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LETTER

Interactions between soil and tree roots accelerate long-term soil carbon decomposition

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Abstract

Decomposition of soil organic carbon (SOC) is the main process governing the release of CO_2 into the atmosphere from terrestrial systems. Although the importance of soil–root interactions for SOC decomposition has increasingly been recognized, their long-term effect on SOC decomposition remains poorly understood. Here we provide experimental evidence for a rhizosphere priming effect, in which interactions between soil and tree roots substantially accelerate SOC decomposition. In a 395-day greenhouse study with Ponderosa pine and Fremont cottonwood trees grown in three different soils, SOC decomposition in the planted treatments was significantly greater (up to 225%) than in soil incubations alone. This rhizosphere priming effect persisted throughout the experiment, until well after initial soil disturbance, and increased with a greater amount of root-derived SOC formed during the experiment. Loss of old SOC was greater than the formation of new C, suggesting that increased C inputs from roots could result in net soil C loss.

Keywords

^{13}C labelling, decomposition, Fremont cottonwood, Ponderosa pine, priming effect, rhizosphere, roots, SOC turnover, soil organic carbon, tree species.

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INTRODUCTION

The amount of organic C stored in the soil (1.5×10^{18} g of C) is globally about twice that of the total C in the atmosphere (Schlesinger 1997). Small changes in soil organic carbon (SOC) can significantly affect the global atmospheric CO_2 concentration and climate system. The amount of SOC storage is a function of its decomposition rate as well as of C inputs and of other C loss pathways. Factors such as, the quality of plant litter, the microbial decomposer community and the abiotic soil environment affect the soil organic matter (SOM) and litter decomposition (Melillo *et al.* 1982; Nadelhoffer *et al.* 1991; Zheng *et al.* 1997; Parton *et al.* 2007). But often, evidence for the importance of these factors comes from the studies where the decomposition was measured in the absence of plants (e.g. Nadelhoffer *et al.* 1991; Giardina & Ryan 2000; Fang *et al.* 2005). However, when plants are present, as has been shown in recent experiments involving annual plant species, SOC decomposition can increase substantially, up to 380%, (Cheng *et al.* 2003) compared with the standard soil incubations lacking plants. This root-induced increase in SOM decomposition is known as the rhizosphere priming effect. Nevertheless, our understanding of rhizosphere priming effects on SOC decomposition is very limited, despite its importance for long-term soil C storage and nutrient mineralization (Kuzyakov *et al.* 2000; Fontaine *et al.* 2004; Cheng & Kuzyakov 2005; Phillips 2007).

Indirect evidence for rhizosphere priming effects on SOC decomposition in the field comes from studies where the plant productivity and root activity were altered by manipulating the atmospheric CO_2 concentration. A CO_2-induced stimulation of SOC decomposition occurred during the first 2 years in a *Populus x euramericana* plantation (Hoosbeek *et al.* 2004, 2006) and in a *Populus deltoides* plantation (Trueman & Gonzalez-Meler 2005). It was suggested that this was caused by greater (root) litter inputs under elevated CO_2. Similarly, in a grassland study in TX, USA, labile soil C increased under elevated CO_2 offsetting the loss of older mineral-associated organic matter (Gill *et al.* 2002), suggesting a greater rhizosphere priming effect under elevated CO_2. In contrast, decomposition shifted from older SOC to more easily degraded rhizodeposits under elevated CO_2 in a California grassland (Cardon *et al.* 2001). Increased plant productivity with elevated atmospheric CO_2 concentration is sometimes accompanied with a considerable

increase in plant nitrogen (N) uptake. This increase has been ascribed to greater root exploration of the soil and N uptake from deep soil layers (Finzi *et al.* 2006; Norby & Iversen 2006). More recently, it has been suggested that rhizosphere priming effects on SOM decomposition and N mineralization should also be considered to explain the increase in plant N supply with elevated atmospheric CO_2 concentration (Reich *et al.* 2006).

Measuring SOC decomposition in the presence of plants remains difficult, and has only been reported in short-term studies using disturbed soils (Helal & Sauerbeck 1984; Liljeroth *et al.* 1994; Cheng 1996; Cardon *et al.* 2001; Cheng *et al.* 2003; Bader & Cheng 2007) and in studies where the atmospheric CO_2 concentration was manipulated (Hoosbeek *et al.* 2004; Trueman & Gonzalez-Meler 2005). It is largely unknown whether rhizosphere priming effects on SOC decomposition will persist long after the initial soil disturbance or how it relates to plant productivity and root activity. There is a circumstantial evidence that the soil adjacent to roots in undisturbed temperate forest sites has larger C mineralization rates than in bulk soil (Phillips & Fahey 2006), but the significance of tree rhizosphere priming effects on SOC decomposition remains unclear.

We used a continuous ^{13}C-labelling technique to study rhizosphere priming effects of Ponderosa pine (POPI) (*Pinus ponderosa* P.&C. Lawson) and Fremont cottonwood (FRCO) (*Populus fremontii* S. Wats) seedlings on SOC decomposition in three different soil types. We grew plants for 395 days in a greenhouse. We showed that SOC decomposition significantly increased when the plants were present and that this rhizosphere priming effect was long-lasting and increased with increased formation of new SOC.

MATERIALS AND METHODS

Greenhouse experiment

We performed our experiment in a temperature and CO_2-controlled greenhouse at the University of California, Santa Cruz. We added ^{13}C-depleted CO_2 ($\delta^{13}C = -38‰$) to the greenhouse from a gas tank. The CO_2 concentration inside the greenhouse, monitored and controlled with an infrared gas analyzer (IRGA, LI-COR 820, LI-COR, Lincoln, NE, USA), was kept at 760 ± 2 p.p.m. (SD) to reduce the CO_2 $\delta^{13}C$ value to a desirable level. This labelling method has previously been tested successfully in a growth chamber and greenhouse (Dijkstra *et al.* 2006; Dijkstra & Cheng 2007). The CO_2 inside the greenhouse was regularly sampled for ^{13}C analysis (see below) and the $\delta^{13}C$ value of the CO_2 was stable (mean = −21.6 ± 0.7‰ SD) throughout the experiment. We filled 20 bottom-capped PVC pots (diameter 15 cm, height 40 cm) either with 'Blodgett', 'UCSC grassland' or 'Marshall field' soil (total of 60 pots). The 'Blodgett' soil was collected from UC Berkeley's Blodgett Forest Research Station, a mixed-conifer forest dominated by POPI (*Pinus ponderosa*), in the Sierra Nevada foothills, CA, USA. The 'UCSC grassland' soil was collected from an open oak savanna, dominated by invasive annual grasses, in the UC Santa Cruz campus. Both POPI and FRCO (*Populus fremontii*) species grow nearby in the adjacent UCSC Arboretum. The 'Marshall field' soil was collected from a POPI grove on a coastal terrace in West Marshall field, Santa Cruz, a part of the UCSC campus reserve. None of the soils contained carbonates. Physical and chemical characteristics of these three soils are listed in Table 1. Soils were air-dried and sieved (4 mm) before pots were filled. All pots were inoculated with Blodgett soil (50 g/pot) to ensure adequate mycorrhizal infection of all POPI seedlings. Eight pots of each soil type were planted with 10-months old POPI seedlings and eight pots with FRCO cuttings (the four remaining pots were used as controls) and grown inside the greenhouse. Pots were watered daily. Half of the plants (four pots of each species of each soil type) were harvested after 107 days of planting and the other half after 398 days of planting.

Table 1 Soil characteristics of the three soil types (average ± SE)

	Blodgett	UCSC grassland	Marshall field
Texture	Loam	Sandy loam	Loam
pH	5.0	5.0	4.4
Total C (g kg^{-1})	52 ± 3	14 ± 2	23 ± 2
$\delta^{13}C$ (‰)	−25.0 ± 0.2	−26.3 ± 0.3	−27.3 ± 0.3
Labile C (g kg^{-1})	1.56 ± 0.12	0.42 ± 0.08	0.47 ± 0.05
k (d^{-1})	0.006 ± 0.001	0.014 ± 0.002	0.012 ± 0.001
Total N (g kg^{-1})	2.2 ± 0.2	1.2 ± 0.1	2.0 ± 0.1
C : N	23.7 ± 1.4	11.8 ± 0.8	11.6 ± 0.7
$NH_4^+ + NO_3^-$ (mg kg^{-1})	14 ± 2	22 ± 3	19 ± 1

Sampling and analyses

We measured the soil respiration on day 24, 60, 100, 156, 206, 296 and 395 after planting (Cheng 1996). Before each measurement, we sealed pots above the soil and around the base of each plant with two component silicone rubber. Residual CO_2 inside the pot was removed before sampling by circulating the isolated air through soda lime. We then measured soil respiration by circulating the soil atmosphere for 15 min in every 4 h through a solution of NaOH during a period of 48 h. The CO_2 trapping efficiency of this system was > 99.9% (Cheng 1996). Each time we sampled soil respiration we also sampled CO_2 inside the greenhouse by

circulating greenhouse atmosphere continuously through a NaOH solution for 48 h. An aliquot of each NaOH solution was analysed for total C (Shimadzu TOC-5050A carbon analyzer, Shimadzu, Columbia, MD, USA) and another aliquot was precipitated as $SrCO_3$. Dried samples of $SrCO_3$ were analysed for ^{13}C (PDZ Europa continuous flow IR-mass spectrometer, Europa Scientific, Crewe, UK). The $\delta^{13}C$ values measured in the NaOH solution were corrected for contamination from carbonate in the NaOH, in the stock solution and from sample handling (Cheng *et al.* 2003). The $\delta^{13}C$ of CO_2 inside the greenhouse showed constant isotopic values throughout the experiment (mean ± SD: −22.0 ± 0.7‰).

We separated harvested plants into leaf/needle, stem and root biomass. Plant biomass samples were dried (65 °C), weighed, ground and analysed for ^{13}C (PDZ Europa continuous flow IR-mass spectrometer). The average $\delta^{13}C$ values of plant biomass were −44.7 and −46.9‰ for POPI and FRCO, respectively (average of two harvests). At the end of the experiment, soil samples from each pot were dried (105 °C), ground and analysed for total C and ^{13}C (PDZ Europa continuous flow IR-mass spectrometer).

We estimated the initial amount of labile C (C_l) and its decomposition rate constant (k) in each of the three soils by fitting a two-order model through soil respiration rates measured at different times in the control treatments (Dijkstra *et al.* 2005):

$$R_t = C_l k\, e^{-kt} + c \quad (1)$$

where R_t is the daily soil respiration rate at time t, and c is the soil respiration rate of more resistant C.

The continuous labelling of plants with depleted ^{13}C allowed us to separate plant-derived from soil-derived CO_2-C in soil respiration. We calculated soil-derived CO_2-C in the planted treatments using the following equation:

$$CO_2\text{-}C_{soil} = CO_2\text{-}C_{tot}(\delta^{13}C_{plant} - \delta^{13}C_{tot})/(\delta^{13}C_{plant} - \delta^{13}C_{control}) \quad (2)$$

where $CO_2\text{-}C_{soil}$ is the efflux of CO_2-C derived from the non-labelled SOC (i.e. SOC that was present at the start of the experiment) in the planted treatments, $CO_2\text{-}C_{tot}$ is the total efflux of CO_2-C from soil respiration in the planted treatments, and $\delta^{13}C_{tot}$, $\delta^{13}C_{control}$ and $\delta^{13}C_{plant}$ are the $\delta^{13}C$ values of the total efflux of CO_2-C in the planted treatments, the efflux of CO_2-C in the control treatments and plant biomass, respectively. We used the weighted average $\delta^{13}C$ of leaf, stem, and roots of FRCO for $\delta^{13}C_{plant}$ (first harvest values for respiration measured on day 24, 60 and 100, and second harvest values for respiration measured on day 156, 206, 296 and 395 after planting). For POPI, we used the weighted average $\delta^{13}C$ of needles and roots for $\delta^{13}C_{plant}$, because after 107 and 398 days of labelling, stems remained slightly less depleted in ^{13}C (by 3.7 and 1.0‰, respectively) than roots and needles, suggesting that a small fraction of unlabelled C was still present in the POPI stems. We calculated 'primed CO_2-C' as the difference in soil-derived CO_2-C between planted and non-planted control treatments. We calculated 'cumulative soil-derived CO_2-C' and 'cumulative primed C' by multiplying the average daily rate of soil-derived and primed CO_2-C between two measuring dates by the time interval between two measuring dates, and by adding the preceding soil-derived and primed CO_2-C, respectively. During the experiment we also grew POPI seedlings in two pots filled with sand that did not contain C, and measured root/rhizosphere respired CO_2 (i.e. all plant-derived CO_2-C) from the two pots to check whether plant-derived CO_2-C had similar $\delta^{13}C$ values as plant biomass C. As we started with 10-month-old POPI seedlings, plant-derived CO_2-C may have partly stemmed from unlabelled plant C, particularly during the early stage of the experiment. After the plants in the sand pots had grown for 24, 60 and 100 days, the $\delta^{13}C$ value of the rhizosphere CO_2 was −39.8, −41.6 and −41.0‰, respectively. All these $\delta^{13}C$ values were within 1.5‰ of the $\delta^{13}C$ value of the plant biomass measured after 107 days (−41.3‰), indicating that the plant biomass $\delta^{13}C$ provided a good estimate of plant-derived CO_2-C, even during the early stage of the experiment.

We calculated the amount of plant-derived SOC formed during the experiment through root exudation and death (C_{gain}) using the following equation:

$$C_{gain} = C_{end}(\delta^{13}C_{start} - \delta^{13}C_{end})/(\delta^{13}C_{start} - \delta^{13}C_{root}) \quad (3)$$

where C_{end} is the total amount of SOC at the end of the experiment (including labelled plant-derived SOC and unlabelled SOC), and $\delta^{13}C_{start}$, $\delta^{13}C_{end}$ and $\delta^{13}C_{root}$ are the $\delta^{13}C$ values of SOC at the start and end of the experiment and of root biomass, respectively.

We used analysis of variance (ANOVA) to test for significant plant species and soil type effects and interactions on primed CO_2-C, cumulative soil-derived CO_2-C, cumulative primed C, new plant-derived SOC and net change in soil C. We used analysis of covariance (ANCOVA) with C input via roots into the soil as a covariate to test for significant plant species and soil type effects and interactions on cumulative primed C. All statistical analyses were carried out with JMP (version 4.0.4).

RESULTS

We observed large rhizosphere priming effects on SOC decomposition in all soil-plant combinations that persisted after 395 days, long after initial soil disturbance (Fig. 1).

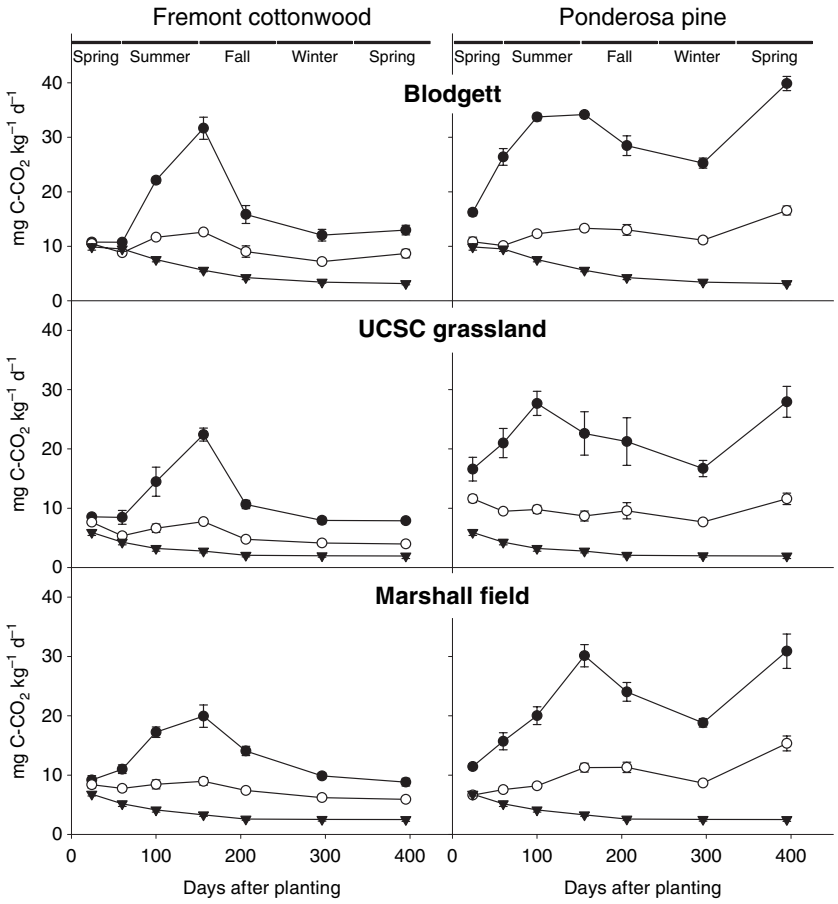

Figure 1 Average soil respiration rates during a 395-day experiment (error bars are ± 1 SE). Filled circles show total soil CO_2 efflux in the planted treatments (plant- and soil-derived CO_2-C), open circles show soil organic carbon (SOC) decomposition rates (as measured by soil-derived CO_2-C) in the planted treatments, and closed triangles show SOC decomposition rates in the unplanted control treatments. The difference in decomposition rates between the planted and control treatments is primed C.

Table 2 ANOVA results for primed C (soil-derived CO_2-C in the planted minus soil-derived CO_2-C in the non-planted control treatments)

Days after planting	Plant species		Soil type		Plant species × soil type	
	F	*P*	*F*	*P*	*F*	*P*
24	5.4	0.03	11.2	0.0009	10.8	0.001
60	35.9	< 0.0001	25.1	< 0.0001	13.4	0.0003
100	8.4	0.01	0.5	0.60	4.2	0.03
156	9.4	0.007	8.0	0.003	0.7	0.51
206	34.5	< 0.0001	3.0	0.08	0.1	0.89
296	116.9	< 0.0001	13.9	0.0003	3.1	0.07
395	167.9	< 0.0001	12.1	0.0005	0.7	0.52

Rhizosphere priming effects on SOC decomposition were always significantly larger for POPI than for FRCO ($P < 0.05$), and largest in the UCSC grassland soil during the first 60 days and largest in the Blodgett soil after 156 days (Fig. 1, Table 2). Cumulative amounts of primed C after 395 days were on average significantly larger for POPI than for FRCO (by 113%, $P < 0.0001$) and largest in the Blodgett soil (Fig. 2a). Using root biomass $\delta^{13}C$ values, rather than 'whole plant' biomass $\delta^{13}C$ values for $\delta^{13}C_{plant}$ in eqn 2 did not change our results in any meaningful way.

In the control treatments, soil respiration showed a typical decline over time in all three soils because of the depletion of more rapidly decomposing labile C compounds. We estimated the initial amount of labile C (C_l) and its decomposition rate constant (k) in each of the three soils according to eqn 1. The Blodgett soil had the highest amount of labile C with the lowest decomposition rate

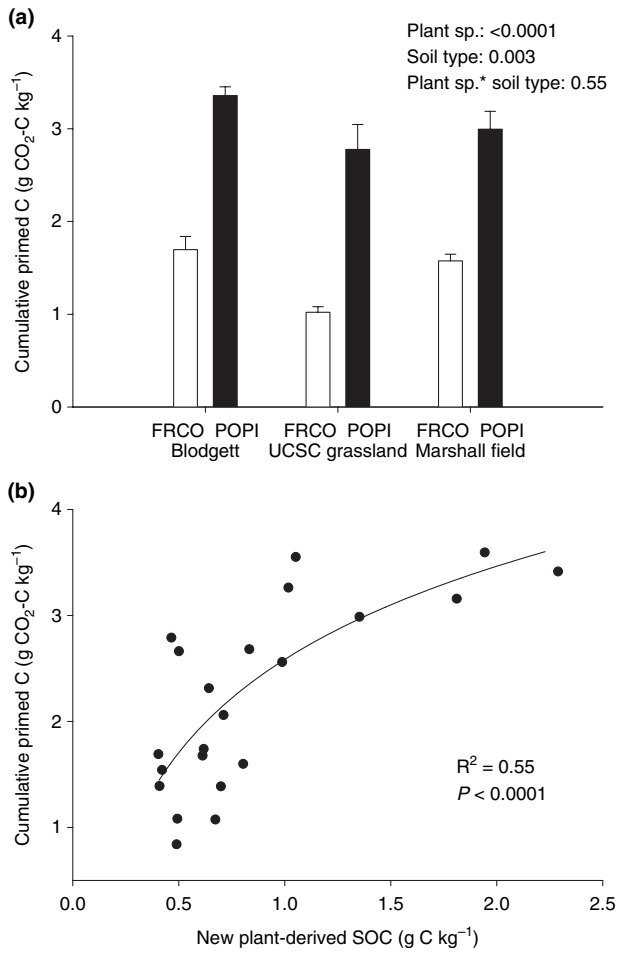

Figure 2 Cumulative primed C (the cumulative amount of soil-derived CO_2-C in the planted treatments minus the cumulative amount of soil-derived CO_2-C in the control treatments) after 395 days of planting. (a) Cumulative primed C among different plant species (FRCO, Fremont cottonwood; POPI, Ponderosa pine) and soil type. (b) Cumulative primed C as a function of new plant-derived soil organic carbon formed during the experiment.

constant (Table 1). Most of the labile C was decomposed in all three soils after 300 days (i.e. nearly flat soil respiration in control treatments after 300 days, Fig. 1). Rhizosphere priming effects on SOC decomposition increased at the end of the experiment in most plant–soil combinations and cumulative amounts of primed C after 395 days were always larger than initial labile C pools in the three soils.

We observed a strong positive relationship between plant-derived SOC and cumulative primed C (Fig. 2b). This relationship was stronger than the relationship between total plant biomass ($R^2 = 0.14$, $P = 0.07$) or root biomass ($R^2 = 0.22$, $P = 0.02$) and cumulative primed C. After effects of plant-derived SOC were corrected for via ANCOVA with plant C input as a covariate, plant species and soil type effects on cumulative primed C remained significant ($P < 0.05$). This indicates that species and soil type effects on cumulative primed C were not solely a result of their effects on the formation of plant-derived SOC.

The amount of C lost through decomposition was always larger than the amount gained with new plant-derived SOC at the end of the experiment, causing a net loss in soil C (Table 3). The net loss was significantly larger for POPI than for FRCO ($P < 0.0001$) and smallest in the UCSC grassland soil. We calculated the net loss in soil C by subtracting total soil C measured at the start of the experiment from total soil C at the end of the experiment. Calculated this way, there was a C loss in all soil type and plant species combinations, but with greater variance.

DISCUSSION

Rhizosphere priming effects on SOC decomposition persisted in all soil–plant combinations. Labile C pools in the soil were mostly depleted after 300 days, but rhizosphere priming effects on SOC decomposition increased after 395 days in most of the plant–soil combinations. The cumulative amount of primed C was always larger than the labile C pool in the soil. Therefore, the presence of plants must have increasingly enhanced decomposition of relatively resistant SOC. While a rhizosphere priming effect on SOC decomposition has only been reported in short-term studies using disturbed soils (Helal & Sauerbeck 1984; Liljeroth *et al.* 1994; Cheng 1996; Cheng *et al.* 2003), our results suggest that initial soil disturbance did not cause these rhizosphere priming effects on SOC decomposition.

The significant positive relationship between new plant-derived SOC formation and cumulative primed C suggests that the presence of plants increased SOC decomposition because of C inputs through rhizodeposition. It has been suggested that root exudation may cause rhizosphere priming effects on SOC decomposition (Kuzyakov *et al.* 2000; Cheng & Kuzyakov 2005). Root exudation may have caused rhizosphere priming effects on SOC decomposition during the first 200 days of the experiment. However, after 200 days (in the fall) FRCO dropped all their leaves (leaves were sampled and not returned to the soil). Root exudate production at that time was likely small for these plants, but rhizosphere priming still occurred, probably because of continuing root death. In a previous study, we have shown that primed C was significantly positively related to plant biomass of sunflower and soybean (Dijkstra *et al.* 2006). Although we observed positive relationships between cumulative primed C and plant biomass of POPI and FRCO, the relationships were not as strong as for plant-derived SOC formation, suggesting that formation of new plant-derived SOC is a better indicator for rhizosphere priming than whole plant or root biomass.

Table 3 Average cumulative soil derived-CO_2 (C_{loss}), new plant-derived SOC formed during the experiment (C_{gain}), and net change in soil C (± 1 SE) after 395 days

Plant sp.	Soil type	C_{loss} g kg^{-1} C	C_{gain} g kg^{-1} C	Net change	
				$C_{gain}-C_{loss}$ g kg^{-1} C	$C_{end}-C_{start}$ g kg^{-1} C
FRCO	Blodgett	3.7 ± 0.1	0.7 ± 0.1	−3.0 ± 0.1	−3.3 ± 1.5
	UCSC grass	2.1 ± 0.1	0.6 ± 0.1	−1.6 ± 0.1	−2.1 ± 0.6
	Marshall	2.9 ± 0.1	0.5 ± 0.1	−2.4 ± 0.1	−3.0 ± 0.3
POPI	Blodgett	4.9 ± 0.1	1.8 ± 0.3	−3.1 ± 0.2	−5.8 ± 0.5
	UCSC grass	3.7 ± 0.3	0.9 ± 0.1	−2.8 ± 0.2	−0.2 ± 0.5
	Marshall	3.8 ± 0.1	0.8 ± 0.3	−3.0 ± 0.2	−5.0 ± 0.7
ANOVA results (*P*-values)					
Plant sp.		< 0.0001	0.0005	< 0.0001	0.79
Soil type		< 0.0001	0.001	< 0.0001	0.03
Plant sp. × Soil type		0.19	0.03	0.005	0.19

FRCO, Fremont cottonwood; POPI, Ponderosa pine; SOC, soil organic carbon. C_{end} and C_{start} are the amounts of soil C measured at the end and at the start of the experiment. C_{gain} was from root input only.

Species and soil type effects on cumulative primed C remained significant after correcting for new plant-derived SOC formation. It is unclear why POPI increased SOC decomposition significantly more than FRCO. One possible explanation is that these species are associated with different fungal symbionts. Ponderosa pine roots are associated with ectomycorrhizae, whereas FRCO roots are associated with arbuscular mycorrhizae. While it has been assumed that mycorrhizae completely depend on C from their plant hosts (Smith & Read 1996), a recent study indicated that tree species hosting ectomycorrhizae caused larger rhizosphere effects on SOC decomposition than tree species hosting arbuscular mycorrhizae (Phillips & Fahey 2006). Unfortunately, we did not measure mycorrhizal infection. The larger rhizosphere priming effects on SOC decomposition in the Blodgett soil than in the other two soils could have been a result of greater amounts of total soil C (Table 1). However, when we expressed cumulative primed C per unit of total soil C, then the amount of cumulative primed C was still significantly different among soils ($P < 0.0001$) with now the UCSC grassland soil having the largest and the Blodgett soil having the smallest amount, suggesting that other soil factors, such as soil fertility and mineralogy, affected the rhizosphere priming effect on SOC decomposition as well. It has been suggested that high N availability and low C : N ratio in soil may enhance the rhizosphere priming effect on SOC decomposition (Hoosbeek *et al.* 2006; Rasmussen *et al.* 2007). The high inorganic N concentration and low C : N ratio in the UCSC grassland soil may have increased the rhizosphere priming effect per unit of total soil C in this soil. However, larger priming effects on soil C decomposition in soils with greater N limitation have also been observed (Fontaine *et al.* 2004). Priming effects on soil C decomposition have also been related to soil texture (Bol *et al.* 2003) and mineralogy (Rasmussen *et al.* 2007). Differences in soil texture and mineralogy of the three soils we used may have influenced the priming effect in our study.

We are confident that our continuous labelling method reliably measured rhizosphere priming effects on SOC decomposition. Plant biomass $\delta^{13}C$ values were at least 16.2‰ more negative than the $\delta^{13}C$ values of soil respiration in control treatments, while standard errors of $\delta^{13}C$ in plant biomass and soil respiration in control treatments were smaller than 0.6‰ ($n = 4$). For POPI, the $\delta^{13}C$ value of plant-derived CO_2-C during the first 60 days may have been up to 1.5‰ higher than the plant biomass $\delta^{13}C$ value measured after 107 days (see Materials and Methods), which would have caused a deviation of 2.9% in the cumulative amount of primed C. We further assumed that the $\delta^{13}C$ signature of soil respiration in the control treatments was the same as the $\delta^{13}C$ signature of soil-derived CO_2-C in the planted treatments. The $\delta^{13}C$ signature of soil respiration in the control treatments remained relatively constant throughout the experiment (−24.0 ± 0.2, −26.2 ± 0.3 and −26.7 ± 0.3‰ for the Blodgett, UCSC grassland and Marshall field soil, respectively, mean ± SE, $n = 7$), and showed no temporal trend, despite progressive depletion of labile C pools during the experiment. This indicates that SOC pools with different turnover times had similar $\delta^{13}C$ signatures, and therefore the $\delta^{13}C$ values most likely remained the same for soil-derived CO_2-C both in the planted treatments and in the unplanted control pots.

Our results indicate increased SOC turnover when plants are present. We observed the largest rhizosphere priming effects when new plant-derived SOC formation was largest. In other words, the loss of soil C because of increased decomposition of resistant SOC in the presence of plants

was replaced by new C that entered the soil via roots. After 395 days, total C loss through decomposition was larger than formation of new SOC, resulting in a net loss in soil C. Because the plants were grown in an environment with roughly twice the ambient atmospheric CO_2 concentration, rhizosphere priming effects may have been larger than under ambient CO_2 concentration (Cheng 1999). Aboveground litter production during the experiment was not added to the soil, which would otherwise have increased C input, but perhaps would also have further increased SOC decomposition. Plant C inputs and rhizosphere priming effects on SOC decomposition may also be different for mature trees than what we observed for tree seedlings. Decomposition of old SOC increased under elevated CO_2 with or without an increase in newly formed SOC (Hoosbeek *et al.* 2004, 2006; Trueman & Gonzalez-Meler 2005), while decomposition of older SOC decreased under elevated CO_2 when mineral nutrients were added (Cardon *et al.* 2001). Here, we show for the first time a direct positive relationship between the rate of new SOC formation and old SOC decomposition. Recently, in a theoretical framework, Fontaine & Barot (2005) also showed that the supply rate of energy-rich litter could increase the decomposition rate of recalcitrant SOC.

Our results have shown that rhizosphere priming effects on SOC decomposition are large and persist long after initial soil disturbance. Increased C input into the soil does not necessarily lead to increased soil C storage, but may actually enhance SOC decomposition that could result in a significant net soil C loss. Indeed, several recent field studies have shown an increase in soil C input but reduced soil C storage under elevated atmospheric CO_2 concentration (Hoosbeek *et al.* 2004; Heath *et al.* 2005; Trueman & Gonzalez-Meler 2005; Carney *et al.* 2007). In contrast, most global models indicate a considerable capacity of terrestrial ecosystems to store large amounts of C in the coming century because of CO_2 enrichment (Intergovernmental Panel on Climate Change 2001). However, these models do not account for rhizosphere priming effects. We believe it necessary to incorporate rhizosphere priming effects on SOC decomposition in more models to better predict soil C dynamics under a changing global environment.

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