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Rhizosphere priming effect of *Populus fremontii* obscures the temperature sensitivity of soil organic carbon respiration

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Abstract

C efflux from soils is a large component of the global C exchange between the biosphere and the atmosphere. However, our understanding of soil C efflux is complicated by the "rhizosphere priming effect," in which the presence of live roots may accelerate or suppress the decomposition of soil organic C. Due to technical obstacles, the rhizosphere priming effect is under-studied, and we know little about rhizosphere priming in tree species. We measured the rates of soil-derived C mineralization in root-free soil and in soil planted with cottonwood (*Populus fremontii*) trees. Live cottonwood roots greatly accelerated (a rhizosphere priming effect) or suppressed (a negative rhizosphere priming effect) the mineralization of soil organic C, depending upon the time of the year. At its maximum, soil organic C was mineralized nine times faster in the presence of cottonwood roots than in the unplanted controls. Over the course of the experiment, approximately twice as much soil organic C was mineralized in pots planted with cottonwoods compared to unplanted control pots. Soil organic C mineralization rates in the unplanted controls were temperature-sensitive. In contrast, soil organic C mineralization in the cottonwood rhizosphere was unresponsive to seasonal temperature changes, due to the strength of the rhizosphere priming effect. The rhizosphere priming effect is of key importance to our understanding of soil C mineralization, because it means that the total soil respiration is not a simple additive function of soil-derived and plant-derived respiration.

Keywords: Soil organic carbon; Rhizosphere; Priming effect; Soil respiration; Temperature sensitivity; *Populus fremontii*

1. Introduction

Live roots interact extensively with the soil, and many ecosystem processes are controlled or directly influenced by roots. CO_2 efflux from the soil is the result of two simultaneous but distinct processes: (1) rhizosphere respiration of plant-derived C, including root respiration and microbial metabolism of material originating from live roots, and (2) mineralization of soil organic C by microbial respiration. Plants clearly mediate rhizosphere respiration, but common laboratory techniques such as soil incubations require the tacit assumption that the mineralization of soil organic C is plant-independent. However, numerous studies now indicate that live roots significantly influence soil organic C decomposition (Cheng and Kuzyakov, 2005). Roots can either accelerate the mineralization of soil organic C (a "rhizosphere priming effect", e.g. Helal and Sauerbeck, 1984; Cheng et al., 2003) or suppress it (a negative rhizosphere priming effect, e.g. Reid and Goss, 1982; Cheng, 1996).

Rhizosphere priming effects represent a major barrier to predictions of soil C efflux, because they can be large and difficult to predict. Decomposition of soil organic C in pots planted with soybean (*Glycine max* L.) and wheat (*Triticum aestivum* L.) was accelerated by as much as 383% and 287%, respectively, relative to pots without plants (Cheng et al., 2003). Conversely, Kuzyakov and Cheng (2001) measured a 50% suppression of soil organic C mineralization in the rhizosphere of *T. aestivum* roots. The magnitude and direction of the rhizosphere priming effect can change with time. For instance, in a two-year study Sallih and Bottner (1988) found suppression of soil organic C mineralization in the presence of *T. aestivum* roots during the first 200 days and stimulation thereafter. The causes of this phenomenon remain under dispute. Soil organic C-rich

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soils may produce larger priming effects than infertile soils (Hart et al., 1986; Kuzyakov et al., 2000). Other important factors are thought to be plant species and phenology (Cheng et al., 2003), photosynthetic intensity (Kuzyakov and Cheng, 2001), nutrient status of the soil (Merckx et al., 1987; Liljeroth et al., 1994; Ehrenfeld et al., 1997), and plant biomass (Dijkstra et al., 2006).

Temperature also affects the respiration of soil organic C. Numerous studies (e.g. Lloyd and Taylor, 1994; Trumbore et al., 1996; Sanderman et al., 2003) have demonstrated that warmer temperatures lead to an acceleration of soil respiration. However, other studies show that soil respiration is temperature-insensitive, or exhibits only a transient temperature response (e.g. Peterjohn et al., 1994; Giardina and Ryan, 2000; Luo et al., 2001). These conflicting results may be explained in part by the confounding influence of rhizosphere effects. Because of the difficulty of separating rhizosphere respiration from SOC decomposition, field experiments generally use total belowground CO_2 efflux as a proxy for soil respiration. Yet the components of soil CO_2 efflux may respond differently to temperature; rhizosphere respiration is coupled to photosynthesis (Högberg et al., 2001; Kuzyakov and Cheng, 2001) and may respond transiently to temperature, while SOC decomposition may be more temperature-dependent. SOC decomposition rates in the laboratory are typically measured using incubations of root-free soils, with the implicit assumption that rhizosphere processes do not affect the results (e.g. Parton et al., 1987; Dalias et al., 2001). Whether in the lab or in the field, rhizosphere effects cannot be measured without special techniques. We are therefore ignorant of how the rhizosphere influences the temperature sensitivity of SOC decomposition.

Because plant species is a driver of the rhizosphere priming effect, rhizosphere priming effects observed in herbaceous species cannot be extrapolated to tree species. Forests are a major terrestrial biome and considerable attention has been devoted to C movement through forest ecosystems. However, because of the technical difficulty of partitioning respiration into plant respiration and mineralization of soil organic C, nearly all studies of the rhizosphere priming effect have focused on herbaceous plants, especially crops. Because of this, almost nothing is known about the rhizosphere priming effect of tree species (Cheng and Kuzyakov, 2005). Because trees are often more deeply rooted than herbaceous species, the rhizosphere priming effect of trees could be important even in deeper soil horizons. Our objective was to measure the rhizosphere priming effect of Fremont cottonwood (*Populus fremontii*), a riparian tree common in the southwestern United States. We hypothesized that this tree species would exhibit a rhizosphere priming effect similar to that observed in studies of herbaceous species. Measurements of respiration were repeated well after the end of the growing season in order to observe long-term changes in the rhizosphere priming effect. We also measured air temperatures throughout the experiment, in order to examine the relationship between temperature and respiration in both treatments.

2. Materials and methods

2.1. Soil

The soil used for this study is a clay loam Mollisol from the Konza Prairie Long-Term Ecological Research Site in Kansas. At this site C_4 grasses have historically been dominant and the soil C consequently has a $\delta^{13}C$ value of about −14.2. The soil was taken from the upper 30 cm of the soil profile. It has about 20 g C kg^{-1} and 1.9 g N kg^{-1}, and has a pH of 7.6. After collection, we sieved the soil through a 4 mm mesh, then air-dried it before use.

2.2. Experiment setup

The experiment took place at the University of California at the Santa Cruz research greenhouse facility on the roof of the Sinsheimer building. Airtight pots made from a PVC pipe with bottom caps (15 cm diameter, 40 cm high) were filled with 8 kg of air-dried Kansas soil per pot. The pots were then watered, then moved outside and allowed to equilibrate for a week before planting. *P. fremontii* cuttings were rooted in Perlite in a misting bed until roots began to develop, then were transplanted to pots on April 17, 2003; the experiment ran until March 24, 2004, 342 days later. After transplanting, the pots remained outside. Every 4 h, aquarium pumps pumped ambient air through the soil in order to compensate for oxygen consumed by respiration in the airtight pots. In the beginning, the experiment consisted of 12 planted pots, 8 unplanted controls, and 2 transparent pots covered with foil designed for the observation of root growth. At 144 days after planting (DAP), four each of the planted and control pots were destructively sampled in order to measure plant and soil properties.

2.3. Water management

After planting, we adjusted soil moisture in each pot to 80% of field capacity. Once the autumn rains began, the pots were moved to the shelter of an overhanging roof to avoid saturation. Periodically, we weighed the pots then watered them to maintain the soil moisture near 80% of field capacity (on June 22 the target weight was readjusted to 75% of field capacity to improve water retention). During the summer, we watered the pots daily; during cooler months watering did not need to occur as frequently. We provided additional water to the plant treatment to account for the mass of the plant and the greater drying effect caused by the plants. After the final harvest we back-calculated the gravimetric soil water content using a linear model to estimate the plant mass and water loss, in order to insure that the plant and