Litter priming and trenching greatly affect soil respiration in a mature subtropical evergreen broadleaf forest in Southwestern China

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ABSTRACT

Global warming will stimulate primary production, which is likely to drive shifts in litter production and lead to an increase in carbon (C) inputs to soil. However, the effects of such changes on soil C cycling in subtropical forests remain largely unknown. In a typical subtropical evergreen broadleaved forest in Southwestern China we conducted a controlled experiment that included addition and removal of litter, and trenching. Annual soil respiration in control, trenching, litter addition, and litter removal treatments were 1083.47, 521.50, 1363.30, and 896.15 g C m^{-2} y^{-1}, respectively. Soil respiration was significantly related to temperature in all treatments, but was independent of soil moisture, except in control plots. Q_{10} values in control, trenching, litter addition, and litter removal treatments were 3.46, 6.36, 2.72, and 4.85, respectively. Litter addition reduced Q_{10}, but litter removal and trenching increased it. Average heterotrophic soil respiration produced C in the amount equivalent to 48 % of the efflux from the soil. Soil respiration in the litter addition treatment was 25 % higher than in the control treatment; this increase is about 8 % larger than the 17 % decrease in soil respiration caused by litter removal. This implies a priming effect on soil respiration. Our results suggest that increases in litter production in response to human disturbances and global warming could have rapid and important consequences on soil respiration in subtropical evergreen broadleaved forests.

Key words: soil respiration, heterotrophic respiration, litter, litter addition, litter removal.

Soil respiration (R_S) is acknowledged to be the second largest source of carbon (C) flux between terrestrial ecosystems and the atmosphere, and it strongly affects the global C cycle [Raich, Schlesinger, 1992; Schlesinger, Andrews, 2000]. The magnitude of C flux from soil respiration is approximately 11-fold greater than fossil fuel and deforestation sources combined [Marland et al., 2000], therefore even small changes in total fluxes will influence atmospheric chemistry and heat balance. Considerable effort has been devoted to the quantification of fluxes of carbon dioxide (CO_2) from soils [Schimel et al., 2000; Houghton, Goodale, 2002], however, there remains a great deal of uncertainty about it [Ryan, Law, 2005; Trumbore, 2006].

Soil respiration is often related to soil temperature [Davidson et al., 2006], soil moisture, and their interaction [Hanson et al., 2000]. The simple empirical temperature dependence equation can generally be described as exponential ''Q_{10}'' (the change in reaction rate with a 10 °C temperature increase), and has been widely proved to have the predictive capacity to accurately model R_S at individual sites and on a global scale; however, sometimes it needs to be amended by a scalar, depending on water availability [Raich, Schlesinger, 1992; Hibbard et al., 2005; Davidson et al., 2006]. Rapid water input may cause a large increase in R_S, described as the ''Birch effect'' [Lee et al., 2004], while it is lower in dry soils where low soil water content reduces respiration by limiting microbial contact with available substrate [Baldocchi et al., 2006]. However, the correlation between soil respiration and environmental conditions has been challenged by several recent studies [Janssens et al., 2001; Bhupinderpal-Singh et al., 2003; Hibbard et al., 2005], suggesting that such factors as aboveground photosynthetic activity and soil organic carbon storage and input (from the sources like litterfall and root turnover) may impact R_S as strongly or more strongly than soil temperature and moisture [Bhupinderpal-Singh et al., 2003]. While the underlying mechanisms controlling R_S are not totally clear, it is important to attempt to better understand these mechanisms, which will significantly influence our comprehensive understanding of the carbon balance in terrestrial ecosystems.

Aboveground plant litter fluxes are strongly correlated with R_S on a global scale [Raich, Schlesinger, 1992], and locally, litter manipulations have shown to have strong effects on R_S [Fontaine et al., 2004; Sulzman et al., 2005; Sayer et al., 2007; Leff et al., 2012]. As aboveground litter provides organic carbon and nutrients to the soil for root and microbial growth [Sayer, 2006; Sayer et al., 2006], it also can cause a release of dissolved organic carbon which can cause a priming effect [Park et al., 2002; Kalbitz et al., 2007]. It is likely that changes in aboveground litter production will have significant consequences for R_S [Sayer et al., 2007], and it is important to elucidate how predicted changes in litter inputs and removal might affect R_S in various ecosystems [Townsend et al., 2011].

Soil respiration is usually separated into two components: heterotrophic respiration and autotrophic respiration [Hanson et al., 2000]. Here, heterotrophic respiration is the decomposition of complex compounds, such as litter and soil organic matter [Högberg et al., 2009], and autotrophic respiration is that of live roots and closely associated microorganisms that are dependent on the flux of recent photosynthate [Högberg, Read, 2006]. Heterotrophic and autotrophic respiration alone releases into the atmosphere approximately 98 ± 12 Pg of C per year [Lamberty, Thomson, 2010]. The two components of R_S may respond differently to environmental changes, which may have profound implications for the ecosystem C balance. Therefore, it is necessary to define the variables controlling each component to help us better understand the effects of climate change on C cycling [Ohashi et al., 2000; Bond-Lamberty et al., 2004]. Currently, trenched plots are extensively used in studies of R_S because of their simplicity and low cost [Hanson et al., 2000]. This method terminates all root functions and has been extensively used to separate respiration of roots and associated rhizospheric microbes from that of soil heterotrophs [Schaefer et al., 2010].

The subtropical forest in Southern China represents about one-third of the total forested area of China; it has a unique subtropical monsoon climate with abundance of rainfall, heat and light [Tang et al., 2006]. The subtropical evergreen broadleaved forest is distributed

across over 10 latitudes in China and is the largest and the most typical evergreen broad-leaved forest in the world; large portions of landscapes at the same latitude in other areas of the world are covered by deserts [Sheng et al., 2010]. Despite the importance of this forest in national C budgets and in the climatic system, R_S of the system is poorly understood and there are limited accurate estimates of the forest C budget. Therefore, separating R_S components to understand their determinants is very important.

In this study, we conducted an experiment consisting of a trenching plot, and monthly litter removal and litter addition treatments in a subtropical evergreen broadleaved forest. Our specific objectives were to (1) separate heterotrophic and autotrophic respiration; (2) quantify annual fluxes of R_S components and their relative contributions in the forest ecosystem; (3) understand the R_S dynamics under different disturbances in a large area of the subtropical forest in East Asia.

MATERIALS AND METHODS

1. Site description and experiment design

The research site is located near the West China Subalpine Botanical Garden, Institute Of Botany, Chinese Academy of Science, Dujiangyan, in the province of Sichuan, Western China (30°44′ N, 103°27′ E). The site receives an annual average of 1243 mm of precipitation, and the monsoon climate produces the wet season from May through October and the dry season from November through April. The mean annual temperature is 15.2 °C. This relatively undisturbed forest is dominated by the subtropical evergreen broad-leaved species *Cyclobalanopsis oxyodon, Lithocarpus harlandii, Phoebe zhennan, Symplocos laurina, Castanopsis carlesi, Pittosporaceae xylocarpum, Aphananthe aspera,* and *Ficus henryi.* On the experimental plots, tree density was 1895 ha^{-1}, mean diameter at breast height was 15 cm (ranged from 1 to 38.3), and mean tree height was 10.2 m.

A random design of the three treatments (root trenching, litter removal and litter addition) with three replications was used to separate the effects of above- and belowground

carbon inputs on R_S from those of root uptake of nutrients and water. Three permanent fixed plots 20 × 30 m were set up in the subtropical forest, and within each plot, four 1 × 1 m subplots were randomly assigned as control (untrenched and litter keeping, UTC), root trenching and litter keeping (TL), untrenched and litter removal (UTL-), and untrenched and litter addition (UTL+) in the forest ecosystem.

The trenches were cut to a depth of 50 cm because the main root biomass is vertically distributed in the 0−50 cm of soil layer [Peng, Hao, 2005]. The trenches were lined with polyethylene sheets at the sides, but not at the bottom and were repacked carefully with the soil. For UTL-, all litter and organic humus above the mineral soil were carefully removed to eliminate any effects of previous aboveground litter on R_S rates. For UTL+, all litter and organic humus collected from each 1 × 1 m subplot of UTL- were added to each 1 × 1 m subplot of UTL+. Polyvinyl chloride (PVC) collars (20 cm inside diameter × 6 cm height) were randomly installed for the measurement of R_S in each subplot. Collars were kept in the same locations for continuity throughout the study period. Field measurements were usually conducted monthly, in the beginning of the month, from August 2009 to November 2010.

2. Measurements protocols

2.1. Soil respiration. Soil respiration was measured using an automated soil CO_2 flux system (Li-8100, LI-COR Inc., Lincoln, NE, USA) equipped with the 20 cm survey chamber (Model 8100-103). Before sampling, plants inside these chamber bases were clipped, and any regrowth was removed prior to obtaining each measurement. To avoid any pulse effect of precipitation on R_S, measurements were performed on the third day after a rainfall. All R_S measurements were made between 09:00 and 11:00 (local time), when R_S is approximately representative of daily average R_S [Tang et al., 2006]. Each measurement took 3−4 min to obtain.

2.2. Soil temperature and water content. At the time of R_S measurement, a probe equipped with the LI-8100 system was used to auto-

matically measure soil temperature and soil moisture at a depth of 10 and 0−5cm, respectively.

2.3. Litter production. Litter was collected from 12 1-m^2 traps at permanent random locations in each 20×30 m plot from January 2010 to December 2010. Litter was dried to a constant weight at 80 °C. Litter C content was calculated as $0.48 \times$ litter biomass [Wieder et al., 2009].

3. Parameters calculations

Trenching cuts off the supply of aboveground photosynthesis to roots and causes rapid root mortality. Therefore, only heterotrophic respiration (R_H) persists after the roots have been disabled, and autotrophic respiration (R_A) is estimated as the difference in R_S between the trenching and litter keeping treatments and control. We calculated the annual fluxes of R_H and R_A (g C m^{-2} yr^{-1}) and relative contribution of R_A to total soil surface CO_2 flux (R_C, %) as:

$$R_A = R_S - R_H, \tag{1}$$

$$R_C = R_A / R_S \times 100, \tag{2}$$

where R_S is the total soil surface CO_2 flux. The relationship between seasonal R_S, soil temperature, and soil moisture was examined using linear and nonlinear regression models:

$$R = ae^{bT}, \tag{3}$$

$$R = mW + n, \tag{4}$$

$$R = ae^{bT}W^c, \tag{5}$$

where R is either R_A or measured R_H (μmol-CO_2 m^{-2} s^{-1}), T is the soil temperature (1 °C) at a depth of 10 cm, W is volumetric soil moisture (cm^3 cm^{-3}), and a, b, c, m, and n are constants fitted by the least-square technique.

The Q_{10} value, the increase in the rate of R_S when the soil temperature increases by 10 °C, which represents the temperature sensitivity of R_S, was calculated as follows:

$$Q_{10} = e^{10b}. \tag{6}$$

4. Statistical test

The annual R_S in each treatment was estimated by extrapolating measurement data. The significance of all regression equations was analyzed using the F-test at a 5 % level. The soil respiration values in UTL+, UTC, UTL-, and TL treatments were analyzed using one-way ANOVA. If significant differences were found, the Duncan test was used to determine mean differences between treatments. All statistical analyses, including the test for homogeneity of variance, were performed using the SPSS 17.0 package (SPSS 2000).

RESULTS AND DISCUSSION

1. Environment factors and litter inputs

Soil temperatures varied seasonally from approximately 5 to 22 °C, and there were no significant differences in temperature between treatments (Fig. 1). Maximum temperatures occurred in July, and minimum temperatures − in January. Annual soil moisture at a depth of 0−5 cm varied significantly between the treatments; annual soil moisture in TL, UTL-, UTC, and UTL+ was 31.22, 27.55, 31.45, and 29.26 cm^3 cm^{-3} (Fig. 2), respectively. Soil moisture of UTL- was lower than the others' treatments. Annual average litterfall was 863.98 g m^{-2} yr^{-1} in the UTC plots; maximum litterfall in UTC plots occurred in May, and minimum litterfall − in January (Fig. 3).

2. Soil respiration in the litter addition and removal treatments

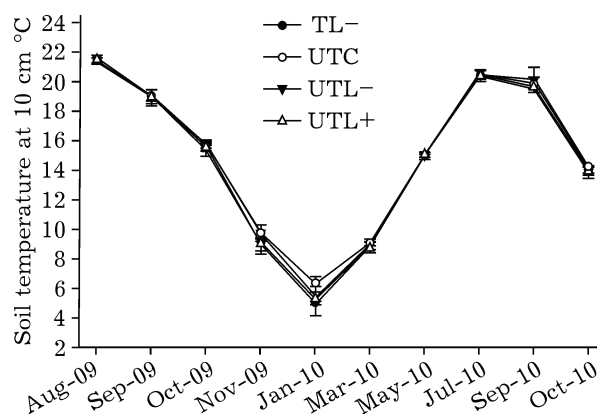The mean annual R_S for the UTC, UTL−, and UTL+ was 1083.47, 896.15 and

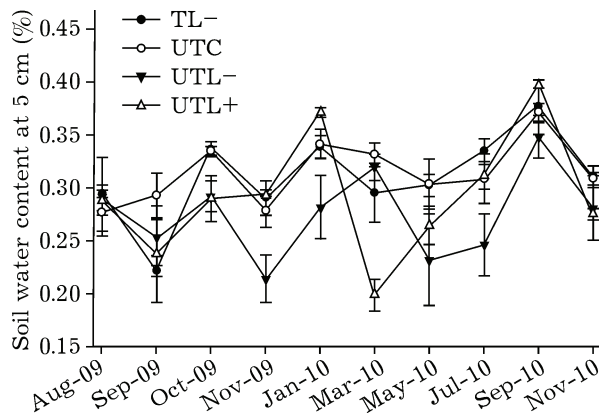*Fig. 1.* Temporal changes of soil temperature (at 10 cm depth) (mean ± SE) on the treatment plots

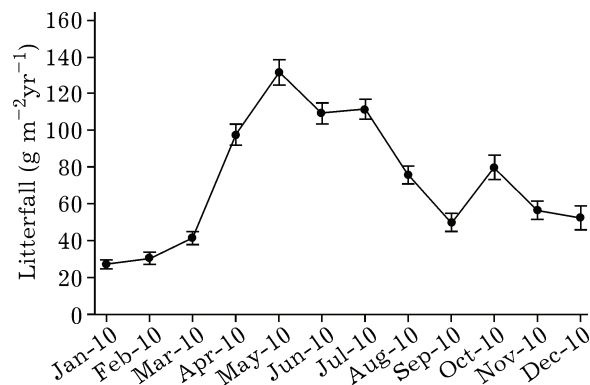*Fig. 2*. Temporal changes of soil moisture content (at 5 cm depth) (mean ± SE) on the treatment plots

Fig. 3. The litterfall measured in relation to the control plot in the subtropical forest, southwest China, from August 2009 to December 2010

1363.30 g C m^{-2} y^{-1}, respectively. R_S varied significantly seasonally, and was high in summer and low in winter. Litter manipulation significantly affected R_S. Generally, the UTL+ treatment had the highest R_S; in UTL+, R_S was 25.83 % higher than that of the control (Fig. 4). The increase in R_S induced by litter addition was higher than the decrease in R_S induced by litter removal. R_S in the UTL− treatment was 17.29 % lower than that of the control.

3. Soil respiration in the trenched and untrenched treatments

The mean annual R_S in TL and UTC was 521.50 and 1083.47 g C m^{-2} y^{-1}, respectively. The overall seasonal pattern of R_S in TL and UTC followed seasonal changes in soil temperature (see Fig. 1, 4). The mean instantaneous rates of R_S in TL and UTC were 3.25 and 3.89 μ
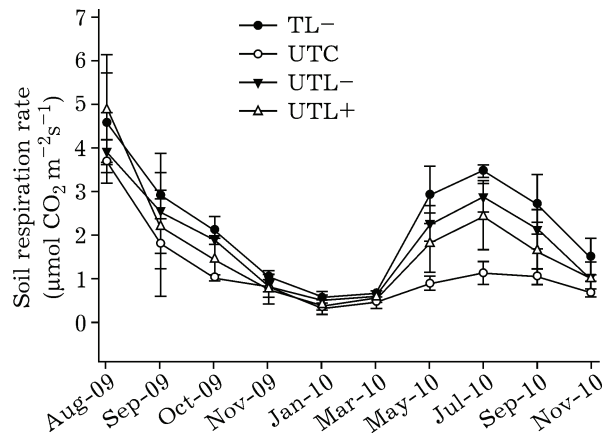

Fig. 4. Temporal and treatment effects of litter addition (UTL+), litter removal (UTL-) and trenching (TL) in relation to the control plots (UTC) on soil respiration rates (mean ± SE of x replica) from August 2009 to December 2010

mol CO_2 $m^{-2}s^{-1}$, respectively. The difference between R_S in UTC and TL in the second year was much higher than that of the first year.

4. Variation in soil respiration related to temperature and soil water content

The temperature at a depth of 10 cm accounted for more than 60 % of the variation in R_S in the UTL+, UTC, UTL- and TL treatments (Fig 5). However, the correlation between R_S and temperature decreased by 16 % for R^2 in the UTL- and TL treatments. Q_{10} values were 2.72, 3.46, 4.85, and 6.36 in UTL+, UTC, UTL-, and TL, respectively; trenching and litter removal both increased Q_{10}, while litter addition decreased it.

The exponential temperature model explained most of the variation in R_S. The soil moisture functions (Eq. 4, 5) performed poorly for UTL+, UTL-, and TL treatments, and performed well for UTC. The regression model of soil temperature together with soil moisture also described R_S well.

5. Effects of environmental factors on soil respiration

It is commonly accepted that temperature is the major factor controlling R_S [Raich, Schlesinger, 1992; Lamberty, Thomson, 2010]. Our results also showed a strongly exponential pos-
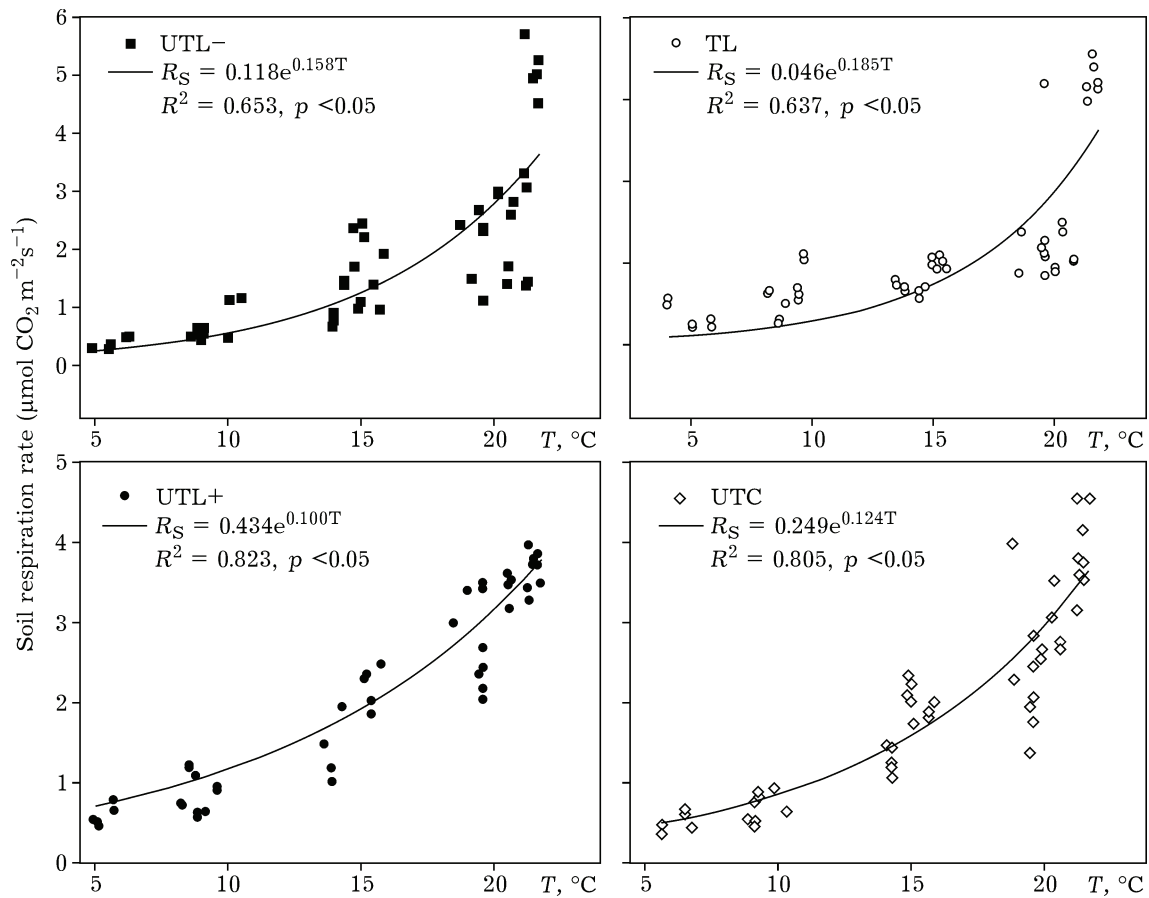
Fig. 5. Annual soil respiration rates

itive correlation between R_S and soil temperature (Fig. 6). This finding is consistent with those of previous studies from tropical forests [Raich, Schlesinger, 1992; Schaefer et al., 2009]. The Q_{10} values have commonly been used as an indicator of soil temperature sensitivity. In our study, the Q_{10} values corresponding to the treatments occurred in the following order: UTL < UTC < UTL < TL. It is worthwhile to note
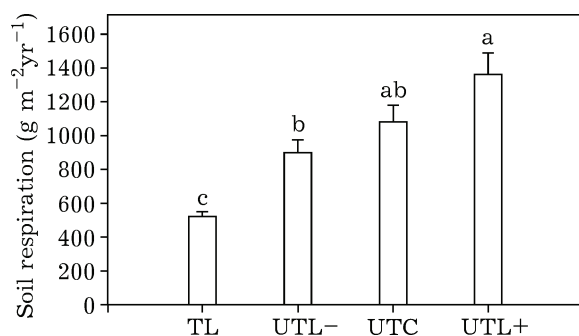

Fig. 6. Annual soil respiration rates for the 4 treatments. Columns with different low case letters are significantly different at $p < 0.05$

that the apparent Q_{10} value increased after trenching and litter removal, and decreased after litter addition; this indicates that litter removal enhanced the temperature sensitivity of R_S. Overall, there is still uncertainty about the mechanisms mediating the variability of Q_{10}. The Q_{10} value may be affected by a range of factors, including soil water availability, temperature range, soil depth, substrate quality, and microbial activities [Xu, Qi, 2001; Wang et al., 2006]. A girdling experiment in a Scott pine forest of Sweden suggested that bulk R_S was more sensitive to that of tree root [Bhupinderpal et al., 2003].

Soil water availability is another important factor influencing R_S at the ecosystem level [Raich, Schlesinger, 1992; Davidson et al., 1998; Law et al., 2001]. However, except for UTC, the correlation between R_S and soil moisture was relatively poor in the treatments. That is perhaps a result of the plentiful rainfall at the research site; because of this, tree root activities were seldom limited by soil water availa-

bility, soils seldom underwent prolonged drought, and the seasonal variation in soil moisture did not limit the activities of microbes most of the time, as reported by Zhang et al. [2001].

6. *Litter change and soil respiration*

A global dataset indicated that C released by annual R_S is, on average, three times higher than that contained in annual litterfall [Raich, Tufekcioglu, 2000]. Our result showed that C release by annual R_S was 1.26, 2.16, 2.61, and 3.28 times higher than that contained in litterfall in the TL, UTL-, UTC, and UTL+ plots, respectively. The 17.29 % reduction in R_S observed in UTL- is similar to the 20 % decrease in an old-growth, moist lowland tropical forest in Panama after one year of litter removal [Sayer et al., 2007], but is lower than the 47.15 % decrease observed after 3 years of litter removal in a subtropical moist forest in the Ailao Mountains Nature Reserve forest in China [Schaefer et al., 2009]. The decrease that occurred during our study could be attributed principally to a reduction in heterotrophic respiration because of the withdrawal of fresh substrate, since there were no significant differences in soil temperature or soil water content between the treatments.

The addition of plant litter increased soil respiration by 25.83 % (see Fig. 6). About 8 % of the increase in R_S in the UTL+ treatment was the result of litter addition, and the decrease in R_S in the UTL- treatment that resulted from litter removal suggests that aboveground litter has a priming effect on R_S [Sayer et al., 2007; Dilly, Zyakun, 2008]. The priming effects of litter addition are also reported in a large number of studies [Sayer et al., 2007; Fontaine et al., 2007; Crow et al., 2009; Schaefer et al., 2009]. After 2 years of treatment in a tropical rain forest, Leff et al. [2012] found that annual R_S was increased by approximately 15 % in the litter addition plots, but decreased by 22 % in the litter removal plots. Li et al. [2004] found that annual R_S decreased by approximately 51 % after 7 years of litter removal in pine plantation and secondary forest plots in Puerto Rico. This suggests that litter addition, besides increasing the amount of readily degradable C, may also cause substan-

tial losses of CO_2 from the soil [Sayer et al., 2007; Schaefer et al., 2009].

7. *Annual fluxes of soil respiration components*

In this study, the measured soil CO_2 efflux rates from the UTC plot was within the range of reported values for subtropical forests [Hanson et al., 2000; Subke et al., 2006; Tan et al., 2013]. Hanson et al. [2000] summarized about 50 reports and calculated mean ratios of autotrophic respiration to total R_S of 48 for forest ecosystems. In our study this ratio was 52 and therefore very similar. However, our value is much higher than those reported in other studies, for example for temperate beech/spruce mixed forest [30, Andersen et al., 2005], Coastal Douglas fir forest [35, Lalonde, Prescott 2007], and subtropical forest of Southwestern China [33, Schaefer et al., 2009].

At the beginning of plot trenching (early August of 2009), the difference between R_S in UTC and TL was very small (see Fig. 4), however, as treatments progressed, the difference increased. One possible explanation for this phenomenon is that in August, the hottest month in Southwestern China, microbial activity was the highest and soil organic matter decomposed quickly, therefore R_S was high. However, in the growing season of the following year, soil organic matter decomposition was almost complete and R_S was reduced. Our results demonstrate that R_S in the TL treatment was always smaller than that of the UTC treatment; this result is different from those of previous studies [e.g., Lee et al., 2003; Wang, Yang, 2007; Schaefer et al., 2009]. The reason for this may be that our study was conducted in the summer, and the high temperature promoted R_S in all treatments. Trenching severed roots and reduced R_S by 52 % in the mature broadleaf forest in Southwestern China, which indicates the significance of autotrophic respiration in forest ecosystems.

In conclusion, our results demonstrate that there was a strongly exponential positive correlation between R_S and soil temperature, while the correlation between R_S and soil moisture was poor except UTC. Litter addition caused a decrease in Q_{10}, but litter removal and

trenching caused it to increase. Our results also indicate that litter addition had a priming effect on R_S, therefore human disturbance and global warming might have rapid and important consequences on soil respiration and may alter the mechanisms controlling soil C mineralization and stabilization in the subtropical forest.

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