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Above- and belowground carbon inputs affect seasonal variations of soil microbial biomass in a subtropical monsoon forest of southwest China

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ABSTRACT

Soil microbial activity drives carbon and nutrient cycling in terrestrial ecosystems. Soil microbial biomass is commonly limited by environmental factors and soil carbon availability. We employed plant litter removal, root trenching and stem-girdling treatments to examine the effects of environmental factors, above- and belowground carbon inputs on soil microbial C in a subtropical monsoon forest in southwest China. During the experimental period from July 2006 through April 2007, 2 years after initiation of the treatments, microbial biomass C in the humus layer did not vary with seasonal changes in soil temperature or water content. Mineral soil microbial C decreased throughout the experimental period and varied with soil temperature and water content. Litter removal reduced mineral soil microbial C by 19.0% in the ungirdled plots, but only 4.0% in girdled plots. Root trenching, stem girdling and their interactions influenced microbial C in humus layer. Neither root trenching nor girdling significantly influenced mineral soil microbial C. Mineral soil microbial C correlated with following-month plant litterfall in control plots, but these correlations were not observed in root-trenching plots or girdling plots. Our results suggest that belowground carbon retranslocated from shoots and present in soil organic matter, rather than aboveground fresh plant litter inputs, determines seasonal fluctuation of mineral soil microbial biomass.

1. Introduction

Soil microbial biomass is important for carbon and nutrient cycling in terrestrial ecosystems. Soil heterotrophic respiration and the decomposition of fresh and old organic materials are associated with soil microbial activity. Soil microbial C fluctuates seasonally in various forests (Maithani et al., 1996; Bohlen et al., 2001; Ruan et al., 2004). The dynamics of soil microbial C are associated with varying environmental factors including temperature, soil moisture and rainfall. In a mixed-oak forest with warm moist summer and cool dry winter, soil microbial C had significant positive correlations with both soil moisture and mean air temperature (Devi and Yadava, 2006).

Besides the influence of environmental factors on soil microbial C, soil available C is recognized to drive soil microbial growth (Wardle, 1992). Zak et al. (1994) suggested that plant litter production controlled the biomass of soil microorganisms. Leachates from or the decomposition products of fresh plant litter and organic layers provide labile organic carbon to stimulate soil microbial activity (Garcia-Oliva et al., 2003). The exclusion of plant litterfall would reduce labile organic C and nutrients for soil microbes and could also alter microclimatic conditions. However, Fisk and Fahey (2001) found no significant change in microbial biomass C on forest organic layers between their control ($5.8\ \mathrm{mg\,C\,g^{-1}}$) and fresh litter ($O_i$ layer) removal ($5.5\ \mathrm{mg\,C\,g^{-1}}$) treatments.

Microbial activity may increase with root exudates (Hütsch et al., 2002) and the decomposition of root debris and old organic matter (Gottlicher et al., 2006). Belowground carbon manipulations, such as root trenching and stem girdling preventing the flow of photosynthates from canopy to soils, should therefore influence soil microbial C. Thirteen years after trenching, soil microbial C in trenched plots was within 25–75% of the control plot value in a coniferous forest (Hart and Sollins, 1998). Li et al. (2004) found that root trenching decreased it by 45.4% in a tropical pine plantation 7 years after the initiation of treatments. Högberg and Högberg (2002) demonstrated that soil microbial C was 41% lower in stem-girdling plots than in the control plots 1 month after the girdling, while it was 23% lower 3 months after the stem-girdling treatment.

The effects of above- and belowground carbon inputs on seasonal variations of soil microbial C are not well understood. In

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a subarctic tundra, Olsrud and Christensen (2004) used ^{14}C tracing to demonstrate that photosynthates were transferred to roots and appeared as dissolved organic carbon in soil water, which reached its highest level at the end of the growing season. In a tropical wet forest, Ruan et al. (2004) observed that monthly changes in soil microbial C were not synchronized with aboveground litterfall but rather preceded litterfall by 1 month in both control and litter-removal plots. They proposed that belowground processes such as the translocation of carbohydrates before leaf senescence or changes in competition for nutrients between plant roots and soil microbes were the potential mechanisms for seasonal variations of soil microbial C. Stem girdling prevents the flow of photosynthates from shoots to stem and roots below the girdles, and root trenching terminates carbon transfer to soil through live plant roots, as well as plant uptake of water and nutrients. These two treatments can allow us to test whether the retranslocation of photosynthates from canopy to belowground would stimulate soil microbial growth before plants shed their leaves.

This study explored to what extent the above- and belowground C inputs affect seasonal variation of soil microbial C in a subtropical monsoon forest of Ailao Mountains, southwest China. We employed litter removal (Li et al., 2005), root trenching (Liu and Zou, 2002) and stem girdling (Högberg et al., 2001) to separate the effects of aboveground litterfall and belowground root exudates and root debris on soil microbial C. We predicted that soil microbial C would be reduced by terminating aboveground plant litter and organic layers, and it would correlate with plant litterfall occurring in the current or preceding month in the intact plots, but not in the litter-removal plots. We expected that soil microbial C would respond to litterfall occurring currently or in the post-months in the control plots because of carbon resorption from leaves in evergreen forests (Lal et al., 2001), but it would not be the case for soil microbial C in girdling and root-trenching plots.

2. Materials and methods

2.1. Study sites

The research was conducted at the Ailao Field Station for Forest Ecosystem Studies (24°32′ N, 101°01′ E), 2476 m a.s.l., in Yunnan Province, southwest China. This relatively undisturbed forest is covered by subtropical evergreen broad-leaved species dominated by *Lithocarpus chintungensis*, *Rhododendron leptothrium*, *Vaccinium ducluoxii*, *Lithocarpus xylocarpus*, *Castanopsis wattii*, *Schima noronhae*, *Hartia sinensis*, and *Manglietia insignsis* (Li, 1983). The site receives an average of 1840 mm rainfall per year and has mean monthly temperatures ranging between 5.4 °C and 23.5 °C. The region has a strong dry–wet seasonality, with the wet season from May through October and the dry season from November though April (Zhang, 1983). The soils are Alfisols with pH of 4.5 and 4.2, soil organic carbon 304 g kg^{-1} and 116 g kg^{-1}, soil organic nitrogen 18 g kg^{-1} and 7 g kg^{-1} in humus and 0–10 cm mineral soil layers, respectively (Chan et al., 2006).

2.2. Experimental design

We employed a split-plot design to carry out this study. Eight 20 × 20 m plots were established in early February 2004, with four plots randomly selected for stem girdling and the other four acting as the ungirdled. Within each 20 × 20 m plot, four 2 × 3 m subplots were randomly chosen as control, litter removal, root trenching and litter removal plus root trenching. Therefore, there were four combinations in each ungirdled plot: CCK (control), CNL (control, litter removal), CNLR (control, litter removal plus root trenching), CNR (control, root trenching), and four in each girdled plot: GCK (girdling), GNL (girdling, litter removal), GNLR (girdling, litter removal plus root trenching) and GNR (girdling, root trenching). All the subplots were positioned to avoid woody stems. In the four 20 × 20 m stem-girdled plots, a 5-cm width band was peeled down to xylem on all trees (diameter > 2 cm) at breast height (Högberg et al., 2001) and those plot perimeters were trenched down to 40 cm below ground surface with the trenches lined with plastic sheets and refilled with soil (Liu and Zou, 2002). In the litter-removal subplots, wooden structures covered with 1 mm nylon mesh were constructed at 1 m above ground to intercept aboveground plant litter (Ruan et al., 2004) and organic layers above the mineral soil were removed. The perimeters of the root-trenching subplots were trenched as described above for the girdled plots. In the stem-girdled plots, most of the trees began dying and shed their leaves in the summer of 2007.

2.3. Field sampling and laboratory analyses

Soil samples from 32 subplots were collected at the end of each month from July 2006 through April 2007. Humus consisting of well-decomposed material was sampled using a wooden frame (20 × 20 cm). Within each subplot, humus samples were pooled together to obtain adequate amounts of materials for chemical analyses. After the removal of forest organic horizons, the upper 10-cm mineral soils were sampled using a soil corer (50.5 mm diameter, 10 cm height). Soil cores taken from two random locations were bulked together from each subplot.

All samples were sieved through 2 mm mesh stainless steel screen, and stored in polyethylene zipper bags at room temperature. From each composite, a 15–20 g subsample was oven-dried at 105 °C for 24 h to determine gravimetric water content. Soil temperature was measured at 5 cm below the mineral soil surface with a digital thermometer. Soil microbial C was measured with a modified chloroform–fumigation–incubation procedure (Jenkinson and Powlson, 1976; Ruan et al., 2004). Soil microbial C was calculated as (Jenkinson and Powlson, 1976): microbial biomass $B = F/K$, where $B =$ soil microbial C, mg C g soil^{-1}; $F =$ C-CO$_2$ the difference between C-CO$_2$ evolved by fumigated soil and unfumigated soil incubated at the same time under the same conditions; $K = 0.45$, the fraction of the microbial biomass carbon released as CO$_2$ following the fumigation. We collected plant litterfall at the end of each month from June 2006 through May 2007. Litterfall was collected from 7 traps (0.25 m^2) randomly arranged in each 20 × 20 m plot. For plant litter dry weights, all litter samples were oven-dried to constant weight at 80 °C.

2.4. Statistical analyses

We used the SAS Proc Mixed procedure (SAS, 1999) to test the effects of litter removal, root trenching, girdling and seasonal variations on soil microbial C in humus and the mineral soil from July 2006 through April 2007. We examined the correlations between soil microbial C and soil water content and temperature in the humus and the mineral soil layers. We also examined the correlations between soil microbial C in humus and the mineral soil and plant litterfall collected in the preceding 1 month, at the same time and in the following month. As the monthly litterfall data were not normally distributed, they were inverse square root transformed prior to testing for correlations with soil microbial C. Litterfall was tested for correlations with soil microbial C in CNL plots, even though it was excluded from those plots. The purpose of this test was to determine whether processes varying in time along with plant litter inputs could influence soil microbial C. All significant effects were determined at the 0.05 probability level.

3. Results

3.1. Environmental factors

Soil water content varied more in humus layer than in the mineral soil (Fig. 1A, B). Average soil water content of humus and the mineral soil was within the ranges of 55–231% and 62–139%, respectively. They showed similar trends, remaining high from July 2006 through January 2007, and then dropping gradually to the lowest value in March 2007 with a subsequent increase. In the humus layer, soil water content was higher in CNR, GCK and GNR plots than in CCK plots (Fig. 1A). In the mineral soil, litter removal significantly decreased soil water content (Table 1). In the study period, soil temperature had a pronounced seasonal fluctuation, high from July 2007 through September 2007, falling subsequently to the lowest value in January 2007 and then increasing afterwards (Fig. 1C). Girdling ($P = 0.008$) and litter-removal ($P = 0.023$) treatments significantly influenced average soil temperature (Table 1). Root trenching increased soil water content (Fig. 1A, B). Aboveground litterfall in both the ungirdled and girdled plots showed seasonal changes. In the ungirdled plots, high litterfall occurred from February to May with the second highest values in October and November. In the girdled plots, litterfall was high from September through November and from March through May. Stem girdling increased aboveground plant litter input ($P = 0.021$, Fig. 1D).

In the humus layer, soil water content correlated with microbial C only in GCK plots (Table 2). Soil temperature did not correlate with microbial C in any plots (Table 2). In 0–10 cm mineral soil, soil temperature significantly correlated with soil microbial C in CCK, CNL, CNR and GCK plots. Significant correlations between soil water content and soil microbial C were found in CCK, CNL and GCK plots but not in CNR plots (Table 2).

3.2. Soil microbial C

Microbial biomass C of humus layer varied between 1.18 mg C g^{-1} and 4.74 mg C g^{-1}. There was no clear peak of microbial C in the humus layer during the study period, but the lowest level occurred in November 2006 (Fig. 2A). In humus layers, microbial biomass C was not significantly higher in both CNR ($P = 0.149$) and GCK ($P = 0.260$) plots than in CCK plots (Fig. 2A). We found a significant interaction between girdling and root-trenching treatments (Table 1). The time-averaged microbial biomass C of the humus layer in GNR plots was less than that in GCK plots by 35.8%, and less than that in CNR plots by 36.0%.

Soil microbial C in the 0–10 cm mineral soil varied among months (Table 1) within the range of 0.92–3.98 mg C g^{-1}. It decreased from July 2006 through April 2007 (Fig. 2B, C). Soil microbial C was lower in the dormant season (November–April) than in growing season (July–October). Litter removal significantly reduced mineral soil microbial C (Table 1), but to different degrees in the ungirdled plots and stem-girdled plots. Mineral soil microbial C was substantially lower in CNL plots than in CCK plots (Fig. 2B), but this difference was much smaller between GNL and GCK plots (Fig. 2C). There was a significant interaction between girdling and

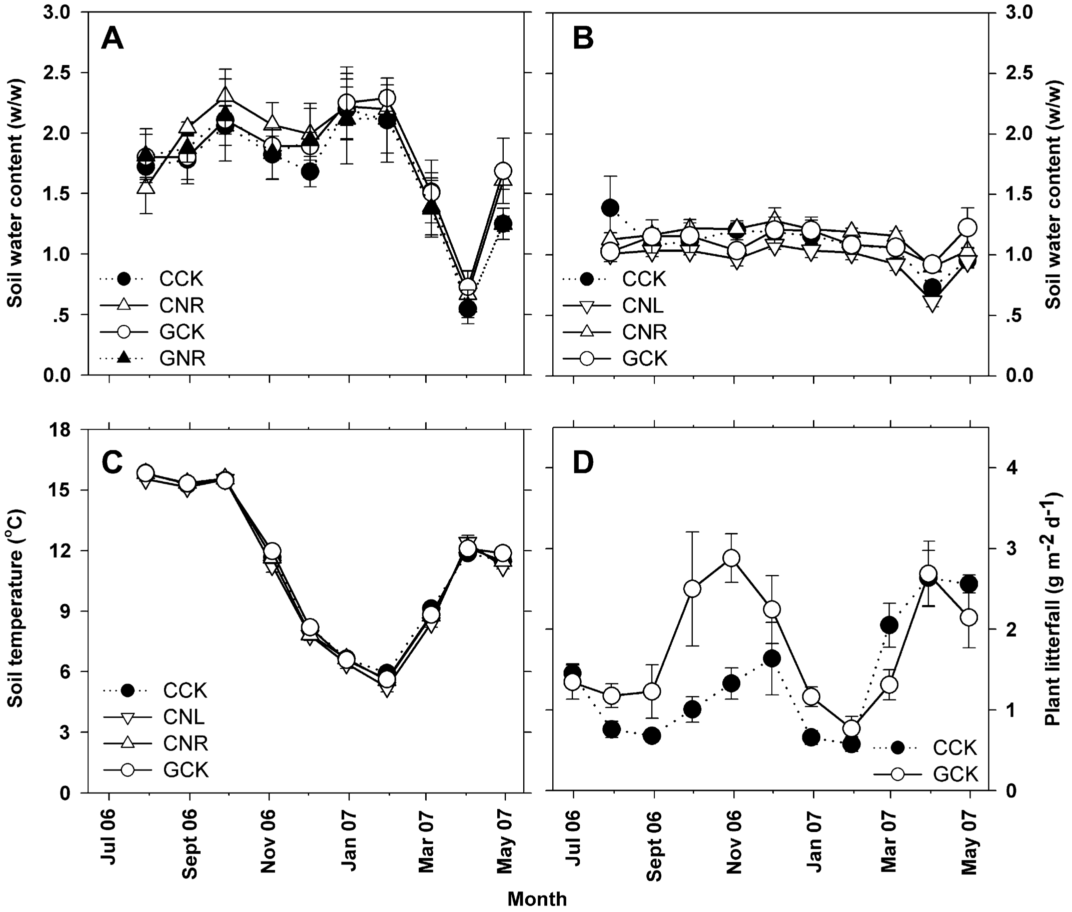

Fig. 1. Soil gravimetric water content (w/w) in humus layer (A) and 0–10 cm mineral soil (B), soil temperature (°C) (C) and plant litterfall (g m^{-2} d^{-1}) (D) in Ailao Mountains, southwest China from June 2006 through May 2007. CCK (control), CNL (control, litter removal), CNR (control, root trenching), GCK (girdling) and GNR (girdling, root trenching). Values are means ± SE, each with four replicates.

Table 1
Analyses of split-plot design for soil microbial C (mg C g^{-1}) and mean soil water content (w/w) and soil temperature (°C) in humus and 0–10 cm mineral soil layers of a subtropical monsoon forest in Ailao Moutains, southwest China, from July 2006 through April 2007.

Effect	Soil microbial C		Mean soil water content		Mean soil temperature
	Humus	Soil	Humus	Soil	Soil
GRL	**0.029***	0.526	0.936	0.774	**0.008***
LTR	–	**0.028***	–	**0.003***	**0.023***
GRL × LTR	–	**0.023***	–	0.475	0.261
TRN	**0.001***	0.517	0.887	0.531	0.417
GRL × TRN	**<.0001***	0.070	0.469	0.920	0.111
LTR × TRN	–	0.108	–	0.775	0.686
GRL × LTR × TRN	–	0.625	–	0.643	0.822
MON	**<.0001***	**<.0001***	–	–	–
GRL × MON	0.262	**0.038***	–	–	–
LTR × MON	–	0.416	–	–	–
GRL × LTR × MON	–	0.214	–	–	–
TRN × MON	0.750	0.318	–	–	–
GRL × TRN × MON	0.878	0.313	–	–	–
LTR × TRN × MON	–	0.468	–	–	–
GRL × LTR × TRN × MON	–	0.992	–	–	–

GRL: stem girdling; LTR: litter removal; TRN: root trenching; MON: months. $^*P < \mathbf{0.05}$.

litter-removal treatments on soil microbial C ($P = 0.023$). Neither root trenching nor stem girdling had significant effects on soil microbial C (Fig. 2; Table 1).

3.3. Correlations between soil microbial C and litterfall

There were no significant correlations between microbial C of humus layer and litterfall occurring in the preceding month, the current month or in the following month in CCK plots. In GCK plots, soil microbial C of humus layer was positively correlated with plant litterfall in the month prior to its sampling time (Table 3). There was a significant positive correlation between mineral soil microbial C and subsequent-month transformed litterfall in CCK plots, but these correlations were absent in CNL, CNR and GCK plots (Table 3). Due to the nature of inverse square root transformation, these positive correlations indicate that microbial biomass C was low the month before high litterfall, and vice versa.

4. Discussion

4.1. Seasonal variations of soil microbial C

Microbial biomass C in the humus layer did not vary significantly except for the lowest value in November 2006 (1.18 mg C g^{-1}). The minimal soil microbial C in November 2006 was probably the result of high water input 5 days before the sampling. This 86.0 mm throughfall and subsequent drying might accelerate CO_2 release from soil (Mariko et al., 2007). Otherwise, the dynamics of microbial biomass C in humus layer were not correlated with soil temperature or soil water content (Table 2). The absence of correlations between microbial biomass C and soil temperature and water content indicates that environmental factors did not influence the seasonal variation of microbial biomass C in humus layer.

Table 2
Correlations of soil microbial C (mg C g^{-1}) in humus and the mineral soil layers with soil water content (w/w) and soil temperature (°C) of a subtropical monsoon forest in Ailao Mountains, southwest China, from July 2006 through April 2007.

Treatments	Soil temperature		Soil water content	
	Humus	Soil	Humus	Soil
CCK	−0.039 NS	**0.392***	−0.003 NS	**0.571***
CNL	–	**0.360***	–	**0.460***
CNR	−0.021 NS	**0.343***	0.073 NS	0.210 NS
GCK	0.135 NS	**0.462***	**0.323***	**0.331***

CCK: the control plots; CNL: the litter-removal plots; CNR: the root-trenching plots; GCK: the girdling plots. NS: $P > 0.05$, $^*P < \mathbf{0.05}$.

Mineral soil microbial C generally decreased throughout the study period (Fig. 2), from the growing season (July–October) through the dormant season (November–April). The seasonality of mineral soil microbial C varies with environmental factors and tree physiology (Myers et al., 2001). In the growing season, plant roots provided labile organic carbon for soil microbes through root exudation. At that time soil temperature and water content should not limit microbial activity. There were significant correlations between mineral soil microbial C and soil temperature in CCK, CNL, CNR and GCK plots. Mineral soil microbial C also correlated with soil water content in CCK, CNL and GCK plots, but not in CNR plots (Table 2). These results demonstrate that soil temperature was an important factor regulating the seasonal variations of mineral soil microbial C. The weak correlations between mineral soil microbial C and soil water content in CNR plots confirmed that soil water content did not affect soil microbial populations where soil water content remained high in this forest.

The correlations between soil microbial C and soil temperature and water content differed between the humus layer and the mineral soil layer. Soil water content was higher and more variable in humus layer than in the mineral soil. The carbon manipulations of root trenching and girdling had larger effects on microbial biomass C in humus layer than in the mineral soil (Table 1). Among the factors associated with soil microbial C, carbon inputs were the primary factors regulating seasonal variation of microbial biomass C in humus layer in this study.

4.2. The influence of aboveground plant litter inputs

Litter removal significantly influenced mineral soil microbial C ($P = 0.028$). Mineral soil microbial C was lower in CNL plots than in CCK plots except for 2 months at the end of the experiment (Fig. 2B). In these treatments, we removed not only fresh plant litter but also old organic layers developed over years or decades. The removal of these organic layers could substantially reduce the labile carbon (Lajtha et al., 2005) available in the mineral soil layer for microorganisms. Much lower mineral soil microbial C in CNL plots than in CCK plots confirms that the humus layer is an important C source for soil microbes. This result was inconsistent with the observed small influence of chronic aboveground C input on microbial biomass C (Brant et al., 2006). However, mineral soil microbial C was only slightly lower in GNL plots than in GCK plots. Subke et al. (2004) also observed that litter removal caused less decrease in microbial

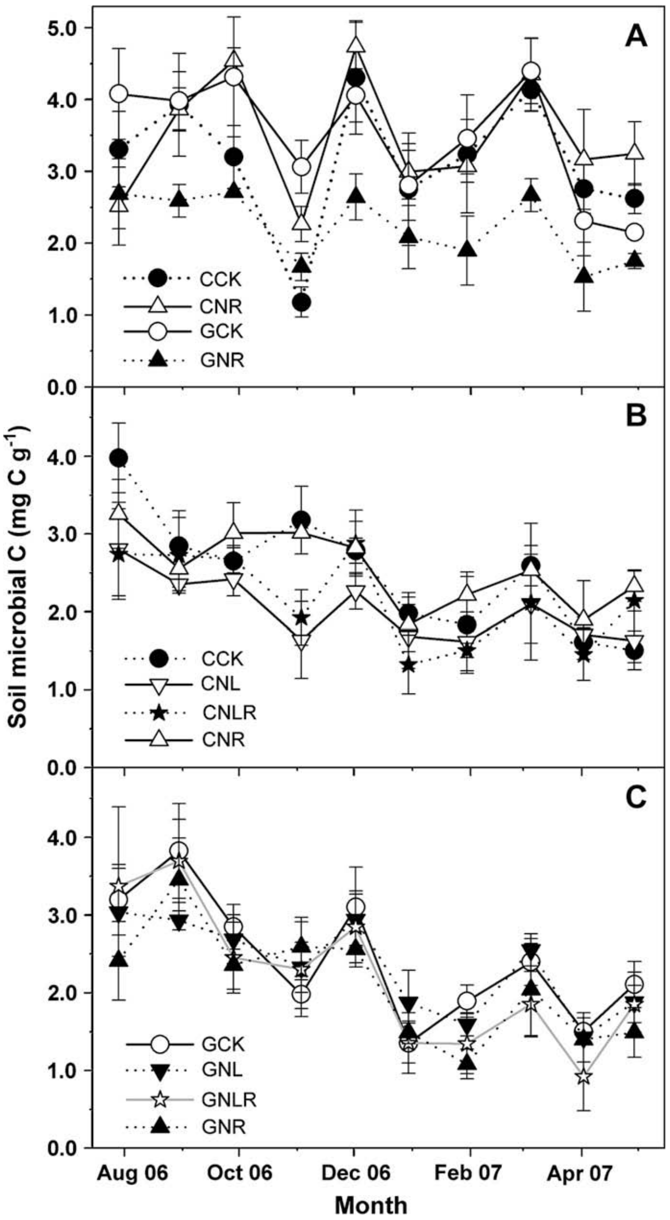

Fig. 2. Soil microbial C (mg C g^{-1}) in humus (A) and 0–10 cm mineral soil layers (B, C) in Ailao Mountains, southwest China from July 2006 through April 2007. CCK (control), CNL (control, litter removal), CNLR (control, litter removal plus root trenching), CNR (control, root trenching), GCK (girdling), GNL (girdling, litter removal), GNLR (girdling, litter removal plus root trenching) and GNR (girdling, root trenching). Values are means ± SE, each with four replicates.

biomass C of the humus layer in girdled plots than in ungirdled plots. Examination of microbial community changes in this experiment would be very useful. Our results showed that the interactions between litter removal and girdling influenced mineral soil microbial C ($P = 0.023$). Removal of the entire forest floor also altered microclimatic conditions. Litter removal reduced soil water content significantly (Table 1) and decreased soil temperature slightly (Fig. 1C). Mineral soil microbial C varied with both soil temperature and soil water content (Table 2).

4.3. The influence of belowground carbon inputs

Microbial biomass C in humus layer was higher in CNR and GCK plots than in CCK plots (Fig. 2A). In CNR plots, most of the labile organic carbon had already been released from root debris since this study began two and a half years after the initiation of treatments. Root trenching probably shifted the soil microbial community towards species tending to utilize recalcitrant carbon. Brant et al. (2006) demonstrated that after root trenching, coniferous forest plots contained larger quantities of actinomycete biomarkers, which have been associated with the degradation of more recalcitrant C compounds (McCarthy and Williams, 1992). Soil microbial C was much lower in GNR plots than in CCK plots. Stem girdling increased plant litterfall during the study period (Fig. 1D). Increased soil microbial activity and biomass were observed with plant litter addition in tropical forests (Sayer et al., 2007). However, the litterfall addition in root-trenching (GNR) plots did not increase microbial biomass C in the humus layer. The additional plant litterfall also could increase the populations of soil mesofauna (Briones et al., 1997), reducing microbial populations in root-trenching plots and/or accelerating the mineralization of soil organic matter. The higher microbial biomass C in humus layer in GCK plots was probably due to more plant litterfall input, even though the termination of carbohydrate supply from shoots reduced organic carbon for soil microbes. In a boreal Scots pine forest, carbon storage in stems was found to provide carbon for soil microbes after the initiation of girdling (Bhupinderpal-Singh et al., 2003). Tree mortality in this study suggested the depletion of carbon stored in stems and roots, and soil microbial C would decrease as a result.

Table 3
Correlations between plant litterfall (mg m^{-2} d^{-1}) and soil microbial C (mg C g^{-1}) in humus and 0–10 cm the mineral soil layers of a subtropical monsoon forest in Ailao Mountains, southwest China, from July 2006 through April 2007.

Treatments	LFB1	LFS	LFA1
Humus			
CCK	0.123 NS	0.016 NS	0.132 NS
CNR	0.169 NS	−0.072 NS	−0.001 NS
GCK	**0.407***	0.137 NS	−0.0179 NS
Soil			
CCK	0.176 NS	0.263 NS	**0.375***
CNL	0.025 NS	0.193 NS	0.297 NS
CNR	0.043 NS	0.168 NS	0.179 NS
GCK	0.070 NS	0.055 NS	−0.026 NS

LF: plant litterfall; B1: litterfall collected during the month prior to the measurement of soil microbial C; S: litterfall collected during the same month as the measurement of soil microbial C; A1: litterfall collected in the following month. CCK: the control plots; CNL: the litter-removal plots; CNR: the root-trenching plots; GCK: the girdling plots. NS: $P > 0.05$, $^*P < \mathbf{0.05}$.

Root trenching and girdling insignificantly decreased mineral soil microbial C (Table 1). Root trenching did not reduce the mineral soil microbial C substantially ($P = 0.517$). The microbial communities in CNR plots might be affected by reduced quality of organic carbon there. Soil labile carbon in root-trenching plots was likely to be depleted rapidly. In stem-girdled plots, tree mortality indicated the depletion of carbon storage in organs below tree girdles, which would subsequently reduce mineral soil microbial C. On the other hand, the girdling treatment led to higher plant litterfall during the study period, particularly in the wet season from July 2006 through November 2006 (Fig. 1D). The leachates and products of decomposition due to litter addition would transport more dissolved organic carbon to the mineral soil. In this subtropical forest, girdling did not reduce soil microbial C as much as it did in a boreal forest (Högberg and Högberg, 2002).

4.4. The correlations between plant litterfall and microbial biomass C

There were no significant correlations between microbial biomass C in humus layer and litterfall in the following month to microbial biomass C measurement in CCK, CNR and GCK plots

(Table 3). This suggests that carbohydrates retranslocated to roots had no significant influence on microbial biomass C in humus layer, or that organic layers provided adequate labile organic carbon for microbial growth. In GCK plots, low microbial biomass C in the humus layer appeared the month before high aboveground litterfall. The retranslocation of carbohydrates occurs before plant litterfall (Lal et al., 2001). Girdling prevented the transport of carbohydrates to roots, and tree mortality in stem-girdled plots indicated less labile organic carbon storage in organs below the girdles.

There were no significant correlations between mineral soil microbial C and plant litterfall in the preceding month in either CCK plots or CNL plots (Table 3). Apparently fresh plant litter by itself does not greatly affect mineral soil microbial C. This suggests that organic layers possibly provided adequate labile organic carbon for microbial growth, or that most of labile organic carbon derived from fresh plant litter might be consumed before their arrival to the mineral soil (Lajtha et al., 2005). Mineral soil microbial C correlated with plant litterfall in the following month only in CCK plots (Table 3). This may be explained by carbon allocated to belowground before trees shed their leaves. Olsrud and Christensen (2004) observed that increased belowground carbon allocation increased root exudation in subarctic tundra. The absence of correlations in CNR and GCK plots suggests that excluding the belowground flow of carbon from canopy to roots influences mineral soil microbial C. However, we did not detect the significant correlation of mineral microbial C with subsequent-month plant litterfall in CNL plots. Since litter-removal treatment also excluded the humus layers and plant roots existing there, carbohydrates transferred to belowground in CNL plots were probably less than in CCK plots.

In this forest, microbial biomass C in the humus layer was more affected by belowground carbon fluxes than by environmental factors. Mineral microbial biomass C was influenced by soil organic matter and carbohydrates retranslocated to roots, and also by soil temperature and moisture.

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References

Bohlen, P.J., Groffman, P.M., Driscoll, C.T., Fahey, T.J., Siccama, T.G., 2001. Plant–soil–microbial interactions in a northern hardwood forest. Ecology 82, 965–978.

Brant, J.B., Myrold, D.D., Sulzman, E.W., 2006. Root controls on soil microbial community structure in forest soils. Oecologia 148, 650–659.

Briones, M.J.I., Ineson, P., Piearce, T.G., 1997. Effects of climate change on soil fauna; responses of enchytraeids, Diptera larvae and tardigrades in a transplant experiment. Applied Soil Ecology 6, 117–134.

Bhupinderpal-Singh, Nordgren, A., Ottosson-Löfvenius, M., Högberg, M.N., Mellander, P.-E., Högberg, P., 2003. Tree root and soil heterotrophic respiration as revealed by girdling of boreal Scots pine forest: extending observations beyond the first year. Plant, Cell & Environment 26, 1287–1296.

Chan, O., Yang, X., Fu, Y., Feng, Z., Sha, L., Casper, P., Zou, X., 2006. 16S rRNA gene analyses of bacterial community structures in the soils of evergreen broad-leaved forests in south-west China. FEMS Microbiology Ecology 58, 247–259.

Devi, N.B., Yadava, P.S., 2006. Seasonal dynamics in soil microbial biomass C, N and P in a mixed-oak forest ecosystem of Manipur, North-east India. Applied Soil Ecology 31, 220–227.

Fisk, M.C., Fahey, T.J., 2001. Microbial biomass and nitrogen cycling responses to fertilization and litter removal in young northern hardwood forests. Biogeochemistry 53, 201–223.

Garcia-Oliva, F., Sveshtarova, B., Oliva, M., 2003. Seasonal effects on soil organic carbon dynamics in a tropical deciduous forest ecosystem in western Mexico. Journal of Tropical Ecology 19, 179–188.

Gottlicher, S.G., Steinmann, K., Betson, N.R., Högberg, P., 2006. The dependence of soil microbial activity on recent photosynthate from trees. Plant and Soil 287, 85–94.

Hart, S.C., Sollins, P., 1998. Soil carbon and nitrogen pools and processes in an old-growth conifer forest 13 years after trenching. Canadian Journal of Forest Research 28, 1261–1265.

Högberg, M.N., Högberg, P., 2002. Extramatrical ectomycorrhizal mycelium contributes one-third of microbial biomass and produces, together with associated roots, half the dissolved organic carbon in a forest soil. New Phytologist 154, 791–795.

Högberg, P., Nordgren, A., Buchmann, N., Taylor, A.F.S., Ekblad, A., Högberg, M.N., Nyberg, G., Ottosson-Löfvenius, M., Read, D.J., 2001. Large-scale forest girdling shows that current photosynthesis drives soil respiration. Nature 411, 789–791.

Hütsch, B.W., Augustin, J., Merbach, W., 2002. Plant rhizodeposition – an important source for carbon turnover in soils. Journal of Plant Nutrition and Soil Science 165, 397–407.

Jenkinson, D.A., Powlson, D.S., 1976. The effects of biocidal treatment on metabolism in soil – V. A method for measuring soil biomass. Soil Biology & Biochemistry 8, 209–213.

Lal, C.B., Annapurna, C., Raghubanshi, A.S., Singh, J.S., 2001. Effect of leaf habit and soil type on nutrient resportion and conservation in woody species of a dry tropical environment. Canadian Journal of Botany 79, 1066–1075.

Lajtha, K., Crow, S.E., Yano, Y., Kaushal, S.S., Sulzman, E., Sollins, P., Spears, J.D.H., 2005. Detrital controls on soil solution N and dissolved organic matter in soils: a field experiment. Biogeochemistry 76, 261–281.

Li, H., 1983. Ecological Characteristics of Vegetation in Xujiaba Region of Ailao Mts. Research of Forest Ecosystem on Ailao Mountains, Yunnan. Yunnan Science and Technology Press, Kunming, China, pp. 63–73.

Li, Y., Xu, M., Zou, X., Xia, Y., 2005. Soil CO_2 efflux and fungal and bacterial biomass in a plantation and a secondary forest in wet tropics in Puerto Rico. Plant and Soil 268, 151–160.

Li, Y., Xu, M., Sun, O., Cui, W., 2004. Effects of root and litter exclusion on soil CO_2 efflux and microbial biomass in wet tropical forests. Soil Biology & Biochemistry 36, 2111–2114.

Liu, Z., Zou, X., 2002. Exotic earthworms accelerate plant litter decomposition in a Puerto Rican pasture and wet forest. Ecological Applications 12, 1406–1417.

Maithani, K., Tripathi, R.S., Arunachalam, A., Pandey, H.N., 1996. Seasonal dynamics of microbial biomass C, N and P during regrowth of a disturbed subtropical humid forest in north-east India. Applied Soil Ecology 4, 31–37.

Mariko, S., Urano, T., Asanuma, J., 2007. Effects of irrigation on CO_2 and CH_4 fluxes from Mongolian steppe soil. Journal of Hydrology 333, 118–123.

McCarthy, A.J., Williams, S.T., 1992. Actinomycetes as agents of biodegradation in the environment – a review. Gene 115, 189–192.

Myers, R.T., Zak, D.R., White, D.C., Peacock, A., 2001. Landscape-level patterns of microbial community composition and substrate use in upland forest ecosystems. Soil Science Society of America Journal 65, 359–367.

Olsrud, M., Christensen, T.R., 2004. Carbon cycling in subarctic tundra: seasonal variation in ecosystem partitioning based on in situ ^{14}C pulse-labeling. Soil Biology & Biochemistry 36, 245–253.

Ruan, H., Zou, X., Scatena, F., Zimmerman, J., 2004. Asynchronous fluctuations of soil microbial biomass and plant litterfall in a tropical wet forest. Plant and Soil 260, 147–154.

SAS, 1999. SAS Institute Inc., SAS Campus Drive, Cary, North Carolina 27513, USA.

Sayer, E.J., Powers, J.S., Tanner, E.V.J., 2007. Increased litterfall in tropical forests boosts the transfer of soil CO_2 to the atmosphere. PLoS ONE 2, e1299.

Subke, J.A., Hahn, V., Battipaglia, G., Linder, S., Buchmann, N., Cotrufo, M.F., 2004. Feedback interactions between needle litter decomposition and rhizosphere activity. Oecologia 139, 551–559.

Wardle, D.A., 1992. A comparative assessment of factors which influence microbial biomass carbon and nitrogen levels in soil. Biology Reviews 67, 321–358.

Zak, D.R., Tilman, D., Parmenter, R.R., Rice, C.W., Fisher, F.M., Vose, J., Milchunas, D., Martin, C.W., 1994. Plant production and soil microorganisms in late-successional ecosystems – a continental-scale study. Ecology 75, 2333–2347.

Zhang, K., 1983. The Characteristics of Mountain Climate in the North of Ailao Mts. Research of Forest Ecosystem on Ailao Mountains, Yunnan. Yunnan Science and Technology Press, Kunming, China, pp. 20–29.