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Rhizosphere priming effects on soil carbon and nitrogen mineralization

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ABSTRACT

Living roots and their rhizodeposits affect microbial activity and soil carbon (C) and nitrogen (N) mineralization. This so-called rhizosphere priming effect (RPE) has been increasingly recognized recently. However, the magnitude of the RPE and its driving mechanisms remain elusive. Here we investigated the RPE of two plant species (soybean and sunflower) grown in two soil types (a farm or a prairie soil) and sampled at two phenological stages (vegetative and mature stages) over an 88-day period in a greenhouse experiment. We measured soil C mineralization using a continuous ^{13}C-labeling method, and quantified gross N mineralization with a ^{15}N-pool dilution technique. We found that living roots significantly enhanced soil C mineralization, by 27–245%. This positive RPE on soil C mineralization did not vary between the two soils or the two phenological stages, but was significantly greater in sunflower compared to soybean. The magnitude of the RPE was positively correlated with rhizosphere respiration rate across all treatments, suggesting the variation of RPE among treatments was likely caused by variations in root activity and rhizodeposit quantity. Moreover, living roots stimulated gross N mineralization rate by 36–62% in five treatments, while they had no significant impact in the other three treatments. We also quantified soil microbial biomass and extracellular enzyme activity when plants were at the vegetative stage. Generally, living roots increased microbial biomass carbon by 0–28%, β-glucosidase activity by 19–56%, and oxidative enzyme activity by 0–46%. These results are consistent with the positive rhizosphere effect on soil C (45–79%) and N (10–52%) mineralization measured at the same period. We also found significant positive relationships between β-glucosidase activity and soil C mineralization rates and between oxidative enzyme activity and gross N mineralization rates across treatments. These relationships provide clear evidence for the microbial activation hypothesis of RPE. Our results demonstrate that root–soil–microbial interactions can stimulate soil C and N mineralization through rhizosphere effects. The relationships between the RPE and rhizosphere respiration rate and soil enzyme activity can be used for explicit representations of RPE in soil organic matter models.

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1. Introduction

Soil organic carbon (SOC) functions as an important source and sink of atmospheric CO_2 (Amundson, 2001). Soil CO_2 efflux is approximately 10 times greater than anthropogenic CO_2 emissions from fossil fuel burning and land use change (Bond-Lamberty and Thomson, 2010). The two main components of soil CO_2 efflux are rhizosphere respiration by roots and microbes utilizing root-derived carbon substrates, and microbial decomposition of native SOC (Kuzyakov, 2006). Globally, SOC decomposition accounts for nearly half of total soil respiration (Hanson et al., 2000; Kuzyakov, 2006), and plays an important role in the global carbon cycle and its feedback to climate change (Davidson and Janssens, 2006; Heimann and Reichstein, 2008).

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Plants can stimulate or inhibit native SOC decomposition through rhizosphere processes (Dormaar, 1990; Kuzyakov, 2002; Paterson, 2003; Cheng and Kuzyakov, 2005; Cheng et al., 2014). Recent syntheses (Zhu and Cheng, 2011a; Cheng et al., 2014) noted that SOC decomposition rate in the presence of live roots can be suppressed by 50% or stimulated by up to 400% compared to unplanted control soils under similar temperature and moisture conditions. It is now becoming generally recognized that rhizosphere priming effects on SOC decomposition can play important roles in the global carbon cycle (Heimann and Reichstein, 2008; Kuzyakov, 2010; Cheng et al., 2014).

The actual mechanisms underlying rhizosphere priming effects still remain elusive (Kuzyakov, 2002; Cheng and Kuzyakov, 2005). The positive rhizosphere effect on SOC decomposition (increased rates of decomposition) has been more frequently reported than the negative rhizosphere effect (Zhu and Cheng, 2011a; Cheng et al., 2014). One mechanism which has been proposed to explain the positive rhizosphere effect relates to root-released available substrates stimulating microbial growth in the rhizosphere thus leading to extracellular enzyme production and enhanced decomposition of native SOM (DeAngelis et al., 2008; Zhu and Cheng, 2011a; Phillips et al., 2011). However, the conditions under which this type of microbial activation occurs (Kuzyakov, 2002; Cheng and Kuzyakov, 2005) have not been clearly delineated.

In response to root-released carbon substrates in the rhizosphere, increases in microbial growth may stimulate microbial demand for nitrogen. This microbial N demand can be met by increasing enzyme synthesis (DeAngelis et al., 2008; Phillips et al., 2011) and gross N mineralization rate in the rhizosphere (Norton and Firestone, 1996; Herman et al., 2006; Koranda et al., 2011). The higher N mineralization rate may eventually lead to higher soil N availability for root uptake due to faster turnover of microbes compared to roots (Frank and Groffman, 2009; Kuzyakov and Xu, 2013). This microbial N mining hypothesis has been invoked as a mechanism to explain increased plant N uptake in elevated CO_2 studies (Zak et al., 1993; Cheng, 1999; Langley et al., 2009; Billings et al., 2010; Phillips et al., 2011), but only few studies (e.g. Herman et al., 2006; Dijkstra et al., 2009) have directly tested this hypothesis.

Here we investigated the rhizosphere priming effect on soil C and N mineralization in an 88-day greenhouse experiment. We measured soil C mineralization rate in the presence of live roots using a novel continuous ^{13}C-labeling method (Cheng and Dijkstra, 2007; Pausch et al., 2013), gross N mineralization rate in freshly sampled soils after root picking using a ^{15}N pool dilution method (Hart et al., 1994a; Herman et al., 2006), microbial biomass carbon by chloroform fumigation–extraction (Vance et al., 1987), and extracellular enzyme activities using fluorometric microplate assays (Saiya-Cork et al., 2002). The experiment included two plant species (a legume soybean (*Glycine max*), a non-legume sunflower (*Helianthus annuus*), and an unplanted control) grown in two soil types (a cultivated farm soil or a pristine prairie soil), and destructively sampled in two phenological stages (vegetative and mature stages). Our main objectives were to (1) investigate the control of rhizosphere priming effect on soil C mineralization by soil type, sampling time, and plant species, (2) test the microbial activation hypothesis for rhizosphere effect on soil C mineralization, and (3) explore the magnitude of rhizosphere effect on soil N mineralization.

2. Materials and methods

2.1. Experimental setup

We performed the experiment in a continuous ^{13}C-labeling greenhouse at University of California, Santa Cruz. During the experimental period, we maintained a constant CO_2 concentration (400 ± 5 ppm) and $\delta^{13}C$ value (-18.0 ± 0.5‰) inside the greenhouse by automatically adjusting the flow rate of CO_2-free air and pure CO_2 into the greenhouse. Details about this continuous ^{13}C-labeling method can be found in Cheng and Dijkstra (2007) and Pausch et al. (2013).

The experiment included two soil types (farm soil and prairie soil, Table 1), two plant species (soybean and sunflower) with an unplanted control, and two destructive samplings (53 and 88 days after planting). There were 8 or 11 replicates for each treatment combination ($2 \times 3 \times 2 = 12$) and 105 pots totally (Table 2).

We used two soil types in this experiment (Table 1). Surface (0–30 cm) soils were collected from a farm on the campus of University of California, Santa Cruz (farm soil) and from a tall-grass prairie at Konza Prairie Biological Station, Kansas (prairie soil). The farm was converted from coastal grassland in 1974 and has been planted with various C_3 crops and vegetables, while the prairie was dominated by C_4 grasses. The farm soil (Alfisol, sandy loam, pH 5.8) contained 14.0 mg C g soil^{-1} and 1.2 mg N g soil^{-1}, while the prairie soil (Mollisol, clay loam, pH 7.1) contained 17.1 mg organic C g soil^{-1} (plus 0.6 mg inorganic C g soil^{-1}) and 1.9 mg N g soil^{-1}. Our previous work using the prairie soil and similar plants (wheat and soybean) showed that soil inorganic carbon did not change significantly among control and planted treatments or during the experimental period (Cheng et al., 2003). Therefore, we are confident that carbonate did not contribute to the measured CO_2 flux from the prairie soil. The $\delta^{13}C$ value of soil organic carbon is −26.8‰ and −15.5‰ for the farm soil and the prairie soil, respectively.

The soils were sieved through a 4-mm screen and air-dried before use. A nylon bag filled with 1500 g washed sand was placed at the bottom of each bottom-capped polyvinyl chloride (PVC) pot (diameter 15 cm, height 40 cm, equipped with an inlet tube at the bottom for aeration and CO_2 trapping). We packed 7.32 kg farm soil or 6.60 kg prairie soil (dry weight equivalent) into each pot at a mean bulk density of 1.29 and 1.17 g cm^{-3}. After adjusting soil moisture to 60% water holding capacity (0.24 and 0.32 mL water g dry soil^{-1} for farm soil and prairie soil), we pre-incubated these 105 pots inside the greenhouse for two weeks. Then we planted five pre-soaked seeds of sunflower or soybean (inoculated with *Bradyrhizobium japonicum*) in 35 "sunflower" or 35 "soybean" pots, and kept 35 "control" pots unplanted. Seedlings germinated within one week and were thinned to one individual plant per pot.

During the experimental period, air temperature inside the greenhouse was maintained below 28 °C during the day (6 am to 6 pm) and above 18 °C during the night (18:00–06:00) by an air conditioner and a heater respectively, and relative air humidity was kept at 50% by a dehumidifier. Supplemental lighting was turned on during cloudy days (light intensity < 800 μmol m^{-2} s^{-1}). Soil moisture in each pot was maintained at 60% water holding capacity by frequent weighing and watering with deionized water.

Table 1
Properties of the two soil types.

Soil property	Farm	Prairie
Soil order	Alfisol	Mollisol
Soil texture	Sandy loam	Clay loam
Vegetation	C_3 crops	C_4 grasses
pH	5.8	7.1
Organic C (g kg^{-1})	14.0	17.1
Total N (g kg^{-1})	1.2	1.9
C:N	11.5	8.8
^{13}C of SOC (‰)	−26.8	−15.5