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ORIGINAL PAPER

Soil mono- and disaccharides and amino acids as influenced by plant litter and root processes in a subtropical moist forest of southwest China

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Abstract Soil mono- and disaccharides (SS) and total free amino acids (AA) can influence soil microbial activities, whether they are derived from decomposition of organic materials or from plant root exudates. To quantify the relative importance of aboveground plant litter input and belowground inputs of root exudates and root debris on SS and AA, we conducted litter removal, root trenching and tree girdling experiments in a subtropical moist forest of southwest China. We found that concentrations of SS and AA had pronounced seasonal fluctuations. Litter removal markedly reduced SS concentrations, but it had no effect on AA concentrations. Concentrations of SS were significantly correlated with litterfall that had occurred 2 months earlier in the control plots, but that correlation was not observed in the litter removal plots. Multiple-linear regressions of soil respiration and soil temperature on AA concentrations were significant in both control and litter removal plots, but not in the root trenching or tree girdling plots. These results suggest that SS levels are likely to be regulated by aboveground plant litter input, and concentrations of AA are affected by microbial activity that fluctuates with soil temperature and belowground carbon input.

Keywords Girdling · Litterfall removal · Root trenching · Soil respiration · Sugars

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Introduction

Ecosystem productivity and the allocation of above- and belowground carbon can be altered under global climate change (Norby et al. 2001; Pregitzer et al. 2000). Such carbon allocation changes may affect the quantity and quality of carbon transferred to soils, which may be observed in the concentrations of soil mono- and disaccharides (SS) and total free amino acids (AA). Leachates and decomposition of aboveground plant litter, as well as root exudates and products of root decomposition supply labile carbon and nitrogen for soil microbes. Labile carbon and nitrogen derived from aboveground plant litter can support a pulse of microbial growth and respiration during the period of high litterfall (Chapin et al. 2002). Dissolved organic carbon can also affect soil microbial activity (Montaño et al. 2007). It is estimated that approximately 5–10% of the net fixed C is exuded from roots (Farrar et al. 2003; Jones et al. 2004). Root exudates are dominated by low molecular weight organic compounds (LMWOCs) such as sugars (e.g. monosaccharides and disaccharides), organic acids and amino acids (Jones 1998). Such compounds are readily available substrates for soil microorganisms (Hütsch et al. 2002; Kraffczyk et al. 1984). Zhang et al. (2006) found that about 90% of soluble sugars from fine roots and more than 50% from coarse and intermediate roots were lost during the first month of root decomposition.

Lipson and Näsholm (2001) found that the hydrolysis of proteins and peptides by extracellular enzymes was a reliable source of amino acids. The rate of proteolysis depends on diverse factors, such as the availability of protein substrates from aboveground plant litter and belowground root inputs, seasonal changes of soil temperature and water content (Lipson and Monson 1998; Lipson et al. 1999), and the amount and variety of proteolytic enzymes produced by the microbial community. Increased soil amino acids concentrations have also been observed after drying–rewetting events (Lipson and Monson 1998).

The relationships between LMWOCs, soil microbial activity, and aboveground and belowground substrate availability are complex. In particular, labile C availability was generally thought to be the major factor constraining soil microbial activity due to the heterotrophic nature of microbial decomposition (Foster et al. 1980; McGill et al. 1986). Sugars and amino acids from root exudates are readily used by rhizospheric microorganisms for growth. Increased microbial activity could keep LMWOCs low; conversely it may accelerate litter decomposition rate and thereby release more labile organic carbon and nitrogen.

However, there are few investigations on how levels of soil LMWOCs are altered by aboveground plant litter input, belowground root debris and exudates, and plant uptake of water and nutrients (Sulzman et al. 2005; Kalbitz et al. 2007). We conducted a field experiment with litter removal (Ruan et al. 2004), root trenching (Li et al. 2005), and tree girdling (Högberg et al. 2001) treatments to examine the effects of aboveground litterfall, belowground root debris, and exudates on SS and AA concentrations in a subtropical moist forest of southwest China. We addressed the following questions: (1) What were the seasonal patterns of surface soil SS and AA concentrations in the subtropical moist forest of southwest China? (2) What were the effects of aboveground input of plant litter, belowground input of root debris and exudates, and plant uptake of water and nutrients on SS and AA concentrations? (3) What were the relationships between soil microbial activity and SS and AA concentrations with the altered above- and belowground processes?

Materials and methods

Study sites

The study was conducted in a subtropical moist forest located at Xujiaba in the Ailao Mountains National Nature Reserve of southwest China. The experimental sites were about 2 km north of the Ailao Field Station for Forest Ecosystem Studies (24°32′ N, 101°01′ E), at an elevation of 2,476 m. Mean monthly temperature varies between 5.4 and 23.5°C, and mean annual precipitation is 1,840 mm. This region has a monsoonal climate with strongly seasonal precipitation. The wet season is from May through October, and the dry season from November through April. Surface soils (0–10 cm) of the area are Alfisols with pH of 4.2 (water). The organic horizon is of 3–7 cm depth (Liu et al. 2002). The forest is dominated by *Lithocarpus chintungensis*, *Rhododendron leptothrium*, *Vaccinium ducluoxii*, *Lithocarpus xylocarpus*, *Castanopsis wattii*, *Schima noronhae*, *Hartia sinensis*, and *Manglietia insignsis* (Wu et al. 1983). Tree density in the experimental plots was 2,738 stems ha^{-1} and median diameter at breast height was 9.5 cm, ranging from 1.3 to 59.7 cm (Z. Feng, unpublished data).

Experimental design

We employed a split-plot design with four block replicates. Within each block, there were two 20 × 20 m plots; one was randomly chosen as the control treatment (plots 2, 3, 6, and 7; Fig. 1) and the other for girdling treatment (plots 1, 4, 5, and 8; Fig. 1). In each plot, there were four 2 × 3 m subplots randomly assigned as control, litter removal,

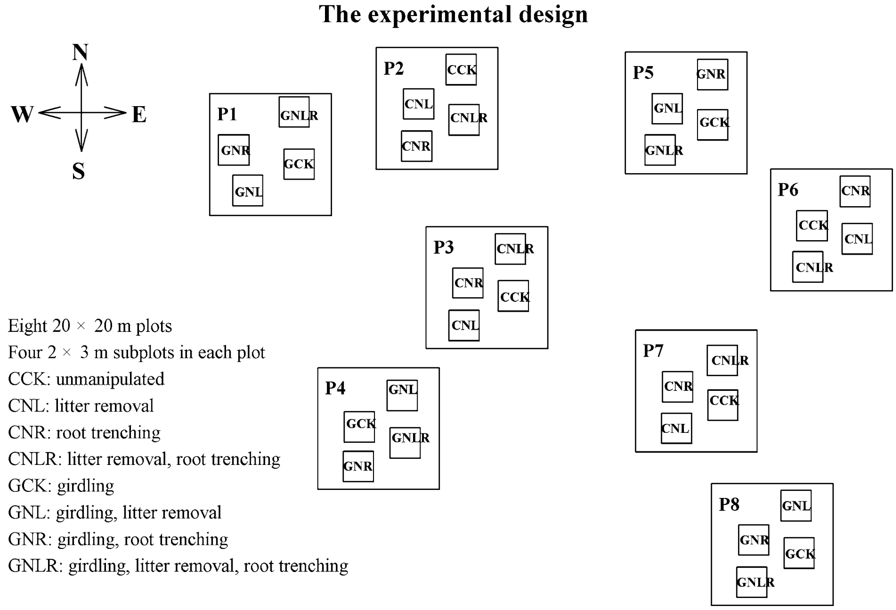

Fig. 1 The experimental design in a subtropical moist forest of southwest China

root trenching, and litter removal plus root trenching, resulting in eight combinations with different treatments: CCK (unmanipulated), CNL (control, litter removal), CNR (control, root trenching), CNLR (control, litter removal plus root trenching), GCK (girdling, control), GNL (girdling, litter removal), GNR (girdling, root trenching), and GNLR (girdling, litter removal plus root trenching). All the 32 subplots were positioned to avoid woody stems. In subplots without plant litter, these inputs were prevented by 1-m-high wooden structures covered with 1 mm mesh fiberglass screens (Ruan et al. 2004), and organic materials above the mineral soil were removed. We trenched the perimeters of all the 20 × 20 m plots to 40 cm and inserted plastic sheets to prevent ingrowth of external roots (Li et al. 2005). The perimeters of the trenched subplots were treated in the same manner. In the girdled plots, a 5-cm width band was peeled down to the xylem on all trees (>2 cm in diameter) at breast height. The girdling treatment was intended to terminate phloem transport of photosynthates from the canopy to roots, but to allow root uptake and xylem transport of water and nutrients before trees eventually die (Högberg et al. 2001). Root trenching prevents carbohydrate transfer from shoots to soils and also plant uptake of water and nutrients. All the treatments were carried out in early February, 2004.

Field sampling and laboratory analyses

Soil samples were collected bimonthly from October 2004 to August 2005. Two soil cores (50.5 mm diameter) from each subplot were randomly selected and collected to a depth of 100 mm from the mineral soil horizon and bulked into a composite sample. Soil samples were transported to the laboratory within 24 h at ambient temperatures. There the soil samples were sieved through 2 mm mesh stainless steel screens. From each composite, a subsample of 15–20 g was oven dried at 105°C for 24 h for soil water content. Soil temperature was measured at 5 cm below the mineral soil surface with a data logger.

Sugars and amino acids were determined by shaking 30 g of the sieved field-moist soil with 150 ml distilled water in polypropylene bottles on a reciprocating shaker (120 rev min^{-1}) for 30 min. The extracts were passed through a glass-fiber filter (5–15 μm) and the filtrates were frozen at −18°C until analysis within two weeks. All soil samples are extracted within 24 h of reaching the laboratory. Filtrate pH values were adjusted to 2–3 with HCl and NaOH. Ion exchange resins (Dowex-50) were used to separate neutral sugars and amino acids with methods described by Kraffczyk et al. (1984) and Zhao and Zheng (1996).

The amino acids fraction was treated with 0.10 ml of 10 M NaOH to dispel NH_4^+ and condensed in a water bath (80°C) to 2–3 ml. The condensed amino acids were transferred to 50-ml colorimetric cylinders and mixed with Na_2HPO_4–KH_2PO_4 buffer solution of pH 6.0 with 0.10 ml 0.3% ascorbic acid and 1.00 ml 2% (w/v) ninhydrin and placed in the water bath (100°C) for color development. After 20 min, the colorimetric cylinders were cooled to room temperature. The solutions were diluted to 50 ml with distilled water and thoroughly mixed. Absorbance was measured at 570 nm against a reagent blank. Concentrations of AA were determined by comparing the optical absorbance with the standard curve for glycine (Yang and Na 1989). The sugar fraction was transferred to 50 ml colorimetric cylinders, mixed with 3.00 ml dinitrosalicylate reagent and placed in a water bath (100°C) for color development. After 10 min, the colorimetric cylinders were cooled to room temperature. The solutions were brought to 50 ml volume with distilled water and thoroughly mixed. Absorbance was measured at 540 nm against a reagent blank. The SS concentrations were determined by comparing the optical absorbance with the standard curve for glucose (Lindsay 1973). All the samples were analyzed in duplicate.

Soil respiration was measured concurrently with soil sampling every 2 months from October 2004 to August 2005, using the alkali trap method (Li et al. 2005). Plant litterfall was collected at the end of each month during the experiment. Litterfall was collected from seven traps (0.25 m^2 each) placed randomly in each 20 × 20 m plot from August 2004 to October 2005. All litter samples were oven dried to constant weights at 80°C.

Statistical analyses

All data were tested for normality using Komologov–Smirnov and transformed if necessary. We used One-way ANOVA to examine the seasonal variation of aboveground litterfall. The repeated measures analysis of Proc Mixed model (SAS 1999) was used to test the effects of litter removal, root trenching, girdling, and months on SS and AA concentrations, soil respiration, soil water content, and temperature. In the multiple linear regression equations, all the variables were transformed using Standardized Transform (SYSTAT Software Inc. 2004) and the coefficients for soil respiration and soil temperature indicated their contributions to the variations in SS and AA concentrations. Statistical differences among the coefficients were determined with *t*-tests. The data transformation and the regression analyses were conducted with SigmaStat (SYSTAT Software Inc. 2004). Correlation analyses were performed between SS concentrations and monthly aboveground litterfall with all possible monthly time-lag intervals between the litter collection and soil sample collection dates. All significance levels were set at alpha = 0.05.

Results

Seasonal variations

There were pronounced seasonal variations (Table 1 and Fig 2) in soil water content ($P = 0.004$), temperature ($P < 0.0001$), and plant litterfall ($P < 0.001$). Soil water content and soil temperature reached the lowest values in April 2005 (69.7%) and December 2004 (4.9°C), respectively, and then increased afterwards (Fig. 2a, b). Plant litterfall decreased slowly from August 2004 to January 2005, and high values were present from February 2005 through June 2005 (Fig. 2c). The interactions of litter removal, root trenching, and girdling did not have significant effects on soil water content or temperature (Table 1). For clarity, soil water and temperature from only the single- treatment plots (CCK, CNL, CNR, and GCK) are presented in Fig. 2.

Concentrations of SS, AA, and soil respiration also showed pronounced seasonality (Table 1). In CCK plots, SS concentrations (Fig. 3) reached the lowest value in October 2004 (3.61 ± 0.11 μg C g^{-1}) and then increased until June 2005 (9.09 ± 1.90 μg C g^{-1}). The highest AA concentrations in CCK plots appeared in October 2004 (0.60 ± 0.02 μg N g^{-1}), then they decreased until February 2005 (0.27 ± 0.07 μg N g^{-1}), followed by an increase (Fig. 4). Soil respiration in CCK plots (Fig. 5) decreased until February 2005 (1.26 ± 0.25 g CO_2 m^{-2} day^{-1}) and then rose steadily, peaking in August 2005 (4.23 ± 0.67 g CO_2 m^{-2} day^{-1}).

Effects of plant litter removal, root trenching and tree girdling

Soil water content in CCK plots was lower than in CNR plots, but higher than in CNL plots. Girdling had

Table 1 The effects of litter removal, root trenching, girdling, and months on SS (μg C g^{-1}), AA (μg N g^{-1}), soil respiration (g CO_2 m^{-2} day^{-1}), soil water content (w/w), and temperature (°C) by using the procedure mixed model in a subtropical moist forest of southwest China from October 2004 through August 2005

Treatments	SS	AA	Soil respiration	Soil water content	Soil temperature
GRL	0.860	0.762	0.012*	0.146	0.692
LTR	0.006*	0.126	<0.0001*	0.981	0.826
TRN	0.669	0.899	0.399	0.011*	0.032*
GRL × LTR	0.759	0.979	0.522	0.247	0.053
GRL × TRN	0.997	0.056	0.481	0.280	0.929
LTR × TRN	0.049*	0.997	0.411	0.217	0.882
GRL × LTR × TRN	0.110	0.099	0.775	0.499	0.055
Mon	<.0001*	0.043*	<0.0001*	0.004*	<0.0001*
GRL × Mon	0.652	0.078	0.091	0.169	0.029*
LTR × Mon	0.691	0.163	0.001*	0.130	0.051
TRN × Mon	0.868	0.066	0.808	0.116	0.254
GRL × LTR × Mon	0.804	0.052	0.967	0.087	0.246
GRL × TRN × Mon	0.624	0.206	0.237	0.094	0.067
LTR × TRN × Mon	0.706	0.072	0.852	0.066	0.089
GRL × LTR × TRN × Mon	0.857	0.185	0.853	0.125	0.175

LTR, litter removal treatment; GRL, tree girdling treatment; TRN, root trenching treatment; Mon, months. * Significant effects (alpha = 0.05)

no significant effect on soil water content (Fig. 2a). Only root trenching treatments had significant effects on soil water content ($P = 0.011$) and temperature ($P = 0.032$).

Litter removal significantly reduced SS concentrations (Table 1), especially during the growing season from April through August. In April, June, and August 2005, the difference of SS concentrations between CCK and CNL plots were 28.5%, 38.8%, and 17.0%, while between GCK and GNL plots they were 54.6%, 66.4%, and 38.2%, respectively (Fig. 3). However, neither root trenching nor tree girdling had pronounced effects on SS concentrations (Fig. 3 and Table 1). Litter removal, root trenching, and girdling treatments did not significantly alter AA concentrations (Table 1). Litter removal ($P < 0.0001$), girdling ($P = 0.012$) and the interaction between litter removal and months ($P = 0.001$) significantly affected soil respiration (Table 1).

Simple sugar and amino acid correlations with litter, soil respiration, and temperature

Concentrations of SS were significantly correlated with litterfall that had occurred in the same month, one month, and two months earlier in CCK plots, but not in CNL plots (Table 2). These correlations were not significant for other lagged time intervals. In contrast, concentrations of AA showed significant multiple linear regressions with soil respiration and soil temperature in CCK and CNL plots, but not in CNR or GCK plots (Table 3). Soil respiration significantly correlated with AA concentrations in CCK, CNL, and CNR plots, but not in GCK plots. Correlations between soil temperature and AA concentrations were significant only in CCK and CNL plots (Table 3).

Discussion

Seasonal variations of mono- and disaccharides and amino acids

We observed a pronounced seasonality in SS concentrations (Table 1). Labile organic carbon derived from fresh plant litter and soil organic matter, as well as the seasonal variation of root-supplied carbon contributed to the temporal changes in SS levels. In CCK plots, SS concentrations had high values in the growing season (from April to August) with the highest in June 2005. Large inputs of plant litter from February to May would release labile organic carbon into soil during the growing season. At the same time, root exudates should increase with plant growth, contributing to elevated SS concentrations. During the growing season, root exudates are enhanced by cell division and elongation of root tips (Neumann

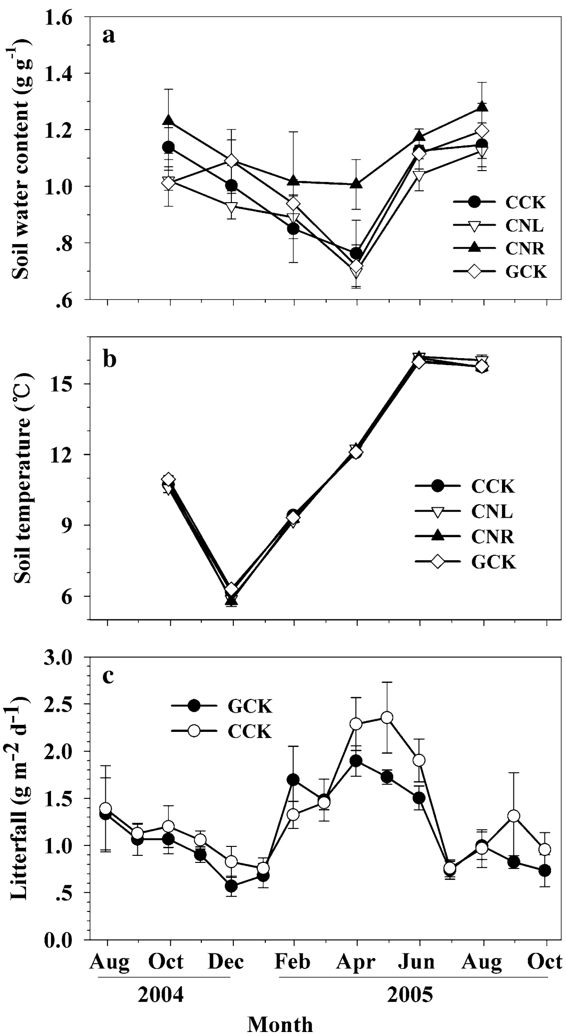

Fig. 2 Seasonal variations of (**a**) soil water content, (**b**) soil temperature, and (**c**) plant litterfall from August 2004 to October 2005 in a subtropical moist forest of southwest China. CCK (unmanipulated); CNL (control, litter removal); CNR (control, root trenching); GCK (girdling, control). Bars indicate means ± SE

and Römheld 2000). Guggenberger and Zech (1994) observed that carbohydrates were released preferentially into soil solution during the growing season through root exudates. The lowest SS concentrations occurred at the end of growing season—October, suggesting that seasonal pattern of plant root activity had an impact. Aboveground plant litterfall at that time is small in this evergreen forest. Moreover, low temperature and soil water contents were not optimal for litter decomposition. In April 2005, SS concentrations in plots with root trenching or girdling

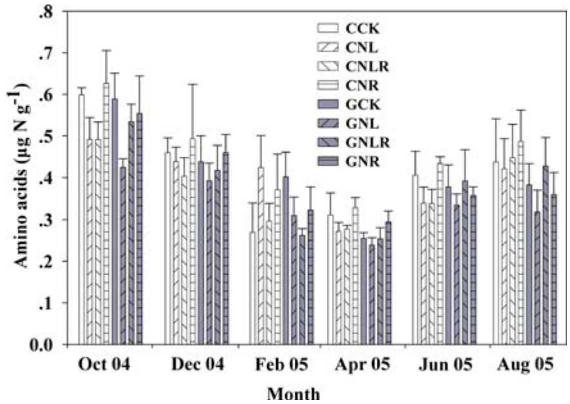

Fig. 3 Seasonal variation of SS concentrations from October 2004 to August 2005 in a subtropical moist forest of southwest China. CCK (unmanipulated); CNL (control, litter removal); CNLR (control, litter removal, root trenching); CNR (control, root trenching); GCK (girdling, control); GNL (girdling, litter removal); GNLR (girdling, litter removal, root trenching), and GNR (girdling, root trenching). LTR: litter removal; TRN: root trenching. Bars indicate means ± SE

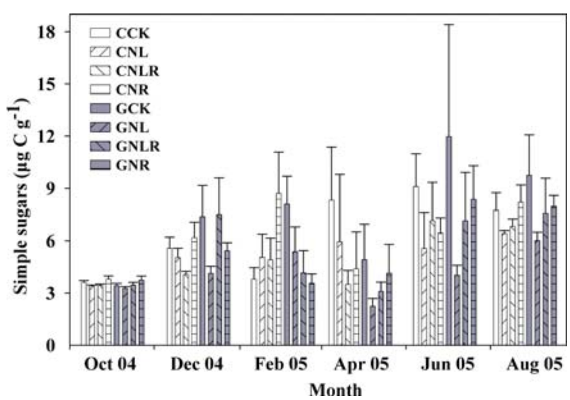

Fig. 4 Seasonal variation of AA concentrations from October 2004 to August 2005 in a subtropical moist forest of southwest China. CCK (unmanipulated); CNL (control, litter removal); CNLR (control, litter removal, root trenching); CNR (control, root trenching); GCK (girdling, control); GNL (girdling, litter removal); GNLR (girdling, litter removal, root trenching), and GNR (girdling, root trenching). LTR: litter removal; TRN: root trenching; GRL: tree girdling. Bars indicate means ± SE

treatments dropped rather than increased as in CCK plots (Fig. 3). This difference of SS concentrations in the beginning of growing season indicates belowground carbon inputs associated with plant phenology influence seasonal pattern of SS concentrations.

Concentrations of AA varied significantly during the study period (Table 1). Changes in soil microbial activity, nitrogen demand for plant growth, root

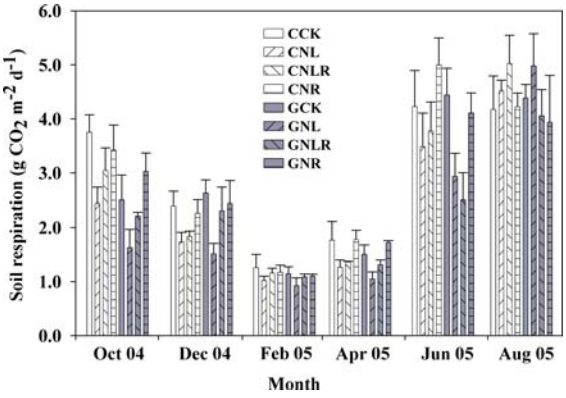

Fig. 5 Seasonal variation of soil respiration from October 2004 to August 2005 in a subtropical moist forest of southwest China. CCK (unmanipulated); CNL (control, litter removal); CNLR (control, litter removal, root trenching); CNR (control, root trenching); GCK (girdling, control); GNL (girdling, litter removal); GNLR (girdling, litter removal, root trenching), and GNR (girdling, root trenching). LTR: litter removal; GRL: tree girdling. Bars indicate means ± SE

exudates associated with plant growth, and the availability of proteinaceous substrates all might influence AA concentrations. In CCK plots, soil respiration and temperature significantly correlated with AA concentration (Table 3), which suggests that soil microbial activity controls the temporal changes of AA in this forest. In the dormant season, low soil temperature and water content may inhibit microbial production of amino acids, even though plant demand for amino acids was low at that time. In the growing season, soil microbial activity also increased along with soil temperature and water content. However, concentrations of AA were lower in August 2005 than those in October 2004. This might result from plant-growth demand for soil labile nitrogen (Jaeger et al. 1999). The seasonality of AA concentrations in other treatments were similar to the control (Fig. 4), so litter removal, root trenching, and girdling did not strongly affect AA concentrations. However, the lowest AA concentrations in other treatments occurred in April 2005, rather than February 2005 in the control. This is probably due to an unusual snowfall in February 2005. The drying–rewetting event should lyse soil microbial cells, leading to the increase in AA concentrations with elevated soil water content. Soil water content in February 2005

Table 2 Correlation coefficients between SS (μg C g^{-1}) and plant litterfall (LF, g m^{-2} day^{-1}) in a subtropical moist forest of southwest China from October 2004 to August 2005

Treatments	R^2				
	LF 2 months earlier	LF 1 month earlier	LF of the same month	LF 1 month later	LF 2 months later
CCK	0.440*	0.542*	0.472*	0.263	0.144
CNL	0.073	0.204	0.259	0.221	0.189
CNR	−0.318	−0.368	−0.099	−0.032	0.196
GCK	0.174	0.168	0.208	0.022	0.174

CCK, unmanipulated; CNL, control, litter removal; CNR, control, root trenching; GCK, girdling, control. * Significant correlations (alpha = 0.05)

Table 3 Multiple linear regressions of concentrations of amino acids (μg N g^{-1}) with soil respiration (g CO_2 m^{-2} day^{-1}) and soil temperature (°C) in a subtropical moist forest of southwest China from October 2004 to August 2005

	Soil respiration				Soil temperature				*n*	R^2_{adj}	*P*
	Coeff (a)	SE	*t*	*P*	Coeff (b)	SE	*t*	*P*			
Amino acids = a × (soil respiration) + b × (soil temperature)											
CCK	0.855	0.184	4.647	<0.001*	−0.495	0.184	−2.690	0.014*	24	0.460	<0.001*
CNL	0.626	0.257	2.432	0.024*	−0.679	0.257	−2.638	0.015*	24	0.198	0.038*
CNR	0.574	0.271	2.119	0.046*	−0.462	0.271	−1.706	0.103	24	0.102	0.124
GCK	0.387	0.255	1.513	0.145	−0.453	0.255	−1.775	0.090	24	0.059	0.203

CCK, unmanipulated; CNL, control, litter removal; CNR, control, root trenching; GCK, girdling, control. * Significant *P* values (<0.05) followed the order: CCK < CNL < GCK < CNR (Fig. 2a).

Effects of aboveground inputs

Litter removal significantly reduced SS concentrations (Table 1; Fig. 3). Concentrations of SS in CNL plots were 28.5%, 38.8%, and 17.0% lower than those in CCK plots in April, June, and August 2005, respectively. A large amount of aboveground plant litter had been removed from CNL plots, and this treatment would exclude the leachates and labile organic carbon from plant litter decomposition. These results indicate that aboveground plant litterfall is an important source of SS. Qualls and Haines (1992) also suggested that fresh litterfall can generate a large amount of carbohydrates. Labile organic carbon is released in the first 1 or 2 months of litter decomposition (Tripathi et al. 2006). We found that SS concentrations were strongly correlated with aboveground plant litterfall in the preceding 1 and 2 months of SS sampling in CCK plots. The absence of such correlations in CNL plots demonstrates that aboveground plant litter regulates SS concentrations, not environmental factors that may co-vary with litter input rates.

Litter removal in tree-girdled plots decreased SS concentrations to a larger extent relative to unmanipulated plots (Fig. 3), especially in the growing season from April through August 2005. Concentrations of SS were less in GNL plots than in GCK plots by 54.6%, 66.4%, and 38.2% in April, June, and August 2005, respectively. More reduction of SS concentrations in tree-girdled plots shows that belowground carbon inputs also influence SS concentrations. Since we removed both fresh plant litter and organic layers, plant roots in the organic layers in unmanipulated plots (CCK) still transported photosynthates to soils, but this flux was prevented in tree-girdled plots (GCK). In addition, the girdling treatment may alter microbial communities and accelerate litter decomposition rate. Subke et al. (2004) suggested that elimination of fresh carbon input by tree girdling resulted in greater fungal abundance than with the removal of aboveground litter only, and this microbial community shift increased soil respiration.

Litter removal treatments did not significantly affect AA concentrations (Table 1). Lipson et al. (2001) showed that protease contributes to the soil amino acid pool in an alpine soil. Weintraub and Schimel (2005), working in an arctic tundra system, suggested that protease activity was not influenced by inputs of fresh proteins from microbial turnover. Our results of marginal effects of litter removal on AA concentrations are consistent with their reports. We found no evidence in the literature that plant litterfall had direct effects on AA concentrations. The correlations of AA concentrations with soil respiration and temperature in CCK plots did not differ from these in CNL plots (Table 3), suggesting that aboveground plant litter inputs alone could not greatly affect AA concentrations.

Effects of belowground processes

Root exudates and the decomposition of root debris are other possible sources of SS (Jones et al. 2004; Zhang et al. 2006), but neither tree girdling nor root trenching substantially reduced SS concentrations (Fig. 3 and Table 1). Although tree girdling limited the transport of carbohydrates from forest canopy to roots, plant roots may have stored carbohydrates such as starches. Högberg et al. (2001) found that an increased apparent heterotrophic respiration in girdled plots because of mobilization of stored starch from roots after girdling. The minor differences between concentrations of SS in CNR and CCK plots might seem inconsistent with decomposition of CNR root debris (Fig. 3). However, as the first measurement of SS was 8 months after root trenching treatment, carbohydrate released from the decomposition of root debris probably preceded the study period (Zhang et al. 2006). The retranslocation of nutrients and carbohydrates to roots occurs before trees senesce their leaves (Killingbeck 1996), and elevated root exudates with increasing belowground carbon allocation were observed in subarctic tundra (Olsrud and Christensen 2004). However, there were no significant correlations between SS and plant litterfall in the subsequent 1 or 2 months in CCK plots, nor in the CNR or GCK plots (Table 2). In this experiment, interrupting the flow of carbohydrates from roots to the soil by trenching and girdling did not affect soil SS concentrations. Therefore, we conclude that other sources of SS (such as litter decomposition discussed previously) are the predominant sources of SS in this forest soil.

Our results showed that AA concentrations were little affected by the substrate supply from belowground root debris or root exudates (Fig. 4 and Table 1). Tree girdling eliminates the transport of carbohydrates from tree canopy to the roots, but amino acids are only a minor component of LMWOCs in root exudates (Hütsch et al. 2002; Jones 1998). Girdling therefore had little capacity to reduce AA concentrations. Soil respiration did not correlate with AA concentrations in GCK plots, differing from CCK plots. This could be another result of soil microbial community changes caused by the girdling treatment (Subke et al. 2004). Root trenching marginally increased AA concentrations (Fig. 4). This may be due to the lack of plant uptake of nutrients including amino acids. Root trenching caused changes in soil temperature (Table 1), which may have further altered the correlations between AA concentrations and soil temperature (Table 3).

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