

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.

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1. Introduction

Live roots interact extensively with the soil, and many ecosystem processes are controlled or directly influenced by roots. CO₂ 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 CO₂ efflux as a proxy for soil respiration. Yet the components of soil CO₂ 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 C₄ grasses have historically been dominant and the soil C consequently has a $\delta^{13}\text{C}$ 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

unplanted treatments had similar average water contents throughout the experiment. During trapping, when a silicone seal prevented the direct evaporation of soil water, we measured transpiration as the loss of mass from planted pots between measurements.

2.4. Temperature

We measured the air temperature with HOBO dataloggers placed in shaded locations on the table among the pots. The temperature during each trapping session was calculated as the mean of the temperature data recorded between the beginning and the end of trapping. Due to a datalogger malfunction, our temperature data begins on May 27 (40 DAP), after the end of the first trapping period (37 DAP); consequently there are no direct temperature data for the first trapping period. We estimated the temperature for this date using air temperature data from the UC Santa Cruz weather station. We compared the weather station temperature data with the datalogger temperature data during the dates for which we had both datasets. This comparison allowed us to correct our temperature estimate for the first trapping session to reflect the slightly warmer conditions observed on the greenhouse roof.

2.5. Plant biomass

In order to measure plant biomass, pots were destructively sampled twice: first immediately after the fourth trapping and again at the end of the experiment. Roots were rinsed free of soil in deionized water. Leaves, stems and roots were then separately dried at 60 °C and weighed. Subsamples were ground in a Certiprep 8000 Spex mill, packed in tin capsules and analyzed for total C concentration and $\delta^{13}\text{C}$ in a PDZ Europa continuous flow isotope ratio mass spectrometer. To calculate the biomass for other

times, we used an empirical allometric equation based on the stem diameter, of the form $\log(\text{Biomass}) = \alpha + \beta \log(\text{Diameter})$.

2.6. Soil organic C mineralization

We measured soil organic C mineralization using the Cheng (1996) stable isotope method (Fig. 1). Briefly, we grew plants in leak-tested PVC containers rather than standard greenhouse pots. Before sampling, we covered the soil surface of each pot with poured silicone rubber to create a seal above the soil and around the base of each plant. We removed residual CO_2 from the soil atmosphere before sampling by circulating the isolated air through a PVC column filled with soda lime. We then replaced the soda lime column with a bottle of 4 M NaOH. For 15 min every 4 h, a pump circulated the soil atmosphere through an airstone in each NaOH bottle. A trapping session lasted up to a week, long enough to insure that total belowground respiration greatly exceeded background contamination in the blanks. This NaOH trapping system captures greater than 99% of the CO_2 in circulation, effectively eliminating the potential pitfall of preferential isotope absorption (Cheng, 1996). We measured the total C content of the NaOH solution using a Shimadzu TOC-5050A carbon analyzer. The C in the NaOH traps was then precipitated as SrCO_3 and rinsed free of NaOH. Dried samples of SrCO_3 were packed in tin capsules and analyzed for total C concentration and $\delta^{13}\text{C}$ in a PDZ Europa continuous flow isotope ratio mass spectrometer.

Cottonwood uses the C_3 photosynthetic pathway which discriminates significantly against the heavier isotope ^{13}C . As a result, CO_2 from plant respiration and respiration of plant-derived compounds contains proportionally less ^{13}C than soil organic C mineralization from the prairie soil. In the pots planted with cottonwood, respiration derived from the C_3 plant C_p (mg C) was separated from soil organic C

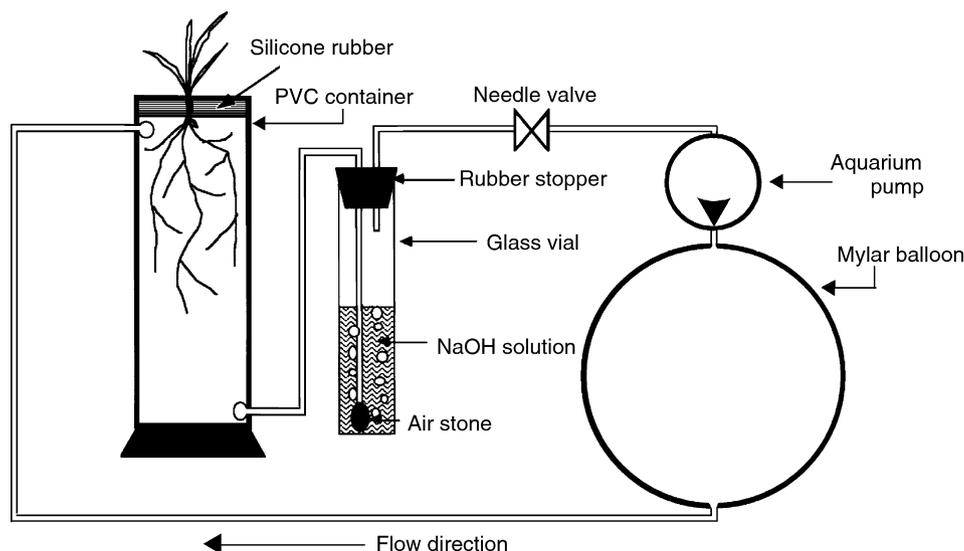


Fig. 1. Schematic of the CO_2 -trapping apparatus.

mineralization C_s (mg C) using this two-endmember simple mixing model (from Cheng, 1996):

$$C_p = C_t(\delta_s - \delta_t)(\delta_s - \delta_p), \quad (1)$$

$$C_s = C_t - C_p, \quad (2)$$

where C_t is the total trapped C (mg), δ_t is the blank-corrected $\delta^{13}\text{C}$ value of the trapped C, δ_s is the $\delta^{13}\text{C}$ of C_4 soil respiration measured in the control pots, and δ_p is the predicted $\delta^{13}\text{C}$ of the C_3 plant respiration. Note that C_p includes both autotrophic root respiration and heterotrophic soil respiration of plant-derived substrates, which are isotopically indistinguishable. Because C isotopes are not significantly fractionated during root respiration (Cheng, 1996), we used the mean $\delta^{13}\text{C}$ signature of roots from a subsample of pots harvested midway through the experiment (-29.18) to define δ_p .

2.7. Statistical analyses

Each pot was considered a replicate. The two treatments (planted pots and unplanted control pots) were compared using a two-tailed Student's *t*-test. To avoid problems with unequal variance among treatments, we used Welch's method to calculate the reduced degrees of freedom. In order to assess the correlation of soil organic C mineralization with temperature in the two treatments, the temperature and C mineralization data from all trapping sessions were combined and used to fit a linear least-squares regression model. R statistical software (R Development Core Team, 2003) was used for all data analysis.

3. Results

Total respiration from the unplanted control pots fluctuated markedly over the course of the experiment, ranging from about $2 \text{ mg C pot}^{-1} \text{ d}^{-1}$ in late December to around $16 \text{ mg C pot}^{-1} \text{ d}^{-1}$ during the warmest days of summer (Table 1). The $\delta^{13}\text{C}$ of this respired C remained approximately constant throughout the experiment; variations were small and did not follow a discernable pattern.

Table 1
Mass and $\delta^{13}\text{C}$ of belowground respiration from the two treatments, ± 1 SE

Trap	DAP	$\text{CO}_2\text{-C, mg pot}^{-1} \text{ d}^{-1}$		$\delta^{13}\text{C}$		<i>n</i>
		Controls	Planted	Controls	Planted	
1	35	9.2 ± 1.2	8.3 ± 1.7	-13.8 ± 0.7	-15.1 ± 0.6	3/3
2	72	15.6 ± 2.8	11.1 ± 1.3	-16.9 ± 0.2	-23.9 ± 0.9	4/4
3	109	9.5 ± 0.8	199.0 ± 39.4	-15.0 ± 0.3	-26.9 ± 0.4	4/3
4	143	4.4 ± 1.0	180.9 ± 9.7	-15.2 ± 0.9	-26.1 ± 0.1	4/3
5	168	6.7 ± 1.2	105.6 ± 42.5	-15.7 ± 0.2	-27.8 ± 0.4	4/4
6	247	1.9 ± 0.2	19.2 ± 4.7	-16.2 ± 0.3	-23.5 ± 1.1	4/4

"Trap" refers to a particular CO_2 -trapping session; DAP is the mean number of days after planting; *n* is the number of replicates (pots) in the control treatment and the planted treatment, respectively.

In the pots planted with cottonwood, total belowground respiration changed dramatically through the growing season, reaching a maximum of around $200 \text{ mg C pot}^{-1} \text{ d}^{-1}$ in early August, during the time of maximum plant growth. High standard errors during trapping sessions three, four, and five reflect the variability in size and vigor among individual plants during this time. The $\delta^{13}\text{C}$ -signature of total belowground C respired in the planted pots was similar to the signature of C from the control pots during the first trapping session; thereafter the signature from the planted pots became more depleted as plant size increased (Table 1). By the time of the last trapping at 247 DAP, the plant contribution to total respiration dropped and the $\delta^{13}\text{C}$ of the respired C increased accordingly.

The mean air temperature was the highest during trapping sessions two, three, and four (late June to early September, Table 2). Gravimetric soil water was slightly lower in the planted pots (maximum $40 \text{ mg water g}^{-1}$ dry soil, mean $10 \text{ mg water g}^{-1}$ dry soil over the course of the experiment). Transpiration from the cottonwoods reached a maximum of about $750 \text{ g water plant}^{-1} \text{ d}^{-1}$ in the fifth trapping session; thereafter the leaves abscised and transpiration dropped dramatically.

In the planted pots, belowground respiration was dominated by plant-derived C (Fig. 2). However, clear differences were apparent between the mineralization of soil C from the planted pots and total respiration from unplanted pots, indicating that live cottonwood roots exert a strong influence on the mineralization rate of soil organic C (Fig. 3). Relative to the unplanted controls, mineralization of soil organic C in the planted treatment was initially suppressed. After about 100 days, however, this effect reversed and soil organic C mineralization in the planted treatment began to surpass total C respiration in the unplanted controls. At its maximum, between 141 and 144 days after planting, soil C was mineralized nine times faster in the pots planted with cottonwood than in the unplanted control pots. The magnitude of the effect then declined during the winter, although a small but significant rhizosphere priming effect was observed in the winter after all of

Table 2
Additional data measured during each trapping session

Trap	$^{\circ}\text{C}$	Gravimetric soil water		Biomass g pot^{-1}	Transpiration $\text{g pot}^{-1} \text{ d}^{-1}$
		Controls	Planted		
1	18.5	0.380 ± 0.001	0.369 ± 0.003	3 ± 1	86 ± 2
2	22.8	0.352 ± 0.001	0.323 ± 0.005	9 ± 2	$188 \text{vmk} \pm 16$
3	20.0	0.355 ± 0.001	0.310 ± 0.008	61 ± 9	669 ± 71
4	18.8	0.352 ± 0.001	0.319 ± 0.004	94 ± 21	668 ± 19
5	16.2	0.352 ± 0.001	0.384 ± 0.008	100 ± 20	751 ± 18
6	12.8	0.395 ± 0.004	0.398 ± 0.022	117 ± 13	42 ± 16

Errors are one standard error of the mean. $^{\circ}\text{C}$ is the mean air temperature. Biomass, expressed as dry plant mass, was calculated using stem diameter in an empirical allometric equation (see Methods).

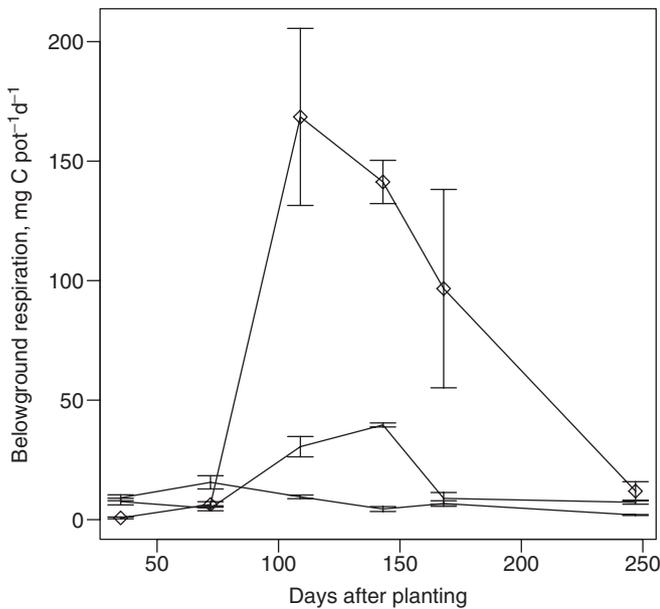


Fig. 2. Respiration rates of soil organic C, ± 1 SE. The three curves represent plant-derived respiration (open diamonds), soil C mineralization in the planted treatment (open circles), and soil C mineralization in the unplanted controls (filled circles).

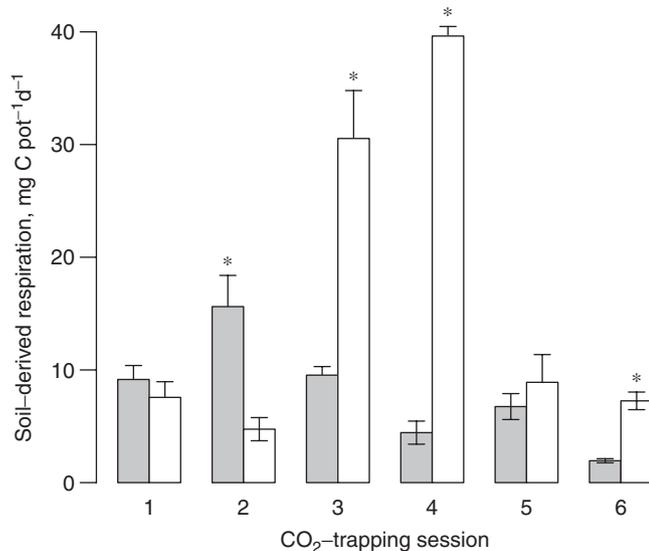


Fig. 3. Mineralization of soil organic C in pots planted with cottonwood (open columns) and unplanted controls (filled columns), ± 1 SE. Asterisks denote treatment groups that were significantly larger (*t*-test, $p < 0.05$) for each trapping session.

the leaves had abscised. Fluctuations in soil organic C mineralization in the control pots correlated well with air temperatures (Fig. 4). Mineralization of soil organic C in the planted pots, in contrast, was not correlated with air temperature. By linearly interpolating between measurements, we estimate that total soil organic C mineralization over the course of the experiment was approximately doubled (102% higher) in the planted pots, compared to the unplanted controls.

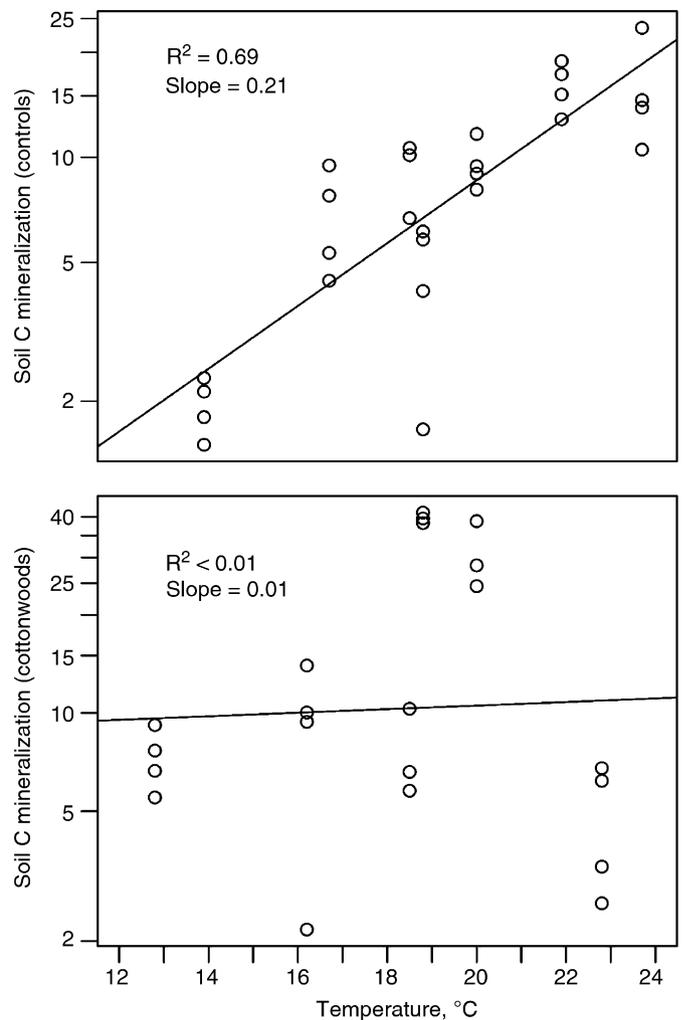


Fig. 4. Relationship of soil organic C mineralization to air temperature in the unplanted pots (upper graph) and in the planted pots (lower graph). Note that y-axis is in the log scale. Soil C mineralization is in the $\text{mg C pot}^{-1} \text{d}^{-1}$. The 95% CI of the slope coefficient is [0.15, 0.27] for the controls and [-0.12, 0.14] for the planted pots.

4. Discussion

Cottonwood roots had a dramatic effect on soil organic C mineralization in the rhizosphere. When total belowground respiration is large, as in trapping sessions three and four, the calculation of soil organic C mineralization is more sensitive to errors in δ_p (Eq. (2)). However, even in trapping sessions three and four, which have the highest total belowground respiration from the planted pots, a large (1) error in δ_p would result in an error in C_s of only 10–12 mg C , so rhizosphere priming is not in doubt. By linearly interpolating between data points, we estimate that the total mineralization of soil C was approximately doubled in cottonwood pots, compared to unplanted pots; i.e. cottonwood was associated with a 102% acceleration of soil organic C mineralization. This level of stimulation is consistent with rhizosphere priming effects observed in herbaceous plants. Published values for similar studies of crop plants range from -37% for wheat (Cheng, 1996) to

208% for soybean (Cheng et al., 2003). Consistent with other studies, the rhizosphere priming effect of cottonwood varied markedly with time. Cottonwood's rhizosphere priming of soil C was very large at 109 DAP and 143 DAP; at other times the rhizosphere priming effect was comparatively small or even negative. The duration of this experiment was therefore of key importance. Had this experiment been run for three months or less, we might have incorrectly concluded that cottonwood consistently suppresses the mineralization of soil organic C.

For approximately the first 100 days of the experiment, soil organic C mineralization was suppressed in the presence of cottonwood roots (Fig. 2). By the third trapping session (109 DAP), the rhizosphere priming effect had become positive (Fig. 3). This pattern of rhizosphere priming is in general agreement with Bottner et al. (1988) and Sallih and Bottner (1988), who reported that planted treatments showed reduced decomposition during the first 150–200 days and accelerated decomposition thereafter, compared to unplanted controls. However, other researchers have observed only positive priming effects that peak during the growing season, with no initial suppression, or small negative priming effects that persist throughout the growing season (e.g., Liljeroth et al., 1994; Cheng et al., 2003). The initial suppression of soil organic C mineralization can be explained in at least two ways. First, competition between plants and microbes for mineral N and other nutrients could have suppressed microbial growth rates (the “competition hypothesis”; Cheng and Kuzyakov, 2005). In this scenario, competition between microbes and plants could gradually precipitate a shift in the soil microbial community by about 100 DAP, favoring strains that more effectively liberate nutrients from soil organic matter. Another explanation for the initial suppression of soil organic C mineralization in the planted pots is that soil microbes preferentially metabolized labile root exudates rather than soil-derived substrates (the “preferred substrate utilization hypothesis”; Cheng and Kuzyakov, 2005). Because we cannot distinguish between plant respiration and microbial mineralization of plant-derived substrates, we would observe decreased soil organic C mineralization due to such a metabolic shift. In this scenario, an increased supply of root exudates could eventually support greater overall soil microbial activity, triggering the switch from suppression to acceleration of soil organic C mineralization by 100 DAP. This latter scenario seems more likely; the Kansas soil used in this experiment is comparatively rich in nutrients, even without fertilization (about 15 g N pot⁻¹), so competition for N probably did not greatly constrain microbial growth, particularly at the beginning of the experiment when plants were small.

Soil organic C mineralization in the control pots was correlated with air temperatures (Fig. 4). Because this experiment was not specifically designed to address temperature–respiration relationships, we do not address the likely differences between air temperature and soil

temperatures and the effect of hysteresis. Nevertheless, the linear correlation between the temperature and the logarithm of soil organic C mineralization is highly significant, with slope 0.21 ± 0.03 ($p < 0.001$). In contrast, soil organic C mineralization in the pots planted with cottonwood had no obvious relationship with temperature (Fig. 4), and the slope of the linear correlation between soil organic C mineralization and temperature was not significantly different from zero. This lack of correlation seems to have been driven by the comparatively large rhizosphere priming effect (Fig. 3), which obscured the temperature sensitivity of soil respiration in the planted pots. Our regression model incorporates measurements recorded at different times, so there is no way to eliminate the possibility that an unknown factor that changes with time, such as soil moisture, causes changes in soil C mineralization. Soil moisture was slightly lower during the warmer months and in the planted treatments (Table 2), and so is negatively correlated with air temperature. However, soil moisture changes of the magnitude we observed should affect soil respiration only slightly (Davidson et al., 2000).

The rate of soil respiration in the unplanted pots was low compared to other experiments using the Konza prairie soil. For example, Fu et al. (2002) measured respiration rates around 30–35 mg CO₂-C pot⁻¹ d⁻¹ from unplanted controls. In contrast, we measured respiration rates between 2 and 16 mg CO₂-C pot⁻¹ d⁻¹ from the same amount of unplanted Kansas soil. However, in the Fu et al. (2002) study, pots were kept in a greenhouse that used supplemental heating to maintain air temperatures above 22–25 °C during cool nights. Therefore, this discrepancy can be attributed to the high observed sensitivity of the Kansas soil to temperature changes in the 12–24 °C range. Another potentially important factor may be the large differences between day and night temperatures in our experiment compared with the more consistent temperatures in the greenhouse. Because of the low respiration rates we observed, the temperature sensitivity of the soil appears very high. However, because the respiratory CO₂ flux is near zero at 12.8 °C, even modest increases in respiration can lead to tripling or quadrupling of total measured respiration. It is therefore not appropriate to extrapolate this sensitivity to higher temperatures.

Our observations of soil organic C mineralization in pots planted with cottonwood confirms that strong rhizosphere priming effects are not restricted to herbaceous species. The discrepancy between soil respiration in unplanted controls and in the presence of live roots illustrates the danger of relying on measurements of respiration in root-free soil to predict the temperature sensitivity of ecosystem soil respiration. Because of the difficulty in partitioning belowground respiration into plant-derived and soil-derived sources, most researchers measure autotrophic and heterotrophic respiration together, and estimate the soil-derived component using incubations of root-free soils. The tacit assumption is that total belowground CO₂ efflux is a

simple additive combination of soil respiration, which is temperature sensitive (Lloyd and Taylor, 1994), and root respiration, which often shows a reduced or transient response to warming compared to root-free soils (Gifford, 1995; Tjoelker et al., 1999). The existence of large rhizosphere priming effects invalidates this assumption. If roots are more important drivers of soil respiration than temperature, then both rhizosphere respiration and soil respiration in natural ecosystems may be influenced by plant characteristics such as photosynthesis rather than temperature. In order to move towards a mechanistic understanding of soil respiration in natural ecosystems, we must recognize the non-additive role of live roots in influencing soil respiration, and that plants may be more important drivers of belowground respiration than currently acknowledged.

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