



# Plant carbon inputs and environmental factors strongly affect soil respiration in a subtropical forest of southwestern China

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## ABSTRACT

Soil respiration is a large component of global carbon fluxes, so it is important to explore how this carbon flux varies with environmental factors and carbon inputs from plants. As part of a long-term study on the chemical and biological effects of aboveground litterfall denial, root trenching and tree-stem girdling, we measured soil respiration for three years in plots where those treatments were applied singly and in combination. Tree-stem girdling terminates the flow of carbohydrates from canopy, but allows the roots to continue water and nutrient uptake. After carbon storage below the stem girdles is depleted, the girdled trees die. Root trenching immediately terminates root exudates as well as water and nutrient uptake. Excluding aboveground litterfall removes soil carbon inputs, but allows normal root functions to continue. We found that removing aboveground litterfall and the humus layer reduced soil respiration by more than the C input from litter, a respiration priming effect. When this treatment was combined with stem girdling, root trenching or those treatments in combination, the change in soil respiration was indistinguishable from the loss of litterfall C inputs. This suggests that litterfall priming occurs only when normal root processes persist. Soil respiration was significantly related to temperature in all treatment combinations, and to soil water content in all treatments except stem girdling alone, and girdling plus trenching. Aboveground litterfall was a significant predictor of soil respiration in control, stem-girdled, trenched and stem-girdled plus trenching treatments. Stem girdling significantly reduced soil respiration as a single factor, but root trenching did not. These results suggest that in addition to temperature, aboveground carbon inputs exert strong controls on forest soil respiration.

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## 1. Introduction

Global soil CO<sub>2</sub> efflux is approximately  $8 \times 10^{16}$  g y<sup>-1</sup> (Raich et al., 2002), 11-fold greater than fossil fuel combustion flux (Marland et al., 2000). Forecasts of soil respiration changes with climate are obviously needed, but they remain highly uncertain (Denman et al., 2007).

Factors affecting soil respiration include temperature (Lloyd and Taylor, 1994; Kirschbaum, 1995; Rustad et al., 2001; Davidson et al., 2006), soil moisture (Hanson et al., 2000) and root exudation (Kuzakov, 2002). Globally, aboveground plant litter fluxes are strongly correlated with soil respiration (Raich and Schlesinger, 1992), and locally, litterfall manipulations have shown strong effects on soil CO<sub>2</sub> efflux (Fontaine et al., 2004; Ruan et al., 2004; Sulzman et al., 2005; Sayer et al., 2007). Litterfall phenology has also been shown to effect soil respiration (DeForest et al., 2006). The response of respiration to temperature was reviewed by

Kirschbaum (2006), with several important conclusions. While illustrating that the response functions can generally be described as exponential “Q<sub>10</sub>” (the change in reaction rate with 10 °C temperature increase), he found that Q<sub>10</sub> values themselves vary with temperature, and with the techniques used to achieve the temperature differences. He also recognized that water and carbon substrate availability can limit soil respiration, and that those factors have complicated relationships with temperature. Rapid water input may cause a large pulse of soil respiration (Lee et al., 2004). Conversely, respiration is reduced in dry soils where conditions are otherwise suitable (Davidson et al., 1998; Baldocchi et al., 2006).

Aboveground litterfall and belowground root turnover and exudation provide organic matter to the soil. An excess of soil respiration over these C inputs represents priming (Bingemann et al., 1953). Priming can result from the application of soluble organic chemicals (Hamer and Marschner, 2005; Dilly and Zyakun, 2008) and cellulose (Fontaine et al., 2004) to soil. Dissolved organic carbon from aboveground litter can cause priming (Park et al., 2002; Kalbitz et al., 2007). Photosynthesis transfers carbon compounds to the root system, where their exudation primes soil

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respiration (Kuzyakov and Larionova, 2005; Göttlicher et al., 2006; Hartley et al., 2007). Carbon isotopic labeling indicates that CO<sub>2</sub> respired is derived in part from soil organic matter, whether the priming input is aboveground litter (Subke et al., 2004) or root exudation (Högberg et al., 2007).

Manipulation of aboveground litter inputs affects soil respiration (Sulzman et al., 2005; Sayer et al., 2007) by providing a surficial organic matter layer for root and microbial growth (Sayer, 2006; Sayer et al., 2006). It also releases dissolved organic C (Lajtha et al., 2005) causing microbial respiration, including the priming effects discussed above. Root trenching has been extensively used to explore roles of roots in many biogeochemical processes, including respiration (e.g., Ewel et al., 1987). This procedure terminates all root functions including water and nutrient uptake, and has been extensively used to separate respiration of roots and associated rhizospheric microbes from that of soil heterotrophs. More recently, tree-stem girdling has been used to interrupt the transfer of photosynthates to roots, while allowing other root functions to continue (Högberg et al., 2001; Andersen et al., 2005; Frey et al., 2006). These girdling studies have demonstrated the strong and rapid effect of root exudation on soil respiration.

In this study we performed litter removal, root trenching and stem girdling treatments, singly and in combination. We measured soil respiration in each of these treatments, along with soil temperature and soil water content for three years, in a subtropical moist forest in China. By these manipulations and observations, we intended to determine the effects of each of these factors on soil respiration in our forest type.

## 2. Materials and methods

### 2.1. Study site

We performed this study in a subtropical moist forest in the Ailao Mountains Nature Reserve (24°32' N, 101°01' E), 2476 m elevation, in the Yunnan Province of southwestern China. This relatively undisturbed forest is dominated by the subtropical evergreen broad-leaved species *Lithocarpus chitungensis*, *Rhododendron leptothrium*, *Vaccinium duclouxii*, *Lithocarpus xylocarpus*, *Castanopsis wattii*, *Schima noronhae*, *Hartia sinensis* and *Manglietia insignis* (Li, 1983). In the experimental plots, tree density was 2728 ha<sup>-1</sup>, median tree height was 9.0 m, median diameter at breast height was 9.5 cm (range 1.3–59.7), and the median basal area in the plots was 91 m<sup>2</sup> ha<sup>-1</sup> (Z. Feng, unpublished data). Mean annual air temperature is 11.3 °C with monthly means from 5.4 to 23.5 °C. The site receives an annual average of 1840 mm precipitation, with 1568–1941 mm y<sup>-1</sup> measured during this study. The monsoon climate produces a wet season from May through October and a dry season from November through April (Zhang, 1983). Soils are loamy Alfisols. The 3–7 cm organic horizon (Liu et al., 2002a) has a pH (water) of 4.5 and organic carbon and total nitrogen contents of 304 and 18 g kg<sup>-1</sup>, respectively (Chan et al., 2006). The top 10-cm mineral soil has a pH (water) of 4.2 and organic C and total N contents of 116 and 7 g kg<sup>-1</sup>, respectively (Chan et al., 2006). The organic horizons removed in this experiment represent approximately 400–800 g C m<sup>-2</sup> (W.T. Feng, unpublished data).

### 2.2. Experimental design

A split-plot design with four block replications of three treatments (litter removal, root trenching and girdling) was used to separate the soil respiration effects of above- and belowground carbon inputs from those of root uptake of nutrients and water. There were two 20 × 20 m plots in each block; one plot was randomly selected for control and the other for tree-girdling treatment. In the girdling plots, all trees' bark and phloem were cut

from 5-cm wide bands at 1.5 m height to interrupt root exudation (Högberg et al., 2001). The girdled plot perimeters were trenched to kill roots from outside the plots. The trenches were cut to 40 cm depth, the trenches were lined with polyethylene sheeting and refilled with soil (Liu and Zou, 2002).

Within each control and girdled plot, four 2 × 3 m subplots were randomly assigned as control, litter removal, root trenching and litter removal plus root trenching. This yielded a total of 32 subplots within the following eight 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).

The CCK and GCK subplots received no further treatments. Above the litter-removal subplots, wooden structures were constructed 1 m high and covered with 1-mm nylon mesh screening to intercept aboveground plant litter. These litter screens were cleared monthly. Organic humus above the mineral soil was also removed from these subplots, to remove any effects of previous aboveground litterfall on soil respiration rates (Ruan et al., 2004). Perimeters of the root-trenching subplots were trenched and backfilled as described above. Plant sprouts in these subplots were clipped monthly. The CNLR and GNLR subplots were subjected to both the litter removal and trenching treatments described here. All the subplots were positioned to avoid woody stems, and all treatments were performed in early February 2004. Most girdled trees showed signs of mortality in the summer of 2007.

### 2.3. Field sampling and laboratory analyses

We measured plant litterfall (starting November 2003) and soil temperature and moisture contents at monthly intervals from April 2004 to April 2007. Litterfall was collected from 7, 0.25 m<sup>2</sup> traps at permanent random locations in each 20 × 20 m plot. Branches, flowers and fruits were removed, and leaf litter was dried to constant weight at 80 °C. Liu et al. (2000) reported leaf litter C content for this forest. The most abundant 3 species averaged 47% C and we used this value to convert litterfall mass fluxes to C fluxes. Air temperature was obtained using a data logger and HOBO Pro sensors (Onset Computer Corp., Bourne, Massachusetts, USA) at 1.5 m aboveground. Soil temperature and moisture were measured concurrently with respiration, using a digital thermometer and a portable TDR (MPKit-B, Institute of Soil Science, Nanjing, China) at 5 random locations around the respiration chambers at 5 cm depth. Monthly soil samples were also retrieved from each subplot from March 2004 through August 2005 for gravimetric water determinations, and these results were used to convert TDR readings to gravimetric water contents throughout the study.

Soil CO<sub>2</sub> efflux was measured by alkali trapping in a single closed chamber in each of the 32 subplots (described below) at approximately monthly intervals from August 2003 to January 2004, prior to the treatments. These measurements were made for 24 h, with excess alkali back-titrated with HCl and fluxes calculated following Coleman et al. (2002). Following the experimental manipulations, soil CO<sub>2</sub> efflux was measured with a portable infrared gas analyzer (LI-COR 820, Lincoln, Nebraska, USA) at monthly intervals from April 2004 to April 2007. Monthly sampling can be a suitable technique for estimating annual soil respiration fluxes (Savage et al., 2008). Within each of the four replicated subplots, we initially installed a single permanent chamber base at a random location, but at least 15 cm from the subplot edges. These bases were PVC pipe (25 cm diameter × 30 cm height), inserted 2 cm into the soil. Plants inside these chamber bases were initially clipped, and any regrowth was removed before each measurement. During CO<sub>2</sub> sampling, each chamber base was covered with a removable PVC cap with inlet and outlet tubes. Circulating air was scrubbed of CO<sub>2</sub>

10–20 ppm below ambient levels, and CO<sub>2</sub> measurements were recorded for 2–3 min after the concentration began increasing steadily. Air circulation exceeded the chamber volume during the measurement period. Soil CO<sub>2</sub> efflux rates were calculated by linear regression of CO<sub>2</sub> concentration versus time, adjusted for temperature and pressure. A pair of (0.1 mm Hg resolution) aneroid barometers in the laboratory (1 km distant) were read before and after respiration measurements and interpolated for flux determinations. The LI-COR 820 internally compensates for pressure effects on IR absorbance. Respiration measurements were typically completed in 2 days, with barometric corrections made each morning and afternoon.

#### 2.4. Statistical analyses

Significant differences between treatment respiration rates were determined by Mann–Whitney ranking, because of unequal variances among the replicated respiration measurements. As there were 28 comparisons among treatments, the  $P < 0.05$  significance level was reduced to  $P < 0.026$  according to the false discovery rate (Benjamini and Hochberg, 1995). Significant effects of soil temperature, moisture and litterfall on soil respiration rates were determined by multiple linear regressions (SigmaStat Version 3.1, Jandel Scientific, San Jose, California) with  $P < 0.05$ . As temperature has an exponential effect on respiration (Wiant, 1967) and the effects of moisture and litter input may also be non-linear, respiration rates were log-transformed for regression analysis. Litter inputs occurring over different intervals before and after the soil respiration measurements were also explored as regression factors.

### 3. Results

#### 3.1. Environmental factors and litterfall inputs

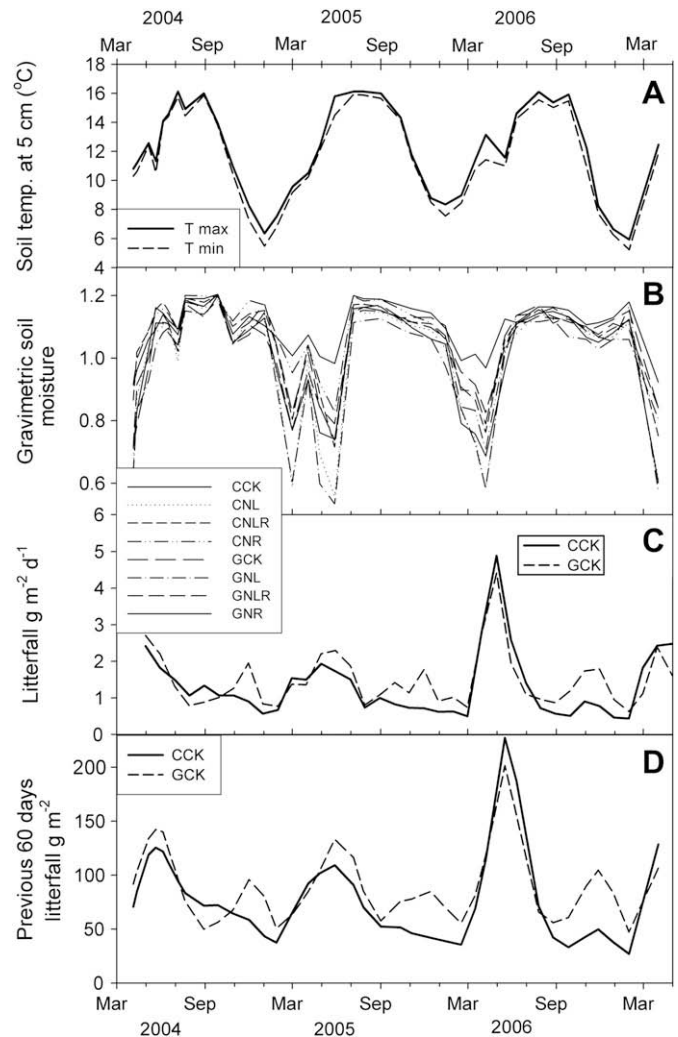
Soil temperatures varied seasonally from approximately 5 to 16 °C, with no significant differences among treatments (Fig. 1A). Maximum temperatures occurred from July to September, with minimums in January. The overall average soil temperature at 5 cm depth was 11.9 °C (Fig. 1A). Based on simultaneous measurements of gravimetric and time-domain reflectometric soil water contents in these plots from March 2004 through August 2005, the following logarithmic regression was developed (Eqn. (1)):

$$\text{Gravimetric/TDR} = -0.0204\text{LN}(\text{TDR}) + 0.1036; \quad R^2 = 0.79 \quad (1)$$

This relationship did not vary among treatments, and so it was applied to all TDR soil data obtained during respiration measurements. The resulting soil water contents through time were highest in the trenched plots and lowest in CCK or GNL plots, and the treatment values on each sampling date are shown in Fig. 1B. Maximum water contents occurred from May to September, with an additional peak in January 2007. Minimum values were observed from March to May, but the 2005 dry season had an increase in soil moisture during May (Fig. 1B).

Annual leaf litterfall averaged 480 and 549 g m<sup>-2</sup> y<sup>-1</sup> in the CCK and GCK treatments, respectively, with much more seasonal variability in the latter (Fig. 1C). Maximum litterfall in CCK plots occurred in April and May, and the October/November secondary peak was much more pronounced in the GCK plots (Fig. 1C). The girdled trees had progressively thinning canopies throughout the study, and were dying by the third year as noted previously.

For the regression models of soil respiration, the litterfall of the current month, the previous month and the sum of those two months had similar predictive power (data not shown). The two-month litterfall sum (LF60) was marginally superior and Fig. 1D



**Fig. 1.** Environmental factors and leaf litterfall measured in the Ailao Mountains forest, Southwest China, from April 2004 to April 2007. A. Soil temperature maximum and minimum among treatments, at 5 cm depth (°C). B. Gravimetric soil moisture (g water g<sup>-1</sup> dry soil) for each of the 8 treatments: CCK = unmanipulated, CNL = control, no litter, CNLR = control, no litter and root trenching, CNR = control and root trenching, GCK = tree stem girdling, GNL = girdling and no litter, GNLR = girdling, no litter and root trenching, GNR = girdling and root trenching (legend extends into panel C). C. Average aboveground leaf litterfall (g m<sup>-2</sup> d<sup>-1</sup>) in the CCK and GCK plots for the 30 days prior to each soil respiration measurement. D. Total aboveground leaf litterfall (g m<sup>-2</sup>) in the CCK and GCK plots during the 60 days prior to each soil respiration measurement.

shows LF60 for the CCK and GCK plots. The average annual leaf litterfall during this study represents a C flux to the forest floor of 226 and 258 g C m<sup>-2</sup> y<sup>-1</sup> in the control and girdled treatments, respectively.

#### 3.2. Treatment effects

##### 3.2.1. Soil respiration fluxes

Soil respiration measured before the initiation of treatments showed no significant differences among the sub-plots assigned to treatments (Fig. 2). Annual and average soil respiration fluxes for each of the 8 treatments are shown in Table 1. The highest fluxes measured each year were in the CCK treatment, averaging 842 g CO<sub>2</sub>-C m<sup>-2</sup> y<sup>-1</sup>. The lowest were in GNLR, with no litterfall or root activity, averaging 362 g CO<sub>2</sub>-C m<sup>-2</sup> y<sup>-1</sup>, or 43% of CCK. Measured respiration values through time and their standard errors are shown in Fig. 2. All 8 treatments exhibited similar overall

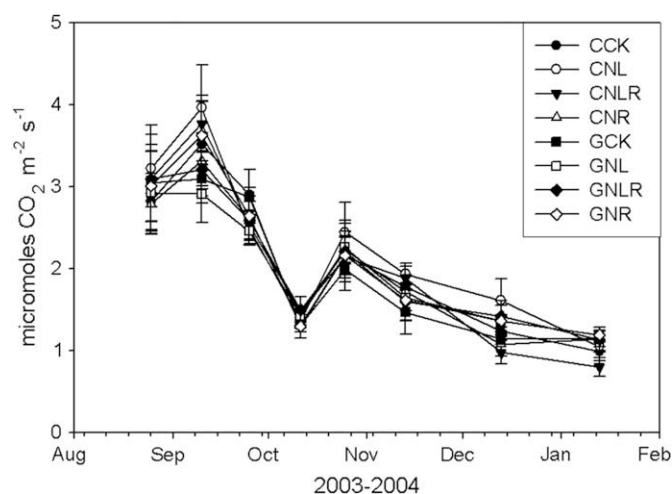


Fig. 2. Soil respiration ( $\mu\text{mol C m}^{-2} \text{s}^{-1}$ ) measured before the initiation of treatments in the Ailao Mountains forest, Southwest China, from August 2003 to January 2004.

patterns: the second and third years follow temperature seasonality, but with higher and more variable fluxes during the first year.

Annual respiration fluxes of the 8 treatments, 3-year averages and their significant differences are shown in Fig. 3. The CNR flux averaged 83% of CCK, but this root-trenching effect was not significant for any year of the study. The GNR flux was 66% of CCK in the second and third years, but not significantly lower in the first year or overall. The GCK flux was significantly lower than CCK in the second and third years, and overall, averaging 72% of CCK.

The litter-removal treatments significantly reduced soil respiration throughout the study. The control treatments (CNLR, CNL) averaged 53% of CCK, while the girdled treatments (GNL and GNLR) averaged 44% of CCK. Here again, it is notable that the trenched treatments had no less soil respiration than did the untrenched ones.

The four treatments with litter had higher fluxes and more temporal variation in the first year than in subsequent years (Fig. 4A). Fluxes in the four treatments without litter were not elevated in the first year, but they were more variable then, compared to later years (Fig. 4B). The relatively low respiration values observed on 21 May 2004 corresponded with a  $2^\circ\text{C}$  decrease in soil temperatures and minor increases in soil moisture (Fig. 1). Relatively high values were observed on 29 August 2004 in CNR and especially in CCK plots. These were accompanied by a  $1.5^\circ\text{C}$  increase in soil temperature, but this same temperature of  $16^\circ\text{C}$  was also attained in the following two years (Fig. 1), and soil respiration did not respond in the same way. Other short-term variations in the first year respiration were not accompanied by

temperature or water changes, and none of them could be related to litterfall patterns (Fig. 1).

In the first year, highly variable soil respiration fluxes were observed in CNR, GCK and GNR plots, but not in their corresponding minus litter treatments. This suggests interactions between litterfall and a pulse of belowground carbon from root damage affected soil respiration flux. However, there was even more year-one variability in CCK plots, with intact root systems. Site disturbance during experimental establishment could be related to these patterns. All plots including those without litter had more variable respiration in the first year, although only those with litter present also showed higher fluxes in that year (Fig. 4).

### 3.2.2. Soil respiration models

Temperature was a significant factor in all 8 regression models, with the coefficients corresponding to  $Q_{10}$  values ranging from 2.6 (CNR) to 4.2 (GNR). Soil water content had a significant positive effect in 4 of the 8 treatments. Litterfall in the preceding 60 days significantly increased respiration in the ungirdled + litter treatments (CCK and CNR), but not in the girdled + litter treatments (GCK and GNR). These regression models explained between 44% (GNR) and 77% (CNR) of the monthly variation in soil respiration. The measured and modeled respiration through time for those two treatments are shown as examples (Fig. 5). Time series plots of the other six treatment models are omitted for brevity, but none of them predicted the first-year respiration variability well. That variability was not present in the measured environmental factors or aboveground litterfall fluxes measured at monthly intervals.

### 3.3. Soil respiration flux differences among treatment pairs

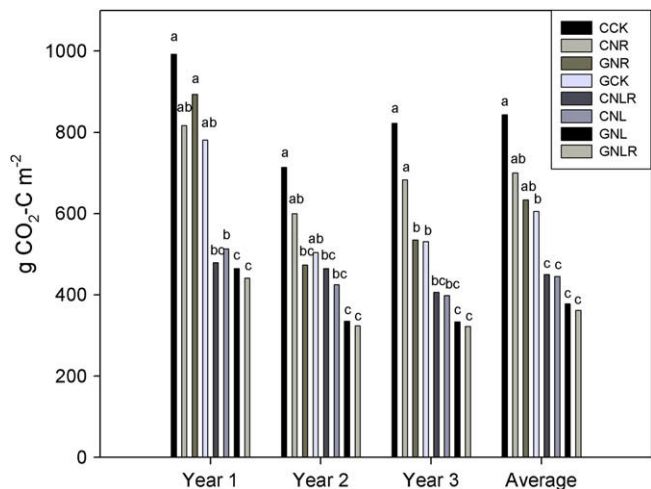
Over all three years, significant differences between treatment pairs were found in 10 of the 17 possible combinations. They represent the effects of one or multiple treatments on soil respiration, and were modeled by multiple linear regression as were the individual treatments. For all of these 10 treatment pairs, the annual and average flux differences, and the multiple linear regression models predicting the differences in carbon flux for the pairs are presented in Table 2. This table follows the format of Table 1, but has 2 additional columns because in CNL–GNLR the difference in soil water content between the treatments was a significant factor in the multiple linear regression.

For each treatment, there are 4 pairs where only that factor is changed. For the litter removal treatment, all 4 pairs had significant flux differences averaged over the 3 years. Those are: litter removal in control plots (CCK–CNL), in girdled plots (GCK–GNL), in trenched plots (CNR–CNLR) and in plots both girdled and trenched (GNR–GNLR). The latter two pairs did not show significant flux differences in all three years (Table 2). For the litter treatment, the largest

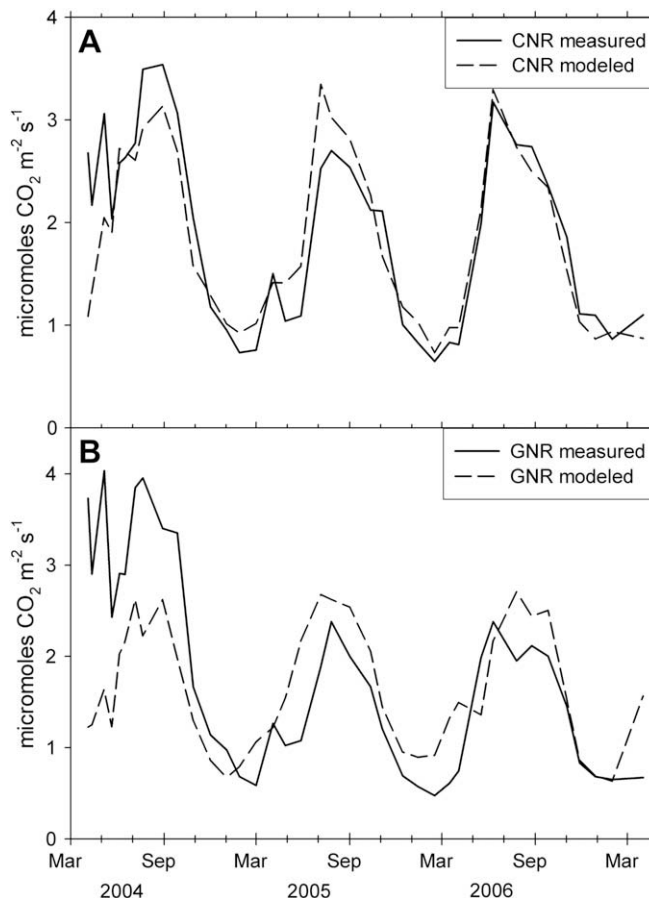
Table 1

Multiple linear regression model coefficients, statistics, and annual and 3-year average soil respiration fluxes ( $\text{g CO}_2\text{-C m}^{-2} \text{y}^{-1}$ ) measured in the Ailao Mountains forest, Southwest China, from April 2004 through March 2007. Treatments (TRTS): CCK = unmanipulated, CNL = control, no litter, CNLR = control, no litter and root trenching, CNR = control and root trenching, GCK = tree stem girdling, GNL = girdling and no litter, GNLR = girdling, no litter and root trenching, GNR = girdling and root trenching. Multiple linear regression models are based on the natural logarithm of soil respiration ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) versus soil temperature ( $^\circ\text{C}$ ), soil water content ( $\text{g water g}^{-1}$  dry soil), and leaf litterfall in the 60 days prior to measurement (LF60;  $\text{g m}^{-2}$ ). Only those factors with  $P < 0.05$  are reported; other cells are blank. All ANOVA  $P$  values were  $< 0.001$ . LF60 was not tested in the no-litter treatments (–).

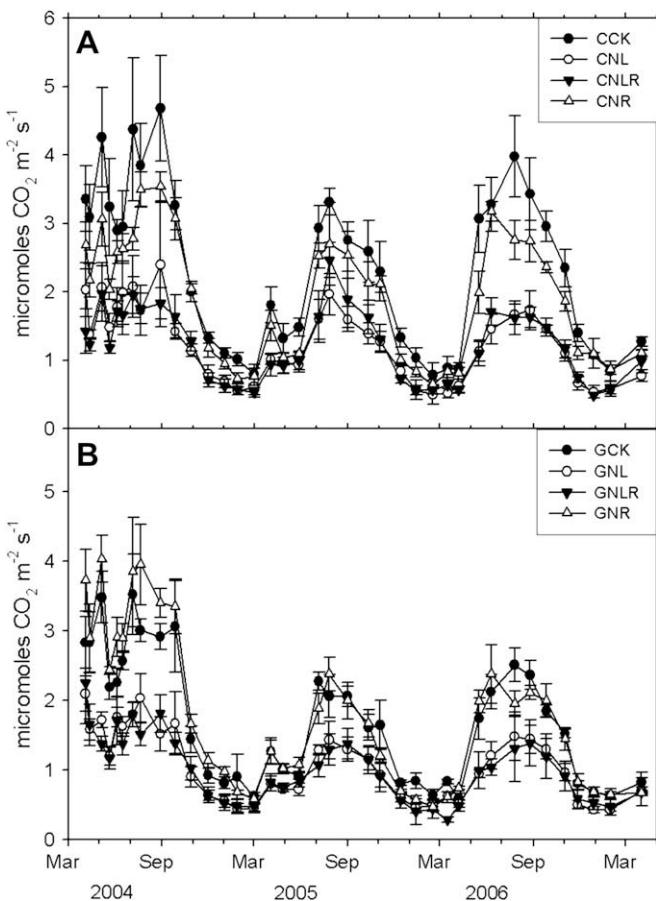
TRTS	Constant	P	Temp	P	Water	P	LF60	P	Adj. $R^2$	ANOVA F	Yr 1	Yr 2	Yr 3	3-yr avg.
CCK	–1.990	<0.001	0.100	<0.001	1.214	<0.001	0.00315	0.024	0.693	28.788	992	714	822	842
CNL	–2.092	<0.001	0.110	<0.001	0.944	0.001	–	–	0.694	42.915	512	425	398	445
CNLR	–1.329	<0.001	0.121	<0.001	–	–	–	–	0.716	94.411	464	407	450	479
CNR	–2.541	<0.001	0.097	<0.001	1.553	<0.001	0.00274	0.017	0.769	42.003	817	600	683	700
GCK	–1.182	<0.001	0.132	<0.001	–	–	–	–	0.505	38.815	781	505	530	606
GNL	–2.118	<0.001	0.114	<0.001	0.751	0.031	–	–	0.599	28.664	464	335	334	378
GNLR	–1.427	<0.001	0.111	<0.001	–	–	–	–	0.479	34.966	440	324	322	362
GNR	–1.306	<0.001	0.143	<0.001	–	–	–	–	0.439	30.006	893	474	535	634



**Fig. 3.** Annual soil respiration fluxes ( $\text{g CO}_2\text{-C m}^{-2}$ ) for each of the 8 treatments measured in the Ailao Mountains forest, Southwest China, from April 2004 to April 2007. Year 1 = April 2004 to March 2005, year 2 = April 2005 to March 2006, year 3 = April 2006 to March 2007 and Average is for those 3 years. Treatments (TRTS): CCK = unmanipulated, CNL = control, no litter, CNLR = control, no litter and root trenching, CNR = control and root trenching, GCK = tree stem girdling, GNL = girdling and no litter, GNLR = girdling, no litter and root trenching, GNR = girdling and root trenching. Bars are displayed in the order of decreasing average fluxes. Different letters within a year indicate significant differences by Mann–Whitney ranking.



**Fig. 5.** A. Measured and modeled soil respiration ( $\mu\text{mol C m}^{-2} \text{s}^{-1}$ ) in the Ailao Mountains forest, Southwest China, from April 2004 to April 2007. CNR = control and root trenching; the treatment for which the multiple linear regression model had the highest adjusted  $R^2$  (0.769, see text for details of the model). B. As in panel A, GNR = girdling and root trenching; the treatment for which the multiple linear regression model had the lowest adjusted  $R^2$  (0.439, see text for details of the model).



**Fig. 4.** Soil respiration ( $\mu\text{mol C m}^{-2} \text{s}^{-1}$ ) and standard error bars ( $N = 4$ ) for each of the 8 treatments measured in the Ailao Mountains forest, Southwest China, from April 2004 to April 2007. A. CCK = unmanipulated, CNL = control, no litter, CNLR = control, no litter and root trenching, CNR = control and root trenching. B. GCK = tree stem girdling, GNL = girdling and no litter, GNL = girdling, no litter and root trenching, GNR = girdling and root trenching.

average flux difference was in CCK–CNL ( $397 \text{ g CO}_2\text{-C m}^{-2} \text{y}^{-1}$ ), with the other 3 pairs all approximately  $240 \text{ g CO}_2\text{-C m}^{-2} \text{y}^{-1}$  (Table 2). For these pairs, litterfall was a significant factor in the regression in CCK–CNL and CNR–CNLR. Temperature was not a significant factor in CNR–CNLR, and water was not in GNR–GNLR.

The single factor of girdling was only significant in the control plots (CCK–GCK), with an average flux difference of approximately  $240 \text{ g CO}_2\text{-C m}^{-2} \text{y}^{-1}$  (Table 2). The difference between these plot pairs was not significant in the first year. When girdling was combined with trenching and litter removal, the girdling treatment did not cause significant respiration differences. For the single factor of trenching, none of the treatment pairs were significant.

For litter removal and girdling together, both control (CCK–GNL) and trenched (CNR–GNLR) pairs showed significant differences, with average flux differences of 464 and  $338 \text{ g CO}_2\text{-C m}^{-2} \text{y}^{-1}$ , respectively (Table 2). Litterfall was a significant factor in the regressions predicting both of these flux differences, and soil water content difference between treatments was significant in CNR–GNLR. For litter removal and trenching together, both control (CCK–CNLR) and girdled (GCK–GNLR) pairs showed significant differences, with average flux differences of 392 and  $244 \text{ g CO}_2\text{-C m}^{-2} \text{y}^{-1}$ , respectively (Table 2). Litterfall was a significant factor in the regression predicting flux differences between CCK and CNLR, but not for GCK–GNLR. All three factors (litter removal, girdling and trenching) were involved in the CCK–GNLR treatment pair. Here the average flux difference was largest of any treatment pair

**Table 2**

Multiple linear regression model coefficients, statistics, and annual and 3-year average soil respiration fluxes ( $\text{g CO}_2\text{-C m}^{-2}\text{y}^{-1}$ ) for significant treatment differences measured in the Ailao Mountains forest, Southwest China, from April 2004 through March 2007. Treatments (TRTs): CCK = unmanipulated, CNL = control, no litter, CNLR = control, no litter and root trenching, CNR = control and root trenching, GCK = tree stem girdling, GNL = girdling and no litter, GNLR = girdling, no litter and root trenching, GNR = girdling and root trenching. Multiple linear regression models are based on the natural logarithm of soil respiration ( $\mu\text{mol m}^{-2}\text{s}^{-1}$ ) versus soil temperature ( $^{\circ}\text{C}$ ), soil water content ( $\text{g water g}^{-1}$  dry soil), difference in water content between treatments and leaf litterfall in the 60 days prior to measurement (LF60;  $\text{g m}^{-2}$ ). Only those factors with  $P < 0.05$  are reported except for two non-significant coefficients in bold; other cells are blank. All ANOVA  $P$  values were  $< 0.001$ .

Trt. Diff.	Const.	$P$	$T$	$P$	$W$	$P$	Water diff.	$P$	LF60	$P$	Adj. $R^2$	ANOVA F	Yr 1	Yr 2	Yr 3	Avg.	Effect
CCK–CNL	–3.844	<0.001	0.106	<0.001	2.095	<0.001			0.00450	0.019	0.649	23.781	480	289	425	397	Litter
GCK–GNL	–4.177	<0.001	0.117	<0.001	2.061	0.002					0.423	14.58	316	169	197	228	Litter (girdled)
CNR–CNLR	–6.110	<0.001	<b>0.057</b>	<b>0.080</b>	4.110	<0.001			0.00513	0.042	0.544	15.743	338	<b>NS</b>	277	250	Litter (trenched)
GNR–GNLR	–2.916	<0.001	0.193	<0.001							0.349	20.29	452	<b>NS</b>	<b>NS</b>	271	Litter (girdled and trenched)
CCK–GCK	–4.093	<0.001	0.135	<0.001	1.736	0.013					0.441	15.599	<b>NS</b>	209	292	238	Girdling
CCK–GNL	–3.324	<0.001	0.094	<0.001	1.850	<0.001			0.00435	0.011	0.678	26.912	528	379	488	464	Litter and girdling
CNR–GNLR	–5.450	<0.001	0.094	<0.001	3.632	<0.001	1.246	0.032	0.00356	0.009	0.794	36.718	376	276	361	338	Litter and girdling (trenched)
CCK–CNLR	–3.622	<0.001	0.084	0.009	2.006	<0.001			0.00513	0.025	0.539	15.418	514	250	416	392	Litter and trench
GCK–GNLR	–5.730	<0.001	0.126	0.002	3.574	0.003					0.416	14.175	340	181	<b>NS</b>	244	Litter and trench (girdled)
CCK–GNLR	–2.944	<0.001	0.126	<0.001	1.477	<0.001					0.681	40.53	552	390	500	481	Litter and girdle and trench

( $481 \text{ g CO}_2\text{-C m}^{-2}\text{y}^{-1}$ ), but litterfall was not a significant factor in the regression (Table 2).

The regression models for treatment differences explained at most 79% (CNR–GNLR) and at least 35% (GNR–GNLR) of the differences in soil respiration. The measured and modeled respiration in those two treatment pairs are shown as examples (Fig. 5).

#### 4. Discussion

##### 4.1. Effects of environmental factors on soil respiration

Temperature had a positive effect on soil respiration in all treatments and in significant treatment differences (Tables 1 and 2) except for CNR–CNLR ( $P = 0.08$ ). Positive temperature coefficients are nearly universal in the soil respiration literature (e.g., Kirschbaum, 2006). However, our multiple regression models demonstrate that temperature alone is inadequate to predict soil respiration rates in the Ailao forest. Multiple linear regression models were also used by Sulzman et al. (2005) to predict soil respiration, but those models included both positive and negative temperature coefficients. This suggests that factors other than temperature may predominate there.

The mean soil (5 cm) temperature at Ailao was  $11.9^{\circ}\text{C}$  (mean air temperature  $11.3^{\circ}\text{C}$ ; Zhang, 1983). Raich and Schlesinger's (1992) global compilation of soil respiration and temperature predicts a soil respiration of  $600 \text{ g CO}_2\text{-C m}^{-2}\text{y}^{-1}$  for Ailao. Our highest treatment average (CCK) was  $842 \text{ g CO}_2\text{-C m}^{-2}\text{y}^{-1}$ , and the lowest (GNLR) was  $362 \text{ g CO}_2\text{-C m}^{-2}\text{y}^{-1}$ . High soil respiration in CCK is probably related to the fact that gravimetric soil moisture rarely fell below 74% there (Fig. 1). Lloyd and Taylor (1994) report field and laboratory respiration rates ranging from  $0.5$  to  $5.0 \mu\text{mol C m}^{-2}\text{s}^{-1}$  at this temperature. In those units CCK averages 2.2, intermediate in their data range.

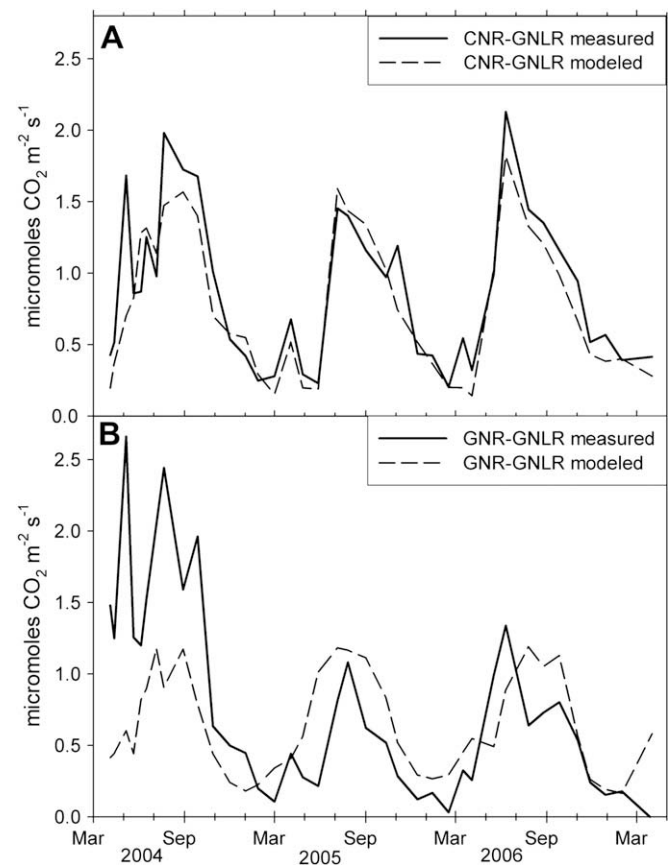
Soil water content had a positive effect soil respiration in all treatments (Table 1) and 9 of the 10 significant treatment differences (Table 2). Only from GNL–GNLR (our weakest regression model) water was excluded as a factor. All treatments had a soil respiration peak on 3 April 2005, corresponding with a temporary increase in soil water content (Figs. 1 and 4). The multiple linear regression models with highest  $R^2$  values reproduced this variation (e.g., Fig. 6).

##### 4.2. Effects of leaf litter on soil respiration

Annual average leaf litterfall of  $480 \text{ g m}^{-2}\text{y}^{-1}$  in the CCK plots fell within the range of  $361$ – $519 \text{ g m}^{-2}\text{y}^{-1}$  reported by Liu et al. (2002b) for 1991 through 1999, while that in the GCK plots ( $549 \text{ g m}^{-2}\text{y}^{-1}$ ) exceeded it. Subsequent leaf litterfall in the GCK

plots will rapidly decline due to tree mortality there, and wood fall will increase. Soil respiration was 3.7 times leaf litterfall C flux in the CCK plots, and 2.3 times this input in the GCK plots. A global compilation of litterfall and soil respiration data showed an average value of 3.0 (Raich and Tufekcioglu, 2000).

Removal of plant litterfall input and the organic humus layer reduced soil respiration by  $397 \text{ g CO}_2\text{-C m}^{-2}\text{y}^{-1}$  in the control subplots (CCK–CNL), by  $228 \text{ g CO}_2\text{-C m}^{-2}\text{y}^{-1}$  in the tree-girdled



**Fig. 6.** A. Measured and modeled soil respiration ( $\mu\text{mol C m}^{-2}\text{s}^{-1}$ ) in the Ailao Mountains forest, Southwest China, from April 2004 to March 2007. CNR–GNLR = control and root trenching minus girdling, no litter and root trenching; the treatment difference for which the multiple linear regression model had the highest adjusted  $R^2$  (0.794, see text for details of the model). B. As in panel A, GNR–GNLR = girdling and root trenching minus girdling, no litter and root trenching; the treatment for which the multiple linear regression model had the lowest adjusted  $R^2$  (0.349, see text for details of the model).

subplots (GCK–GNL) and by  $271 \text{ g CO}_2\text{-C m}^{-2} \text{ y}^{-1}$  in the girdled and trenched subplots (GNR–GNLR; Table 2). The greater reduction in the control plots suggests that aboveground litter has a priming effect on soil respiration (Subke et al., 2004; Sayer et al., 2007; Dilly and Zyakun, 2008) when roots are intact in this forest. Root respiration in the humus layer would also be terminated with the removal of that layer, and could contribute to this greater reduction in the control plot pair. However the CNR respiration was never significantly less than CCK, and fine roots in the humus layer should certainly have died in the three years since trenching. Another alternative explanation would be that some of the humus layer C was also respired in those plots. The 3–7 cm humus layer in this Ailao forest (Liu et al., 2000) remains so at present, and the leaf litterfall has been consistent at least since 1991 (Liu et al., 2002b). The  $400\text{--}800 \text{ g C m}^{-2}$  of the organic humus layer appears to be near a steady-state condition. A definitive test of priming here would involve applying dissolved organic carbon from leaf litter and organic humus to the mineral soil, to determine if the respiration increase exceeds the organic carbon added.

Results of other studies are also consistent with a priming effect. Seven years after trenching in pine plantation and secondary forest plots in Puerto Rico, Li et al. (2004) found that annual soil respiration was approximately  $960$  and  $864 \text{ g CO}_2\text{-C m}^{-2} \text{ y}^{-1}$ , respectively. Litter exclusion there reduced these values to  $444$  and  $240 \text{ g CO}_2\text{-C m}^{-2} \text{ y}^{-1}$ . Litterfall in those forests has not been reported since Lugo's (1992) measurements. Assuming leaf litter to be 50% C, those values were  $192$  and  $324 \text{ g C m}^{-2} \text{ y}^{-1}$ , respectively. In Li et al.'s (2004) trenched plots, respiration was reduced further to  $180$  and  $144 \text{ g CO}_2\text{-C m}^{-2} \text{ y}^{-1}$ , respectively, so litterfall priming apparently occurred there even without roots. Sulzman et al. (2005) also concluded that aboveground litter caused soil respiration priming, but as their experiment did not include litter manipulation in trenched plots, it cannot be determined whether priming was dependent upon root function there.

#### 4.3. Separating heterotrophic and autotrophic respiration

Root trenching and stem girdling have both been used to estimate heterotrophic and autotrophic respiration. The premise is that only heterotrophic respiration persists after the roots have been disabled, and autotrophic respiration is estimated as the difference from control treatments (Hanson et al., 2000). Their literature review found an average of 46% autotrophic respiration in forests. Subsequent reviews would predict 44% (Bond-Lamberty et al., 2004) and 51% (Subke et al., 2006) autotrophic for Ailao forest CCK respiration. However, the CNR "heterotrophic" respiration at Ailao was not significantly less than total soil respiration during any of the three years (Fig. 3), precluding such a calculation. Each of our treatments had only 4 replications and a higher degree of replication might show a significant difference between CCK and CNR. If the treatment-mean values remained the same, autotrophic respiration would be 20% of the total. The GCK respiration was significantly less than total soil respiration in the second and third years, and for that period we estimate autotrophic respiration as 33%. These proportions of autotrophic respiration are low compared to the reviews cited above, and are considered below.

Trenching causes rapid root mortality, but girdling initially prevents root exudation and after carbohydrate reserves are exhausted, the roots die. We offer two possible explanations why trenching caused smaller reductions in soil respiration than did girdling, even in the second and third year of the present study. While root nutrient uptake in the girdling plots continued, there may have been nutrient competition between plant roots and heterotrophic microbes. This competition would decrease total soil

respiration. It was also possible that the 40-cm trenching depth was inadequate to sever and kill all the roots in this forest, but soil coring has not yet been performed in the trenched plots to examine this. Two years of hydrological monitoring by Liu et al. (2003) is consistent with 82% water abstraction by roots 40 cm or shallower, and 18% by roots at greater depth. Roots surviving trenching would reduce our estimate of autotrophic respiration. However, the proliferation of such roots would increase CNR respiration through time, and this has not been observed. Soil respiration measurements continue in these plots, so later root recovery would be detected. Decomposition of roots killed in CNR and CNLR would increase soil respiration and reduce our estimates of autotrophic respiration by difference. Indeed, both of those treatments showed their highest respiration rates in the first year after treatment (Table 1). Respiration in the four girdling treatments was also highest in the first year (Table 1), even though root death was delayed in those treatments until after starch reserves were exhausted. Decomposition of dead roots remains a shortcoming of all techniques that estimate autotrophic respiration by treatments such as root trenching and stem girdling. Continued monitoring may yield consistent asymptotic values for heterotrophic respiration in the CNR, GCK and GNR treatments.

Belowground-C manipulations published since Subke et al. (2006) have also shown low proportions for autotrophic respiration. Using *in situ* soil cores (essentially very small trenched plots), Lalonde and Prescott (2007) found 35% autotrophic respiration in a coastal Douglas fir forest soil. For their total soil respiration of  $1200 \text{ g CO}_2\text{-C m}^{-2} \text{ y}^{-1}$ , the Subke et al. (2006) model predicts 50% autotrophic. Binkley et al. (2006) girdled a Eucalyptus forest in Brazil, but that treatment did not decrease soil respiration. They concluded that the trees had sufficient carbohydrate reserves below the girdles to maintain normal root function for at least 9 months after treatment. Scott-Denton et al. (2006) reported only scarcely significant differences between soil respiration in control and girdled plots of subalpine lodgepole pine. In the present study, CCK and GCK respiration differed significantly in the second and third years (Fig. 3). Stem girdling in a temperate beech/spruce mixed forest reduced soil respiration by approximately 30% (Andersen et al., 2005), and our GCK plots showed 33% reduction in the second and third years (28% over all 3 years; Table 1).

Overall, we found the interpretations of the single and paired treatments complicated because they were non-additive. Our best estimate of autotrophic respiration is 33% or less, lower than predicted by the models of Bond-Lamberty et al. (2004) and Subke et al. (2006). Our strongest conclusion is that litterfall removal plots show the largest effect on soil respiration where root function has not been impaired, and that the reduction in soil respiration was substantially larger than the C flux in annual litterfall. Changing climates may affect plant species distributions (Parmesan, 2006; Williams and Jackson, 2007), litterfall patterns (Peñuelas and Filella, 2001), and the transfer of labile C during the growing season by herbivores or plant disease (Coley, 1998; Logan et al., 2003; Michalzik and Stadler, 2005). Accurate assessments of the sensitivity of soil respiration to climatic changes will require consideration of sources of labile organic C to the soil, not only to temperature.

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