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Rhizosphere respiration varies with plant species and phenology: A greenhouse pot experiment

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Abstract

Two plant–soil systems, C_3 plant - 'C_4 soil' (obtained from a grassland dominated by C_4 grasses) and C_4 plant - 'C_3 soil' (obtained from a pasture dominated by C_3 grasses), were used in this study to monitor the dynamics of rhizosphere respiration (root-derived CO_2-C) at different plant developmental stages. In C_3 plant - 'C_4 soil' system, CO_2-C derived from soybean roots increased significantly from vegetative stage (55.69 mg C d^{-1} pot^{-1}) to flowering stage (132.18 mg C d^{-1} pot^{-1}), and it declined thereafter (83.37-111.63 mg C d^{-1} pot^{-1}). However, no significant change of CO_2-C derived from sunflower roots was observed at different plant developmental stages (67.05–77.66 mg C d^{-1} pot^{-1}). CO_2-C derived from soybean (*Glycine max* (L) Merr) roots was significantly higher than that derived from sunflower (*Helianthus annuus*) roots except for that at vegetative stage. In C_4 plant - 'C_3 soil' system, CO_2-C derived from sorghum roots was significantly higher at flowering stage (169.51 mg C d^{-1} pot^{-1}) than at other stages (75.89–113.26 mg C d^{-1} pot^{-1}). CO_2-C derived from amaranthus roots was the highest at vegetative stage (88.88 mg C d^{-1} pot^{-1}) and it declined significantly thereafter (23.42–53.47 mg C d^{-1} pot^{-1}). CO_2-C derived from sorghum (*Sorghum bicolor*) roots was significantly higher than that from amaranthus (*Amaranthus hypochondriacus*) roots except for that at vegetative stage. In conclusion, rhizosphere respiration varied not only with plant species but also with plant phenology. With the soil volume used in our pots, the overall percentages of cumulative root-derived CO_2-C to total soil respiration were 61.22, 61.14, 81.84 and 67.37% for soybean, sunflower, sorghum and amaranthus, respectively. Specific rhizosphere respiration was also discussed and was used as an index of root activity and vitality.

Introduction

Soil respiration is often used as an index of soil biological activity, and is one of the largest fluxes in the global C cycle. Small changes in the magnitude of soil respiration may have a large effect on concentration of CO_2 in the atmosphere (Schlesinger, 1997; Schlesinger and Andrews, 2000). Soil respiration is the sum of rhizosphere respiration (root respiration and microbial respiration derived from root associated materials) and soil microbial respiration (derived from soil organic matter-SOM). Separating rhizosphere respiration from soil respiration would help us to better understand the C source-sink relationship of plant roots, soil organic matter and soil microbial biomass.

Several methods were developed for separating the total CO_2 efflux into that from microbial respiration of SOM and that from roots and rhizosphere microbial population. Hanson et al. (2000) summarized these methods into three broad categories: Component integration, root exclusion and isotopic approaches. Component integration involves separation of the constituent soil components contributing to CO_2 efflux (i.e. roots, sieved soil and litter) followed by measurements of the specific rates of CO_2 efflux from each component part (Anderson, 1973; Coleman, 1973; Hendrickson and Robinson, 1984; Johnson et al.,

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1994; Nakane, 1980; Phillipson et al., 1975; Trumbore et al., 1995; Uchida et al., 1998). The root exclusion method indirectly estimates root respiration by subtracting the soil respiration without roots from the soil respiration with roots (Anderson, 1973; Brumme, 1995; Edwards, 1991; Ewel et al., 1987; Kelting et al., 1998; Minderman and Vulto, 1973; Nakane et al., 1996). Isotope methods refer to the use of either radioactive ^{14}C (Cheng et al., 1993; Dörr and Münnich, 1986, 1987; Horwath et al., 1994; Swinnen, 1994) or stable ^{13}C isotopes to trace the C origin of soil respiration (Andrew et al., 1999; Robinson and Scrimgour, 1995; Rochette and Flanagan, 1997; Rochette et al., 1999). Isotopic methods have an advantage over component integration and root exclusion because they allow C partitioning between rhizosphere respiration and SOM decomposition *in situ*, and avoid the disturbance to soil.

Recently, the stable ^{13}C method is getting more attention because of its advantages over radioactive ^{14}C labeling (Cheng, 1996). Robinson and Scrimgeour (1995) grew a C_4 species – Bermuda grass (*Cynodon dactylon* L.) on a soil containing only C_3–C. They found that the fraction of the soil CO_2 originated from the plants varied and seemed to be related to the green material in the leaf canopy. Rochette et al. (1999) also planted C_4 crop – maize (*Zea mays*) on a field of previously cultivated C_3 crops, and estimated the contribution of rhizosphere respiration to soil respiration during growing season by taking CO_2 samples from various soil depths. Andrew et al. (1999) estimated the relative contribution of rhizosphere respiration of loblolly pine (*Pinus taeda* L.) to soil respiration using ^{13}C as an isotopic tracer in a FACE (Free Air CO_2 Enrichment) site. The CO_2 used to fumigate the FACE plot was strongly depleted in ^{13}C ($\delta^{13}C = -43.1‰$), which enabled them to partition the C source of CO_2 evolved from plant–soil system. In the present study, we estimated the rhizosphere respiration of different plant species at different developmental stages in two plant–soil systems. We grew C_3 plants in a 'C_4 soil' (obtained from a grassland dominated by C_4 grasses), and C_4 plants in a 'C_3soil' (obtained from a pasture dominated by C_3grasses). The difference in $\delta^{13}C$ values between plant (e.g. $\delta^{13}C$ for C_3 plant is between $-24‰$ and $-29‰$) and soil (e.g. $\delta^{13}C$ for 'C_4 soil' is between $-12‰$ and $-14‰$) enabled us to partition the CO_2-C derived from plant roots and from SOM.

Our objectives were to test the hypothesis that rhizosphere respiration varies with both plant species and phenology, and to compare the rhizosphere respiration in two plant–soil systems.

Materials and methods

Experimental design

This experiment was conducted at the greenhouse of the Department of Biology at University of California, Santa Cruz. During the period of experiment, temperature was maintained at 22 °C to 25 °C and relative humidity was maintained at 450 g kg^{-1} during the day and 700 g kg^{-1} during the night. Two types of soils were selected for this study. 'C_4soil' was obtained from Konza prairie, Kansas, where C_4 grasses dominated, with a $\delta^{13}C$ of $-14.61‰$, C and N contents of 20 g kg^{-1} and 1.9 g kg^{-1}, and a pH of 7.05. The other soil was taken from Santa Cruz pasture, California, 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 root-picked, air-dried and sieved with a 4-mm mesh sieve before use.

PVC (polyvinyl chloride) pots (15 cm in diameter and 40 cm in height) were constructed with a capped bottom and an air outlet tubing at the bottom. Each pot was filled with 8000 g of air-dried either 'C_4 soil' or 'C_3 soil'. Soil moisture of these soils was adjusted to 300 g kg^{-1} prior to the seed's germination. Two C_3 plant species, soybean (*Glycine max* (L) Merr) and sunflower (*Helianthus annuus*), were grown on the 'C_4 soil', and two C_4 plants, sorghum (*Sorghum bicolor*) and amaranthus (*Amaranthus hypochondriacus*) were grown on the 'C_3 soil'. Controls for 'C_4 soil' and 'C_3 soil' were set in the same way except without planting. Germination started on March 27, 2000 with multiple seeds but was thinned to one plant. Soil water content in the pot was maintained at about 300 g kg^{-1} by weighing and watering. Sampling was conducted on May 10 and 11, May 31 and June 1, June 25 and 26, and July 18 and 19, 2000, roughly at the vegetative, flowering, grain-filling and maturity stages of the plants, respectively. There were four replication pots for each plant species and control soils at each sampling time.

Sampling and measurements

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 (3/16 in. I.D.) were taped together to fit the base of the plant. 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. CO_2 accumulated in the PVC pot was pulled out with a pump before the start of the CO_2 trapping. All CO_2 evolved from the root-soil system were trapped for two consecutive diurnal cycles (or 48 h) with a closed circulating system (Cheng, 1996). Briefly, all gases (including CO_2) evolved from the root–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 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 root–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. The inorganic C content of a sub-sample of the solution was measured with a TOC analyzer (Shimadzu TOC-5050A). Another sub-sample was used to form the $SrCO_3$ precipitate with 1 N $SrCl_2$. The $SrCO_3$ precipitate was washed with deionized water until its pH was 7 and then dried in an oven at 105 °C (Harris et al., 1997). Immediately after CO_2 trapping, plant materials were harvested and categorized into stem, leaf and root. Plant materials 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 ^{13}C were measured with a PDZ Europa (Cheshire, UK) 'Hydra 20-20' continuous flow isotope ratio mass spectrometer.

Calculation

In the present study, the term 'soil respiration' was used exclusively as the sum of rhizosphere respiration (root respiration and microbial respiration derived from root associated materials) and soil microbial respiration (derived from SOM). 'Root-derived CO_2–C' was used as rhizosphere respiration and 'soil-derived CO_2-C' as soil microbial respiration from decomposition of SOM. If one grows C_3 plant in a 'C_4soil', the carbon derived from C_3 plant (^{13}C= −24‰ to −29‰) and from 'C_4 soil' (^{13}C = −12‰ to −14‰) will have different ^{13}C values. Root derived CO_2-C was estimated using the following equation (Cerri et al., 1985; Cheng, 1996):

$$C_3 = C_t(d_t - d_4)/(d_3 - d_4)$$

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', d_t is the $\delta^{13}C$ value of C_t, d_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. d_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_3soil', root derived CO_2-C can be estimated using a similar equation:

$$C_4 = C_t(d_t - d_3)/(d_4 - d_3)$$

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', d_t is the $\delta^{13}C$ value of C_t, d_4 is the $\delta^{13}C$ value of theC derived from C_4 plant roots, and d_3 is the $\delta^{13}C$ value of the C derived from decomposition of SOM in 'C_3 soil'.

Root-derived CO_2–C was expressed either on a per pot basis or on root biomass basis. The former was generally referred as 'rhizosphere respiration' and it was used to estimate the contribution of rhizosphere respiration to total soil respiration. The latter was termed as 'specific rhizosphere respiration' and it was used as an index of root activity and vitality.

Cumulative root-derived CO_2–C (on a pot basis) was the sum of the cumulative root-derived CO_2–C of all developmental stages. Cumulative root-derived CO_2–C for a specific developmental stage was calculated by multiplying the duration (days) with the average daily root-derived CO_2–C of the stage. Cumulative soil-derived CO_2–C was estimated likewise.

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

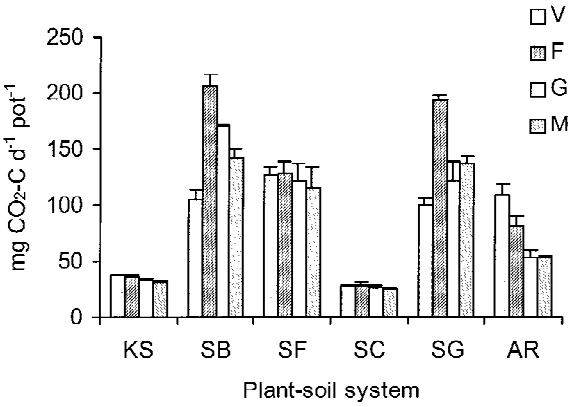

Figure 1. Soil respiration under different plant-soil systems. KS – Kansas 'C_4 soil' control, SB – Soybean planted on 'C_4 soil', SF – Sunflower planted on 'C_4 soil', SC – Santa Cruz 'C_3 soil' control, SG – Sorghum planted on 'C_3 soil', AR – Amaranthus planted on 'C_3 soil'. V, F, G and M represent the vegetative, flowering, grain-filling and maturity stages of the plants.

set at $P<0.05$. Unless otherwise stated, all data were expressed on dry mass basis.

Results

Daily soil respiration

In both C_4 plant – 'C_3 soil' and C_3plant – 'C_4 soil' systems, daily soil respiration was significantly higher under the treatments with plants than those without plants (Figure 1). In C_3 plant – 'C_4 soil' system, daily soil respiration increased significantly from vegetative stage to flowering stage for the soils planted with soybean, however, it did not show any significant change for the soil planted with sunflower from one developmental stage to another. In C_4 plant – 'C_3 soil' system, daily soil respiration increased significantly from vegetative to flowering stage for the soil planted with sorghum, while it declined significantly for the soil planted with amaranthus. The daily soil respiration did not change significantly from grain-filling stage to maturity in all systems (Figure 1).

Rhizosphere respiration

Rhizosphere respiration (root– derived CO_2–C) was estimated based on soil respiration (Figure 1) and $\delta^{13}C$ values of CO_2 evolved from plant roots, control soil and from plant-soil systems (Table1). In C_3 plant – 'C_4 soil' system, CO_2-C derived from soybean roots increased significantly from vegetative stage to flowering stage, and it declined thereafter. However, no significant change of CO_2–C derived from sunflower roots was observed at different plant developmental stages. CO_2–C derived from soybean roots was significantly higher than that derived from sunflower roots from flowering to maturity stage. The percentage of root-derived CO_2–C to soil respiration ranged from 53.22 to 65.25% for soybean, and it ranged from 56.20 to 64.64% for sunflower (Table 2). In C_4 plant – 'C_3 soil' system, CO_2-C derived from sorghum roots increased significantly from vegetative to flowering stage and it declined thereafter. CO_2–C derived from amaranthus was the highest at vegetative stage and it declined with the plant age. CO_2–C derived from sorghum roots was significantly higher than that from amaranthus roots from flowering to maturity stage. The contribution of sorghum roots to soil respiration was relatively stable and it ranged from 75.44 to 86.93% during the experimental period. However, the percentages of CO_2–C derived from amaranthus roots to soil respiration was the highest at vegetative stage (81.97%), and it declined significantly thereafter with the lowest at grain-filling stage (43.09%) (Table 2).

Root biomass and specific rhizosphere respiration

Root biomass increased with plant age for all plant species except that it decreased from grain-filling to maturity stage for amaranthus. Root biomass of sorghum was the highest (2.02–13.36 g pot^{-1}) and that of sunflower (1.69–3.98 g pot^{-1}) was the least. Soybean and amaranthus had similar root biomass (Table 3). When root-derived CO_2-C was normalized with root biomass, it was termed as 'specific rhizosphere respiration'. Table 4 showed that the specific rhizosphere respiration varied significantly with plant age, it declined significantly from physiologically active stages (vegetative and flowering) to inactive stages (grain-filling and maturity) under both plant-soil systems. Specific rhizosphere respiration of soybean (except vegetative stage) and sunflower were significantly higher than that of sorghum and amaranthus.

Contribution of rhizosphere respiration to soil respiration

Cumulative total CO_2–C evolved from soils planted with soybean, sunflower, sorghum and amaranthus were 14.18, 11.54, 12.71 and 7.39 g C pot^{-1}, and cumulative root-derived CO_2–C were 8.68, 7.05, 10.40 and 4.98 g C pot^{-1}, respectively. With the soil volume

Table 1. $\delta^{13}C$ values of CO_2 evolved from soil, plant roots and plant-soil systems at different developmental stages

Plant Species	CO_2 origin	$\delta^{13}C$ (‰) at different developmental stages			
		V[a]	F	G	M
(1) C_3 plant-'C_4 soil' system					
SB[b]	Soil[c]	−11.93[d]	−14.41	−11.63	−12.92
	Roots	−26.96	−25.82	−25.77	−25.71
	System	−19.93	−20.94	−20.86	−20.43
SF	Soil	−11.93[c]	−14.41	−11.63	−12.92
	Roots	−29.55	−28.70	−28.74	−27.99
	System	−22.83	−22.05	−22.68	−21.35
(2) C_4 plant-'C_3 soil' system					
SG	Soil	−24.70	−23.14	−22.72	−26.36
	Root	−12.47	−12.80	−12.61	−12.46
	System	−15.47	−14.17	−14.09	−14.93
AR	Soil	−24.70	−23.14	−22.72	−26.36
	Root	−13.00	−12.65	−12.41	−12.37
	System	−15.11	−16.40	−18.28	−20.28

[a] V, F, G and M represent vegetative, flowering, Grain-filling and maturity stages, respectively.
[b] SB, SF, SG and AR represent plant species of Soybean, Sunflower, Sorghum and Amaranthus.
[c] $\delta^{13}C$ values of CO_2 evolved from 'C_4 soil' and 'C_3 soil' controls are used in C_3 plant-'C_4 soil' system and C_4 plant-'C_3 soil' system, respectively. $\delta^{13}C$ values of plant roots are used as $\delta^{13}C$ values of CO_2 evolved from plant roots since isotope fractionation does not occur during rhizosphere respiration (Cheng, 1996). $\delta^{13}C$ values of total CO_2 evolved from plant-soil systems.
[d] Values are the means of four replicates. Since the coefficient of variation (C.V.) of the data are very small (<5%), the standard errors are not presented to minimize the size of the table.

used in our pots, the rhizosphere respiration accounted for 61.22, 61.14, 81.84 and 67.37% to total soil respiration (Figure 2).

Discussion

Phenological variation of rhizosphere respiration

Growing a C_4 species – Bermuda grass (*Cynodon dactylon* L.) on a soil containing only C_3–C, Robinson and Scrimgeour (1995) found that $\delta^{13}CO_2$ evolved from plant-soil system became less negative during canopy establishment and re-growth following periods of leaf senescence. However, the $\delta^{13}CO_2$ value became more negative as leaf senescence progressed and the canopy consisted of largely of dead leaves. This suggested that root-derived CO_2–C from Bermuda grass (C_4 species) contributed more to soil respiration at active growing stage than at senescence stage. Schönwitz et al (1986) grew C_4 plant – maize (*Zea mays*) on a 'C_3 soil' and also reported that the $\delta^{13}CO_2$ evolved from the plant-soil system was higher (less negative) before harvest than after. It also suggested that the maize roots (C_4 species) delivered more C to soil respiration before the harvest when plants were fruiting than after harvest and plowing. Our results showed that CO_2–C derived from soybean or sorghum roots increased significantly from vegetative to flowering stage, and it declined thereafter. CO_2–C derived from amaranthus was the highest at vegetative stage and it declined with the plant age. No significant change of CO_2–C derived

Table 2. Root-derived CO_2-C (mg C d^{-1} pot^{-1})

Plant species	Plant development stages			
	V[a]	F	G	M
(1) C_3 plant-'C_4 soil' system				
SB[b]	55.69±4.30[c] (53.22%)[d]	132.18±16.01 (63.8%)	111.63±4.0 (65.25%)	83.37±6.01 (58.73%)
SF	77.66±4.49 (61.65%)	75.76±7.12 (59.18%)	77.97±8.07 (64.64%)	67.05±14.38 (56.20%)
(2) C_4 plant-'C_3 soil' system				
SG	75.89±3.76 (75.44%)	169.51±19.43 (86.93%)	104.80±16.81 (85.38%)	113.26±6.29 (82.26%)
AR	88.88±7.01 (81.97%)	53.47±8.98 (64.26%)	22.85±2.89 (43.09%)	23.42±1.53 (43.51%)

[a] V, F, G M represent vegetative, flowering, grain-filling and maturity stages, respectively.
[b] SB, SF, SG and AR represent plant species of soybean, sunflower, sorghum and amaranthus.
[c] Means and standard errors of four replicates.
[d] Percentages of rhizosphere respiration (root-derived CO_2-C) to total soil respiration.

Table 3. Root biomass at different plant developmental stages (g pot^{-1})

Plant species	Plant development stages			
	V[a]	F	G	M
(1) C_3 plant-'C_4 soil' system				
SB[b]	2.29±0.27[c]	4.33±0.30	5.23±1.55	6.30±0.60
SF	1.69±0.44	2.85±0.25	2.94±0.69	3.98±0.79
(2) C_4 plant-'C_3 soil' system				
SG	2.02±0.27	8.05±0.91	9.23±1.43	13.36±1.67
AR	2.54±0.17	5.61±0.48	5.76±0.55	5.12±0.47

[a] V, F, G M represent vegetative, flowering, grain-filling and maturity stages, respectively.
[b] SB, SF, SG and AR represent plant species of soybean, sunflower, sorghum and amaranthus.
[c] Means and standard errors of four replicates.

Table 4. Specific rhizosphere respiration (mg C d^{-1} g^{-1} root)

Plant species	Plant development stages			
	V[a]	F	G	M
(1) C_3 plant-'C_4 soil' system				
SB[b]	25.45±4.03[c]	30.78±3.73	22.63±2.99	13.64±1.78
SF	53.85±10.77	27.22±3.34	27.07±2.60	16.70±0.46
(2) C_4 plant-'C_3 soil' system				
SG	39.49±4.97	21.38±2.56	11.40±1.68	8.70±0.62
AR	35.19±2.89	9.31±1.01	3.96±0.47	4.70±0.59

[a] V, F, G M represent vegetative, flowering, grain-filling and maturity stages, respectively.
[b] SB, SF, SG and AR represent plant species of soybean, sunflower, sorghum and amaranthus.
[c] Means and standard errors of four replicates.

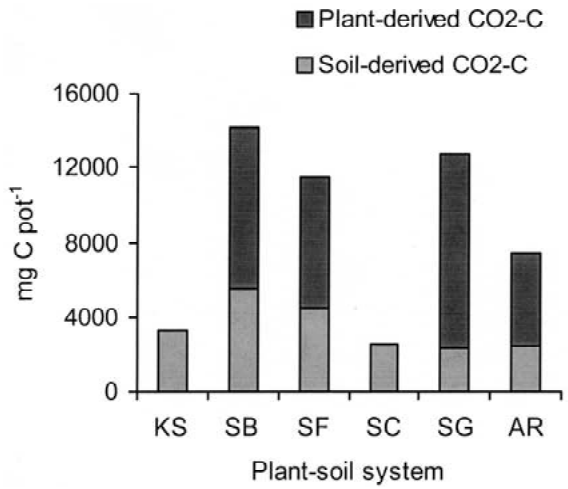

Figure 2. Cumulative root-derived CO_2-C and its contribution to soil respiration under different plant-soil systems. KS – Kansas $1C_4$ soil' control, SB – Soybean planted on 'C_4 soil', SF – Sunflower planted on 'C_4 soil', SC – Santa Cruz 'C_3 soil' control, SG – Sorghum planted on 'C_3 soil', AR – Amaranthus planted on 'C_3 soil'.

from sunflower roots was observed at different plant developmental stages. In conclusion, rhizosphere respiration (root-derived CO_2–C) varied not only with plant species but also with plant phenology. Phenological variation of rhizosphere respiration suggested that timing of the sampling for $\delta^{13}CO_2$ measurement should be mentioned when making comparisons of rhizosphere respiration among various studies.

Specific rhizosphere respiration

Root biomass increased with plant maturity (Table 3) while root activity or/and vitality might decrease concurrently. Therefore, it was difficult to interpret the pattern of rhizosphere respiration when root-derived CO_2–C was expressed on per pot basis. However, specific rhizosphere respiration was used as an index of root activity (e.g. root exudates, secretion) or/and root vitality (e.g. the ratio of live root–dead root) because it was normalized with root biomass. Our results showed that the specific rhizosphere respiration declined significantly from vegetative and flowering to grain-filling and maturity stages under both plant-soil systems. This indicated that root activity or/and root vitality decreased with plant maturity and it was supported by the findings of various studies (Keith et al., 1986; Kuzyakov and Domanski, 2000; Swinnen et al., 1994). They found that the portion of C translocated belowground by cereals and used for root growth, respiration and exudation decreased during plant development. Although the root biomass of sorghum and amaranthus were higher than soybean and sunflower in the present study (Table 3), the specific rhizosphere respiration of sorghum and amaranthus were significantly lower than that of soybean and sunflower in most cases (Table 4). This indicated that the root activities such as root exudation of sorghum and amaranthus were lower or/and the proportion of dead root or senescent root was higher than that of soybean and sunflower at a specific plant developmental stage. Kuzyakov (2001) found that translocation of photosynthate to roots varied significantly with plant species, which provided an indirect evidence for our finding. Simultaneous measurements of root exudation and the ratio of live root–dead root of different plant species would help to better understand the determining factors of rhizosphere respiration.

Methodological limitation

There were advantages and drawbacks for both greenhouse pot study and field study on rhizosphere respiration. One of the advantages of the pot study was able to trap all the CO_2 evolved from a specific plant–soil system using a closed circulating system, and it was convenient to set up systems like C_3 plant – 'C_4 soil' or C_4 plant – 'C_3 soil' used in the present study. The drawbacks of the pot study were that the experimental pots restricted the root growth and blocked the natural water movement and lateral gas diffusion. In the field study, the advantages were that water movement and gas diffusion happened naturally and plant root growth was not restricted. However, it was hard to trap all CO_2

evolved from a specific plant-soil system because there was no naturally closed plant-soil system.

The common problem with both greenhouse pot experiment and field measurement was the ratio of soil volume–root biomass. How much soil was an optimum volume for a plant to grow? Unfortunately, there was not much such information available in the literature. We hypothesized that the ratio of soil volume to root biomass might vary with both soil condition (soil type, fertility and moisture) and plant species. In other words, the ratio of soil volume to root biomass might be different from one experiment to another. This could be one of the reasons causing the variability in carbon partitioning of soil respiration in different studies. In the present study, a pot of 16 cm in diameter × 40 cm in height was used and filled with 8000 g of soil to grow plant. It was unknown that if this was an optimum soil volume for plants in the field. In addition, live roots caused rhizosphere priming effect on decomposition of SOM as illustrated by soil-derived CO_2–C (Figure 2). The intensity and direction of rhizosphere priming effect varied with plant species (Fu and Cheng, 2001), and it would probably vary with the ratio of soil volume–root biomass. Therefore, caution must be taken to interpret the results (e.g. the percentages of rhizosphere respiration to total soil respiration) from our pot study and to compare them with any field measurements.

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