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Rhizosphere priming effects on the decomposition of soil organic matter in C_4 and C_3 grassland soils

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Abstract

Using a natural abundance ^{13}C method, soil organic matter (SOM) decomposition was studied in a C_3 plant – 'C_4 soil' (C_3 plant grown in a soil obtained from a grassland dominated by C_4 grasses) system and a C_4 plant – 'C_3 soil' (C_4 plant grown in a soil taken from a pasture dominated by C_3 grasses) system. In C_3 plant – 'C_4 soil' system, cumulative soil-derived CO_2–C were higher in the soils planted with soybean (5499 mg pot^{-1}) and sunflower (4484 mg pot^{-1}) than that in 'C_4 soil' control (3237 mg pot^{-1}) without plants. In other words, the decomposition of SOM in soils planted with soybean and sunflower were 69.9% and 38.5% faster than 'C_4 soil' control. In C_4 plant – 'C_3 soil' system, there was an overall negative priming effect of live roots on the decomposition of SOM. The cumulative soil-derived CO_2–C were lower in the soils planted with sorghum (2308 mg pot^{-1}) and amaranthus (2413 mg pot^{-1}) than that in 'C_3 soil' control (2541 mg pot^{-1}). The decomposition of SOM in soils planted with sorghum and amaranthus were 9.2% and 5.1% slower than 'C_3 soil' control. Our results also showed that rhizosphere priming effects on SOM decomposition were positive at all developmental stages in C_3 plant – 'C_4 soil' system, but the direction of the rhizosphere priming effect changed at different developmental stages in the C_4 plant – 'C_3 soil' system. Implications of rhizosphere priming effects on SOM decomposition were discussed.

Introduction

The rhizosphere has been recognized as one of the key fine scale components in global carbon cycle research (Coleman et al., 1992). Many important aspects of plant–soil interactions such as plant nutrient acquisition (Uren and Reisennauer, 1988), root colonization by rhizosphere microorganisms (Baker, 1991), and soil organic matter (SOM) decomposition (Cheng and Coleman, 1990; Sallih and Bottner, 1988) are mediated by rhizosphere processes. According to Kuzyakov et al. (2000), priming effects are strong short-term changes in the turnover of soil organic matter caused by comparatively moderate treatments (or disturbance) of the soil. Planting is one of the treatments (or disturbance) of soil, and plant root exudation or rhizosphere deposition may induce rhizosphere priming effect. In the literature, both positive (Helal and Sauerbech, 1984, 1987; Sallih and Bottner, 1988) and negative (Cheng, 1996; Liljieroth et al., 1994) rhizosphere priming effects on SOM decomposition have been reported. The contrasting findings may be explained by the link between SOM decomposition processes, plant carbon allocation and the metabolic status of the rhizosphere microbial community (Cheng and Coleman, 1990). For example, carbon allocation belowground for root growth and exudation may enhance microbial growth resulting in an increase in SOM decomposition. In contrast, plant uptake for nutrients might suppress soil microbial growth in nutrient-limiting soils, consequently, reduces decomposition of SOM (Hu et al., 2001).

The effects of plant roots on SOM decomposition have been studied using ^{14}C labeling technique in two approaches: (1) Label plants with ^{14}C in a soil which was not previously ^{14}C labeled (Helal and

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Sauerback, 1984, 1987; Liljieroth et al., 1994.). (2) Apply ^{14}C labeled plant residue or other material (e.g. ^{14}C labeled glucose) into soil, and it decomposes with the presence of live plants (Cheng and Coleman, 1990; Helal and Sauerback, 1987; Jenkinson, 1977; Reid and Goss, 1982; Sallih and Bottner, 1988). Both approaches enable one to differentiate the origin of CO_2–C evolved from rhizosphere or from SOM. The $^{14}CO_2$ was considered to be that from the decomposition or utilization of ^{14}C labeled plant materials (residues or root exudates) and the $^{12}CO_2$ was from the decomposition or utilization of non-labeled materials (e.g. SOM). Natural abundance ^{13}C tracer method has many advantages over radioactive ^{14}C labeling technique (Cheng, 1996). However, ^{13}C natural tracer method has not been a popular approach for decomposition studies until recent years (Cheng, 1996; Ekblad and Högberg, 2000; Nyberg et al., 2000; Robinson and Scrimgour, 1995; Rochette and Flanagan, 1997; Rochette et al., 1999). Isotope ^{13}C techniques have been employed in decomposition studies in two ways: (1) growing C_4 plants in 'C_3 soil' (derived from C_3 plant) or vice versa (Cheng, 1996; Robinson and Scrimgour, 1995; Rochette and Flanagan, 1997; Rochette et al., 1999). (2) and apply C_4 plant residues or other C_4 materials (e.g. C_4-sucrose) on 'C_3 soil' or vice versa without the presence of live plants (Ekblad and Högberg, 2000; Nyberg et al., 2000). Unfortunately, these studies have not been able to estimate the rhizosphere priming effects on SOM decomposition either because of the absence of live plants (Nyberg et al., 2000) or lack of data from control soils without live plants (Rochette and Flanagan, 1997; Robinson and Scrimgeour, 1995).

In the present study, we established a C_3 plant – 'C_4 soil' and a C_4 plant – 'C_3 soil' systems and investigated the effects of plant roots on SOM decomposition at different plant developmental stage. The soil-derived C to total soil respiration was partitioned using the ^{13}C natural tracer method, and was used as a measure of the decomposition of SOM. Our objective was to test the hypothesis that rhizosphere priming effects on SOM decomposition vary with plant species and plant developmental stages in both C_3 plant – 'C_4 soil' and C_4 plant – 'C_3 soil' systems.

Materials and methods

Soils

Two types of soils were selected for this study. One soil was obtained from Konza Prairie, KS, where C_4 grasses dominated, and the soil was then defined as 'C_4 soil' in the present study. 'C_4 soil' had a $\delta^{13}C$ of $-14.61‰$, C and N contents of 20g kg^{-1} and 1.9g kg^{-1}, and a pH of 7.05. The other soil was taken from a Santa Cruz pasture, CA, where C_3 grasses dominated, and it was defined as 'C_3 soil'. The $\delta^{13}C$ value and soil pH of 'C_3 soil' were $-24.16‰$, 5.49, and soil C and N contents were 19 g kg^{-1} and 1.7 g kg^{-1}, respectively. The soils were sieved with a 4-mm mesh sieve and air-dried before use.

Treatments

PVC (polyvinyl chloride) pots (15 cm in diameter, 40 cm in height, capped bottom, with air outlet tubing at the bottom) were made and used for growing plants. Eight kg of air-dried Kansas 'C_4 soil' or Santa Cruz 'C_3 soil' was put into each PVC pot. Soil moisture of these soils was adjusted to 300 g kg^{-1} prior to planting. Two C_3 plant species, soybean (*Glycine max*) and sunflower (*Helianthus annuus*), were grown in 'C_4 soil', and two C_4 plants, sorghum (*Sorghum bicolor*) and amaranthus (*Amaranthus hypochondriacus*) were grown in 'C_3 soil'. Planting was conducted on March 27, 2000 with multiple seeds but only one plant in each pot was kept for later measurements. Controls for 'C_4 soil' or 'C_3 soil' were set in the same way except without plants. Soil water content in each pot was maintained at about 300 g kg^{-1} by weighing and watering.

This experiment was conducted in a greenhouse of the Department of Biology at University of California, Santa Cruz. During the period of plant growth, photoperiod was set as 14 h with supplement lighting when needed. Temperature was maintained at 22 °C to 25 °C, relative humidity was maintained at 450 g kg^{-1} during the day and 750 g kg^{-1} during the night.

Sampling and measurements

Sampling was conducted on May 10 and 11, May 31 and June 1, June 25 and 26, and July 18 and 19, 2000, representing the vegetative, flowering, grain-filling and maturity stages of the plants, respectively. There were four replication pots for each treatment at

each sampling time. Sampling included CO_2 trapping, plant biomass harvesting and soil collection.

For CO_2 trapping, two pieces of half-moon-shaped Plexiglas sheets connected with Tygon tubing (3.2 mm I.D.) were placed and fitted around the plant base and taped together. Low melting point paraffin wax was melted and poured on the top of the Plexiglas sheets to seal the top of the PVC pot. The Tygon tubing connected to the Plexiglas sheet served as the air inlet during CO_2 trapping. Pots were tested for possible air leaks by pumping air into the pot through the air inlet and submerging the air outlet tubing into water. The CO_2 accumulated in the PVC pot was completely pumped out before the start of the CO_2 trapping. All CO_2 evolved from the plant–soil system were trapped for two consecutive diurnal cycles (or 48 h) with a closed circulating system (Cheng, 1996). The closed circulating system consisted of three major components: Plant–soil system, CO_2 absorber, and an airflow controlling and pressure relief set. All gases (including CO_2) evolved from the plant–soil system were pumped through a CO_2 trapping column (a PVC tube filled with a mixture of 35 ml of 4 N NaOH solution and 350 g burnt and acid-washed fine sand). The coating of NaOH on fine sand particles insured a complete trapping of CO_2, no CO_2 was detected with infrared gas analyzer (IRGA) after all gases traveled through the sand column. The rest of the gases passed a needle valve, a flow meter and a Mylar balloon (filled with CO_2-free air, served as a pressure relief and oxygen source), and was brought back to the plant–soil system. Possible air contamination during the trapping process was corrected by setting the blank CO_2 traps with the same set-ups but bypassing the plant–soil system. The CO_2 trapping columns were brought back to laboratory and the content of each column was washed with deionized water and collected in a sample bottle. After settled down, the inorganic C content of a sub-sample of the solution was measured with a TOC analyzer (Shimadzu TOC-5050A). Another subsample was used to form the $SrCO_3$ precipitate with $SrCl_2$, excess $SrCl_2$ was added to insure a complete precipitation of the carbonate. The $SrCO_3$ precipitate was washed with deionized water until its pH was 7 to minimize the air contamination to the sample (preventing further absorption of air CO_2)and then dried in an oven (Harris, 1997).

Immediately after CO_2 trapping, plant materials were harvested and categorized into stem, leaf and root. Plant roots were washed (e.g. roots) with deionized water and collected in brown paper bags, and dried in an oven at 70 °C. One composite soil sample was taken from each PVC pot and a sub-sample was dried in an oven at 105 °C.

All oven-dried materials ($SrCO_3$ precipitate, plant materials and soils) were ground with a Spex mill (Certiprep 8000), and their $\delta^{13}C$ were measured with a PDZ Europa (Cheshire, UK) 'Hydra 20-20' continuous flow isotope ratio mass spectrometer. The samples were combusted at 1000 °C and the combustion products (N_2 and CO_2) fed into the IRMS via a chromatography column which separated N_2 and CO_2. The isotope ratios were compared to those of reference gas injections.

Calculation

If one grows C_3 plant in a 'C_4 soil', the carbon derived from C_3 plant ($\delta^{13}C$= −24‰ to −29‰) and from 'C_4 soil' ($\delta^{13}C$ = −12‰ to −14‰) will have different $\delta^{13}C$ values. Plant derived CO_2–C was estimated using the following equation:

$$C_3=C_t\ (\delta_t - \delta_4)/(\delta_3 - \delta_4)$$

In the equation, C_t is the total C from soil respiration (C_t= C_3+ C_4), C_3 is the amount of C derived from C_3 plant roots, C_4 is the amount of C derived from decomposition of SOM in 'C_4 soil', δ_t is the $\delta^{13}C$ value of C_t, δ_3 is the $\delta^{13}C$ value of the C derived from C_3 plant roots. Cheng (1996) found that total rhizosphere CO_2 has the same $\delta^{13}C$ value as that of plant roots, i.e. isotope fractionation does not occur during rhizosphere respiration. δ_4 is the $\delta^{13}C$ value of the C derived from decomposition of SOM in 'C_4 soil'. Likewise, if one grows C_4 plant in a 'C_3 soil', plant derived CO_2–C can be estimated using a similar equation:

$$C_4=C_t\ (\delta_t - \delta_3)/(\delta_4 - \delta_3)$$

Here, C_t is the total C from soil respiration (C_t= C_3+ C_4), C_4 is the amount of C derived from C_4 plant roots, C_3 is the amount of C derived from decomposition of SOM in 'C_3 soil', δ_t is the $\delta^{13}C$ value of C_t, δ_4 is the $\delta^{13}C$ value of the C derived from C_4 plant roots, and δ_3 is the $\delta^{13}C$ value of the C derived from decomposition of SOM in 'C_3 soil'.

Cumulative soil-derived CO_2–C through the whole experiment was estimated by extrapolation and it was the sum of the cumulative soil-derived CO_2–C of all plant developmental stages. Cumulative soil-derived CO_2–C for a specific developmental stage was estimated by multiplying the duration (days) with the mean value of daily soil-derived CO_2–C of the stage.

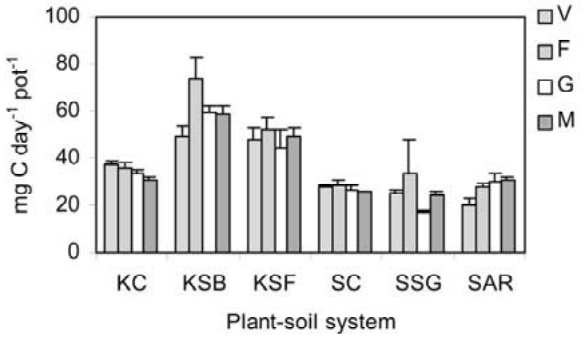

Figure 1. Daily soil-derived CO_2–C under different plant–soil systems. KC – Kansas 'C_4 soil' control; KSB – Soybean planted on 'C_4 soil'; KSF – Sunflower planted on 'C_4 soil'; SC – Santa Cruz 'C_3 soil' control; SSG – Sorghum planted on 'C_3 soil'; SAR – Amaranthus planted on 'C_3 soil'. V, F, G and M represent the vegetative, flowering, grain-filling and maturity stages of the plants. The error bars are standard errors.

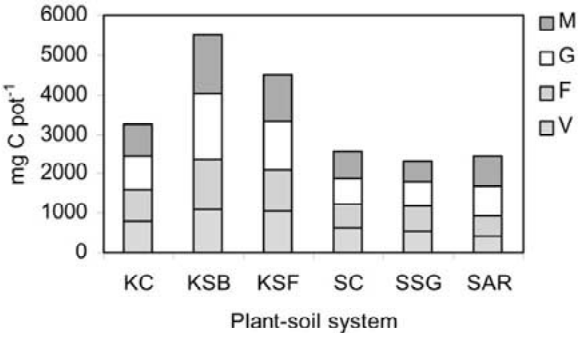

Figure 2. Cumulative soil-derived CO_2–C under different plant–soil systems. KC – Kansas 'C_4 soil' control; KSB – Soybean planted on 'C_4 soil'; KSF – Sunflower planted on 'C_4 soil'; SC – Santa Cruz 'C_3 soil' control; SSG – Sorghum planted on 'C_3 soil'; SAR – Amaranthus planted on 'C_3 soil'. V, F, G and M represent the vegetative, flowering, grain-filling and maturity stages of the plants.

The difference in cumulative soil-derived CO_2–C between a soil with and without plant was defined as rhizosphere-primed soil C. For instance, the rhizosphere-primed soil C under the influence of soybean was calculated by subtracting the cumulative soil-derived CO_2–C of 'C_4 soil' control from the cumulative soil-derived CO_2–C of that soil planted with soybean.

Statistics analysis

Statistical analyses for all data were performed using SAS software (SAS Institute, 1985) GLM procedure. Comparison among means was carried out using the LSD test for equal sample sizes and Scheffe's test for unequal sample sizes. Significance levels were set at $P<0.05$. Unless otherwise stated, all data were expressed on dry mass basis.

Results

Daily soil-derived CO_2–C under different plant–soil systems

Daily soil-derived CO_2–C was the portion of soil respiration that originated from the decomposition of SOM. In C_3 plant – 'C_4 soil' system, daily soil-derived CO_2–C were significantly higher from the soils planted with soybean and sunflower than from 'C_4 soil' control during all developmental stages. Daily soil-derived CO_2–C from the treatment of soybean was significantly lower at vegetative stage than that at later stages. There was no significant difference in daily soil-derived CO_2–C between different developmental stages for the soils planted with sunflower (Figure 1). In C_4 plant – 'C_3 soil', the daily soil-derived CO_2–C was significantly less than that of 'C_3 soil' control at grain-filling stage for sorghum and at vegetative stage for amaranthus, but significantly more at maturity stage for amaranthus (Figure 1).

Cumulative soil-derived CO_2–C and SOM decomposition

The pattern of cumulative soil-derived CO_2–C reflected the dynamics of the decomposition of SOM. In C_3 plant – 'C_4 soil' system, the cumulative soil-derived CO_2–C were higher in the soils with live soybean and sunflower roots than that in 'C_4 soil' control at all developmental stages, illustrating a positive priming effect of live roots on the decomposition of SOM. Over the whole experimental period, the cumulative soil-derived CO_2–C were 5499 and 4484 mg pot^{-1} for soils planted with soybean and sunflower, indicating that the SOM decomposition in soils planted with soybean and sunflower were 69.9% and 38.5% faster than that in 'C_4 soil' control (3237 mg pot^{-1})(Figure 2). Unlike in C_3 plant – 'C_4 soil' system, the direction of rhizosphere priming effect changed at different plant developmental stages in C_4 plant – 'C_3 soil' system. The cumulative soil-derived CO_2–C were lower at vegetative, grain-filling and maturity stages but higher at flowering stage in the soil with live sorghum roots than that in 'C_3 soil' control. The cumulative soil-derived CO_2–C were lower at vegetative and flowering stages but higher at grain-filling and maturity stages in the

Table 1. Correlation between root biomass and rhizosphere-primed soil C

System	R^2				P value			
	V[a]	F	G	M	V	F	G	M
C_3 plant – 'C_4 soil'	0.06[b]	0.37	0.32	0.62	0.84	0.09*	0.14	0.02**
C_4 plant – 'C_3 soil'	0.02	0.09	0.58	0.61	0.79	0.47	0.03**	0.02**
C_3 plant – 'C_4 soil'	0.28 (n=32)				0.0018***			
C_4 plant – 'C_3 soil'	0.05 (n=32)				0.7042			

[a] V, F, G and M represent vegetative, flowering, grain-filling and maturity stages of plants, respectively.
[b] $n = 8$.

soil with live amaranthus roots than that in 'C_3 soil' control. Over the whole experimental period, cumulative soil-derived CO_2–C were 2308 and 2413 mg pot^{-1} for soils planted with sorghum and amaranthus which suggested that the SOM decomposition in soils planted with sorghum and amaranthus were 9.2% and 5.1% slower than that of 'C_3 soil' control (2541 mg pot^{-1})(Figure 2).

Correlation between rhizosphere-primed soil C and root biomass

In C_3 plant – 'C_4 soil' system, there was a significant positive correlation between rhizosphere-primed soil C and root biomass at flowering and maturity stages. In C_4 plant – 'C_3 soil' system, the correlation was significantly negative at grain-filling and maturity stages. Overall, there was a significantly positive correlation between rhizosphere-primed soil C and root biomass in C_3 plant – 'C_4 soil' system; and no significant correlation in C_4 plant – 'C_3 soil' system (Table 1).

Discussion

Helal and Sauerbech (1984, 1987) reported that maize roots significantly enhanced the breakdown of SOM, and thus induced a positive priming effect. However, Liljieroth et al. (1994) found that maize did not cause priming effect on SOM, but they found that wheat suppressed the decomposition of SOM at high N level. Cheng (1996) also found that the presence of living wheat roots suppressed the decomposition of original soil C. Sallih and Bottner (1988) reported that the system with plants lost significantly more native soil organic C than the unplanted control for one soil type but this was not observed for another soil. Our results showed that the overall rhizosphere priming effects on the decomposition of SOM were positive (38.5–69.9% more) for a 'C_4 soil' planted with sunflower and soybean and were negative (5.1–9.2% less) for a 'C_3 soil' planted with amaranthus and sorghum over the whole experimental period. Plant species (Liljieroth et al., 1994), growth conditions (Helal and Sauerbeck, 1984, 1987; Liljieroth et al., 1994), soil nutrient level (Hu, 2001; Wang and Bakken, 1997) and soil types (Kuzyakov et al., 2000; Sallih and Bottner, 1988) seemed to be the factors affecting the direction (positive or negative) of the priming effect. However, none of the studies mentioned the plant phenology. The results of cumulative soil-derived CO_2–C from the present study illustrated that the direction of priming effect of live roots on the decomposition of SOM changed with plant developmental stages in C_4 plant – 'C_3 soil' system (Figure 2). This might be one of the causes for contrasting findings in different studies if the measurements were made at different developmental stages of the plants. Our results suggested that not only plant species but also plant phenology should be taken into account in the studies of rhizosphere priming effects on SOM decomposition.

Rhizodeposition has been shown to be a primer for the mineralization of SOM (Helal and Sauerbeck, 1986). Rhizodeposition includes all the losses of organic substances arising from the plant roots. It consists of water-soluble root exudates, secretion, lysates (e.g. cell walls, sloughed cells and decaying roots) (Whipps, 1990; Whipps and Linch, 1985). Rhizodeposition, as easily decomposable organic substances, can increase microbial activity or microbial biomass turnover, therefore accelerate SOM mineralization (positive priming effect). However, rhizodeposition can be toxic substances to microorganisms, therefore inhibit the microbial activity or their enzymes and suppress SOM decomposition (negative priming effect). The significant correlation between rhizosphere-primed soil C and root biomass at certain plant developmental stages supports that the rhizodeposition is one of the causes for priming effect. Nevertheless, rhizosphere priming effect can not be attributed to rhizodeposition alone. Roots exploration into soil can destabilize soil aggregates and thereby releases previously protected soil organic carbon, and the growth of roots also increases dry-wet cycles and therefore affects the decomposition process of soil organic carbon (Helal and Sauerback, 1987). In addition, competition between living roots and rhizosphere micro-organisms for limited nutrients (i.e. nitrogen) might suppress microbial growth and cause negative priming effect

(Cheng, 1996; Hu et al., 2001; Kuzyakov et al., 2000; Wang and Bakken, 1997). The exact cause for the shift of the direction of rhizosphere priming effect at different plant developmental stages can not be sorted out without simultaneous measurements of the parameters such as: quantity and quality of rhizodeposition, soil moisture and C/N of microbial biomass.

'Litterbag' is still one of the most popular methods employed in decomposition studies (Heneghan et al., 1999; Melillo et al., 1982), and often with the absence of live plants. The major drawback of the 'litterbag' method is that it ignores the influence of plant roots on the decomposition of SOM. Our findings also illustrate that careful assumptions (i.e. if rhizosphere priming effect is negligible) must be made for the use of root exclusion method to estimate root respiration under field conditions. Our results suggest that the rhizosphere priming effect on SOM decomposition should be taken into account in further C budgeting and modeling.

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