Plant inter-species effects on rhizosphere priming of soil organic matter decomposition

Johanna Pausch [a,c,*], Biao Zhu [b], Yakov Kuzyakov [c], Weixin Cheng [b]

[a] Department of Soil Science of Temperate Ecosystems, University of Göttingen, Büsgenweg 2, 37077 Göttingen, Germany
[b] Department of Environmental Studies, University of California, Santa Cruz, CA 95064, USA
[c] Department of Agroecosystem Research, University of Bayreuth, BayCEER, Universitätsstr. 30, 95440 Bayreuth, Germany

ARTICLE INFO

ABSTRACT

Living roots and their rhizodeposits can stimulate microbial activity and soil organic matter (SOM) decomposition up to several folds. This so-called rhizosphere priming effect (RPE) varies widely among plant species possibly due to species-specific differences in the quality and quantity of rhizodeposits and other root functions. However, whether the RPE is influenced by plant inter-species interactions remains largely unexplored, even though these interactions can fundamentally shape plant functions such as carbon allocation and nutrient uptake.

In a 60-day greenhouse experiment, we continuously labeled monocultures and mixtures of sunflower, soybean and wheat with ^{13}C-depleted CO_2 and partitioned total CO_2 efflux released from soil at two stages of plant development for SOM- and root-derived CO_2. The RPE was calculated as the difference in SOM-derived CO_2 between the planted and the unplanted soil, and was compared among the mono-cultures and mixtures.

We found that the RPE was positive under all plants, ranging from 43% to 136% increase above the unplanted control. There were no significant differences in RPE at the vegetative stage. At the flowering stage however, the RPE in the soybean–wheat mixture was significantly higher than those in the sunflower monoculture, the sunflower–wheat mixture, and the sunflower–soybean mixture. These results indicated that the influence of plant inter-specific interactions on the RPE is case-specific and phenology-dependent. To evaluate the intensity of inter-specific effects on priming, we calculated an expected RPE for the mixtures based on the RPE of the monocultures weighted by their root biomass and compared it to the measured RPE under mixtures. At flowering, the measured RPE was significantly lower for the sunflower–wheat mixture than what can be expected from their monocultures, suggesting that RPE was significantly reduced by the inter-species effects of sunflower and wheat. In summary, our results clearly demonstrated that inter-species interactions can significantly modify rhizosphere priming on SOM decomposition.

© 2012 Elsevier Ltd. All rights reserved.

1. Introduction

Soil organic carbon (C) functions as both an important source and a sink of atmospheric CO_2. Many uncertain parameters of the global C cycle are associated with complex soil processes and biological communities, which are both difficult to measure and highly sensitive to disturbance (Moyes et al., 2010). Soil CO_2 mainly consists of (1) root-derived CO_2, including root respiration and microbial decomposition of rhizodeposits from living roots (rhizomicrobial respiration), and (2) CO_2 derived from microbial decomposition of soil organic matter (SOM) (Kuzyakov, 2006). Both sources are linked through the rhizosphere priming effect (RPE) which describes changes in the rate of SOM decomposition in the presence of living roots (Kuzyakov, 2002; Cheng and Kuzyakov, 2005). Plant roots can alter microbial activities by providing organic substances (rhizodeposits) (Paterson, 2003), by competing with microorganisms for mineral nutrients (Schimel et al., 1989; Wang and Bakken, 1997), and by changing the physical and chemical conditions in the rhizosphere (e.g. water, pH) (Shields and Paul, 1973; Jenkinson, 1977). These alterations can lead to either stimulation (positive RPE) or retardation (negative RPE) of SOM

decomposition with rates ranging from 70% reduction to as high as 330% increase compared to an unplanted control (Cheng and Kuzyakov, 2005). The direction and magnitude of RPE on SOM decomposition depend on both the plant and the soil. The amount of decomposable organic C and the mineral nitrogen (N_{min}) content of the soil have been identified as two of the main soil factors that significantly influence RPE (Liljeroth et al., 1994; Cheng and Johnson, 1998; Bottner et al., 1999; Kuzyakov, 2002). On the other hand, plant species and their developmental stages (Fu and Cheng, 2002; Cheng et al., 2003) also strongly influence the RPE, possibly through differences in the quality and quantity of rhizodeposits (Van der Krift et al., 2001; Nguyen, 2003; Jones et al., 2004).

Since the RPE is plant-species specific (Fu and Cheng, 2002; Cheng et al., 2003), it may also vary with plant inter-species interactions. It was proposed that with higher plant diversity the diversity of root exudates may also increase (Lavelle et al., 1995; Hooper et al., 2000). This wider spectrum of root exudates from mixed plant species may support a higher microbial biomass and activity in the rhizosphere (Hooper et al., 2000; Spehn et al., 2000; Stephan et al., 2000) whereby, the production of extracellular enzymes can be enhanced. Consequently, the potential for a positive RPE may increase (Fontaine et al., 2003). In contrast, Dijkstra et al. (2010) suggested a plant-diversity-induced decrease in SOM decomposition for systems with low water availability. With higher plant richness, belowground resources, especially N, are being complementarily used (Hooper and Vitousek, 1997; Von Felten et al., 2009). This may result in a lower availability of belowground resources and thus, in a decline in the decomposition of SOM (Dijkstra et al., 2010).

In this study monocultures and mixtures of sunflower, soybean and wheat were continuously exposed to ^{13}C-depleted CO_2. The soil CO_2 efflux was measured at an early stage of plant development (day 29–30 after planting), and at flowering of sunflower and soybean (day 55–56 after planting). Based on its $\delta^{13}C$ values the total soil CO_2 efflux was separated into root- and SOM-derived CO_2. The RPE was calculated as the difference in SOM-derived CO_2 between planted and unplanted treatments. To our knowledge, up to now the experimental work of Dijkstra et al. (2010) is the only study investigating the effect of plant diversity on the RPE, although inter-specific effects on carbon allocation belowground (Sanaullah et al., 2012) and on the activity of microorganisms (Sanaullah et al., 2011) are known. Although the results of Dijkstra et al. (2010) provide evidence that plant–plant interactions modify RPE, no firm conclusions on general patterns could be drawn, which necessitates future research on this topic.

Therefore, the aim of this study was to gain a more comprehensive understanding of modified RPE due to plant inter-species interactions. We hypothesized that the modulation of RPE by inter-species interactions is specific to the plant species composition and dependent on plant developmental stage.

2. Materials and methods

2.1. Experimental set-up

Monocultures of sunflower (Sun) (*Helianthus annuus* L.), soybean (Soy) (*Glycine max* L. Merr.) and spring wheat (Wh) (*Triticum aestivum* L.) and mixed cultures of sunflower/soybean (Sun/Soy), sunflower/wheat (Sun/Wh), soybean/wheat (Soy/Wh) and sunflower/soybean/wheat (Sun/Soy/Wh) were grown in PVC pots (15 cm diameter, 40 cm height, equipped with an inlet tube at the bottom for aeration and soil CO_2 trapping) with four replicates of the monocultures and six replicates of the mixed cultures. Including two-species mixtures in our study allowed investigation of possible patterns of individual species' influence on RPE when

they were grown in mixtures. In addition four unplanted pots were prepared. A nylon bag filled with 1500 g sand was placed at the bottom of each PVC pot to improve air circulation. The pots were then filled with 7.9 kg of air-dried, sieved (<4 mm) soil taken from the plough horizon (top 30 cm) of a sandy loam from a farm on the campus reserves of the University of California, Santa Cruz. Air drying and sieving allowed us to achieve a high degree of soil homogeneity and reduced the variability among the treatments and replicates. The soil contained 1.1% organic C and 0.1% N, had a $\delta^{13}C$ value of −26.0‰ and a pH value of 5.8. All filled pots were wetted to 20% gravimetric soil moisture content (equivalent of 80% of the water holding capacity) with deionized water.

Seeds were presoaked over night in deionized water before planting. For the mixed cultures we used one individual plant of each species. For all monocultures we used two individual plants per pot to establish comparable growing conditions for all treatments. To get one individual plant, six seeds of wheat, two of sunflower and three of soybean were planted and thinned to one after seedling emergence. The soil moisture content was measured gravimetrically and adjusted daily to 80% of the water holding capacity. To maintain homogeneous soil moisture and good soil structure, water was added through perforated tubes (inner diameter 0.32 cm, total length 180 cm, buried length approximately 140 cm) as described by Dijkstra and Cheng (2007). The location of the pots in the greenhouse was changed weekly by mixing them randomly to guarantee similar growing conditions for the plants.

The experiment was conducted from January to March 2011 in a greenhouse equipped with continuous labeling by ^{13}C-depleted CO_2 at the University of California, Santa Cruz. Plants were continuously, i.e. from the emergence of the first leaf till harvest, exposed to ^{13}C-depleted CO_2 (−15‰). The continuous labeling technique allows us to quantitatively differentiate root-derived CO_2 from native SOM-derived CO_2 since both C pools differ in their isotopic composition after labeling (Table 1). During plant growth the day time air temperature inside the greenhouse was maintained at 28 °C by two AC units. The night time temperature was kept above 18 °C. Artificial lighting (1100 W lights, P.L. Light Systems, Beamsville, ON) was used when the natural light intensity was less than 900 W m^{-2}. The photoperiod was set from 6 AM to 6 PM. The relative air humidity was kept at 45% by a dehumidifier (Kenmore Elite 70 pint, Sears, Chicago, IL, USA). We continuously labeled the plants with naturally ^{13}C-depleted CO_2 using the method described in detail by Cheng and Dijkstra (2007). Briefly, a constant CO_2 concentration of 400 ± 5 ppm and a constant $\delta^{13}C$ value (see below) was maintained inside the greenhouse by regulating the flow of pure, ^{13}C-depleted CO_2 (99.9% CO_2, −35‰) from a tank and setting CO_2-free air flow rate proportional to the leakage rate of the greenhouse (Zhu and Cheng, 2012). The CO_2-free air was produced from compressed air passed through six soda lime columns (20 cm diameter, 200 cm length) filled with approximately 40 kg soda lime each. The CO_2-free air flow was set at 120 L/min.

Table 1
End member values (±SEM) used in two-source isotopic mixing models in order to calculate the contribution of SOM-derived CO_2 to total soil CO_2 of the planted treatments.

Treatment	Root-derived CO_2 [‰]	SOM-derived CO_2 of the unplanted soil [‰]
Sun	−39.6 ± 0.09	T1
Soy	−37.0 ± 0.3	−23.9 ± 0.2
Wh	−39.4 ± 0.4	T2
Sun/Soy	−39.2 ± 0.1	−23.7 ± 0.1
Sun/Wh	−39.6 ± 0.06	
Soy/Wh	−39.4 ± 0.2	
Sun/Soy/Wh	−39.1 ± 0.07	