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Plant biomass influences rhizosphere priming effects on soil organic matter decomposition in two differently managed soils

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Abstract

We used a continuous labeling method of naturally ^{13}C-depleted CO_2 in a growth chamber to test for rhizosphere effects on soil organic matter (SOM) decomposition. Two C3 plant species, soybean (*Glycine max*) and sunflower (*Helianthus annus*), were grown in two previously differently managed soils, an organically farmed soil and a soil from an annual grassland. We maintained a constant atmospheric CO_2 concentration at 400 ± 5 ppm and $\delta^{13}C$ signature at $-24.4‰$ by regulating the flow of naturally ^{13}C-depleted CO_2 and CO_2-free air into the growth chamber, which allowed us to separate new plant-derived CO_2–C from original soil-derived CO_2–C in soil respiration. Rhizosphere priming effects on SOM decomposition, i.e., differences in soil-derived CO_2–C between planted and non-planted treatments, were significantly different between the two soils, but not between the two plant species. Soil-derived CO_2–C efflux in the organically farmed soil increased up to 61% compared to the no-plant control, while the annual grassland soil showed a negligible increase (up to 5% increase), despite an overall larger efflux of soil-derived CO_2–C and total soil C content. Differences in rhizosphere priming effects on SOM decomposition between the two soils could be largely explained by differences in plant biomass, and in particular leaf biomass, explaining 49% and 74% of the variation in primed soil C among soils and plant species, respectively. Nitrogen uptake rates by soybean and sunflower was relatively high compared to soil C respiration and associated N mineralization, while inorganic N pools were significantly depleted in the organic farm soil by the end of the experiment. Despite relatively large increases in SOM decomposition caused by rhizosphere effects in the organic farm soil, the fast-growing soybean and sunflower plants gained little extra N from the increase in SOM decomposition caused by rhizosphere effects. We conclude that rhizosphere priming effects of annual plants on SOM decomposition are largely driven by plant biomass, especially in soils of high fertility that can sustain high plant productivity.

Keywords: ^{13}C; Nitrogen uptake; Plant biomass; Priming; Rhizosphere effects; Soil organic matter decomposition

1. Introduction

Plants can stimulate or inhibit native soil organic matter decomposition (e.g., Reid and Goss, 1982; Helal and Sauerbeck, 1986; Fu and Cheng, 2002). While it has been recognized that these rhizosphere effects on soil organic matter decomposition play an important role in the global carbon cycle (Coleman et al., 1992), mechanisms and potential benefits for plants from rhizosphere effects remain unclear.

Plants can influence composition and stimulate activity of soil micro-organisms by producing labile carbon compounds through root exudation (De Nobili et al., 2001; Marschner et al., 2004; Paterson, 2003). Plants can also inhibit microbial activity by competing with microbes for nutrients and water (Fisher and Gosz, 1986; Van Veen et al., 1989; Ehrenfeld et al., 1997; Wang and Bakken, 1997). Plant-induced changes in microbial activity and composition in return can increase plant growth through enhanced soil organic matter decomposition and plant nutrient acquisition (Hamilton and Frank, 2001; Kuzyakov, 2002) or decrease plant growth through competition for resources or attraction of pathogens (Westover and Bever, 2001; Bever, 2002; Reynolds et al., 2003).

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Rhizosphere effects on microbial activity, soil organic matter decomposition and nutrient acquisition depend both on plant species and soil properties (Fu and Cheng, 2002; Kuzyakov et al., 2000; Veneklaas et al., 2003; Van Veen et al., 1989). Plant species differ in the amount and type of labile C released from living roots (Jones et al., 2004; Van der Krift et al., 2001) and in their competition with microbes for nutrients (Priha and Smolander, 2003; Cheng and Bledsoe, 2004). Soil differences in the amount and nature of organic matter, microbial composition, and structure can influence rhizosphere effects on soil organic matter decomposition (Cheng and Kuzyakov, 2005).

Most studies investigating rhizosphere effects on soil organic matter have used continuous labeling or natural tracer techniques with ^{13}C or ^{14}C isotopes to separate plant-derived CO_2–C from SOM-derived CO_2–C effluxes (Andrews et al., 1999; Meharg, 1994; Nguyen et al., 1999; Swinnen et al., 1994). Pulse labeling does not allow for separation of total plant-derived CO_2–C from SOM-derived CO_2–C because it does not uniformly label all plant C (Kuzyakov and Cheng, 2004). Continuous ^{14}C labeling is hazardous and requires special facilities that only exist in a few places around the world. The use of ^{13}C as a natural tracer has been used successfully in the past, but is limited to studies where C4 plants are grown in soils developed under C3 plant-dominated vegetation or vice versa (Cheng, 1996; Qian et al., 1997; Rochette and Flanagan, 1997). We developed a continuous ^{13}C labeling method (similar to the method used by Schnyder, 1992) that allowed us to separate plant-derived CO_2–C from SOM-derived CO_2–C for different plant species grown in different soils in a full factorial design under ambient atmospheric CO_2 concentrations (Cheng and Dijkstra, unpublished).

Here we study rhizosphere effects on soil organic matter decomposition for soybean (*Glycine max*) and sunflower (*Helianthus annuus*) grown in soil from an annual grassland (dominated by C3 grasses) and soil nearby the grassland that has been organically farmed. We hypothesized that each soil has different properties that define the maximum potential for rhizosphere effects on SOM decomposition to occur. Because the grassland and organically farmed soil were managed differently (e.g., greater disturbance in the organically farmed soil) causing them to have different soil properties (e.g., lower total soil C, but higher inorganic N pools in the organically farmed soil than in the grassland soil, and different soil structure), the two soils would show different potential for rhizosphere effects on SOM decomposition. We further hypothesized that rhizosphere effects on SOM decomposition are strongly affected by plant species. Soybean is a N-fixing plant that depends less on soil-derived N for growth and therefore competes less for N with microbial decomposers living close to the roots. These microbes may become increasingly C-limited with increased N-fixation, and respond more strongly to root exudation. We therefore hypothesized that rhizosphere effects on SOM decomposition would be stronger for soybean than for sunflower. We further examined the potential for plants to increase N uptake due to rhizosphere effects on SOM decomposition by comparing soil-derived plant N pools with increases in C respiration and associated N mineralization caused by rhizosphere effects.

2. Materials and methods

2.1. Experimental design

The two soils used in this experiment came from an annual grassland (dominated by C3 grasses, 'grassland soil') and from the organic farm of the Agroecology Center that has been organically farmed (without use of synthetic fertilizer) for over 30 years ('organic farm soil'), both located on the campus of the University of California, Santa Cruz (both Alfisols). Both soils have the same physical properties (sandy loams, 10% clay, 32% silt, 58% sand, formed on calcareous bedrock). The soils we used did not contain carbonates based on the lack of effervescence with addition of 10% HCl. Soil characteristics are shown in Table 1. Soils were homogenized by sieving (2 mm) and air-dried before use. Large aggregates were destroyed by sieving, which may have reduced potential differences in structure between the two soils.

A nylon bag filled with 2500 g playground sand was placed at the bottom of 24 PVC pots (diam. 15 cm, height 40 cm, closed at the bottom except for an air outlet) to improve air circulation, and then filled with 7500 g of air-dried soil. Twelve pots were filled with grassland soil and another twelve with organic farm soil. For each of the two differently managed soils, four pots were planted with soybean (*Glycine max*), four with sunflower (*Helianthus annuus*), and four were not planted (control). Plants were grown from seeds, one plant in each pot in a growth chamber (2800 L) with 12 h of light (approximately 800 $\mu mol\,m^{-1}\,s^{-1}$), at 25 °C when lights were on and 20 °C when lights were off, and 40% relative humidity.

We continuously labeled plants inside the growth chamber with naturally ^{13}C-depleted CO_2 (Cheng and Dijkstra, unpublished). We maintained a constant CO_2 concentration (400 ppm) inside the growth chamber when growth chamber lights were on by regulating the flow of ^{13}C-depleted CO_2 generated from natural gas

Table 1
Soil characteristics of the grassland and organic farm soil

	Grassland soil	Organic farm soil
Bulk density ($g\,cm^{-3}$)	1.21	1.25
Total C (%)	1.53	1.06
Total N (%)	0.12	0.10
C:N	12.8	10.6
$\delta^{13}C$ (‰)	−27.46	−25.93
Extractable $NH_4^+ + NO_3^-$ ($mg\,kg^{-1}$ soil)	22	47
pH (water, S:W ratio 1:2)	6.04	5.8

($\delta^{13}C = -37.7‰$) and CO_2-free air (ambient air led through a soda lime column removing the CO_2) into the growth chamber. The CO_2 concentration inside the growth chamber was monitored and controlled with an infrared gas analyzer (IRGA, LI-COR 820). When the CO_2 concentration fell below 390 ppm, the IRGA opened a solenoid valve to let ^{13}C-depleted CO_2 into the growth chamber. The valve closed at 400 ppm. Two hours before the start of day light period, CO_2-free air was led into the growth chamber at a rate of 55 L min^{-1}. The flow of CO_2-free air was discontinued when lights went off and CO_2 concentrations inside the growth chamber were allowed to increase (due to soil and plant respiration) until two hours before lights went on again. Air CO_2 inside the growth chamber was sampled every other day when growth chamber lights were on by pumping air through a 4 M NaOH solution (from half hour after lights were on until half hour before lights went off, total of 11 hours). Samples were analyzed for $\delta^{13}C$ (see below). The $\delta^{13}C$ signature of the CO_2 inside the growth chamber was relatively constant and highly depleted in ^{13}C (average $\delta^{13}C = -24.4‰$, minimum of –23.4 and maximum of –25.8‰).

The pots were watered daily with deionized water and maintained at 80% water holding capacity by weighing the pots before watering. Disturbances in CO_2 concentration and ^{13}C signature inside the growth chamber during light hours were kept at a minimum by watering during the dark period.

2.2. Sampling and measurements

We measured soil respiration on day 34 and 54 after planting. The first soil respiration measurements occurred when plants were still in vegetative stage, the second occurred after flowering. Before measurement, we sealed the top of the pots by placing two half-moon-shaped Plexiglass on top of the soil inside the pot around the base of the plant, and pouring two-component silicone rubber (Circle K Products, Temecula, CA) on top of the Plexiglass. An air inlet was created by attaching plastic tubing to the Plexiglass. Through closed circulation of air, initial CO_2 inside the root-soil system was removed with a soda lime column and subsequent CO_2 evolved inside the root-soil system was trapped in a CO_2 trapping column (a PVC tube filled with 350 g burnt and acid-washed sand and 35 ml of 4 M NaOH) during a 72 h period (Cheng et al., 2003). The CO_2 trapping efficiency of this system was > 99% as checked by an infrared gas analyzer (Model LI-6262, LI-COR, Lincoln, NE, Cheng et al., 2003). Sub-samples of the solution containing CO_2 trapped from soil respiration and growth chamber air (see above) were measured for inorganic C on a TOC analyzer (Shimadzu TOC-5050A). A 0.3 M $SrCl_2$ solution was added to another sub-sample to form $SrCO_3$ precipitate. The $SrCO_3$ precipitate was repeatedly rinsed with deionized water until a solution pH $\approx$ 7, then dried at 105 °C (Harris et al., 1997).

We measured plant available N in the soil with Plant Root Simulator Probes (PRS™), which consist of anion or cation exchange membranes imbedded in plastic stakes (Western Ag Innovations, Inc., Saskatoon, Canada). These probes are thought to provide a better indicator of plant available N than standard soil analyses, as they are meant to simulate a root (Hangs et al., 2004). The probes have been shown to be responsive to both water and soil nutrient levels (Johnson et al., 2005). Under dry conditions, for example, it is possible that standard soil tests would yield high mineral N values, yet N availability to plants would be limited by moisture. The counter-ions on the resin membranes are Na^+ and HCO_3^-. The PRS probes were inserted to 10-cm depth in each of the pots at the time of planting. We removed the PRS probes from the soil after 30 days and replaced them with new ones. The second set of PRS probes were removed at the time of harvesting. The PRS probes were sent to Western Ag Innovations, Saskatoon, Canada for extraction. At Western Ag, the probes were extracted with 17.5 ml of 0.5 N HCl for 1 h in a zip lock bag, and the extractant was analyzed for NH_4^+ and NO_3^- using a Technicon Autoanlyzer.

All plants were harvested after the second soil respiration measurement (57 days after planting). Plants were separated into stems, leaves, reproductive organs, and roots, were then dried (65°C), weighed, and ground. All $SrCO_3$ precipitate samples, ground plant material samples, and ground soil samples were analyzed for $\delta^{13}C$ on a Hydra 20–20 continuous flow isotope mass spectrometer (PDZ Europa, Chesire, UK). Plant stem and leaf material were combined for $\delta^{13}C$, $\delta^{15}N$ and total N analysis.

2.3. Calculations and statistical analyses

We separated soil respiration into plant-derived CO_2–C (root respiration, and microbial respiration of root associated materials) and soil-derived CO_2–C (microbial respiration of SOM) using the following equation:

$$C_s = C_t(\delta^{13}C_p - \delta^{13}C_t)/(\delta^{13}C_p - \delta^{13}C_s), \quad (1)$$

where C_s is the efflux of CO_2–C derived from soil, C_t is the total efflux of CO_2–C from soil respiration (plant-derived plus soil-derived), and $\delta^{13}C_t$, $\delta^{13}C_s$, and $\delta^{13}C_p$ are the $\delta^{13}C$ values of the total efflux of CO_2–C from soil respiration, the efflux of soil-derived CO_2–C and plant-derived CO_2–C respectively. We used the $\delta^{13}C$ value measured from soil respiration in control pots (no plants) for $\delta^{13}C_s$ and from plant biomass in each pot for $\delta^{13}C_p$.

The $\delta^{13}C$ values measured in the NaOH CO_2 traps were corrected for contamination from carbonate in the NaOH stock solution and from sample handling using the following equation (Cheng et al., 2003):

$$\delta^{13}C_j = (C_t\delta^{13}C_t - C_c\delta^{13}C_c)/(C_t - C_c), \quad (2)$$

where $\delta^{13}C_j$ is the $\delta^{13}C$ value of a sample after correction, $\delta^{13}C_t$ is the $\delta^{13}C$ value of a sample before correction, $\delta^{13}C_c$ is the $\delta^{13}C$ value of the contaminant C (−6‰), C_t is the

total amount of C in the sample solution including contaminant C, C_c is the amount of C in blank control solutions.

For soybean, we separated plant N assimilation into soil-derived N and N fixed from the atmosphere using the following equation (after Shearer and Kohl, 1993):

$$N_s = N_t(\delta^{15}N_{SB} - \delta^{15}N_{\text{fixed N}})/(\delta^{15}NSF - \delta^{15}N_{\text{fixed N}}), \quad (3)$$

where N_s is the amount of soil-derived plant N, N_t is the total amount of plant N, and $\delta^{15}N_{SB}$, $\delta^{15}N_{SF}$, and $\delta^{15}N_{\text{fixed N}}$ are the $\delta^{15}N$ values of soybean, sunflower (reference plant) and atmospherically fixed N (for soybean $\delta^{15}N_{\text{fixed N}} = -1.5$, Shearer and Kohl, 1993), respectively. Soybean and sunflower had similar rooting patterns inside the pot and we further assumed that they were taking up the same form of N from the soil. We realize that this last assumption may not be true, and therefore the interpretation of the fraction of plant N derived from N-fixation that we calculated should be considered cautiously.

We used analyses of variance (ANOVA) to test for plant and soil effects and their interaction on $\delta^{13}C$ values of plant biomass, soil-derived CO_2–C from soil respiration, difference in soil-derived CO_2–C between planted and control pots ('primed soil C'), plant-available N, and plant N pools. We used post-hoc tests (Tukey's test) to test for differences in soil-derived C among all treatments. We also used analyses of covariance (ANCOVA) to test for plant and soil effects on primed soil C with plant biomass as a covariate to account for plant biomass differences among treatments. All statistical analyses were done with JMP (version 4.0.4).

3. Results

We successfully labeled plants with ^{13}C-depleted CO_2 using our continuous ^{13}C labeling method. Plants grown inside the growth chamber were highly depleted in ^{13}C with $\delta^{13}C$ values ranging between –47.7‰ and –41.6‰ (Table 2), or at least 14 units more negative than the soils we used. Sunflower was more productive than soybean and its biomass was more depleted in ^{13}C than for soybean. Plants, and in particular sunflower plants, grown in the organic farm soil were more productive than in the grassland soil. Interestingly, $\delta^{13}C$ values of stem + leaf and root material differed also between the two soils. Especially for roots, differences between soils were relatively large. The $\delta^{13}C$ values of root samples collected in the grassland soil were less negative and more variable than of aboveground biomass, which could be an indication that root samples were contaminated with soil C.

The large difference in the $\delta^{13}C$ signature between soil and plant C allowed us to calculate soil-derived CO_2–C from soil respiration (Eq. (1)) by using the weighted average $\delta^{13}C$ value of the different plant parts for $\delta^{13}C_p$ (Fig. 1). The efflux of soil-derived CO_2–C in control pots was significantly higher in the grassland soil than in the organic farm soil, likely because of the greater total soil C content in the grassland soil. The presence of plants did not significantly alter the efflux of soil-derived CO_2–C after 34 days of planting, but significantly increased the efflux after 54 days of planting in the organic farm soil (on average by 61%). No differences were observed between soybean and sunflower. We found similar results when we used aboveground biomass $\delta^{13}C$ values for $\delta^{13}C_p$ (not shown).

The difference in the efflux of soil-derived CO_2–C between planted and non-planted control pots, or primed soil C, was significantly higher ($P = 0.0006$) for the organic farm soil than for the grassland soil, but was not significantly different between soybean and sunflower after 54 days of planting (ANOVA, Fig. 2). However, significant soil effects on primed soil C could be related to greater plant biomass in the organic farm soil. For instance, leaf biomass was significantly related to primed soil C ($P = 0.02$), while the soil effect disappeared in the ANCOVA (Fig. 2). Leaf biomass showed the highest positive correlation with primed soil C, although total aboveground (stem + leaves + reproductive organs), total belowground (roots), and total biomass also showed

Table 2
Mean biomass and $\delta^{13}C$ values ± standard error for plant biomass with ANOVA results

Plant type	Soil	Stem + leaf		Reproductive organs		Roots		Whole plant	
		Biomass ($g\,pot^{-1}$)	$\delta^{13}C$ (‰)	Biomass ($g\,pot^{-1}$)	$\delta^{13}C$ (‰)	Biomass ($g\,pot^{-1}$)	$\delta^{13}C$ (‰)	Biomass ($g\,pot^{-1}$)	$\delta^{13}C^a$ (‰)
Soybean	Grassland	2.1 ± 0.1	−43.34 ± 0.28	0.7 ± 0.3	−42.90 ± 0.63	1.0 ± 0.2	−41.59 ± 0.68	3.7 ± 0.3	−42.82 ± 0.45
	Organic farm	5.7 ± 0.5	−43.87 ± 0.24	2.0 ± 0.6	−43.49 ± 0.52	0.9 ± 0.1	−43.49 ± 0.29	8.6 ± 1.0	−43.77 ± 0.29
Sunflower	Grassland	1.9 ± 0.2	−47.67 ± 0.08	0.2 ± 0.1	−45.36 ± 0.62	1.0 ± 0.1	−42.33 ± 1.02	3.1 ± 0.1	−45.36 ± 0.62
	Organic farm	15.6 ± 0.5	−45.96 ± 0.12	8.6 ± 0.4	−45.04 ± 0.13	3.0 ± 0.1	−45.39 ± 0.28	27.3 ± 0.5	−45.60 ± 0.13
ANOVA results (*P*-values)									
Plant type		< 0.0001	< 0.0001	< 0.0001	0.002	< 0.0001	0.06	< 0.0001	0.0002
Soil		< 0.0001	0.01	< 0.0001	0.79	< 0.0001	0.002	< 0.0001	0.18
Plant type[a] soil		< 0.0001	0.0001	< 0.0001	0.39	< 0.0001	0.39	< 0.0001	0.41

[a]Weighted average of stem + leaf, reproductive organs and roots.

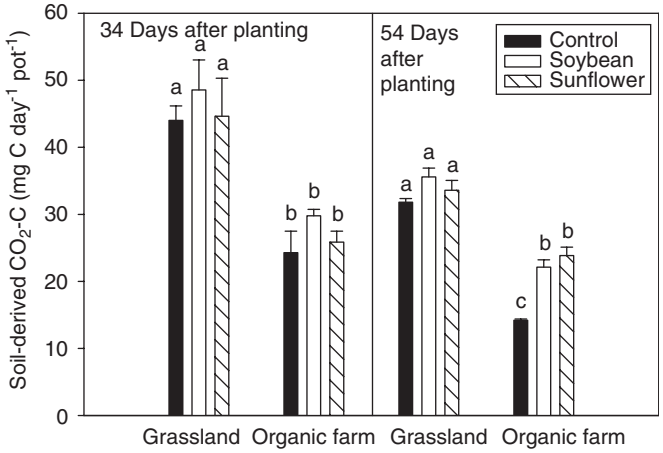

Fig. 1. Average soil derived CO_2–C in soil respiration measured 34 and 54 days after planting affected by soil treatment (grassland and organic farm soil) and plant treatment (control: without plants, soybean, and sunflower). Error bars are standard errors. In each panel, different letters denote significant differences ($P<0.05$, post hoc Tukey's test).

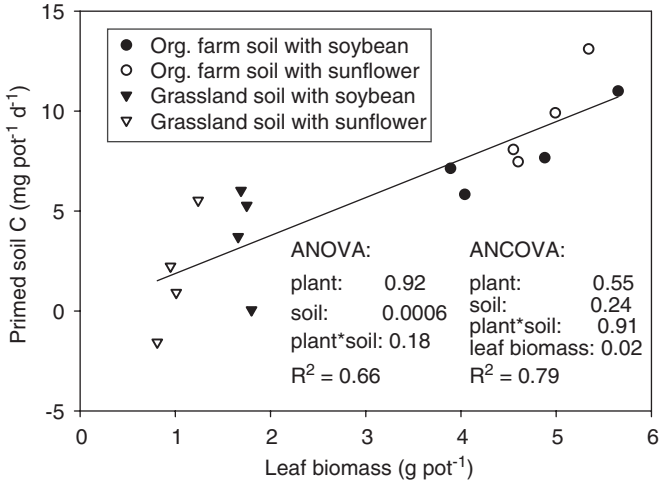

Fig. 2. Primed soil C (difference in soil-derived CO_2–C between planted and control pots) as a function of leaf biomass 54 days after planting.

Table 3
Correlation coefficients between plant biomass parameters and primed soil C and total biomass for all pots

Plant biomass parameter	Primed soil C	Total biomass
Belowground biomass	$+0.52^{*}$	$+0.90^{***}$
Leaf biomass	$+0.86^{***}$	$+0.81^{***}$
Aboveground biomass	$+0.71^{**}$	$+0.99^{***}$
Total biomass	$+0.70^{**}$	

$^{*}P<0.05$, $^{**}P<0.01$, $^{***}P<0.001$.

significant positive correlations with primed soil C (Table 3). Because these measurements of different plant parts were highly correlated to one another (Table 3), it is unclear from our data if priming of soil C is promoted more by aboveground or by belowground plant growth.

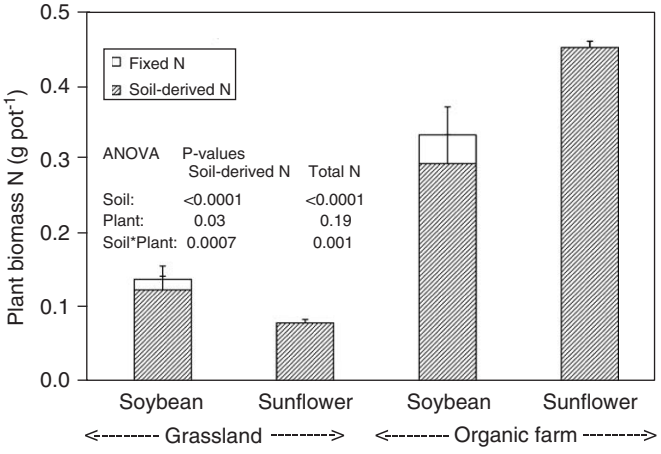

Fig. 3. Average soil-derived N and fixed N in plant biomass 57 days after planting for soybean and sunflower in grassland and organic farm soil. Error bars are standard errors.

Total plant N after 57 days of growth was significantly higher in the organic farm soil than in the grassland soil, while the soil-derived N in sunflower was significantly higher than in soybean in the organic farm soil (Fig. 3). We observed no significant differences in plant available N (PRS probe N) in the soil among treatments after 30 days of planting, but plant available N decreased significantly after 57 days in the organic farm soil planted with soybean and sunflower, and to a smaller degree in the grassland soil with soybean (Fig. 4). Greater amounts of total plant N corresponded with smaller amounts of plant available N in the soil after 57 days. Plant available N in the control pots of the organic farm soil did not decrease after 57 days, but did decrease in the grassland soil control pots.

Plants grown in the organic farm soil most likely gained little extra N through rhizosphere effects on SOM decomposition. The flux of primed soil C in the organic farm soil after 54 days was on average 7.9 mg C day^{-1} pot^{-1} for soybean and 11.7 mg C day^{-1} pot^{-1} for sunflower. Rhizosphere effects on SOM decomposition in the organic farm soil only occurred during the last 23 days of the experiment. Assuming that the flux of primed soil C measured at the end of the experiment was constant during the last 23 days of the experiment, the total amount of primed soil C in the organic farm soil was then roughly 182 mg C pot^{-1} for soybean and 269 mg C pot^{-1} for sunflower. Using the C:N ratio (10.6) of the organic farm soil we calculated that decomposition of organic N could have increased by 17 mg pot^{-1} for soybean and by 25 mg pot^{-1} for sunflower, or only 6% of the total amount of soil-derived N taken up by soybean and sunflower by the end of the experiment. Actual increases in organic N decomposition and plant available N caused by rhizosphere effects were most likely even smaller, because the actual SOM that decomposed during this experiment was most likely relatively young and most likely had a higher C:N ratio than 10.6.

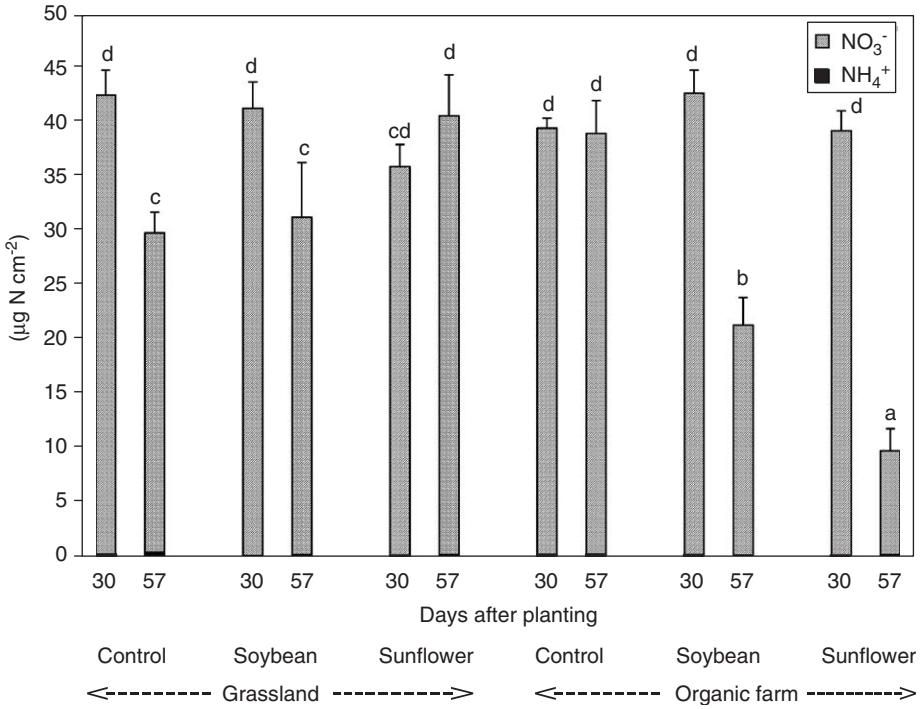

Fig. 4. Plant available N in the soil 30 and 57 days after planting affected by soil treatment (grassland and organic farm soil) and plant treatment (control: without plants, soybean and sunflower). Error bars are standard error. Different letters denote significant differences in total plant available N ($NH_4^+ + NO_3^-$, $P<0.05$, post hoc Tukey's test).

4. Discussion

We hypothesized that soil characteristics affected by management practices alter the soil's potential for rhizosphere effects on SOM decomposition. After 54 days of planting rhizosphere effects on SOM were higher in the organically farmed soil, with greater rhizosphere priming effects on SOM decomposition, despite containing less total soil C and having lower soil respiration rates than the grassland soil. Therefore, rhizosphere priming effects on SOM decomposition in our plant-soil system appear to be less related to total soil C content, but may be more related to soil properties such as fertility (inorganic nutrient pools) and soil C quality, or to microbial composition. Cheng et al. (2003) found that NPK fertilization did not significantly alter rhizosphere effects on SOM decomposition. Fu and Cheng (2002) grew C3 plants in soils developed under a C4 plant community (C4 soil) and C4 plants in a C3 soil and only observed rhizosphere priming effects in the C4 soil, suggesting that soil C quality could play a role in rhizosphere priming effects. However, because they did not grow the same plants in different soils, they were unable to separate soil effects from plant species effects. We observed a smaller rate of soil respiration per unit of soil C in the organic farm control pots (0.32 and 0.19 mg C $pot^{-1}\,d^{-1}$ g soil C^{-1} after 34 and 54 days, respectively) than in the grassland soil (0.40 and 0.29 mg C $pot^{-1}\,d^{-1}$ g soil C^{-1} after 34 and 54 days, respectively), indicating that the average soil C in the organic farm soil was less labile than in the grassland soil. Root exudates could possibly trigger the activity of microbes to synthesize extracellular enzymes specialized in the decomposition of less labile soil C (Fontaine et al., 2003), causing a greater rhizosphere priming effect in the organic farm soil. Root growth could also affect SOM decomposition through destruction of soil aggregates (Helal and Sauerbeck, 1986). In our study, soil structure effects on rhizosphere priming may have been minimal because we destroyed soil aggregates larger than 2 mm (by sieving) before the soil was put into the pots. Disturbance of the soil when placing the soil in the pots may also have induced C and N flushes and may have changed the microbial community in the soil, thereby affecting rhizosphere effects on SOM decomposition. Although the soils we used experience frequent and severe disturbances in their natural settings (tillage in the organic farm soil and gopher activity in the grassland soil), we caution that our results may not be directly relevant to undisturbed soils.

Differences in the rhizosphere priming effect on SOM decomposition between the two soils could largely be explained by differences in plant biomass. Plant biomass, and especially leaf biomass, was positively related to primed soil C. Plants grew bigger in the organically farmed soil (likely because of greater fertility), and within the organically farmed soil variation in plant biomass (leaf biomass) was positively related to rhizosphere priming of SOM decomposition. Many plants that are not under direct abiotic or biotic stress may exert little direct control

over the exudation of labile C (Jones et al., 2004), and a study review by Pinton et al. (2001) indicated that roots exude a relative constant fraction (3–5%) of C fixed in photosynthesis as labile C compounds. Therefore plants that have high leaf production and photosynthetic capacity may exude a greater total amount of labile C into the soil and have a greater potential to prime native soil C. Priming of soil C has also been positively related to root biomass (Fu and Cheng, 2002), and has been shown to change with plant phenology (Cheng et al., 2003; Fu and Cheng, 2002). It is possible that we observed a stronger relationship with leaf biomass than with root biomass, because of greater uncertainties with quantifying root growth than leaf growth. From our results it is also unclear if rhizosphere priming of SOM decomposition would occur in the grassland soil if plants were bigger, or if rhizosphere priming of SOM decomposition in the grassland soil just had a low potential for priming of SOM decomposition.

Contrary to our hypothesis, we observed no greater priming of soil C in soybean than in sunflower. Because soybean depends less on soil-derived N for growth and therefore competes less for N with microbes than sunflower, we expected greater priming of soil C in soybean. Our results contradict other studies that showed greater priming of soil C in soybean compared to wheat (Cheng et al., 2003) and sunflower (Fu and Cheng, 2002). One reason we did not find greater priming of soil C in soybean is that competition for N between plants and microbes may have been small, even for sunflower, in the relative fertile organic farm soil. Also, the amount of N fixed from the atmosphere by soybean was relatively small compared to total N uptake, which may not have resulted in significant differences in plant-microbe competition for N between soybean and sunflower. However, the amount of atmospherically fixed N in soybean may have been different than we calculated with Eq. (3) if soybean and sunflower did not take up the same form of N from the soil. Another reason is that the length of the experiment in this current study was much shorter than the experimental duration of the previous two studies that showed a stronger priming effect with soybean plants during later growing stages. Other mechanisms such as increased drying-rewetting (Cheng and Kuzyakov, 2005), and increased destruction of aggregates (Helal and Sauerbeck, 1986) have been suggested to cause rhizosphere priming effects. Although not incongruent with these mechanisms, our results suggest that plant biomass, and particularly leaf biomass, drove rhizosphere priming effects on SOM decomposition (i.e., leaf biomass explained 74% of the variation in primed soil C among soils and plant species).

Overall soil organic matter decomposition was greater in the grassland soil (i.e., higher efflux of soil derived CO_2–C), but plant productivity and plant N assimilation were smaller than in the organic farm soil. SOM decomposition most likely contributed little to plant available N during the experiment and differences in plant N assimilation between the two soils were likely caused by differences in initial inorganic N pools in the soil. The relatively high initial inorganic N pools (47 mg kg^{-1} soil or 330 mg pot^{-1}) and the large reduction in PRS probe N by the end of the experiment (Fig. 4) in the organic farm soil suggest that much of the plant N uptake came from the soil inorganic N pool. The PRS probe N (plant available N) patterns at day 57 in both soils were the inverse of those for total plant biomass N (Figs. 3 and 4), suggesting that plant N uptake depleted existing sources of available N in the soil, as has been noted in previous studies (Hangs et al., 2004). Rhizosphere effects on SOM decomposition in the organic farm soil most likely contributed even smaller amounts to plant N assimilation. We calculated that no more than 6% of the soil-derived N in both soybean and sunflower could have come from increased SOM decomposition as a result of rhizosphere effects in the organic farm soil. Rhizosphere effects on SOM decomposition and associated N mineralization may be more important for growth of plant species that grow longer and have smaller N uptake rates than sunflower and soybean, but have otherwise similar rhizosphere effects on SOM decomposition. However, to our knowledge only fast-growing annual plants have been used in studies addressing rhizosphere effects on SOM decomposition (Kuzyakov et al., 2000; Cheng and Kuzyakov, 2005), and it remains to be seen if slower growing perennial species can cause significant rhizosphere priming effects on SOM decomposition and N mineralization.

We conclude that rhizosphere priming effects of annual plants on SOM decomposition are largely driven by plant biomass, and in particular leaf biomass, when the potential for priming effects is present in the soil. This means that for fast-growing agricultural plants such as soybean and sunflower rhizosphere priming effects on SOM decomposition are more likely to occur in soils of relatively high fertility that can sustain high plant productivity, and possibly in soils with overall less labile C compounds. However, increased SOM decomposition and associated N mineralization caused by rhizosphere effects likely contribute relatively little N to these fast growing plants.

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