



Water limitation and plant inter-specific competition reduce rhizosphere-induced C decomposition and plant N uptake

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ABSTRACT

Plants can affect soil organic matter decomposition and mineralization through litter inputs, but also more directly through root-microbial interactions (rhizosphere effects). Depending on resource availability and plant species identity, these rhizosphere effects can be positive or negative. To date, studies of rhizosphere effects have been limited to plant species grown individually. It is unclear how belowground resources and inter-specific interactions among plants may influence rhizosphere effects on soil C decomposition and plant N uptake. In this study, we tested the simple and interactive effects of plant diversity and water availability on rhizosphere-mediated soil C decomposition and plant N uptake. The study was conducted in the greenhouse with five semi-arid grassland species (monocultures and mixtures of all five species) and two water levels (15 and 20% gravimetric soil moisture content). We hypothesized that microbial decomposition and N release would be less in the low compared to high water treatment and less in mixtures compared to monocultures. Rhizosphere effects on soil C decomposition were both positive and negative among the five species when grown in monoculture, although negative effects prevailed by the end of the experiment. When grown in mixture, rhizosphere effects reduced soil C decomposition and plant N uptake compared to monocultures, but only at the low-water level. Our results suggest that when water availability is low, plant species complementarity and selection effects on water and N use can decrease soil C decomposition through rhizosphere effects. Although complementarity and selection effects can increase plant N uptake efficiency, plant N uptake in the mixtures was still lower than expected, most likely because rhizosphere effects reduced N supply in the mixtures more than in the monocultures. Our results indicate that rhizosphere effects on C and N cycling depend on water availability and inter-specific plant interactions. Negative rhizosphere effects on soil C decomposition and N supply in mixtures relative to monocultures of the component species could ultimately increase soil C storage and possibly influence how plant communities in semi-arid grasslands respond to global climate change.

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1. Introduction

There is considerable evidence that storage and cycling of soil C and N are affected by plant species composition and diversity (Hooper and Vitousek, 1997, 1998; Wardle et al., 1999; Craine et al., 2001; Zak et al., 2003; Dybzinski et al., 2008; Fornara and Tilman, 2008). Greater storage and cycling of soil C and N with increased plant species richness has been associated with increased plant litter inputs resulting from enhanced plant productivity (Zak et al., 2003; Dijkstra et al., 2005; Fornara and Tilman, 2008). However, Steinbeiss et al. (2008) observed a positive effect of plant diversity

on soil C storage in a temperate grassland in Germany that could not be totally explained by greater plant biomass production. Similarly, greater plant productivity could not completely explain more rapid N mineralization with increased plant diversity in a tall grass prairie in Minnesota (Zak et al., 2003). These results indicate that plant diversity can affect ecosystem C and N cycling through mechanisms other than effects on plant litter production.

Plants can also affect soil organic matter (SOM) decomposition through direct root-microbe interactions (rhizosphere effects, Cheng and Kuzyakov, 2005). For instance, plant roots can enhance SOM decomposition by supplying the decomposer soil microbial community with labile C substrates (rhizosphere priming effect, Kuzyakov, 2002). This rhizosphere priming effect appears to be plant species-specific (Cheng et al., 2003; Cheng and Kuzyakov, 2005) and can be more pronounced in soils with greater water

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availability (Dijkstra and Cheng, 2007b) and smaller N availability (Liljeroth et al., 1990; Fontaine et al., 2004). With rhizosphere priming, N transfer from the inactive SOM pool into the active microbial pool may be enhanced, which ultimately may increase plant N availability (Hungate, 1999; Paterson, 2003). However, it has also been suggested that plant water uptake and competition for nutrients could reduce microbial activity, SOM decomposition and net N mineralization (Van Veen et al., 1989; Ehrenfeld et al., 1997; Wang and Bakken, 1997). Indeed, agricultural field studies from the 1960s and 70s have shown that decomposition of labeled plant material is markedly lowered in the presence of plants (Führ and Sauerbeck, 1968; Shields and Paul, 1973; Jenkinson, 1977).

Given that rhizosphere effects vary with species identity, water and N availability, they might also vary with plant diversity, and therefore influence effects of plant diversity on C and N cycling. Plant diversity could influence rhizosphere effects through species-specific differences in inputs of labile C and/or inter-specific competition for belowground resources. A greater diversity of organic compounds produced by more diverse plant communities could stimulate a more diverse microbial decomposer community (Lodge, 1997; Hooper et al., 2000; Stephan et al., 2000). A greater chemical diversity of organic compounds could also stimulate a greater diversity of extracellular enzyme production thereby increasing the probability of occurrence of a rhizosphere priming effect (Fontaine et al., 2003). On the other hand, Loreau (2001) suggested that a greater organic compound diversity could have negative effects on soil C decomposition and N cycling because of an increased likelihood that some of the organic compounds will not be consumed by decomposers. Plant diversity might also decrease belowground resource availability through complementarity and selection effects (Tilman et al., 1996, 1997; Hooper and Vitousek, 1997), thereby potentially reducing rhizosphere effects on microbial SOM decomposition and N mineralization. To our knowledge, rhizosphere effects on SOM decomposition (i.e., SOM decomposition measured in the presence of live roots) in plant species mixtures have never been examined, and empirical studies of rhizosphere effects on N cycling in non-N fixing plant species mixtures are rare (Saj et al., 2007; Nilsson et al., 2008).

Here we compared rhizosphere effects on soil C decomposition and plant N uptake between monocultures of five different semi-arid grassland species and mixtures of all five species grown in a greenhouse experiment at two water levels. We also included treatments without plants. Throughout the experiment we continuously labeled the plants with depleted ^{13}C . We used ^{13}C isotope analyses in respiration measurements to separate the soil-derived $\text{CO}_2\text{-C}$ flux (soil C decomposition) from the plant-derived $\text{CO}_2\text{-C}$ flux while plants were present. After 85 days of growth we analyzed plant material for N content (g pot^{-1}) as a measure of plant N uptake. We hypothesized that differences in the rhizosphere effect on soil C decomposition and plant N uptake between low and high water levels and between mixtures and monocultures would be driven by their effects on water and N availability. Specifically, we predicted that reduced water availability in the low-water treatments and reduced water and N availability in the mixtures (due to selection and complementarity effects) would reduce rhizosphere-mediated soil C decomposition and plant N uptake in these treatments.

2. Materials and methods

2.1. Experimental design

We filled 70 polyvinyl chloride (PVC) pots (diam. 20 cm, height 40 cm) with a sandy loam soil (Aridic Argiustoll, Ascalon series) from the USDA-ARS Central Plains Experimental Range in the

shortgrass steppe region of north-eastern Colorado. The pots were closed at the bottom except for an air inlet (see Dijkstra et al., 2010). The soil was taken from the top 20 cm. The soil contained no carbonates based on the lack of effervescence with addition of 10% HCl, had a pH of 6.6, 0.95% C, 0.09% total N, and 23 mg kg^{-1} inorganic N ($\text{NH}_4^+ + \text{NO}_3^-$) at the start of the experiment. We placed a nylon bag filled with 3 kg sand at the bottom of each pot before filling the pots with 14 kg sieved (4 mm), air-dried soil. The pots were then watered to field capacity (30% gravimetric soil moisture content). We transplanted seedlings (grown in peat pellets for two weeks) of *Artemisia frigida* Willd. (sub-shrub), *Linaria dalmanica* [L.] Mill. (forb), *Bouteloua gracilis* [Willd. ex Kunth] Lag. Ex Griffiths (C_4 grass), *Hesperostipa comata* [Trin. & Rupr.] (C_3 grass), and *Pascopyrum smithii* [Rybd.] A. Love (C_3 grass) to the pots. All species are native to the shortgrass steppe, except for the invasive weed *L. dalmanica*. Each species was grown as a monoculture (five plants per pot) in 10 pots for each species. In another 10 pots, we grew all species together (All, one plant of each species per pot). We further included 10 pots without plants (control).

The experiment was conducted in a greenhouse facility of the USDA-ARS Crops Research Laboratory in Fort Collins, Colorado. To label the plants with C depleted in ^{13}C we raised the atmospheric CO_2 concentration inside the greenhouse to a constant level of $780 \pm 50 \mu\text{L L}^{-1}$ (average \pm standard deviation) by adding pure CO_2 depleted in ^{13}C ($\delta^{13}\text{C} = -39.7\text{‰}$). We should note that rhizosphere effects on SOM decomposition (see below) may be different than under ambient CO_2 concentration (Cheng, 1999), but a doubling of atmospheric CO_2 concentration by the end of this century is not unlikely (Forster et al., 2007). The CO_2 was added through a ventilation system to ensure uniform distribution of the CO_2 concentration inside the greenhouse. The CO_2 concentration was continuously monitored and the CO_2 supply was computer-controlled (Argus Control Systems Ltd, White Rock, BC). This continuous labeling method has been tested successfully in other greenhouse and growth chamber experiments (Dijkstra and Cheng, 2007a,b). During the experiment, air temperature inside the greenhouse was kept between 27 and 29 °C during the day and between 16 and 18 °C during the night using computer-controlled air conditioners and heaters (York International, York, PA). Light inside the greenhouse was supplemented with 600 W lights (P.L. Light Systems, Beamsville, Ontario) that were on for 12 h during the day. The light intensity inside the greenhouse was $\sim 200 \text{ W m}^{-2}$ during the day. The relative humidity inside the greenhouse was $24 \pm 5\%$ during the day and $30 \pm 5\%$ during the night.

During the first week after transplanting, all pots were maintained at 30% soil moisture content. After the first week, half of all pots (or 5 pots of each monoculture and mixture, and 5 pots without plants) were allowed to dry down to 15% (low-water treatment), and the other half to 20% (high water treatment). Pots were then maintained at these water levels by watering the pots three times a week. Pots were weighed once every week and watered up to their target weights. The amount of water added during the other two times of the week was calculated based on previous water loss from each pot. We calculated total water use for each pot as the total amount of water added to each pot during the experiment. Inside the greenhouse the 70 pots were placed in five blocks (14 pots per block, each block containing one replicate of each treatment). Treatments within each block were randomly assigned.

2.2. Measurements and analyses

We measured pot respiration 48, 69, and 83 days after transplanting (DAT). At each time, we placed opaque PVC chambers (diam. 20 cm, height 45 cm for the planted pots and 15 cm for the pots without plants) on top of the pots. The chambers were fitted

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