. Ten pots were covered by the shading cloth and moved randomly every two days. The light intensity in shading treatment was approximately 54% of that in no-shading treatment, which was measured by LI-250 (LI-COR, Lincoln, NE, USA). There were two destructive sampling times, namely at the vegetative growth stage (T_{14}, shading for 14 days) and the flowering period (T_{35}, shading for 35 days). The experiment was set up as a complete factorial randomized design with five replicates for each treatment and the control.

During the experimental period, the air temperature inside the greenhouse was kept at 25 °C during the daytime and about 15 °C during the night by two air conditioning units and heaters. The relative air humidity was maintained at 50% by a dehumidifier. Supplemental lighting (1100-W lights) was used to ensure an adequate light intensity. Soil moisture content was measured gravimetrically and maintained at 60% water holding capacity. To avoid deterioration of the soil structure, deionized water was added through perforated tubes on the surface of each pot. To prevent anaerobic conditions, ambient air was forced into each pot twice per night (20:00–20:30 p.m., 4:00–4:30 a.m.) by timer-controlled aquarium pumps. The location of the pots in the greenhouse bench top was randomly changed weekly to guarantee similar growing conditions for the soybeans.

2.2. Measurements and calculations

2.2.1. Soil CO_2 efflux and RPE

Soil CO_2 efflux from each pot was measured with a closed circulation CO_2 trapping system (Cheng et al., 2003) at 14 days (T_{14} treatment) and 35 days (T_{35} treatment) after shading. Prior to measurement, each pot was sealed with two-components silicone rubber placed around the base of the plant, and residual CO_2 within the pot was absorbed by circulating the isolated air through a soda lime column (3 cm diameter, 50 cm length) for 1 h. The CO_2 produced subsequently was trapped in 300 mL of a 0.3 M NaOH solution for 24 h in planted pots and 48 h in non-planted pots. Three blanks were used to correct for handling errors. An aliquot of the NaOH solution was analyzed for total inorganic C with a Shimadzu analyzer (TOC 5050A). Another aliquot of the trapping solution was precipitated as $SrCO_3$ (Harris et al., 1997), and the $\delta^{13}C$ of the oven-dried precipitate was analyzed with a PDZ Europa ANCA-GSL elemental analyzer interfaced with a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK).

A two-source mixing model was used to separate the total soil CO_2 efflux (CO_2-C_{total}) into soil-derived CO_2 (SOM decomposition, CO_2-C_{soil}) and root-derived CO_2 (CO_2-C_{root}):

$$CO_2\text{-}C_{soil} = CO_2\text{-}C_{total}\ (\delta^{13}C_{total} - \delta^{13}C_{root})/(\delta^{13}C_{soil} - \delta^{13}C_{root}) \quad (1)$$

$$CO_2\text{-}C_{root} = CO_2\text{-}C_{total} - CO_2\text{-}C_{soil} \quad (2)$$

where $\delta^{13}C_{total}$ is the $\delta^{13}C$ value of the total CO_2 efflux in planted treatments and $\delta^{13}C_{root}$ is the $\delta^{13}C$ value of root-derived CO_2. Given the isotopic fractionation between roots and root-respired CO_2, the $\delta^{13}C_{root}$ was calculated according to the $\delta^{13}C$ value of roots and the ^{13}C depletion of root-derived CO_2 compared with roots (1.71‰, Zhu and Cheng, 2011; Pausch et al., 2013). The $\delta^{13}C_{soil}$ is the mean $\delta^{13}C$ value of SOM-derived

CO_2, which was measured in the unplanted control treatments.

The observed primed C (referred to as the RPE) was calculated by subtracting soil-derived CO_2 in the planted treatments (CO_2-$C_{S\text{-planted}}$) from that in the control treatments (CO_2-$C_{S\text{-control}}$):

$$\text{Primed C} = CO_2\text{-}C_{S\text{-planted}} - CO_2\text{-}C_{S\text{-control}} \quad (3)$$

2.2.2. Harvesting and soil analyses

Before CO_2 trapping, soil dissolved organic C (DOC) from each pot was measured at two growth stages (i.e., T_{14} and T_{35}). A plastic bottle was connected with the inlet tube at the bottom of pot, and the other end was linked to an aquarium pump. We added the deionized water to the pot through the perforated tubes, and soil solutions (500 mL) were collected in the plastic bottle. An aliquot of each solution was analyzed for total organic C with a Shimadzu TOC-5050A analyzer. Another aliquot of the water sample was measured to obtain the $\delta^{13}C$ of DOC with an O.I. Analytical Model 1030 TOC Analyzer (Xylem Analytics, College Station, TX) interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK) and a GD-100 Gas Trap Interface (Graden Instruments).

After CO_2 trapping, the pots were immediately sampled destructively. Harvested plants were separated into shoots and roots, and the fine roots were collected by hand-picking. Each plant sample was dried in an oven at 65 °C for 48 h and weighted, ground in a ball mill and analyzed for total C and $\delta^{13}C$ using a Carlo Elba 1108 elemental analyzer interfaced to an isotope ratio mass spectrometer (PDZ Europa 20-20). One subsample of about 1000 g of homogenized fresh soil was taken from each pot, stored in a refrigerator at 4.0 °C and used for further analysis. Another soil sample was dried at 85 °C for 48 h, weighed to determine the soil moisture, and measured for total C and $\delta^{13}C$ with a mass spectrometer.

Soil microbial biomass C (MBC) was measured via the chloroform fumigation–extraction method (Vance et al., 1987). Briefly, a subsample of fresh soil (50 g) was exposed to ethanol-free chloroform for 48 h in the dark under vacuum and then extracted with 80 mL 0.5 M K_2SO_4. Another nonfumigated control was extracted by 80 mL of a 0.5 M K_2SO_4 solution. Total organic C in the extracts was determined by the TOC analyzer. The difference in extractable C between the fumigated and non-fumigated soils was assumed to have been released by lysed soil microbes. The released C was converted to MBC by a proportionality coefficient ($K_{EC} = 0.45$).

The soil aggregate size fractions were separated as coarse macro-aggregates (>2000 μm), fine macro-aggregates (250–2000 μm), micro-aggregates (53–250 μm), and silt and clay fractions (<53 μm) through a wet sieving method (Six et al., 2000). Briefly, one subsample (100 g of dried soil) was placed on the top of a nest of three sieves with 2000-, 250- and 53-μm openings, and submerged in deionized water for 5 min. The sieves were then manually moved up and down 3 cm with 50 repetitions during 2 min. The fraction remaining on each sieve and silt & clay fraction that passed through the 53-μm sieve was collected in beakers and dried at 85 °C for 48 h in an oven. All aggregate-size fractions were ground in a ball mill and analyzed for total C and $\delta^{13}C$ with a mass spectrometer.

2.3. Statistical analyses

We used one-way analysis of variance (ANOVA) to test for significant differences in all measured data among the control, shading and full light treatments. Differences among treatments were assessed by post-hoc tests using Fisher's protected least significant difference (LSD) test for all variables, and the significance level was set at 0.05. Linear regression analysis was conducted to identify the relationships of the RPE with root respiration, root, shoot and total biomass in shading and full light treatments, respectively. We used SPSS Statistics 23 (SPSS. Inc., Chicago, IL, USA) to perform the ANOVA and R statistical software v3.2.4 (R Development Core Team, 2016) to perform the regression analysis.

3. Results

3.1. Plant biomass and ^{13}C values

Soybeans grew normally in the greenhouse. At the first sampling time (14 days after shading, T_{14}), soybeans were at the vegetative growth stage. Both shoot and root biomass were significantly higher in the full light than that in the shading treatment ($P < 0.05$). This pattern became stronger at the second sampling time (35 days after shading, T_{35}) when soybeans were at the flowering period (Table 1).

The $\delta^{13}C$ value of shoots and roots ranged from −35.34 to −37.33‰ and −33.05 to −35.46‰, respectively (Table 1), showing that the soybeans were successfully labeled with ^{13}C-depleted CO_2 compared to those values in the unlabeled tissues (−24 to −27‰). On average, all plant tissues in the shading treatments were 1.64–2.24‰ more ^{13}C-depleted than those in the no-shading ones, and shoots were 1.82–2.64‰ more ^{13}C-depleted than roots (Table 1).

3.2. Soil CO_2 efflux and rhizosphere priming effect (RPE)

The total CO_2 efflux from the soil ranged from 12.7 to 17.1 mg C day^{-1} kg^{-1} soil in the unplanted soils, which is significantly lower than that in the planted soils (36.3–55.3 mg C day^{-1} kg^{-1} soil) across two sampling times ($P < 0.05$). The total CO_2 efflux in the shading treatment was significantly lower than that in the full light systems ($P < 0.05$, Table 1). Total CO_2 efflux was partitioned into root- and soil-derived components according to Eqs. (1) and (2). Root-derived CO_2 efflux was 48.27% and 49.89% higher in the full light treatment than that in the shading treatment at T_1 and T_2, respectively (Fig. 1).

Table 1
Shoot and root biomass and $\delta^{13}C$ values, and total CO_2 efflux (C_{total}) and total $\delta^{13}C$ value. Values represent mean ± standard errors ($n = 5$). Significant differences ($P < 0.05$) between the treatments at one sampling date are indicated by different letters.

Sampling stage	Treatment	Shoot biomass (g per pot)	Root biomass (g per pot)	Root–shoot ratio	Shoot $\delta^{13}C$ (‰)	Root $\delta^{13}C$ (‰)	C_{total} (mg C day^{-1} kg^{-1} soil)	C_{total} $\delta^{13}C$ (‰)
T_{14} (14 days)	Control						17.08 ± 1.47a	−15.57 ± 0.22b
	Shading	8.01 ± 0.76a	4.24 ± 0.34a	0.53 ± 0.02a	−37.33 ± 0.19a	−34.69 ± 0.22a	36.30 ± 0.66b	−22.90 ± 0.30a
	Full light	10.40 ± 0.42b	5.79 ± 0.37b	0.56 ± 0.04a	−35.61 ± 0.10b	−33.05 ± 0.18b	44.74 ± 2.43c	−23.61 ± 0.26a
T_{35} (35 days)	Control						12.72 ± 0.31a	−15.46 ± 0.25b
	Shading	22.98 ± 1.24a	4.48 ± 0.29a	0.20 ± 0.01a	−37.29 ± 0.31a	−35.46 ± 0.25a	42.83 ± 1.57b	−24.60 ± 0.46a
	Full light	30.94 ± 1.71b	7.42 ± 0.39b	0.24 ± 0.01b	−35.34 ± 0.22b	−33.22 ± 0.18b	55.31 ± 2.41c	−24.90 ± 0.37a

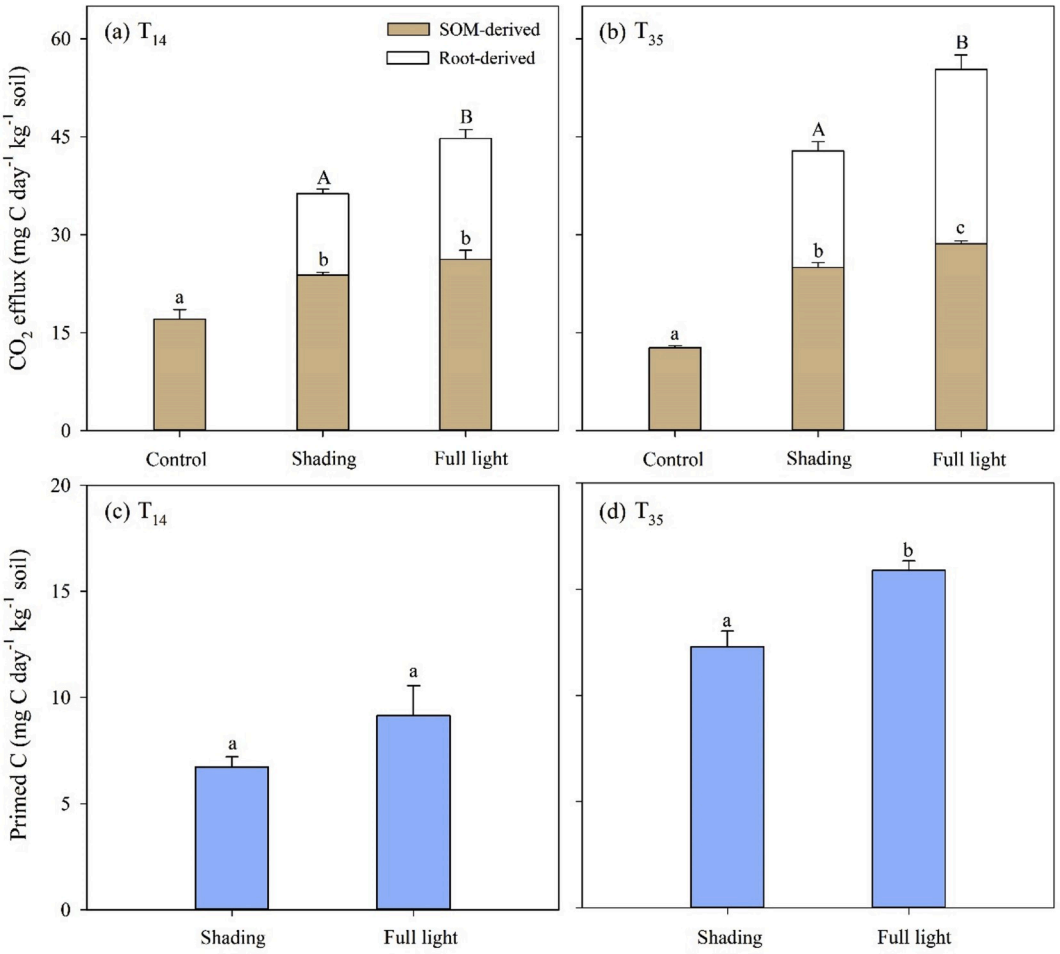

Fig. 1. CO_2 effluxes (root- and SOM-derived) and primed C after 14 (T_{14}, a and c) and 35 days (T_{35}, b and d) of shading. Different letters indicate significant differences ($P < 0.05$) among treatments. Error bars indicate the standard errors ($n = 5$).

The primed C (referred to as the RPE) was calculated as the difference in soil-derived CO_2 efflux between the planted and unplanted treatments (Eq. (3)). SOC decomposition rate in soil-plant combinaions were increased by 39–125% compared to that in the unplanted control treatment. The primed C in shading and full light treatments was 6.7 and 9.1 mg C kg $soil^{-1}$ day^{-1} respectively at T_{14}, and 12.3 and 15.9 mg C kg $soil^{-1}$ day^{-1} at T_{35}. The primed C was significantly higher in full light treatment than in shading treatment at T_{35}, but not at T_{14} (Fig. 1). The primed C increased linearly with root-derived CO_2 efflux, total and shoot biomass across two sampling times in both full light and shading treatments, but did not change significantly with root biomass (Fig. 2).

3.3. Soil aggregate structure and ^{13}C values in each fraction

The distribution of soil aggregate fractions as a proportion of the whole soil mass varied little, but significantly among three treatments (i.e., control, full light, shading; Fig. 3). At T_{14}, the proportion of coarse macro-aggregates (>2000 μm) in control was higher than that in shading treatment ($P < 0.05$), and marginally higher than that in full light treatment ($P = 0.07$). The proportion of fine macro-aggregates (250–2000 μm) in control was smaller than that in shading treatment ($P < 0.05$), but no significant difference was found between control and full light treatment. The micro-aggregates (53–250 μm) increased in the order: control < shading < full light, but there were no significant differences among treatments in the silt and clay fractions (<53 μm, Fig. 3a). These results suggested that roots slightly increased the breakdown of coarse macro-aggregates at T_{14}. At T_{35}, there was no change in macro-aggregate fractions, the proportion of micro-aggregates was higher in the planted than the unplanted treatments, but the silt and clay fractions decreased in the order: control > shading > full light (Fig. 3b). Overall, roots enhanced the abundance of micro-aggregates at T_{35}.

The SOC concentration and its $\delta^{13}C$ values of each fraction were also measured. The sampling time and shading treatment did not significantly affect SOC concentration in the whole soil or aggregate fractions (Table S1). Moreover, the $\delta^{13}C$ values of macro-aggregates showed no significant difference among treatments at either T_{14} or T_{35}, but the $\delta^{13}C$ values of micro-aggregates in the planted treatment were less negative than those in the control. The opposite trend was observed for the $\delta^{13}C$ values of silt and clay fractions (Fig. 3c and d), and no changes were showed in SOC concentration among different treatments, displaying that root-derived C was mainly incorporated into the silt and clay fractions.

3.4. Microbial biomass C (MBC) and DOC

Compared with the unplanted treatment, MBC was higher in the shading treatment ($P < 0.05$), but showed no difference in the full light treatment at T_{14}. MBC was 28% and 44% higher in the shading and full light treatments than in the control treatment at T_{35}, respectively. Meanwhile, shading induced an 11% decrease in MBC compared with the full light treatment ($P < 0.05$, Fig. 4b).

The deionized water was percolated downward through the soil layers to obtain the leachate of each treatment. The color of the leachate

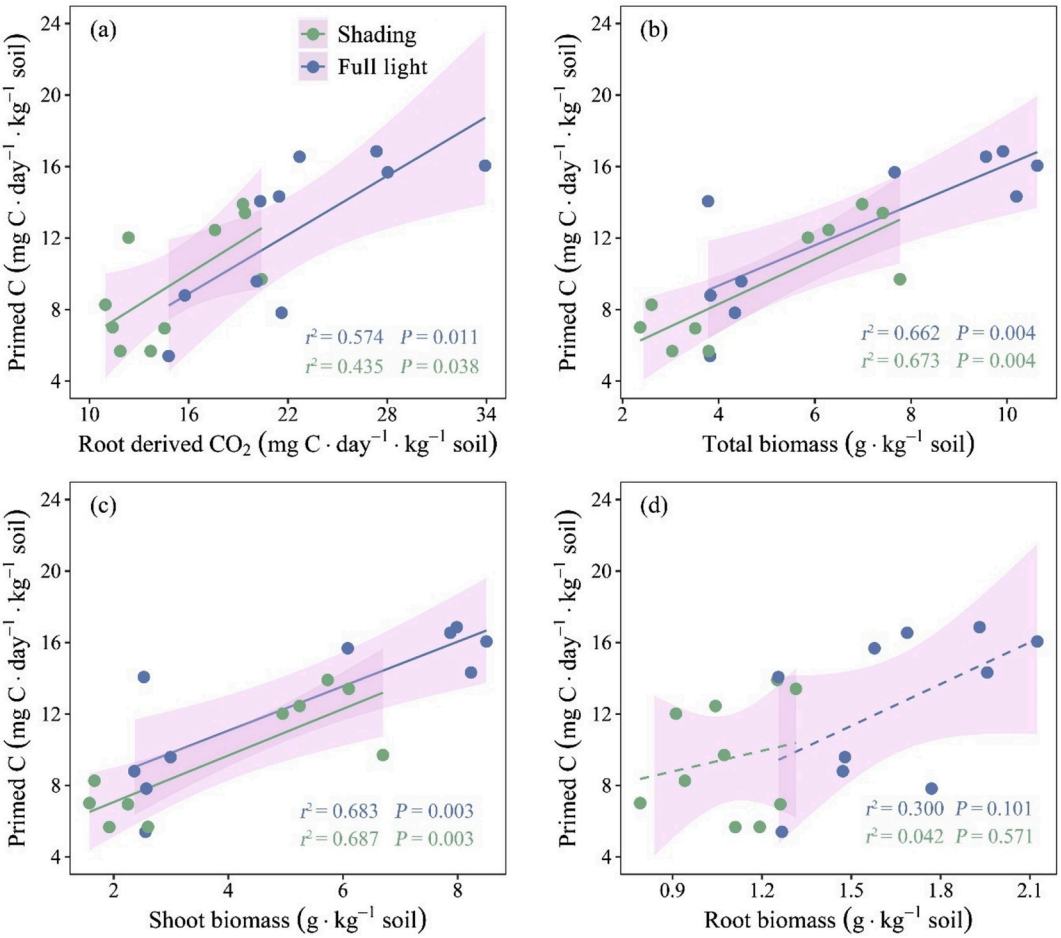

Fig. 2. Relationships of primed C with root-derived CO_2 flux (a), root biomass (b), shoot biomass (c) and plant total biomass (d). Data for (a), (b), (c) and (d) include two samplings and two treatments (green circles indicate shading; blue circles indicate the full light treatment). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

in planted systems was more intense than that in the control (Fig. 4a). The concentration of DOC was 22% and 45% higher in the shaded and full light treatments than in the control treatment at T_{14}, respectively, and 46% and 36% higher at T_{35}. However, DOC in the shading treatment did not significantly differ from that in the full light treatment at either T_{14} or T_{35} ($P > 0.05$, Fig. 4c). Meanwhile, no significant difference in the $\delta^{13}C$ of DOC was observed among all the treatments (Fig. 4d), and the more negative ^{13}C signal (−35‰) of the plant-derived C was absent in DOC samples from all planted treatments, showing that the increased DOC in the planted treatments primarily came from SOM, not from root exudates that should have a $\delta^{13}C$ value of approximately −35‰ similar to that of roots.

4. Discussion

4.1. Rhizosphere priming effect (RPE) driven by photosynthesis

Aboveground assimilation of CO_2 (i.e., plant photosynthesis) strongly controls belowground respiratory processes (Högberg et al., 2001; Heimann and Reichstein, 2008). Our study showed that shading decreased the RPE on SOC decomposition (i.e., primed C) and that the 'primed C' was positively correlated with root-derived CO_2 and total plant biomass (Figs. 1 and 2), suggesting a tight coupling between photosynthesis and rhizosphere processes. A recent study also displayed that clipping-induced decrease in photosynthesis dramatically reduced soil respiration and the RPE within 24 h (Shahzad et al., 2012). As the control of plant photosynthesis on the RPE were confirmed across different soil and plant types (Kuzyakove and Cheng, 2001, 2004; Tang et al., 2019), gross primary productivity might be a useful index to incorporate the RPE into models at the ecosystem and global scales.

The primed C were positively correlated with root-derived CO_2 efflux and shoot biomass within each treatment (Fig. 2a and c), indicating the regulatory influence of root exudation on the RPE (Paterson and Sim, 2013; Shahzad et al., 2015). In this study, shading decreased the growth rate and shoot biomass (Table 1), possibly inducing a lower rate of root exudation (as indicated by root-derived CO_2). Although we did not directly measure root exudation, it is reasonable to assume that the level of exudation is proportional to the root-derived CO_2 (Bahn et al., 2009; Zhu et al., 2014; Yin et al., 2018). Subsequently, the decrease of root exudation after shading caused a smaller PRE. Meanwhile, our results showed that the RPE increased with microbial biomass at T_{35} (Figs. 1 and 4b). On the basis of the microbial activation mechanism, the exuded organic compounds and sloughed-off root cells, which largely stem from photosynthetically fixed C as the energy source, might stimulate the activity of soil microorganisms and production of extracellular enzyme, thereby accelerating the native SOC decomposition (Fig. 5a, Fontaine et al., 2011; Phillips et al., 2012; Dijkstra et al., 2013; Yin et al., 2019). However, in our experiment, no significant relationship between the RPE and root biomass were observed either in shading or full light treatments (Fig. 2d), which is largely in accordance with previous studies (Zhu et al., 2014; Huo et al., 2017). These results might imply the much less contribution of root litter to the RPE than root exudates (Shahzad et al., 2015).

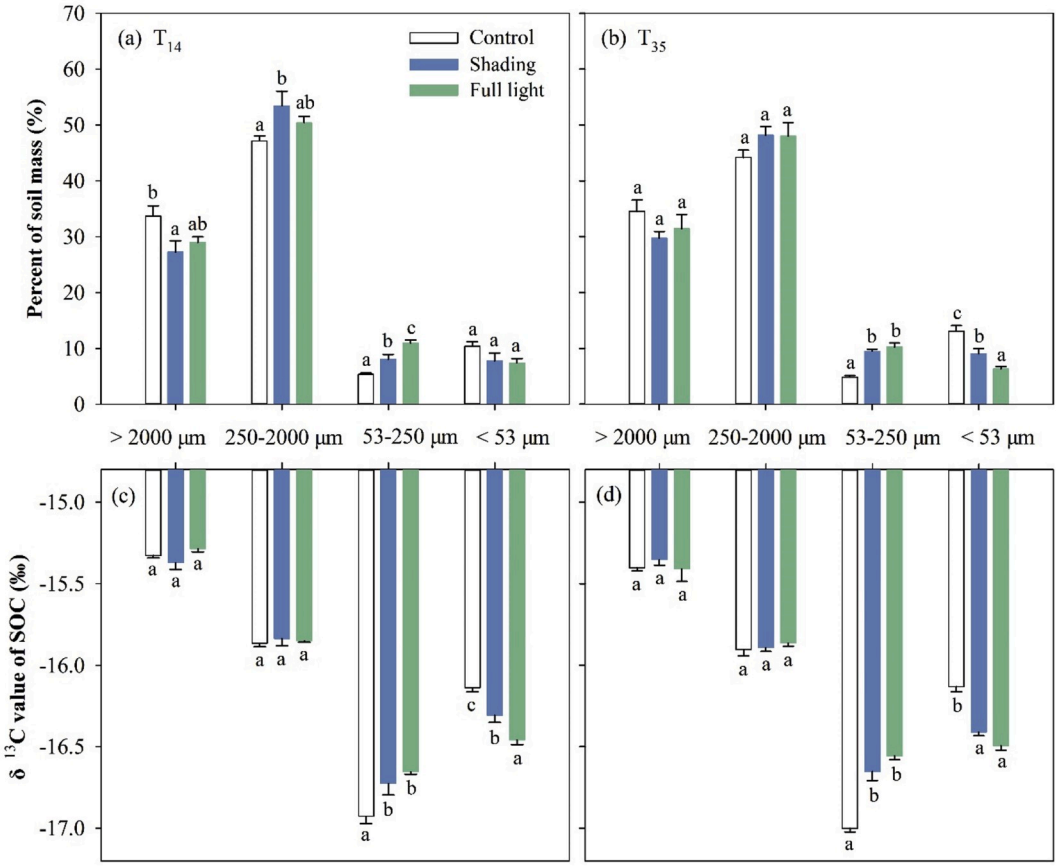

Fig. 3. Proportion of soil aggregates (a and b) and $\delta^{13}C$ of SOC (c and d) within soil aggregate fractions (coarse macro-aggregates, >2000 μm; small macro-aggregates, 250–2000 μm; micro-aggregates, 53–250 μm; silt and clay fractions, <53 μm) after 14 (T_{14}) and 35 days (T_{35}) of shading. Different letters indicate significant differences ($P < 0.05$) among treatments. Error bars indicate the standard errors ($n = 5$).

4.2. RPE regulated by destabilization of aggregate-protected soil C

The RPE can be affected by changes in soil structure, because microbial access to substrate C is strongly limited by the soil physical structures (i.e., soil aggregates and mineral–organic associations) in most soils (Ohm et al., 2007; Rasmussen et al., 2007; Keiluweit et al., 2015). By using a soil aggregate fractionation technique, we showed that the proportion of coarse macro-aggregates in the planted soil was lower than that in bare soil at T_{14}, but the proportions of micro-aggregates exhibited the opposite patterns. Meanwhile, the $\delta^{13}C$ value of micro-aggregates in the control was more depleted than that in the planted treatments (Fig. 3). Together, these changes indicated that coarse macro-aggregates might be broken down into fine macro- and micro-aggregates, which was probably caused by root penetration and compression, and increased wet–dry cycling of the adjacent soil (Materechera et al., 1994; Angers et al., 1997; Gale et al., 2000; Bronick and Lal, 2005; Zhu and Cheng, 2013). We hypothesized that following the fragmentation of coarse macro-aggregates, the organic compounds originally protected by aggregates were exposed to soil microbes, extracellular enzymes and oxygen (Six et al., 2000; von Lützow et al., 2007), then resulting in a positive RPE (Fig. 5b). Given that these net changes in aggregate fractions due to roots and rhizosphere effects were not as high as expected, further studies on this potential mechanism are definitely needed, especially the potential effect of roots on soil aggregate turnover rates which was not quantified in this current study.

The planted treatments had more negative $\delta^{13}C$ values in the silt and clay fractions compared to the control (Fig. 3c and d), but no change in SOC concentration (Table S1), indicating that new plant-derived C was incorporated into the silt and clay fractions through adsorption processes (Hassink and Whitmore, 1997; Six et al., 2002). Sorption of organic compounds to mineral (i.e., clay and silt particles) surfaces provided reactive places for physical and chemical stabilization, formed intricate associations, and led to a long-term stabilization of SOM (Kleber et al., 2007; Lehmann and Kleber, 2015; Newcomb et al., 2017). However, root exudates (including the oxalic acid and citrate molecules) act as ligands liberating C from previously protective associations with minerals through complexation and dissolution reactions, causing SOM destabilization (Clarholm et al., 2015; Keiluweit et al., 2015). Therefore, new plant-derived C incorporated into the silt and clay fractions in our study could promote the accessibility of the original protected C to microbes and enzymes, inducing positive RPE (Fig. 5b). Our study suggests that the destruction of coarse macro-aggregates induced by roots and/or replacement of originally protected C in silt and clay fractions with root exudates could significantly modulate the RPE, and future investigations should focus on quantifying their relative contributions in different soil matrix.

4.3. RPE modulated by the release of DOC

Pedogenic DOC plays an important role in soil biogeochemical processes, as it acts as a substrate for microorganisms, enables redox-related activities, and contributes to the C balance of terrestrial ecosystems (Qualls and Haines, 1992; Neff and Asner, 2001; Kindler et al., 2011). We found that soil DOC concentration was 22%–46% higher in the planted than the unplanted treatments across two sampling times, but there was no significant difference in the $\delta^{13}C$ signal of DOC between planted and unplanted treatments (Fig. 4c and d) and the ^{13}C-depleted root-derived C was absent in DOC samples. These results clearly indicated that the increased DOC in the planted treatments primarily originated from SOM, not from plant-derived rhizodeposits. The potential

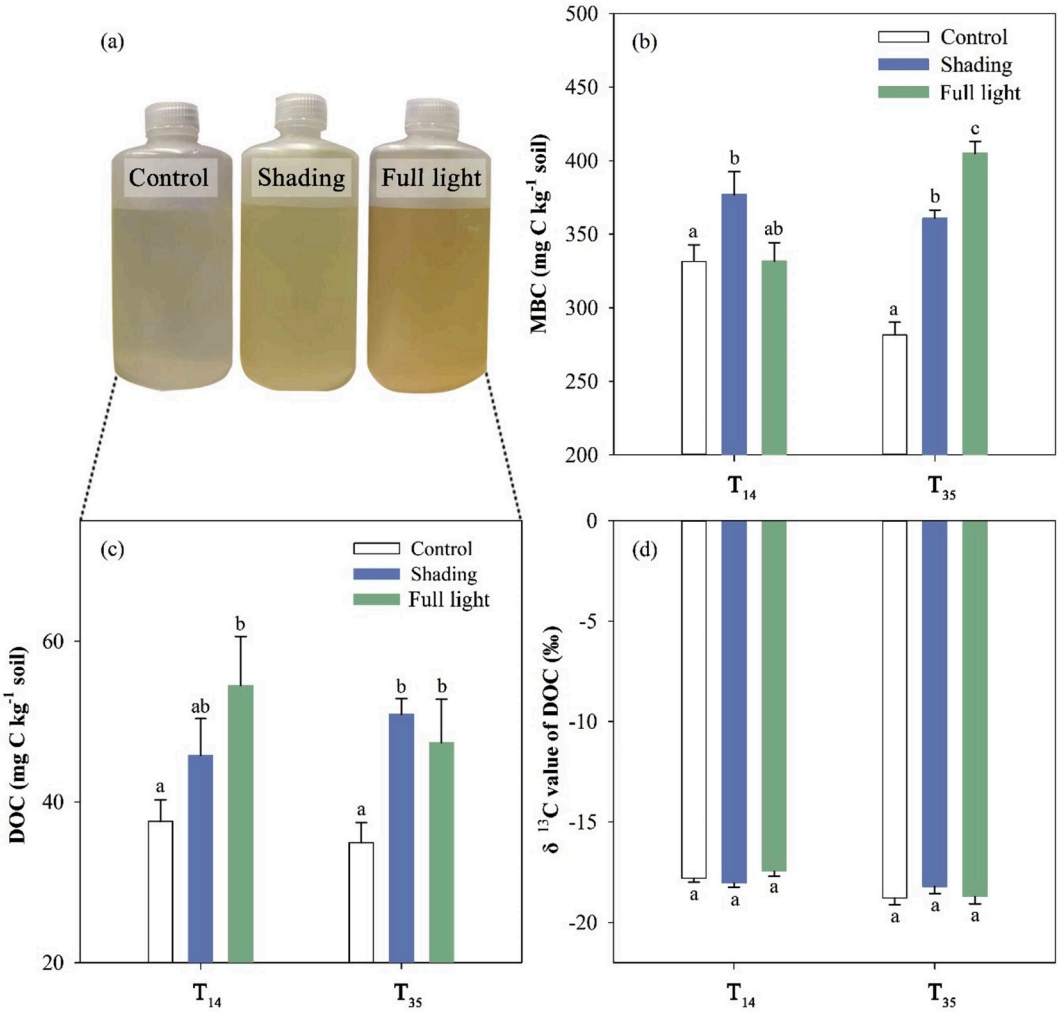

Fig. 4. The photograph (a) shows the leachate from different treatments after 35 days of shading. Microbial biomass carbon (MBC, b), dissolved organic carbon (DOC, c) and its $\delta^{13}C$ (d) after 14 and 35 days of shading. Bars labeled by different letters indicate significant differences ($P < 0.05$) among treatments. Error bars indicate standard errors of the mean ($n = 5$).

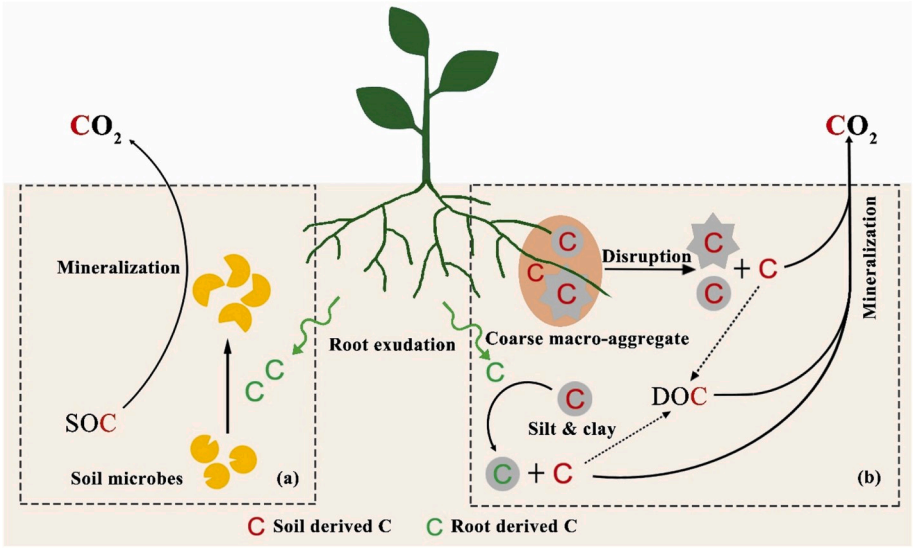

Fig. 5. Mechanisms of rhizosphere priming on soil organic matter decomposition. **(a)** The traditional view is that roots exudates provide a readily bioavailable supply of energy for the decomposition of native soil carbon through stimulating microbial growth and activity. **(b)** The alternative mechanism proposed here takes into account that large quantities of soil C are inaccessible to microbes owing to soil physical protection. Plant roots facilitate the breakdown of coarse macro-aggregates and destabilize the originally protected C. Meanwhile, root exudates are incorporated into the silt and clay fractions and destabilize old C. The disruption of coarse macro-aggregates and the release of C from the silt and clay fractions, promoting that the original protected organic C converges on DOC pools and exposed to the decomposed microbes.

sources of DOC release in the planted system might be new root exudates in exchange for stabilized SOC, the physical disruption of the aggregates, and the desorption processes of original organo-mineral complexes. Mechanical disruption of macro-aggregates likely release SOM protected by soil physical structure, increase the extractability of the non-biomass SOM, enhance DOC leaching and microbial activity (Miller et al., 2005; Mueller et al., 2012). In addition, new root exudates absorb or co-precipitate with reactive mineral phases, mobilize and replace the originally sorbed ones (Sanderman et al., 2008; Kaiser and Kalbitz, 2012), which could partly explain the remarkable rise in DOC. Our results revealed an alternate mechanism that living roots and their exudates destabilize SOM supramolecules to release DOC for local microbes, indicating that rhizosphere processes would be a quantitatively important driver for the release of nutrients.

Since DOC is considered as an easily decomposable substrate for soil microorganisms (Zsolnay, 1996; Marschner and Kalbitz, 2003), the activation of SOM-derived DOC would accelerate SOC decomposition, thereby inducing a positive RPE (Fig. 5), which have major implications to SOC stabilization and sequestration. DOC is a reactive intermediate pool that stabilizes and possibly primes deep soil C. DOC and its movement through soils would be a source of the stabilized C occurring in subsoil horizons (Schmidt et al., 2011). Meanwhile, DOC provides essential energy for soil microbes, and thus reactivate the decomposition of deep SOC (Fontaine et al., 2007). Soil DOC is also a potential source of the organic C in aquatic systems, the rhizosphere-enhanced DOC release may contribute to widespread increases in DOC in the surface waters of glaciated landscapes (Monteith et al., 2007; Kaiser and Kalbitz, 2012). It is critical to further investigate root-activated soil DOC at ecosystem and landscape levels, given its important role in the C cycle.

4.4. Implications for terrestrial carbon cycling

Results from this experiment and many previous studies (e.g., Wang et al., 2016; Lu et al., 2018; Yin et al., 2018) distinctly suggest that SOC decomposition significantly influenced by the RPE. Therefore, current model parameterization based on observations from bare soil incubation and root exclusion experiments might be unrealistic (Cheng, 2009). Furthermore, both plant and soil variables can substantially control the magnitude of the RPE. Global change factors such as N deposition, warming, drought, and elevated CO_2, are likely to affect the RPE through regulating leaf photosynthesis, root exudations, and rhizosphere microbes (Drigo et al., 2008; Phillips et al., 2011; Okubo et al., 2015; Zhou et al., 2018). How the RPE may respond to global change deserves further studies. Next-generation land surface models may need to incorporate the RPE into biogeochemical processes for better forecasting the long-term changes in SOC under global climate change scenarios.

Conventional frameworks considered soil C in aggregation and organo-mineral associations protected from microbial decomposition (Torn et al., 1997; Baisden et al., 2002; Six et al., 2002; Chenu and Plante, 2006). Emerging view suggests that any natural organic compound could be mineralized when the decomposer communities gain access to such substrates (Fontaine et al., 2007; Schmidt et al., 2011). Here we suggest an alternative mechanism controlling the RPE on SOC decomposition, where roots could mobilize soil matrix-protected C through fragmentation of coarse macro-aggregates and/or destabilize C from the silt and clay fractions, thereby stimulating the release of DOC in the soil profile. By enhancing microbial access to previously matrix-protected C, the RPE can accelerate the loss of stabilized soil C. These results underscore the importance to fully understand the mechanisms controlling the RPE so that we can improve our capability of predicting future trends in terrestrial C-cycling under a changing environment.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

The authors thank the chief editor and three anonymous reviewers for their insightful comments and suggestions. We thank Dr. John Blair for helping us obtain the valuable Tallgrass prairie soil used in this experiment and Mr. Colin Carney for isotope analysis. Laboratory assistance from the following people is acknowledged: Kelsey Forbush, Catherine Takata, Peng Wang and Junjie Lin. This research was financially supported by the National Natural Science Foundation of China (Grant Nos. 31901200, 31770559 and 31600387), the U.S. National Science Foundation (Grant No. DEB-1926438), Shanghai Sailing Program, a scholarship fund from China Scholarship Council, and a Faculty Research Grant awarded by the Committee on Research from the University of California, Santa Cruz.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.soilbio.2020.107787.

References

Angers, D.A., Recous, S., Aita, C., 1997. Fate of carbon and nitrogen in water-stable aggregates during decomposition of $^{13}C^{15}N$-labelled wheat straw in situ. European Journal of Soil Science 48, 295–300.
Badri, D.V., Vivanco, J.M., 2009. Regulation and function of root exudates. Plant, Cell and Environment 32, 666–681.
Bahn, M., Schmitt, M., Siegwolf, R., Richter, A., Brüggemann, N., 2009. Does photosynthesis affect grassland soil-respired CO_2 and its carbon isotope composition on a diurnal timescale? New Phytologist 182, 451–460.
Bais, H.P., Weir, T.L., Perry, L.G., Gilroy, S., Vivanco, J.M., 2006. The role of root exudates in rhizosphere interactions with plants and other organisms. Annual Review of Plant Biology 57, 233–266.
Baisden, W.T., Amundson, R., Cook, A.C., Brenner, D.L., 2002. Turnover and storage of C and N in five density fractions from California annual grassland surface soils. Global Biogeochemical Cycles 16, GB1117.
Bronick, C.J., Lal, R., 2005. Soil structure and management: a review. Geoderma 124, 3–22.
Brzostek, E.R., Greco, A., Drake, J.E., Finzi, A.C., 2013. Root carbon inputs to the rhizosphere stimulate extracellular enzyme activity and increase nitrogen availability in temperate forest soils. Biogeochemistry 115, 65–76.
Cheng, W.X., 1999. Rhizosphere feedbacks in elevated CO_2. Tree Physiology 19, 313–320.
Cheng, W.X., 2009. Rhizosphere priming effects: its functional relationships with microbial turnover, evapotranspiration, and C-N budgets. Soil Biology and Biochemistry 41, 1795–1801.
Cheng, W.X., Johnson, D.W., Fu, S.L., 2003. Rhizosphere effects on decomposition: controls of plant species, phenology, and fertilization. Soil Science Society of America Journal 67, 1418–1427.
Cheng, W.X., Kuzyakov, Y., 2005. Root effects on soil organic matter decomposition. In: Zobel, R.W., Wright, S.F. (Eds.), Roots and Soil Management: Interactions between Roots and the Soil. Agronomy Monograph No 48. American Society of Agronomy/Crop Science Society of America/Soil Science Society of America, Madison, WI, USA, pp. 119–143.
Cheng, W.X., Parton, W.J., Gonzalez-Meler, M.A., Phillips, R., Asao, S., McNickle, G.G., Brzostek, E., Jastrow, J.D., 2014. Synthesis and modeling perspectives of rhizosphere priming. New Phytologist 201, 31–44.
Chenu, C., Plante, A.F., 2006. Clay-sized organo-mineral complexes in a cultivation chronosequence: revisiting the concept of the 'primary organo-mineral complex'. European Journal of Soil Science 57, 596–607.
Clarholm, M., Skyllberg, U., Rosling, A., 2015. Organic acid induced release of nutrients from metal-stabilized soil organic matter – the unbutton model. Soil Biology and Biochemistry 84, 168–176.
Dijkstra, F.A., Carrillo, Y., Pendall, E., Morgan, J.A., 2013. Rhizosphere priming: a nutrient perspective. Frontiers in Microbiology 4, 1–8.
Dijkstra, F.A., Cheng, W.X., 2007a. Interactions between soil and tree roots accelerate long-term soil carbon decomposition. Ecology Letters 10, 1047–1053.
Dijkstra, F.A., Cheng, W.X., 2007b. Moisture modulates rhizosphere effects on C decomposition in two different soil types. Soil Biology and Biochemistry 39, 2264–2274.

Drigo, B., Kowalchuk, G.A., van Veen, J.A., 2008. Climate change goes underground: effects of elevated atmospheric CO_2 on microbial community structure and activities in the rhizosphere. Biology and Fertility of Soils 44, 667–679.
Finzi, A.C., Abramoff, R.Z., Spiller, K.S., Brzostek, E.R., Darby, B.A., Kramer, M.A., Phillips, R.P., 2015. Rhizosphere processes are quantitatively important components of terrestrial carbon and nutrient cycles. Global Change Biology 21, 2082–2094.
Fontaine, S., Barot, S., Barré, P., Bdioui, N., Mary, B., Rumpel, C., 2007. Stability of organic carbon in deep soil layers controlled by fresh carbon supply. Nature 450, 277–280.
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.
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.
Gale, W.J., Cambardella, C.A., Bailey, T.B., 2000. Root-derived carbon and the formation and stabilization of aggregates. Soil Science Society of America Journal 64, 201–207.
Hamer, U., Marschner, B., 2005. Priming effects in different soil types induced by fructose, alanine, oxalic acid and catechol additions. Soil Biology and Biochemistry 37, 445–454.
Harris, D., Porter, L.K., Paul, E.A., 1997. Continuous flow isotope ratio mass spectrometry of carbon dioxide trapped as strontium carbonate. Communications in Soil Science and Plant Analysis 28, 747–757.
Hassink, J., Whitmore, A.P., 1997. A model of the physical protection of organic matter in soils. Soil Science Society of America Journal 61, 131–139.
Heimann, M., Reichstein, M., 2008. Terrestrial ecosystem carbon dynamics and climate feedbacks. Nature 451, 289–292.
Högberg, P., Nordgren, A., Buchmann, N., Taylor, A.F.S., Ekblad, A., Högberg, M.N., Nyberg, G., Ottosson-Löfvenius, M., Read, D.J., 2001. Large-scale forest girdling shows that current photosynthesis drives soil respiration. Nature 411, 789–792.
Huo, C., Luo, Y., Cheng, W., 2017. Rhizosphere priming effect: a meta-analysis. Soil Biology and Biochemistry 111, 78–84.
Jobbágy, E.G., Jackson, R.B., 2000. The vertical distribution of soil organic carbon and its relation to climate and vegetation. Ecological Applications 10, 423–436.
Kaiser, K., Kalbitz, K., 2012. Cycling downwards-dissolved organic matter in soils. Soil Biology and Biochemistry 52, 29–32.
Keiluweit, M., Bougoure, J.J., Nico, P.S., Pett-Ridge, J., Weber, P.K., Kleber, M., 2015. Mineral protection of soil carbon counteracted by root exudates. Nature Climate Change 5, 588–595.
Kindler, R., Siemens, J., Kaiser, K., Walmsley, D.C., Bernhofer, C., Buchmann, N., Cellier, P., Eugster, W., Gleixner, G., GrüNwald, T., Heim, A., Ibrom, A., Jones, S.K., Jones, M., Klumpp, K., Kutsch, W., Larsen, K.S., Lehuger, S., Loubet, B., Mckenzie, R., Moors, E., Osborne, B., Pilegaard, K., Rebmann, C., Saunders, M., Schmidt, M.W.I., Schrumpf, M., Seyfferth, J., Skiba, U., Soussana, J.-F., Sutton, M.A., Tefs, C., Vowinckel, B., Zeeman, M.J., Kaupenjohann, M., 2011. Dissolved carbon leaching from soil is a crucial component of the net ecosystem carbon balance. Global Change Biology 17, 1167–1185.
Kleber, M., Eusterhues, K., Keiluweit, M., Mikutta, C., Mikutta, R., Nico, P.S., 2015. Mineral–organic associations: formation, properties, and relevance in soil environments. Advances in Agronomy 130, 1–140.
Kleber, M., Sollins, P., Sutton, R., 2007. A conceptual model of organo-mineral interactions in soils: self-assembly of organic molecular fragments into zonal structures on mineral surfaces. Biogeochemistry 85, 9–24.
Kuzyakov, Y., 2010. Priming effects: interactions between living and dead organic matter. Soil Biology and Biochemistry 42, 1363–1371.
Kuzyakov, Y., Cheng, W., 2001. Photosynthesis controls of rhizosphere respiration and organic matter decomposition. Soil Biology and Biochemistry 33, 1915–1925.
Kuzyakov, Y., Cheng, W., 2004. Photosynthesis controls of CO_2 efflux from maize rhizosphere. Plant and Soil 263, 85–99.
Kuzyakov, Y., Xu, X., 2013. Competition between roots and microorganisms for nitrogen: mechanisms and ecological relevance. New Phytologist 198, 656–669.
Lehmann, J., Kleber, M., 2015. The contentious nature of soil organic matter. Nature 528, 60–68.
Lu, J., Dijkstra, F.A., Wang, P., Cheng, W., 2018. Rhizosphere priming of grassland species under different water and nitrogen conditions: a mechanistic hypothesis of C-N interactions. Plant and Soil 429, 303–319.
Magid, J., Kjærgaard, C., Gorissen, A., Kuikman, P.J., 1999. Drying and rewetting of a loamy sand soil did not increase the turnover of native organic matter, but retarded the decomposition of added 14C-labelled plant material. Soil Biology and Biochemistry 31, 595–602.
Marschner, B., Kalbitz, K., 2003. Controls of bioavailability and biodegradability of dissolved organic matter in soils. Geoderma 113, 211–235.
Materechera, S.A., Kirby, J.M., Alston, A.M., Dexter, A.R., 1994. Modification of soil aggregation by watering regime and roots growing through beds of large aggregates. Plant and Soil 160, 57–66.
McCormack, M.L., Guo, D., Iversen, C.M., Chen, W., Eissenstat, D.M., Fernandez, C.W., Li, L., Ma, C., Ma, Z., Poorter, H., Reich, P.B., Zadworny, M., Zanne, A., 2017. Building a better foundation: improving root-trait measurements to understand and model plant and ecosystem processes. New Phytologist 215, 27–37.
Mikutta, R., Kleber, M., Torn, M.S., Jahn, R., 2006. Stabilization of soil organic matter: association with minerals or chemical recalcitrance? Biogeochemistry 77, 25–56.
Miller, A.E., Schimel, J.P., Meixner, T., Sickman, J.O., Melack, J.M., 2005. Episodic rewetting enhances carbon and nitrogen release from chaparral soils. Soil Biology and Biochemistry 37, 2195–2204.
Monteith, D.T., Stoddard, J.L., Evans, C.D., de Wit, H.A., Forsius, M., Høgåsen, T., Wilander, A., Skjelkvåle, B.L., Jeffries, D.S., Vuorenmaa, J., Keller, B., Kopácek, J., Vesely, J., 2007. Dissolved organic carbon trends resulting from changes in atmospheric deposition chemistry. Nature 450, 537–540.
Mueller, C.W., Schlund, S., Prietzel, J., Kögel-Knabner, I., Gutsch, M., 2012. Soil aggregate destruction by ultrasonication increases soil organic matter mineralization and mobility. Soil Science Society of America Journal 76, 1634–1643.
Nagel, K.A., Schurr, U., Walter, A., 2006. Dynamics of root growth stimulation in Nicotiana tabacum in increasing light intensity. Plant, Cell and Environment 29, 1936–1945.
Neff, J.C., Asner, G.P., 2001. Dissolved organic carbon in terrestrial ecosystems: synthesis and a model. Ecosystems 4, 29–48.
Newcomb, C.J., Qafoku, N.P., Grate, J.W., Bailey, V.L., De Yoreo, J.J., 2017. Developing a molecular picture of soil organic matter–mineral interactions by quantifying organo–mineral binding. Nature Communications 8.
Okubo, T., Liu, D., Tsurumaru, H., Ikeda, S., Asakawa, S., Tokida, T., Tago, K., Hayatsu, M., Aoki, N., Ishimaru, K., Ujiie, K., Usui, Y., Nakamura, H., Sakai, H., Hayashi, K., Hasegawa, T., Minamisawa, K., 2015. Elevated atmospheric CO_2 levels affect community structure of rice root-associated bacteria. Frontiers in Microbiology 6.
Ohm, H., Hamer, U., Marschner, B., 2007. Priming effects in soil size fractions of a podzol Bs horizon after addition of fructose and alanine. Journal of Plant Nutrition and Soil Science 170, 551–559.
Pausch, J., Zhu, B., Kuzyakov, Y., Cheng, W., 2013. Plant inter-species effects on rhizosphere priming of soil organic matter decomposition. Soil Biology and Biochemistry 57, 91–99.
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.
Phillips, R.P., Finzi, A.C., Bernhardt, E.S., 2011. Enhanced root exudation induces microbial feedbacks to N cycling in a pine forest under long-term CO_2 fumigation. Ecology Letters 14, 187–194.
Phillips, R.P., Meier, I.C., Bernhardt, E.S., Grandy, A.S., Wickings, K., Finzi, A.C., 2012. Roots and fungi accelerate carbon and nitrogen cycling in forests exposed to elevated CO_2. Ecology Letters 15, 1042–1049.
Qualls, R.G., Haines, B.L., 1992. Biodegradability of dissolved organic matter in forest throughfall, soil solution, and stream water. Soil Science Society of America Journal 56, 578–586.
Rasse, D.P., Rumpel, C., Dignac, M.-F., 2005. Is soil carbon mostly root carbon? Mechanisms for a specific stabilisation. Plant and Soil 269, 341–356.
Rasmussen, C., Southard, R.J., Horwath, W.R., 2007. Soil mineralogy affects conifer forest soil carbon source utilization and microbial priming. Soil Science Society of America Journal 71, 1141–1150.
Sanderman, J., Baldock, J.A., Amundson, R., 2008. Dissolved organic carbon chemistry and dynamics in contrasting forest and grassland soils. Biogeochemistry 89, 181–198.
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.
Schlesinger, W.H., 1997. Biogeochemistry: an Analysis of Global Change, second ed. Academic Press, San Diego, Calidornia, USA.
Schulten, H.-R., Leinweber, P., 2000. New insights into organic-mineral particles: composition, properties and models of molecular structure. Biology and Fertility of Soils 30, 399–432.
Shahzad, T., Chenu, C., Repinçay, C., Mougin, C., Ollier, J.-L., Fontaine, S., 2012. Plant clipping decelerates the mineralization of recalcitrant soil organic matter under multiple grassland species. Soil Biology and Biochemistry 51, 73–80.
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.
Six, J., Bossuyt, H., Degryze, S., Denef, K., 2004. A history of research on the link between (micro)aggregates, soil biota, and soil organic matter dynamics. Soil and Tillage Research 79, 7–31.
Six, J., Conant, R.T., Paul, E.A., Paustian, K., 2002. Stabilization mechanisms of soil organic matter: implications for C-saturation of soils. Plant and Soil 241, 155–176.
Six, J., Elliott, E.T., Paustian, K., 2000. Soil structure and soil organic matter: II. A normalized stability index and the effect of mineralogy. Soil Science Society of America Journal 64, 1042–1049.
Smith, P., Fang, C., Dawson, J.J.C., Moncrieff, J.B., 2008. Impact of global warming on soil organic carbon. Advances in Agronomy 97, 1–43.
Tang, M., Cheng, W.X., Zeng, H., Zhu, B., 2019. Light intensity controls rhizosphere respiration rate and rhizosphere priming effect of soybean and sunflower. Rhizosphere 9, 97–105.
Torn, M.S., Trumbore, S.E., Chadwick, O.A., Vitousek, P.M., Hendricks, D.M., 1997. Mineral control of soil organic carbon storage and turnover. Nature 389, 170–173.
Vance, E.D., Brookes, P.C., Jenkinson, D.S., 1987. An extraction method for measuring soil microbial biomass C. Soil Biology and Biochemistry 19, 703–707.
van der Heijden, M.G.A., Bardgett, R.D., van Straalen, N.M., 2008. The unseen majority: soil microbes as drivers of plant diversity and productivity in terrestrial ecosystems. Ecology Letters 11, 296–310.
Wang, X., Tang, C., Severi, J., Butterly, C.R., Baldock, J.A., 2016. Rhizosphere priming effect on soil organic carbon decomposition under plant species differing in soil acidification and root exudation. New Phytologist 211, 864–873.
Yin, L.M., Dijkstra, F.A., Wang, P., Zhu, B., Cheng, W.X., 2018. Rhizosphere priming effects on soil carbon and nitrogen dynamics among tree species with and without intraspecific competition. New Phytologist 218, 1036–1048.

Yin, L.M., Corneo, P.E., Richter, A., Wang, P., Cheng, W.X., Dijkstra, F.A., 2019. Variation in rhizosphere priming and microbial growth and carbon use efficiency caused by wheat genotypes and temperatures. Soil Biology and Biochemistry 134, 54–61.

Zhou, G., Zhou, X., Nie, Y., Bai, S.H., Zhou, L., Shao, J., Cheng, W., Wang, J., Hu, F., Fu, Y., 2018. Drought-induced changes in root biomass largely result from altered root morphological traits: evidence from a synthesis of global field trials. Plant, Cell and Environment 41, 2589–2599.

Zhu, B., Cheng, W.X., 2011. Rhizosphere priming effect increases the temperature sensitivity of soil organic matter decomposition. Global Change Biology 17, 2172–2183.

Zhu, B., Cheng, W.X., 2013. Impacts of drying-wetting cycles on rhizosphere respiration and soil organic matter decomposition. Soil Biology and Biochemistry 63, 89–96.

Zhu, B., Gutknecht, J.L.M., Herman, D.J., Keck, D.C., Firestone, M.K., Cheng, W.X., 2014. Rhizosphere priming effects on soil carbon and nitrogen mineralization. Soil Biology and Biochemistry 76, 183–192.

Zsolnay, A., 1996. Dissolved humus in soil waters. In: Piccolo, A. (Ed.), Humic Substances in Terrestrial Ecosystems. Elsevier, Amsterdam, pp. 171–223.