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Wenting Feng · Douglas A. Schaefer Xiaoming Zou · Min Zhang

Shifting sources of soil labile organic carbon after termination of plant carbon inputs in a subtropical moist forest of southwest China

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Abstract Labile organic carbon (LOC) is a critical component of soil organic carbon (C) because of its intimate association with soil heterotrophic respiration and role in the decomposition of resistant soil organic matter. In a subtropical moist evergreen broad-leaved forest of southwest China, we examined changes of LOC and its potential turnover time, microbial biomass C (MBC), and soil microbial activity of the organic and the 0-10 cm mineral soil layers with aboveground plant litter and belowground root treatments. In February of 2004, removal of organic layer, root-trenching, and tree-girdling treatments were applied alone and in combination to manipulate plant-C inputs. In 2006, root-trenching and tree-girdling treatments did not significantly change LOC in the organic layer. In the 0-10 cm mineral soil layer, LOC increased substantially due to tree-girdling treatment, especially in the plots of tree-girdling and the combinations of three treatments, but this increase was absent in 2007. Soil MBC in these two layers generally did not change markedly after plant-C inputs manipulations except significant increase under tree-girdling treatment in 2006. The potential turnover times of LOC increased in all plots with the plant-C inputs manipulations. The lack of influence of

W. Feng · D. A. Schaefer Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, 88 Xuefu Road, Kunming 650223 Yunnan, People's Republic of China

X. Zou

Institute for Tropical Ecosystem Studies, University of Puerto Rico, PO Box 70377, San Juan, Puerto Rico 00936-8377, USA

M. Zhang

Department of Tea Science, Zhejiang University, 268 Kaixuan Road, Hangzhou 310029 Zhejiang, People's Republic of China

W. Feng (🖂)

Earth and Environmental Science, University of Pennsylvania, 240 South 33rd street, Philadelphia, PA 19104-6316, USA E-mail: fengwen@sas.upenn.edu Tel.: +1-215-5738502 Fax: +1-215-8980964 plant-C inputs manipulations on LOC pools is likely due to high total soil organic C here, while insignificant changes of MBC suggest the soil microbes are not C limited in this forest. The changes of the potential turnover time of LOC imply that the sources of LOC have been shifted from fresh plant litter or root exudates to old soil organic C. Our results suggest that LOC recently derived from plants is preferred by microbes when available, but microbes can also use LOC from soil organic matter when fresh plant C is not available.

Keywords Girdling \cdot Microbial biomass carbon \cdot Sequential fumigation incubation \cdot Soil labile organic carbon \cdot Trenching \cdot Turnover time

Introduction

Soil organic carbon (C) exceeds atmospheric C by a factor of two and thus has substantial effects on the global C cycle (Schlesinger 1995). Among the components of soil organic C, labile organic C (LOC) is particularly important because of its intimate association with soil microorganisms. Since soil microbes control heterotrophic respiration, they could accelerate decomposition of resistant soil organic matter by the priming effect of LOC (Kuzyakov 2002; Hamer and Marschner 2005).

Soil organic C with a turnover time of less than a few years is defined as labile organic C. Soil LOC includes low molecular-weight compounds from plant rhizodeposition (Jones et al. 2004), C leachates and decomposition products from plant litter (Chapin et al. 2002), and microbial biomass C (MBC). Hence, changes in soil microbial biomass, dissolved organic C (DOC), and plant rhizodeposition will change LOC. These components of LOC are regulated by C inputs from aboveground plant litterfall and belowground plant roots. It is generally thought that soil microbial biomass C is energy limited, and affected by the seasonality of plant litterfall (Zak et al. 1994) and belowground C inputs from plant roots (Feng et al. 2009). Both fresh plant litterfall and existing soil organic matter can influence soil LOC extractable as DOC (Park and Matzner 2003; Don and Kalbitz 2005). It is not clear how soil LOC may respond to changes in aboveground litterfall and belowground root inputs.

Reflecting its complexity, several different methods have been used to estimate soil LOC, including acid hydrolysis (Blair et al. 1995; Leite et al. 2003; Jiang and Xu 2006), density fractionation (Gregorich and Janzen 1996; Carter et al. 1998; Roscoe and Buurman 2003), aqueous extractions (Sparling et al. 1998; Ghani et al. 2003), MBC by fumigation-incubation (Jenkinson and Powlson 1976) or fumigation-extraction (Vance et al. 1987), and mineralizable C (Alvarez and Alvarez 2000). However, these methods do not provide soil LOC turnover time unless accompanied by radiocarbon measurements. As soil microbes are generally energy limited, soil LOC estimate based on biological availability seems appropriate. Sequential fumigation-incubation was proposed by Zou et al. (2005) to evaluate biological LOC as microbially degradable C over a period of time. In this technique, field-moist soil samples are incubated at optimal temperature and moisture and then fumigated and re-incubated for several cycles until no further LOC is released as CO₂. The accumulated CO₂ respired against incubation time is used to extrapolate LOC based on its exponential degradation (Olson 1963). Compared to other LOC analyses, this method has the advantage of simultaneously providing concentrations and potential turnover rates of LOC.

In this study, we determined changes in concentrations and potential turnover times of soil LOC with manipulations of above- and belowground plant-C inputs to a subtropical evergreen forest of southwest China. We removed the organic layer and excluded aboveground plant litter. Separately and in combination, we used root trenching (Li et al. 2005) to terminate all biogeochemical functions of roots and tree-stem girdling (Högberg et al. 2001) to prevent transport of photosynthates to roots. During a multi-year experiment manipulating plant-C inputs in these ways, we addressed the following questions: (1) how would concentrations and potential turnover times of soil LOC change, and (2) how would the contribution of MBC to soil LOC be changed by plant-C inputs manipulations?

Materials and methods

Experimental sites

Our experimental sites are located in the Ailaoshan Nature Reserve of southwest China, about 2 km north of the Ailaoshan Forest Ecosystem Research Station (24°31'N, 101°01'E) administered by Xishuangbanna Tropical Botanical Garden of the Chinese Academy of Sciences. The climate is monsoonal with distinct dry (November–April) and wet (May–October) seasons. Mean monthly temperatures range from 5.4 to 15.2° C, and the annual rainfall averages 1,840 mm. The study site is a broad-leaved evergreen forest, dominated by *Lithocarpus chintungensis, Vaccinium ducluoxii*, and *Rhododendron leptothrium* (Wu et al. 1983). The soil is an Alfisol with pH of 4.2 (water 3:1). The soil is loamy, having 16.9% soil particles (<1 µm), 16.7% soil particles (10–50 µm), and 48.7% soil particles (50–1,000 µm) (Gan et al. 1997).

To control above- and belowground plant-C inputs, we removed the organic layer and aboveground litter inputs, and conducted root trenching (Li et al. 2005) and tree girdling (Högberg et al. 2001). Four pairs of 20×20 m plots were established; within each pair one was randomly assigned as the control and the other as tree girdling. Within each of these 20×20 m plots, there were four 2×3 m subplots—control, removal of organic layer, root trenching, and removal of organic layer plus root trenching. This generated eight combinations: CCK (control), CNL (removal of organic layer), CNR (root trenching), CNLR (removal of organic layer plus root trenching), GCK (tree girdling), GNL (girdled, removal of organic layer), GNR (girdled, root trenching), and GNLR (girdled, removal of organic layer plus root trenching). In these subplots, soil organic layer was removed down to the mineral soil layer and plant litterfall was intercepted with tents 1 m above the ground surface. Perimeters of root-trenched subplots were excavated to 40 cm, two layers of polyethylene sheets were inserted, and the trenches were back filled. Tree girdling was accomplished by cutting tree bark and phloem on a 5-cm band at 1.5 m height on all tree stems, and the perimeters of tree-girdled plots were also trenched and edged with polyethylene sheets as described above. Detailed descriptions of the treatments were previously presented (Schaefer et al. 2009). The treatments were set up in early February 2004.

Field sampling and laboratory analyses

Soil samples were collected on 13 October 2003, 28 August 2006, and 3 November 2007. Organic layers were sampled with a wood frame (20×20 cm), and soils from the 0 to 10 cm mineral soil layer with a 50.5-mm-diameter corer. Two mineral soil cores were taken from each of the 32 subplots and combined to form 32 composites.

Before sieving, rocks and animals were picked out of the soil samples. Then soils were passed through a 2-mm sieve and the material not passing was discarded. Visible plant roots below the sieve were removed with tweezers. Subsamples of 15–20 g were oven dried at 105°C for 24 h to determine moisture correction factors, and fieldmoist soils were used for incubations.

The sequential chloroform fumigation-incubation method for LOC estimation is based on the chloroform fumigation-incubation method for MBC determination as illustrated in Fig. 1 (Jenkinson and Powlson 1976; Zou et al. 2005). Specifically, two 30-g subsamples of



Fig. 1 Procedure for the estimates of soil labile organic carbon and microbial biomass carbon. Subscript "c" means the control and subscript "f" means the fumigated. Microbial biomass C can be calculated based on the difference between C_{c1} and C_{f1} . In this study, *i* refers to the time of repeated incubation cycle

each soil were weighed, one as the control and the other fumigated with ethanol-free chloroform for 18-24 h in darkness. Both the control and the fumigated soils then received 1 g of fresh soil as inoculum, and were incubated for 10 days in darkness within 1.5-1 sealed jars. Each jar also contained 20 mL of 1 mol l^{-1} NaOH in a beaker to absorb released CO₂ and a piece of moistened filter paper to maintain humidity. The procedure of fumigation and incubation with 1-g inoculum for 10 days was repeated seven times in this experiment. The total CO₂–C released from each fumigated sample beyond that of the control during the incubation series was identified as LOC according to the following details. The released soil CO₂–C during the *t*th fumigation– incubation was calculated using the formula modified from Carter (1993):

$$C_t = [(A_t - V_t)N_t E - Q_t]/w,$$

where A_t refers to the volume (milliliters) of acid needed to titrate the NaOH for the blank; V_t refers to the volume (milliliters) of acid needed to titrate NaOH for the fumigated soils; N_t is the normality of the acid; E = 6, the equivalent weight; and w is the initial weight of soil in each fumigation treatment.

$$Q_t = C'/(r+1) + \sum [C_{t-1}/(r+1)],$$

 $t = 1, 2, ..., n, Q_t$ is a correction factor for the soil inoculum added after each fumigation, where $C_{t-1} = 0$ when

t = 1; C' is the amount of CO₂–C from the control soil during the first 10-day incubation; and r is the initially fumigated-inoculated soil weight ratio. The accumulated CO₂–C (M_t , t = 1,..., n) from the fumigated soil is calculated according to Stanford and Smith (1972):

$$M_t = C_{\text{labile}} (1 - \mathrm{e}^{-kt}),$$

where C_{labile} is soil LOC and k is the potential turnover rate (day⁻¹). Potential turnover time (days) of soil LOC is calculated as the inverse of k multiplied by 10 as each cycle lasted 10 days. Values for C_{labile} and k can be calculated by linear regression using the transformed equation as follows:

$$\ln(C_t) = \ln(kC_{\text{labile}}) - kt,$$

where t is 1, 2, ..., n, k is the absolute value of the slope, ln (kC_{labile}) is the intercept (a), and $C_{\text{labile}} = e^a/k$.

Soil MBC was assessed as the difference of CO_2 released between the control and the fumigated in the first 10-day incubation of LOC measurement, and divided by 0.45 (Vance et al. 1987). Other components of LOC were that remaining after subtracting MBC (value after dividing by 0.45).

Two to four days before each field soil sampling, soil respiration was measured by alkali trapping in all 32 subplots (Li et al. 2005). There were two replicates in each subplot.

Statistical analyses

All data were tested for normality and transformed if necessary. We used the mixed procedure model (SAS Institute Inc. 1999) to test the effects of tree girdling, removal of organic layer, and root trenching on LOC concentrations and its potential turnover times, MBC, the other components of LOC in the organic and the 0-10 cm mineral soil layers, and soil respiration. Where the organic layer was removed, we could only test the effects of tree girdling and root trenching on variables in the mineral soil layer. The regressions between the potential turnover time of LOC and LOC, MBC, and the other components of LOC in October 2003, August 2006, and November 2007 were determined. Significance levels for all tests were set at alpha = 0.05.

Results

Soil labile organic C

Before plant-C inputs manipulations, LOC of the organic and the 0–10 cm mineral soil layers averaged 15.7 and 4.8 mg C g⁻¹ in the control plots (CCK), respectively. In the organic layer, neither tree girdling nor root trenching had significant effects on LOC at any sampling time (Table 1). In the 0–10 cm mineral soil layer, tree girdling and the interactions among tree girdling, removal of

Table 1 The statistical results of labile organic carbon (LOC, mg C g^{-1}), potential turnover times of LOC (days), microbial biomass carbon (MBC, mg C g^{-1}), and components of LOC other

than MBC (other LOC, mg C g^{-1}) of the organic soil in a subtropical forest of Ailao Mountains, southwest China in October 2003, August 2006, and November 2007

Year	Effect	LOC	Turnover time	MBC	Other LOC
2003	Tree girdling (A)	0.474	0.567	0.146	0.864
	Root trenching (B)	0.952	0.795	0.701	0.843
	$A \times B$	0.051	0.218	0.111	0.076
2006	Tree girdling (A)	0.844	0.146	0.203	0.621
	Root trenching (B)	0.271	0.819	0.133	0.337
	A×B	0.105	0.097	0.167	0.111
2007	Tree girdling (A)	0.220	0.253	0.658	0.194
	Root trenching (B)	0.567	0.662	0.350	0.612
	$A \times B$	0.363	0.858	0.534	0.517

* Significant effects (alpha = 0.05)

Table 2 The statistical results of labile organic carbon (LOC, mg C g^{-1}), potential turnover times of LOC (days), microbial biomass carbon (MBC, mg C g^{-1}), and components of LOC other

than MBC (other LOC, mg C g^{-1}) of the 0–10 cm mineral soil in a subtropical forest in the Ailao Mountains, southwest China in October 2003, August 2006, and November 2007

Year	Effect	LOC	Turnover time	MBC	Other LOC	Soil respiration
2003	Tree girdling (A)	0.017*	0.973	0.076	0.041*	0.884
	Organic layer removal (B)	0.507	0.568	0.688	0.196	0.174
	Root trenching (C)	0.471	0.641	0.633	0.151	0.327
	$A \times B$	0.037*	0.768	0.194	0.048*	0.460
	$A \times C$	0.915	0.251	0.494	0.460	0.519
	$B \times C$	0.374	0.946	0.614	0.092	0.770
	$A \times B \times C$	0.797	0.501	0.152	0.395	0.732
2006	Tree girdling (A)	0.001*	0.058	0.009*	0.002*	0.007*
	Organic layer removal (B)	0.719	0.700	0.431	0.455	< 0.001*
	Root trenching (C)	0.862	0.331	0.699	0.898	0.028*
	$A \times B$	0.568	0.590	0.785	0.538	0.331
	$A \times C$	0.905	0.293	0.798	0.992	0.035*
	$B \times C$	0.862	0.086	0.153	0.987	0.744
	$A \times B \times C$	0.001*	0.098	0.702	0.001*	0.581
2007	Tree girdling (A)	0.314	0.165	0.389	0.169	0.055
	Organic layer removal (B)	0.357	0.961	0.915	0.250	0.002*
	Root trenching (C)	0.513	0.964	0.647	0.466	0.604
	$A \times B$	0.848	0.288	0.099	0.981	0.553
	$A \times C$	0.942	0.861	0.299	0.855	0.862
	$B \times C$	0.311	0.210	0.443	0.206	0.159
	$A \times B \times C$	0.943	0.494	0.339	0.851	0.652

* Significant effects (alpha = 0.05)

organic layer, and root trenching significantly changed LOC in August 2006 (Table 2). None of the treatments markedly affected LOC in November 2007. The largest changes in LOC concentrations among eight plots were observed in August 2006 and the smallest in October 2003 (Fig. 2b). Greater differences in LOC between 2003 and 2006 were observed in tree-girdling (GCK) and the combination of tree-girdling and removal of organic layer plus root-trenching (GNLR) plots (Fig. 2b). Greater differences in LOC between seen in root-trenching (CNR), tree-girdling (GCK), and the combination of tree-girdling and root-trenching (GNR) plots (Fig. 2b).

Potential turnover time of soil labile organic C

In October 2003 before treatment initiation, LOC potential turnover times of the organic and the 0–10 cm

mineral soil layers were 25–28 and 18–20 days, with only minor variations among plots (Fig. 3a, b). In the organic layer, potential turnover times of LOC were similar in August 2006 and November 2007, and were about twice that in October 2003 (Fig. 3a; Table 1). However plant-C inputs treatments did not alter potential turnover times of LOC in August 2006 or November 2007 (Table 1). In the 0–10 cm mineral soil layer, potential turnover times of LOC in both August 2006 and November 2007 were longer compared to pre-treatment values in October 2003 (Fig. 3b). Labile organic C in tree-girdling plus removal of organic layer (GNL) plots and tree girdling plus root trenching (GNR) had slower turnover in November 2007 than in August 2006 (Fig. 3b).

In the organic layer, LOC potential turnover times were significantly correlated with LOC concentrations at each sampling time (Table 3). It was only significantly correlated with MBC in October 2003 and with



а 2003 80 2006 Potential turnover time of LOC (days) 60 40 20 0 b 120 90 60 30 0 CNLR GNLR SS CNR GNR GCK Ч GR Treatment

Fig. 2 In a subtropical moist forest of southwest China, labile organic carbon (mg C g⁻¹) of **a** the organic and **b** the 0–10 cm mineral soils in October 2003, August 2006, and November 2007 in CCK (control), CNL (removal of organic layer), CNLR (removal of organic layer plus root-trenching), CNR (root-trenching), GCK (tree-girdling), GNL (girdled, removal of organic layer), GNLR (girdled, removal of organic layer), and GNR (girdled, root-trenching) plots. Data are mean \pm SE (n = 4)

components of LOC other than MBC in August 2006 and November 2007 (Table 3). In the 0–10 cm mineral soil layer, LOC potential turnover times were significantly correlated with LOC concentrations and components of LOC other than MBC in August 2006 and November 2007. However, there were no significant correlations between LOC potential turnover time and MBC at any sampling time (Table 3).

Soil microbial biomass C

In the organic layer, MBC was slightly higher in October 2003 than after treatments (Fig. 4a). There were no significant treatment effects on MBC in the organic layer at any sampling time. In the 0–10 cm mineral soil layer, MBC was higher in August 2006 than in October 2003, especially in tree-girdled plots (GCK, GNL, GNLR, and GNR) (Fig. 4b). Tree girdling had significant effects on MBC in the 0–10 cm mineral soil layer (Table 2). However, MBC was not greatly changed in November 2007 compared to that in October 2003 (Fig. 4b).

Fig. 3 In a subtropical moist forest of southwest China, potential turnover times of labile organic carbon (days) of **a** the organic and **b** the 0–10 cm mineral soils in October 2003, August 2006, and November 2007 in CCK (control), CNL (removal of organic layer), CNLR (removal of organic layer plus root-trenching), GCK (tree-girdling), GNL (girdled, removal of organic layer), GNLR (girdled, removal of organic layer plus root-trenching), and GNR (girdled, root-trenching) plots. Data are mean \pm SE (n = 4)

Soil respiration

Soil respiration flux rates were 0.53-0.62, 0.60-1.31, and $0.43-0.71 \ \mu\text{mol}\ \text{m}^{-2}\ \text{s}^{-1}$ in the October 2003, August 2006, and November 2007, respectively (Fig. 5). Soil respiration did not differ among plots before treatments in October 2003. In August 2006, soil respiration in organic layer removal, root-trenching, tree-girdling, both the tree-girdling and root-trenching plots were significantly lower than that in the control plot (Table 2). In November 2007, markedly low soil respiration was only observed in organic layer removal plots (Fig. 5; Table 2).

Discussion

Changes of soil labile organic C

Before the plant-C inputs manipulations, LOC was much higher in the organic layer (15.7 mg C g^{-1}) than in the 0–10 cm mineral soil layer (4.8 mg C g^{-1}), with small variations among plots (Fig. 2). Two or three years after plant-C inputs manipulations, LOC in the

Table 3 Regressions between potential turnover times of labile organic carbon (LOC) and LOC (mg C g^{-1}), microbial biomass carbon (MBC, mg C g^{-1}), and components LOC other than MBC

(other LOC, mg C g^{-1}) for the organic and 0–10 cm mineral soils in a subtropical forest in the Ailao Mountains, southwest China in October 2003, August 2006, and November 2007

Year	Organic 1	Organic layer			0-10 cm mineral soil layer			
	Slope	Intercept	R^2	Р	Slope	Intercept	R^2	Р
LOC								
2003	0.76	14.39	0.21	0.043*	0.09	18.34	< 0.01	0.876
2006	2.28	19.27	0.71	< 0.001*	1.12	34.63	0.17	0.011*
2007	2.12	26.38	0.58	< 0.001*	5.19	18.20	0.54	< 0.001*
MBC								
2003	1.77	18.95	0.25	0.029*	0.99	16.28	< 0.01	0.319
2006	6.57	37.42	0.14	0.083	-1.87	53.20	< 0.01	0.386
2007	2.22	50.96	< 0.01	0.601	-1.35	61.13	< 0.01	0.837
Other LC	C							
2003	0.59	19.66	0.04	0.226	-0.41	19.70	< 0.01	0.592
2006	2.71	21.21	0.76	< 0.001*	1.48	35.03	0.25	0.002*
2007	2.39	30.52	0.70	< 0.001*	6.33	25.88	0.67	< 0.001*

* Significant effects (alpha = 0.05)



Fig. 4 In a subtropical moist forest of southwest China, microbial biomass carbon (mg C g^{-1}) of **a** the organic and **b** the 0–10 cm mineral soils in October 2003, August 2006, and November 2007 in CCK (control), CNL (removal of organic layer), CNLR (removal of organic layer), CNLR (removal of organic layer), GNLR (tree-girdling), GNL (girdled, removal of organic layer), GNLR (girdled, root-trenching) plots. Data are mean \pm SE (n = 4)

organic layer was still twice that in the 0–10 cm mineral soil layer (Fig. 2). These results are consistent with another study showing higher soil DOC reflecting LOC in topsoil than in subsoil (Park and Matzner 2003). With a large amount of aboveground plant litter and shallow



Fig. 5 In a subtropical moist forest of southwest China, soil respiration (μ mol m⁻² s⁻¹) measured in October 2003, August 2006, and November 2007 in CCK (control), CNL (removal of organic layer), CNLR (removal of organic layer plus root-trenching), CNR (root-trenching), GCK (tree-girdling), GNL (girdled, removal of organic layer), GNLR (girdled, removal of organic layer), and GNR (girdled, root-trenching) plots. Data are mean \pm SE (n = 4)

root distributions in this forest, relatively little plant labile C may move deep into mineral soil horizons.

In the organic layer, LOC concentrations were not affected by tree-girdling or root-trenching treatments (Fig. 2a; Table 1), but they were slightly higher only in August 2006 than pre-treatment values (Fig. 2a). This was probably due to high initial organic C content in this forest soil.

In the 0–10 cm mineral soil layer, LOC was higher in August 2006 than before treatments especially in CNL, GCK, GNL, GNLR, and GNR plots (Fig. 2b; Table 2). This suggests that sources of LOC shifted from fresh plant litter or root exudates to the existing old soil organic C under plant-C inputs manipulations. Park and Matzner (2003) found that both fresh plant litter and soil organic matter were important sources of LOC as measured by DOC. A strong influence of belowground plant-C inputs on LOC (as DOC) was also reported by Dannenmann et al. (2009). Additionally, the markedly higher LOC in the August 2006 than in the November 2007 in the removal of organic layer (CNL) and the interactions between tree girding and the removal of organic layer (GNL) plots suggest that rhizosphere disruption by the tree-girdling treatment influenced LOC dynamics in mineral soils.

In contrast to a large increase of LOC in August 2006 relative to pre-treatments, LOC in November 2007 was only slightly higher. This was probably related to the exhaustion of LOC stored in trees below girdling level available for growth or respiration (Gough et al. 2009). Girdled trees began dying in the summer of 2007. Higher LOC in 2006 might also result from different sampling times; August 2006 was in the growing season and November 2007 was in the dormant season for this forest. Using the same method for LOC evaluation, Zhang and Zou (2009) found that soil LOC concentrations were higher in the growing season than in the dormant season in a tropical forest of southwest China. Rapid decomposition of plant litter and root debris in August 2006 compared to November 2007 may have also contributed to this difference.

Potential turnover time of soil labile organic C

The LOC potential turnover times of the organic layer soils in August 2006 (50-73 days) and November 2007 (55-65 days) were about twice those measured before treatments (25-28 days) (Fig. 3a). In the 0-10 cm mineral soil layer, LOC potential turnover times in August 2006 and November 2007 were 38-57 days and 40-90 days, respectively, much longer compared to pretreatment times (18-20 days). There were only small variations of LOC potential turnover times in the organic and the mineral soil layers among treatments during this experimental time (Tables 1, 2). In this period of time, increases of LOC potential turnover time in the control might be related to annual variations in chemistry of plant litter inputs driven by climate or other factors. The potential turnover time of LOC was longer in the organic layer than in the 0-10 cm mineral soil layer, and MBC accounted for a smaller portion in the organic layer than in the 0-10 cm mineral soil. Together, these suggest that components of soil LOC other than MBC are more closely related to the potential turnover times of soil LOC. By manipulating plant-C inputs, we found that components of LOC other than MBC were significantly correlated with the potential turnover times of LOC in both the organic and the 0-10 cm mineral soil layers (Table 3). It suggests that the sources of LOC included not only plant rhizodeposition and photosynthates but also plant decomposition products which appear to be less readily available to soil microbes.

As soil LOC is heterogeneous, different components can respond differently to plant-C inputs. Soil respiration includes heterotrophic C decomposition and "autotrophic" microbial and root activity based directly on photosynthates (Högberg et al. 2001). Soil MBC is a fraction of LOC with a relatively short turnover time, and the other LOC fractions have relatively longer turnover times.

In August 2006, soil respiration was significantly affected by plant-C inputs manipulations. The removal of organic layer and tree girdling decreased soil respiration, and root trenching increased it only in non-girdled plots (Fig. 5; Table 2). In November 2007, soil respiration was reduced only by removing organic layer (Fig. 5; Table 2). These results demonstrate that soil microbial respiration was strongly and directly affected by both aboveground plant litter and by belowground C derived from photosynthates fluctuating seasonally.

For microbial biomass C, influences of plant-C inputs were minor in both soil layers (Fig. 4; Tables 1, 2). In August 2006, MBC was reduced in the organic layer, but it increased in tree-girdled plots in the 0–10 cm mineral soil layer (Fig. 4). These differences suggest that the soil microbial community may have shifted from bacterial to fungal dominance under plant-C inputs reductions (personal communication with Shi LL). In November 2007, MBC did not vary among eight plots. Brant et al. (2006) also reported a minor effect of aboveground litter removal on soil microbial biomass in a temperate coniferous forest. Therefore, soil LOC derived from microbial cells seems only slightly affected by plant-C inputs during this experiment.

The difference between LOC and MBC represents other components of LOC. In the organic layer, this fraction accounted for more than 70% of LOC, and it was not significantly changed by tree-girdling or roottrenching treatments (Table 1). In the 0–10 cm mineral soil layer, this fraction increased during the experiment (Fig. 4). In November 2007, tree girdling and interactions between tree girdling and removal of organic layer affected the other components of LOC, but in August 2006 only tree girdling influenced it. Our results suggest that removal of organic layer affected the other components of LOC early, and effects of tree girdling and root trenching came later. Decomposing root debris from the tree-girdling and root-trenching treatments were likely responsible for changes in the other components of LOC. Because it took time for the girdled trees to die and to generate root debris, the decomposition products of root debris slowly contributed to sources of the other components of LOC with relatively long turnover times.

In this study, continued monitoring of this ongoing experiment will provide additional information about how above- and belowground plant-C inputs influence soil organic C and its different fractions. Acknowledgments We are grateful to the Bureau of Nature Reserve of Jingdong County for giving the permission to carry out this experiment in the Ailao Mountain Nature Reserve. We thank Yun Fu for the help for the chemical analyses, and Lingling Shi for providing unpublished data on the soil microbial community. We also appreciate the support in the field by the staff of the Ailaoshan Nature Reserve. This is a research contribution from the Ailaoshan Station for Subtropical Forest Ecosystem Studies (ASSFE), Chinese Academy of Sciences, and the Ailaoshan National Ecosystem Observation Research Network Station, Chinese Ecological Research Network, Jingdong, Yunnan, P. R. China. This study was financially supported by the Natural Science Foundation of Yunnan (2005C0056M), Wang K. C. Foundation, and Xishuangbanna Tropical Botanical Garden of the Chinese Academy of Sciences.

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