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 CO2 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
13C labelling, decomposition, Fremont cottonwood, Ponderosa pine, priming effect, rhizosphere, roots, SOC turnover, soil organic carbon, tree species.

INTRODUCTION
The amount of organic C stored in the soil (1.5X1018 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 CO2 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 CO2 concentration. A CO2-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 CO2. Similarly, in a grassland study in TX, USA, labile soil C increased under elevated CO2 offsetting the loss of older mineral-associated organic matter (Gill et al. 2002), suggesting a greater rhizosphere priming effect under elevated CO2. In contrast, decomposition shifted from older SOC to more easily degraded rhizodeposits under elevated CO2 in a California grassland (Cardon et al. 2001). Increased plant productivity with elevated atmospheric CO2 concentration is sometimes accompanied with a considerable

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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 CO2 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 CO2 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 13C-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 CO2-controlled greenhouse at the University of California, Santa Cruz. We added 13C-depleted CO2 ($\delta^{13}C = -38^{\circ/o}$) to the greenhouse from a gas tank. The CO2 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 CO2 $\delta^{13}C$ 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 CO2 inside the greenhouse was regularly sampled for 13C analysis (see below) and the $\delta^{13}C$ value of the CO2 was stable (mean = $-21.6 \pm 0.7^{\circ/o}$ 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.

**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 CO2 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 CO2 trapping efficiency of this system was $>99.9\%$ (Cheng 1996). Each time we sampled soil respiration we also sampled CO2 inside the greenhouse by

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

<table>
<thead>
<tr>
<th>Texture</th>
<th>Blodgett</th>
<th>UCSC grassland</th>
<th>Marshall field</th>
</tr>
</thead>
<tbody>
<tr>
<td>pH</td>
<td>5.0</td>
<td>5.0</td>
<td>4.4</td>
</tr>
<tr>
<td>Total C (g kg⁻¹)</td>
<td>52 ± 3</td>
<td>14 ± 2</td>
<td>23 ± 2</td>
</tr>
<tr>
<td>$\delta^{13}C$ (%)</td>
<td>-25.0 ± 0.2</td>
<td>-26.3 ± 0.3</td>
<td>-27.3 ± 0.3</td>
</tr>
<tr>
<td>Labile C (g kg⁻¹)</td>
<td>1.56 ± 0.12</td>
<td>0.42 ± 0.08</td>
<td>0.47 ± 0.05</td>
</tr>
<tr>
<td>$k$ (d⁻¹)</td>
<td>0.006 ± 0.001</td>
<td>0.014 ± 0.002</td>
<td>0.012 ± 0.001</td>
</tr>
<tr>
<td>Total N (g kg⁻¹)</td>
<td>2.2 ± 0.2</td>
<td>1.2 ± 0.1</td>
<td>2.0 ± 0.1</td>
</tr>
<tr>
<td>C : N</td>
<td>23.7 ± 1.4</td>
<td>11.8 ± 0.8</td>
<td>11.6 ± 0.7</td>
</tr>
<tr>
<td>NH₄⁺ + NO₃⁻ (mg kg⁻¹)</td>
<td>14 ± 2</td>
<td>22 ± 3</td>
<td>19 ± 1</td>
</tr>
</tbody>
</table>
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 SrCO₃. Dried samples of SrCO₃ were analysed for ¹³C (PDZ Europa continuous flow IR-mass spectrometer, Europa Scientific, Crewe, UK). The δ¹³C 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 δ¹³C of CO₂ 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 ¹³C (PDZ Europa continuous flow IR-mass spectrometer). The average δ¹³C 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 ¹³C (PDZ Europa continuous flow IR-mass spectrometer).

We estimated the initial amount of labile C (C₀) 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):

\[ R_t = C_0 e^{-kt} + i \]

where \( R_t \) is the daily soil respiration rate at time \( t \), and \( i \) is the soil respiration rate of more resistant C.

The continuous labelling of plants with depleted ¹³C allowed us to separate plant-derived from soil-derived CO₂-C in soil respiration. We calculated soil-derived CO₂-C in the planted treatments using the following equation:

\[ CO₂-C_{\text{plant}} = CO₂-C_{\text{tot}}(\delta^{13}C_{\text{plant}} - \delta^{13}C_{\text{tot}})/\left(\delta^{13}C_{\text{plant}} - \delta^{13}C_{\text{control}}\right) \]

where \( CO₂-C_{\text{plant}} \) is the efflux of CO₂-C derived from the non-labelled SOC (i.e. SOC that was present at the start of the experiment) in the planted treatments, \( CO₂-C_{\text{tot}} \) is the total efflux of CO₂-C from soil respiration in the planted treatments, and \( \delta^{13}C_{\text{tot}}, \delta^{13}C_{\text{control}} \) and \( \delta^{13}C_{\text{plant}} \) are the δ¹³C values of the total efflux of CO₂-C in the planted treatments, the efflux of CO₂-C in the control treatments and plant biomass, respectively. We used the weighted average δ¹³C of leaf, stem, and roots of FRCO for \( \delta^{13}C_{\text{plant}} \) (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 δ¹³C of needles and roots for \( \delta^{13}C_{\text{plant}} \) because after 107 and 398 days of labelling, stems remained slightly less depleted in ¹³C (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 CO₂-C’ as the difference in soil-derived CO₂-C between planted and non-planted control treatments. We calculated ‘cumulative soil-derived CO₂-C’ and ‘cumulative primed C’ by multiplying the average daily rate of soil-derived and primed CO₂-C between two measuring dates by the time interval between two measuring dates, and by adding the preceding soil-derived and primed CO₂-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 CO₂ (i.e. all plant-derived CO₂-C) from the two pots to check whether plant-derived CO₂-C had similar δ¹³C values as plant biomass. As we started with 10-month-old POPI seedlings, plant-derived CO₂-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 δ¹³C value of the rhizosphere CO₂ was −39.8, −41.6 and −41.0‰, respectively. All these δ¹³C values were within 1.5‰ of the δ¹³C value of the plant biomass measured after 107 days (−41.3‰), indicating that the plant biomass δ¹³C provided a good estimate of plant-derived CO₂-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 (Cgain) using the following equation:

\[ C_{\text{gain}} = C_{\text{end}}(\delta^{13}C_{\text{start}} - \delta^{13}C_{\text{end}})/(\delta^{13}C_{\text{start}} - \delta^{13}C_{\text{control}}) \]

where \( C_{\text{end}} \) is the total amount of SOC at the end of the experiment (including labelled plant-derived SOC and unlabelled SOC), and \( \delta^{13}C_{\text{start}}, \delta^{13}C_{\text{end}} \) and \( \delta^{13}C_{\text{control}} \) are the δ¹³C 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 CO₂-C, cumulative soil-derived CO₂-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).
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 \(\delta^{13}C_{\text{plant}}\) 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 \((\text{Cl})\) and its decomposition rate constant \((\text{k})\) 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
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.

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**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.
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 mycorrhizal species 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/oo 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/oo ($n = 4$). 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/oo 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 ($\approx24.0 \pm 0.2$, $\approx26.2 \pm 0.3$ and $\approx26.7 \pm 0.3$ for the Blodgett, UCSC grassland and Marshall field soil, respectively, mean $\pm$ 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 CO2 concentration, rhizosphere priming effects may have been larger than under ambient CO2 concentration (Cheng 1999). Above-ground 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 CO2 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 CO2 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 CO2 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 CO2 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.

ACKNOWLEDGEMENTS

This research was supported by the National Research Initiative of the USDA Cooperative State Research, Education and Extension Service (Grant no. 2006-35107-17225) and by a research grant from Kearney Foundation of Soil Science. We thank Drs Sarah Hobbie, Peter Reich and two anonymous referees for the comments on a previous draft of this manuscript. We thank Reginaldo Gomez and Paul Tran for their assistance with watering plants and laboratory work, and David Harris for isotope analyses.

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© 2007 Blackwell Publishing Ltd/CNRS


Editor, Richard Bardgett
Manuscript received 24 May 2007
First decision made 11 June 2007
Second decision made 3 July 2007
Manuscript accepted 6 July 2007

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