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# Estimates of soil respiration and net primary production of three forests at different succession stages in South China

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## Abstract

**Soil respiration (heterotropic and autotropic respiration, $R_g$) and aboveground litter fall carbon were measured at three forests at different succession (early, middle and advanced) stages in Dinghushan Biosphere Reserve, Southern China. It was found that the soil respiration increases exponentially with soil temperature at 5 cm depth ($T_s$) according to the relation $R_g = a\exp(bT_s)$, and the more advanced forest community during succession has a higher value of $a$ because of higher litter carbon input than the forests at early or middle succession stages. It was also found that the monthly soil respiration is linearly correlated with the aboveground litter carbon input of the previous month. Using measurements of aboveground litter and soil respiration, the net primary productions (NPPs) of three forests were estimated using nonlinear inversion. They are 475, 678 and 1148 $\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ for the Masson pine forest (MPF), coniferous and broad-leaf mixed forest (MF) and subtropical monsoon evergreen broad-leaf forest (MEBF), respectively, in year 2003/2004, of which 54%, 37% and 62% are belowground NPP for those three respective forests if no change in live plant biomass is assumed. After taking account of the decrease in live plant biomass, we estimated the NPP of the subtropical MEBF is 970 $\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ in year 2003/2004. Total amount of carbon allocated below ground for plant roots is 388 $\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ for the MPF, 504 $\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ for the coniferous and broad-leaf MF and 1254 $\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ for the subtropical MEBF in 2003/2004. Our results support the hypothesis that the amount of carbon allocation belowground increases during forest succession.**

*Keywords:* inversion, litter fall, net primary production, soil respiration, subtropical forest

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## Introduction

The subtropical area in South China is strongly influenced by monsoons from the western Pacific and north Indian Oceans. Warm and humid southeast or southwest winds in summer, together with the influence of typhoons in summer and autumn, bring much precipitation to this region (Kong *et al*., 1997). In Dinghushan Biosphere Reserve (DBR), forests at three succession phases have been reserved and studied as part of China's contribution to the International Biosphere Program (IBP) in the early 1970s. They are the coniferous Masson pine forest (MPF), the coniferous and broad-leaf mixed forest (MF) and the subtropical monsoon evergreen broad-leaf forest (MEBF) from pioneer vegetation community to the local climax vegetation (Peng & Wang, 1995). During vegetation succession, forest ecosystems undergo changes in their community structure, species composition, abundance and consequently their biogeochemical cycles. Such changes can play an important role in soil restoration through the accumulation of vegetation biomass and improved soil fertility (Kovel *et al*., 2000; Feldpausch *et al*., 2004). It was also found that the soil carbon would gradually increase as broad-leaves species invade the conifer species-dominated forests as a result of increase in litter fall, root and microbial activities in soil from the pioneering forest community to locally stable climax vegetation (Peng & Wang, 1995).

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Extensive field studies have been conducted at these three forests at DBR over the last three decades (Ehleringer *et al*., 1987; Brown *et al*., 1995; Peng & Zhang, 1995). More recently, a comprehensive field measurement program has been established to quantify heat, water and carbon exchange between the forests and atmosphere (Yan *et al*., 2002; Yi *et al*., 2003; Zhou *et al*., 2004). As part of this field measurement program, we measured respiration from soil and litter layer weekly and aboveground litter fall monthly. The objective of this study is to quantify the annual soil respiration and net primary production (NPP) using the measurements of soil respiration and litter fall, and test the hypothesis that the fraction of NPP allocated belowground increases during forest succession because of an increase in competition for soil nutrients and water.

Because of the difficulties in measuring belowground root production, direct estimates of NPP have not been possible for all three forests. All three forests have not experienced significant human disturbance over the last 40 year, and are speculated to allocate a significant fraction of photosynthetic carbon belowground (Zhou & Yan, 2000, 2001). A study by Raich & Nadelhoffer (1989) showed that total belowground carbon allocation accounts for about two-thirds of total NPP in mature forests. However, their analysis did not provide a separate contribution to soil respiration by roots from that by the decomposition of soil organic matter (SOM). In this study, we estimated belowground allocation by applying nonlinear inversion to the measurements of soil respiration and soil carbon pool sizes in all three forests, and compared with the estimates from the estimates from the regression equation developed by Raich & Nadelhoffer (1989) or Davidson *et al*. (2002). We also studied the contribution of surface litter to soil respiration by comparing respiration of soil with surface litter with that without surface litter.

## Material and methods

### *Field sites description*

The DBR lies in the middle part of Guangdong Province, South China, 84 km west of Guangzhou, at latitude 23°9′ to 23°12′ N and longitude 112°31′ to 112°34′ E. The rocks at DBR are sandstone and shale belonging to the Devonian Period. The terrain is quite hilly with an altitude varying from 100 to 700 m above sea level in most areas. The reserve has a subtropical monsoon humid climate with an annual mean temperature of 20.9 °C. The highest and lowest monthly mean temperatures are 28.0 °C in July and 12.0 °C in January, and the highest and lowest extreme temperature, 38.0 °C and −0.2 °C, respectively. The annual average rainfall is 1956 mm, and the rainfall from April to September is more than 80% of the annual total, with distinctive wet and dry seasons within a year.

The predominant soil types at DBR are lateritic red-earth in the lower altitude region and yellow earth in the higher altitude region. Soil pH is about 3.9, with a rich humus layer at the surface. Three types of natural vegetation community are common. They are subtropical MEBF with age of more than 400 years, coniferous and broadleaf MF and coniferous MPF (Table 1). They are considered to represent different succession stages, with a climax community of MEBF, dominated by *Cryptocarya concinna*, *Schima superba* and *Castanopsis chinensis*. The flora includes 260 families, 864 genera and 1740 species of wild plants and a further 349 species of cultivated plants.

### *Soil respiration measurements*

Six plots were randomly located within each forest type, and a permanent chamber base was pushed 3 cm deep into the soil, and was covered with a chamber and sealed during measurements. Litter was removed from three of the six plots in each forest for studying the effect of surface litter on soil respiration.

The chamber system consists of a base with an annular collar on which is placed the chamber with a diameter of 50 cm. The chamber is made from stainless steel with the top being covered by cotton pad to reduce heat exchange. The bases were permanently pushed 3 cm into the soil at least 4 weeks before the first sampling. The sample tube was connected to the upper part of the chamber. Two small electric fans were installed for air mixing inside the chamber. During

**Table 1** Some characteristics of the study sites

| Stand type | Elevation (m) | Soil pH value | SOC ($g\,C\,m^{-2}$) | Stand age (year) | LAI | Dominant species |
|---|---|---|---|---|---|---|
| MPF | 200–300 | 3.92 | 6510 | 50–60 | 4.3 | *Pinus massoniana* |
| MF | 220–300 | 3.86 | 7442 | –100 | 6.5 | *Castanopsis chinensis*, *Castanopsis chinensis*, *Schima superba* |
| MEBF | 220–300 | 3.96 | 9104 | –400 | 7.8 | *Cryptocarya concinna*, *Machilus chinensis*, *Cryptocarya chinensis* |

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SOC and LAI represent soil organic carbon in the top 60 cm depth and leaf area index, respectively.
MPF, Masson pine forest; MF, mixed forest; MEBF, monsoon evergreen broad-leaf forest.

measurements, the chamber was water sealed by filling water into the pedestal's trough where the chamber sits. Gas sample was taken using a gas-tight syringe through a septum-covered access port immediately and every 10 min after chamber closure. Five gas samples were collected for laboratory analysis during each measurement.

Samples were analyzed for $CO_2$ concentration using an HP4890D gas chromatograph (Agilent, Wilmington, DE, USA) equipped with flame ionization detectors (FID). $CO_2$ fluxes were calculated from linear regressions of the concentration vs. time curves from the chambers according to

$$F_c = \rho \frac{V}{A} \frac{\Delta c}{\Delta t}, \tag{1}$$

where $\rho$ is the density of air in the chamber ($g\,m^{-3}$), $V$ is chamber volume ($m^3$) and $A$ is ground area covered by the chamber ($m^2$), $c$ is $CO_2$ concentration in the chamber at time $t$ (ppm) and $\Delta c/\Delta t$ represents the slope of the linear part of the relationship between $c$ and $t$ after chamber closure. We found that $c$ increases linearly with time for all our measurements with $r^2$ for the linear regression between $c$ and $t$ being greater than 0.98 for all measurements. Positive values of $F_c$ indicate an emission of $CO_2$ from the ground to the atmosphere.

Hourly soil respiration was measured for each plot between 9:00 and 12:00 hours once per week and 24-hourly respiration was measured once per month. All measurements reported here were conducted from March 2003 to April 2004.

### *Temperature and soil moisture measurements*

Continuous measurements of soil moisture and temperature were taken using time-domain reflectometry (Campbell Scientific Inc., Logan, UT, USA) in the top 10 cm of soil and thermistors at 5 cm depth at each chamber site. The measurements were stored onto a data logger for weekly retrieval using a personal computer.

### *Litter fall measurements*

Fifteen 1 $m^2$ square litter traps were placed in each forest randomly. The trap was made of a plastic net that allows water to percolate easily but retain litter. The trap was installed at 50 cm above the ground. Litter material in the trap was collected weekly since 1996, and was air dried, then separated into leaves, branches, barks and flower and fruit. The unidentified fine litter material was combined with flower and fruit litter. All litter material was dried in an oven at 65 °C until constant weight was obtained. The final dry weight of each component in all samples was recorded.

### *Estimation of NPP*

To help interpret the field measurements of soil respiration and aboveground litter fall carbon, we developed a theoretical framework that relates the annual NPP to these two entities.

Annual NPP of a forest ($P_{npp}$) is calculated as

$$P_{npp} = \sum_j \int_1^{365} D_j(t)\,dt + \Delta C_{plant} + \Delta C_{cwd}, \tag{2}$$

where $D_j$ is daily litter carbon input of different plant biomass components ($g\,C\,m^{-2}\,day^{-1}$) ($j = 1$, 2 and 3 for leaves, woody material excluding coarse wood debris (CWD) and roots, respectively), and $\Delta C_{plant}$ and $\Delta C_{cwd}$ represent net change in live plant biomass and dead CWD in 1 year. We assumed that decomposition of CWD is insignificant over 1 year.

Contribution from litter fall carbon to $P_{npp}$ is by far the largest term on the right-hand side of Eqn (2) for the three forests that have not been subject to any significant human disturbance over the last 40 years or more to our best knowledge. Belowground litter carbon can be a significant fraction of annual NPP for forests (Davidson *et al*., 2002), but is not directly measured in this study because of well-known difficulties. In this study, we develop a novel method to estimate the belowground litter fall input and NPP by applying nonlinear inversion to a soil carbon model using measurements of soil respiration and aboveground litter fall of all three forests.

Litter fall provides substrate for soil microbial activities and, therefore, is closely related to heterotrophic respiration, which cannot be separated from root respiration when only soil respiration is measured. To relate litter fall carbon to soil respiration, we used the Rothamsted soil carbon model (Jenkinson, 1990). In the model, plant litter carbon is considered to enter two litter carbon pools: the decomposable plant material (pool d) and resistant plant material (pool r). Partitioning coefficients for leaf, branch, and root into pools d and r are taken from Polglase & Wang (1992) for a tropical forest. Soil carbon is separated into microbial biomass (pool b) and humus (pool h) (Jenkinson, 1990). Decomposition of carbon in each pool follows the first-order kinetics:

$$\frac{dC_i}{dt} = L_i - \kappa_i C_i;\ i = \mathrm{d},\ \mathrm{r},\ \mathrm{b\ or\ h}, \tag{3}$$

where $C_i$ is the size of carbon pool in $g\,C\,m^{-2}$, $L_i$ is the carbon input to pool $i$ ($g\,C\,day^{-1}$) and $\kappa_i$ is the decay rate of pool $i$ ($day^{-1}$).

Carbon inputs to different litter and soil carbon pools ($L_i$) are calculated as

$$L_d = \sum_j f_j D_j; \quad j = \text{leaf, branch or root}, \tag{4}$$

$$L_r = \sum_j (1 - f_j) D_j, \tag{5}$$

$$L_b = \frac{\beta}{1 + m_c} \sum_i \kappa_i C_i; \quad i = \text{d, r, b or h}, \tag{6}$$

$$L_h = \frac{1 - \beta}{1 + m_c} \sum_i \kappa_i C_i; \quad i = \text{d, r, b or h}, \tag{7}$$

where $f_j$ is the fraction of plant litter entering $L_d$, and $\beta$ and $m_c$ are empirical constants. When litter carbon decomposes, a fraction of the decomposed litter carbon, $m_c/(1 + m_c)$, is released as $CO_2$ (heterotrophic respiration), and the rest enters SOM with a fraction of $\beta/(1 + m_c)$ and the soil microbial biomass carbon pool with a fraction of $(1 - \beta/(1 + m_c)$. Parameter $m_c$ is a function of cation exchange capacity ($\text{C mol kg}^{-1}$ of soil) (see Jenkinson, 1990).

$CO_2$ emission of SOM decomposition, $R_s$, is calculated as

$$R_s = \frac{m_c}{1 + m_c} \sum_i \kappa_i C_i. \tag{8}$$

The decay rate, $\kappa_i$, is also assumed to be dependent on soil temperature at 5 cm depth. That is

$$\kappa_i = \kappa_{i,25} f_T, \tag{9}$$

where $\kappa_{i,25}$ is the decay rate at a soil temperature of 25 °C (see Table 4), and $f_T$ is calculated as

$$f_T = a_1 \exp(\alpha_g (T_s - 25)), \tag{10}$$

where $a_1$ represents the relative soil organic carbon decomposition rate at 25 °C, $\alpha_g$ is the temperature coefficient of SOM decomposition ($^\circ C^{-1}$) and $T_s$ is soil temperature at 5 cm depth.

On the other hand, soil respiration, $R_g$, comprises $CO_2$ release of the SOM decomposition ($R_s$) and root respiration ($R_r$):

$$R_g = R_s + R_r. \tag{11}$$

Root respiration, $R_r$, is modeled as

$$R_r = a_2 W_r \exp(\alpha_{\text{root}} (T_s - 25)), \tag{12}$$

where $a_2$ is specific root respiration rate at a root temperature of 25 °C ($\text{g C g}^{-1}\,\text{day}^{-1}$), $\alpha_{\text{root}}$ is the temperature coefficient of root respiration ($^\circ C^{-1}$) and $W_r$ is carbon of live roots ($\text{g C m}^{-2}$).

As only aboveground litter fall was measured, we, therefore, assume that belowground NPP was proportional to the aboveground litter fall carbon. That is

$$D_{\text{root}} = a_3 (D_{\text{leaf}} + D_{\text{branch}}), \tag{13}$$

where $a_3$ is a parameter to be estimated. Using the measurements of $D_{\text{leaf}}$ and $D_{\text{branch}}$, $T_s$, the initial carbon pool sizes and the root biomass carbon, we calculate the $R_g$ for given estimates of $a_1$, $a_2$ and $a_3$ with Eqns (3)–(12). Using nonlinear optimization package PEST (Doherty, 2002), we obtained the optimal estimates of $a_1$, $a_2$ and $a_3$ by minimizing the following cost, $J$:

$$J = \sum_n \frac{(R_g - R_{\text{obs}})^2}{\sigma_R^2} + \frac{\left(\sum_i C_i - C_{\text{obs}}\right)^2}{\sigma_C^2} \tag{14}$$

where $R_{\text{obs}}$ is the measured soil respiration ($\text{g C m}^{-2}\,\text{day}^{-1}$) and $C_{\text{obs}}$ is the measured soil organic carbon down to 60 cm depth ($\text{g C m}^{-2}$), and $\sigma_R$ and $\sigma_C$ represent the measurement errors in soil respiration and soil carbon, respectively.

Using the estimate of $a_3$, measurements of $D_{\text{leaf}}$ and $D_{\text{branch}}$ and $\Delta C_{\text{plant}}$ and $\Delta C_{\text{cwd}}$, we calculated the NPP of a forest using Eqn (2). If changes in live plant biomass and CWD are ignored, the fraction of NPP that is allocated belowground is given by $a_3/(1 + a_3)$.

## Results

### *Responses of soil respiration to soil temperature and moisture*

Measurements show that the diurnal variation of soil respiration is quite small (data not shown). Mean soil respiration from 9:00 to 12:00 hours is a very good approximation of the 24-hourly mean rate of the same day (Fig. 1). The slopes of linear regressions between the mean soil respiration rates as measured from 9:00 to 12:00 hours and that from 0 to 24:00 hours are not significantly different from 1. Similar results were also found by Davidson *et al*. (1998). Their soil respiration measurements were made between 9:00 and 12:00 hours, when the average flux of the diurnal cycle occurred. They were able to use the morning measurements to make daily estimates. Therefore, daily mean soil respiration rates were calculated as averages of measurements taken from 9:00 to 12:00 hours or 24 hourly, and are used in subsequent analysis.

We plotted the daily mean soil respiration rates, $y_1$, and daily mean soil temperature at 5 cm over the measurement periods and fitted the following regression to the data for each treatment:

$$y_1 = a \exp(bT_s). \tag{15}$$

We found that the above regression can explain 80–95% of total variance in the measured mean soil respiration over a period of 12 months for all six plots (Fig. 2). Table 2 lists the values of regression coefficients and $r^2$ for all six plots.

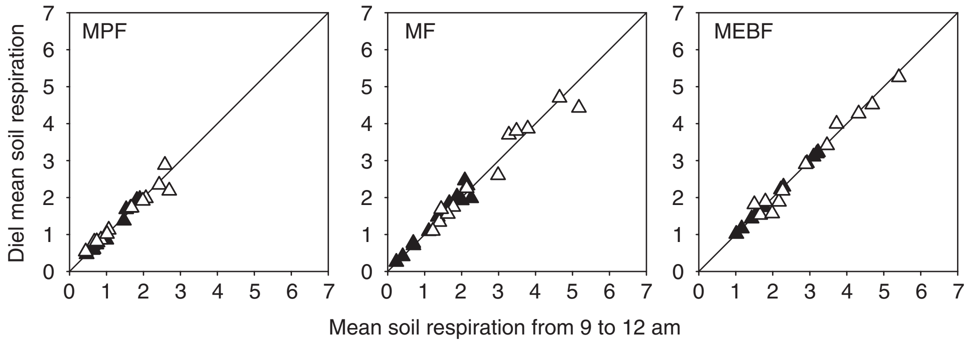

**Fig. 1** A comparison of the mean hourly rate (μmol $m^{-2}$ $s^{-1}$) of soil respiration from 9:00 to 12:00 hours with the 24-hourly diel mean rate (μmol $m^{-2}$ $s^{-1}$) of soil respiration in the same days for the three sites. Note that the solid line is the 1 : 1 line. The open and filled triangles represent the treatments of soil + litter and soil, respectively.

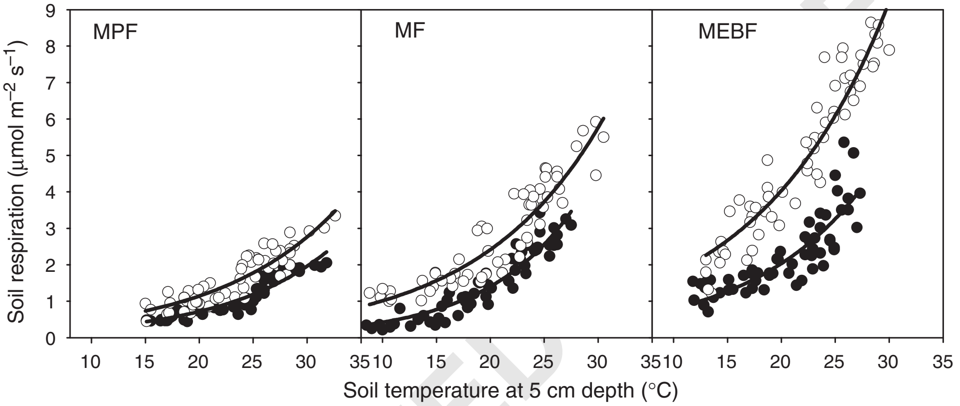

**Fig. 2** Response of soil (filled circle) or soil and litter (open circle) respiration to soil temperature at 5 cm depth for three forest types in Dinghushan Biological Reserve. The curves are fitted using Eqn (15).

Both regression coefficients are well within the ranges of values found for other forests (Raich & Schlesinger, 1992). Equivalent values of $Q_{10}$ ( = exp(10*b*)) range from 2.2 for MEBF (S + L) to 3.3 for MF(*S*), and respiration rate at 0°C (coefficient *a*) is more variable, ranging from 0.1 to 0.8 μmol $m^{-2}$ $s^{-1}$. Statistical tests also show that coefficient *a* is significantly higher but coefficient *b* significantly lower for the plot with litter than for that without litter for the same forest type (see Table 3). Calculations using these sets of coefficients in the two different treatments suggest that the relative contribution of $CO_2$ respired from litter to total soil respiration decreases with an increase in soil temperature for all three forest types.

Figure 2 also shows that the respiration at the same soil temperature is smallest for the MPF forest and highest for the MEBF forest, the local climax vegetation type in the region. These differences are statistically significant (see Table 3).

**Table 2** Values of regression coefficients (*a* and *b*) in $y_1 = a\exp(bT_s)$ and $r^2$, where $T_s$ is soil temperature at 5 cm depth in °C and *y* is soil respiration in μmol $m^{-2}$ $s^{-1}$

| Treatment | *a* | *b* | $r^2$ | $Q_{10}$ | $*r^2$ |
|---|---|---|---|---|---|
| MPF (S + L) | 0.195(0.030) | 0.088(0.005) | 0.81 | 2.42 | 0.83 |
| MPF (S) | 0.095 (0.012) | 0.100 (0.005) | 0.89 | 2.74 | 0.84 |
| MF (S + L) | 0.423 (0.055) | 0.087 (0.005) | 0.86 | 2.39 | 0.88 |
| MF (S) | 0.126 (0.021) | 0.120 (0.007) | 0.89 | 3.34 | 0.83 |
| MEBF (S + L) | 0.772 (0.081) | 0.082 (0.004) | 0.90 | 2.28 | 0.83 |
| MEBF (S) | 0.309 (0.006) | 0.094 (0.008) | 0.73 | 2.57 | 0.82 |

Units are μmol $m^{-2}$ $s^{-1}$ for *a* and $^{\circ}C^{-1}$ for *b*. Values in brackets represent the standard error of the mean. Treatments 'S + L' and 'S' represent ground with and without surface litter, respectively. $Q_{10}$ was calculated as exp(10*b*). Values of $r^2$ in the last column with asterisk are for fitting equation $y = y_1 \times y_2$ to the data. $n = 60$.
MPF, Masson pine forest; MF, mixed forest; MEBF, monsoon evergreen broad-leaf forest.

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**Table 3** *t*-test of significant difference in coefficient *a* (upper triangle in the table and in bold) or *b* (lower triangle in the table and underlined) ($n = 60$)

| | MPF (S + L) | MPF (S) | MF (S + L) | MF (S) | MEBF (S + L) | MEBF (S) |
|---|---|---|---|---|---|---|
| MPF (S + L) | | **−22.19** | **28.63** | | **51.77** | |
| MPF (S) | −12.35 | | | **9.41** | | **26.57** |
| MF (S + L) | 1.31* | | | **−38.96** | **27.50** | |
| MF (S) | | −17.63 | −29.40 | | | **21.96** |
| MEBF (S + L) | 6.13 | | 5.14 | | | **−35.28** |
| MEBF (S) | | | | 18.57 | −9.65 | |

The critical value of 95% significant level is 1.98 for a two-tailed *t*-test. Treatments 'S + L' and 'S' and represent ground with and without surface litter, respectively.

*Indicates that the difference is not statistically significant at the 95% level.

MPF, Masson pine forest; MF, mixed forest; MEBF, monsoon evergreen broad-leaf forest.

Figure 3 shows the responses of daily mean ground efflux, $y_2$, to daily mean volumetric water content in the top 10 cm of soil, $\theta_s$. We fitted the following equation to the data:

$$y_2 = y_0 \exp\left(-0.5\left(\frac{\theta_s - \theta_0}{d}\right)^2\right), \qquad (16)$$

where $y_0$, $\theta_0$ and $d$ are three regression coefficients. Values of $r^2$ here are smaller than the corresponding $r^2$ value using Eqn (15) for corresponding plots. When both soil moisture and temperature are used as independent variables and fitted to the equation $y = y_1 y_2$, where $y$ is the modeled soil respiration, we did not find a significant increase in $r^2$ as compared with those using Eqn (15) for all plots (see Table 2). Because climate in DBR region has wet (April–September) and dry seasons (October–March), air temperature is higher in the wet season than in the dry season; soil temperature and moisture are strongly correlated. Using soil temperature alone can explain most of the variance in the observed soil $CO_2$ efflux; we, therefore, did not include the effects of soil moisture on decay rates of SOM (Eqn (9)).

Using daily mean soil temperature measured at 5 cm and appropriate values of regression coefficients (Table 2) and their standard deviations, we calculated the daily and monthly soil respiration rates from all six plots and their uncertainties ( ± standard deviation), and results are shown in Fig. 4. Mean soil respiration rates in the wet season are significantly higher than those in the dry season for all three forest ecosystems, and contributions of $CO_2$ respired from litter to total soil respiration are 30%, 45% and 29% in the wet season and 26%, 44% and 21% in the dry season for MPF, MF and MEBF, respectively. The annual contributions of surface litter to total soil respiration are 28%, 45% and 27% for MPF, MF and MEBF, respectively.

### *Correlation between soil respiration and litter input*

Soil respiration results from decomposition of ground litter, SOM and plant root respiration. Current theory suggests that SOM decomposition and root respiration both are proportional to the amount of substrate (Parton *et al*., 1987; Jenkinson, 1990). Analytic solution of the Rothamsted soil carbon model shows that soil respiration is proportional to NPP (Wang & Polglase, 1995). Although it is not possible to evaluate the contribution of each component to total soil respiration from the measurements made in this study, we analyzed the litter dynamics in all three forest ecosystems, and found that monthly $CO_2$ efflux from soil and litter linearly correlated with the monthly litter input in all three forest ecosystems, but the correlation differs significantly with the lag between monthly ground efflux and monthly litter input (Fig. 5). The correlation is highest when the lag is 1 month or 6 or 7 months. The correlation between monthly soil respiration with monthly litter input is negative when the lag is equal to 7 months, and is positive when the lag is 1 month (see Fig. 6). We, therefore, consider that a 1-month lag is biologically more plausible, and the 7-month lag results from the seasonal cycle of litter fall and soil respiration.

Figure 5 also shows that soil respiration is always greater than the surface litter input of the same month or previous month in all three forests, and the differences are greater during the wet season (April–September) than during the dry season. Therefore, the accumulated amount of surface litter is greatest at the beginning of the wet season and then declines rapidly owing to high soil microbial activities at high temperature and soil moisture during the wet season. The strong positive and linear correlation between the soil respiration and the amount of surface litter fall of the previous month (see Fig. 6) provides direct evidence to

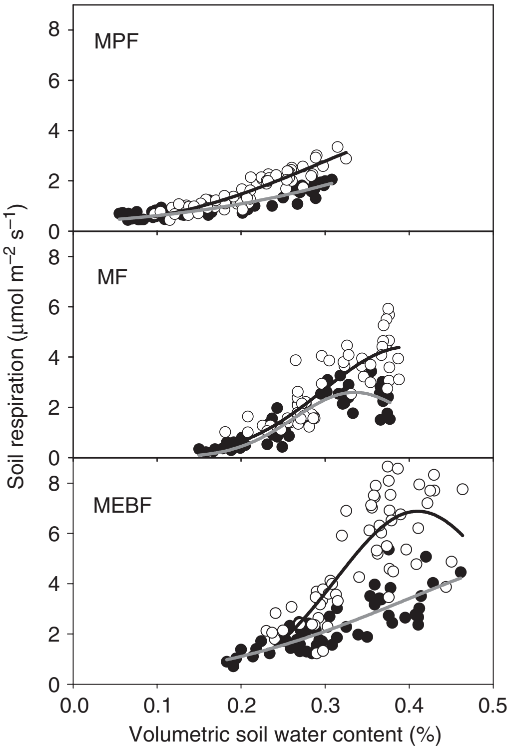

**Fig. 3** Response of soil (filled circle) or soil and litter (open circle) respiration to volumetric soil water content of the top 10 cm soil in three different forests. The fitted response curves are in dark gray and black for soil and soil and litter, respectively. Values of $r^2$ of the fitted curves are 0.85, 0.69 and 0.63 for the response of soil of Masson pine forest (MPF), mixed forest (MF)and monsoon evergreen broad-leaf forest (MEBF), respectively, and are 0.87, 0.81 and 0.63 for the responses of soil and litter of Masson pine forest (MPF), mixed forest (MF)and monsoon evergreen broad-leaf forest (MEBF), respectively, and are significant at the 99% confidence level.

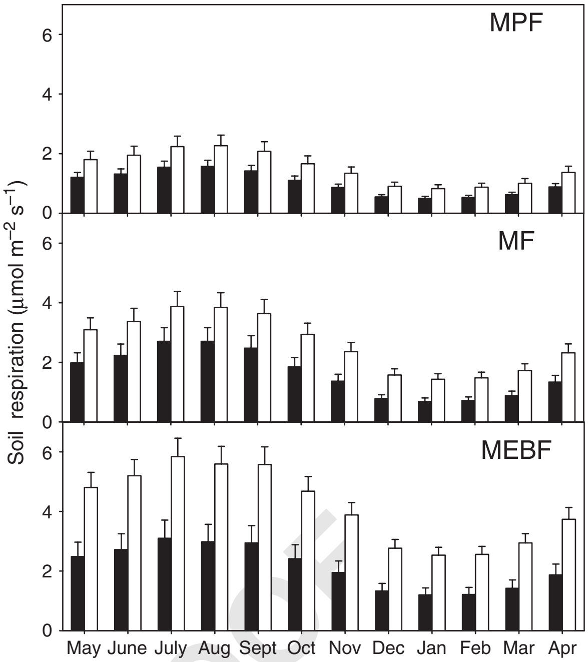

**Fig. 4** Monthly mean and 1 standard deviation of soil $CO_2$ efflux from May 2003 to April 2004 from the sites with (open bar) or without (filled bar) surface litter in three forests. Number of observations for each month is 5.

support that surface litter fall is one of the main drivers for ground biological activities.

At annual time scales, the total soil $CO_2$ effluxes are 578, 1001 and 1586 g C m$^{-2}$ yr$^{-1}$ for MPF, MF and MEBF with ground litter and 382, 624 and 810 g C m$^{-2}$ yr$^{-1}$ for MPF, MF and MEBF without ground litter, respectively. The differences in annual total soil respiration between the ground with and without surface litter are smaller for MPF and MF but significantly larger for MEBF than the amount of surface litter fall (Fig. 7). Removal of surface litter has reduced soil respiration rate by 34%, 38% and 49% for MPF, MF and MEBF, respectively. Given that the mean turnover rate of surface litter is likely greater than 1 year, removal of surface litter has reduced soil respiration rate by removing the $CO_2$ efflux from surface litter itself and slowing down the belowground biological activities of the soil and roots, and this impact is strongest in MEBF, where the reduction of soil respiration rate from litter removal is 1.8 times the annual surface litter input.

The data compiled by Davidson *et al*. (2002) and Raich & Nadelhoffer (1989) showed that the total belowground carbon allocation is about twice the annual aboveground litter fall carbon for mature forests. As shown in Fig. 8, our data agree with the regression from Raich & Nadelhoffer (1989) better than with that from Davidson *et al*. (2002). Data from two forests, MPF and MF, fall outside the 95% confidence intervals of the regression equation of Davidson *et al*. (2002).

As discussed by Davidson *et al*. (2002), the linear regression equations as shown in Fig. 8 should only be applied to forests at approximately steady state, which is true for all three mature forests ($>$50 years old) in this study. Interannual climatic variations may result in significant deviations of either aboveground litter fall or soil respiration from their respective long-term mean. Our measurements show that the mean amount of aboveground litter fall from 2000 to 2004 was 305 ± 19, 446 ± 58 and 359 ± 44 g C m$^{-2}$ yr$^{-1}$ for MPF, MF and MEBF, respectively, as compared with the annual aboveground litter fall carbon of 219, 424 and 438 g C m$^{-2}$ yr$^{-1}$ in the year 2003/2004. The differences may explain some of the departure of our data from regressions for other mature forests worldwide as reported by Davidson *et al*. (2002).

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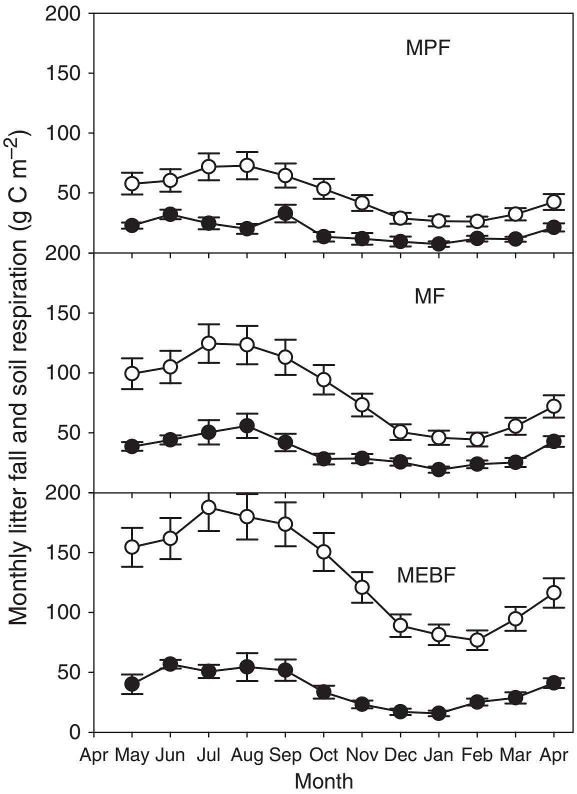

Fig. 5 Monthly litter fall (filled circle) or soil respiration (open circle) in three forests from May 2003 to April 2004. Number of observations for each data point is 5 for soil respiration and 10 for litter fall. Error bar represents one standard deviation.

### *Inferred belowground NPP from soil respiration and litter fall measurements*

Estimates of NPP of forest ecosystems have been problematic because of the difficulty in measuring belowground biomass production (Clark *et al*., 2001). Indirect methods have been developed to estimate belowground NPP (Nadelhoffer & Raich, 1992), but are yet to be validated against a wide range of field measurements. By assuming that the carbon balance of a mature forest ecosystem is at steady state, Davidson *et al*. (2002) estimated the belowground NPP from litter fall and soil respiration measurements. In this study we estimate the belowground NPP and root respiration and their uncertainties by fitting the Rothamsted soil carbon model (Jenkinson, 1990) to the measurements of total soil organic carbon and soil respiration rate.

Estimates of some model parameters are listed in Table 4. They were derived as follows. On the basis of the results in Table 2, we used a temperature coefficient for soil respiration of $0.087^{\circ}\mathrm{C}^{-1}$ for all three forests. Laboratory measurements by Yi *et al*. (2003) showed similar temperature sensitivities of respiration of cut roots from all three forests; a value of $0.1^{\circ}\mathrm{C}^{-1}$ was used for all three forests in the simulation. Estimates of root biomass carbon from the forest inventory by Tang *et al*. (2005) were 405, 440 and 480 g C m$^{-2}$ for MPF, MF and MEBF, respectively.

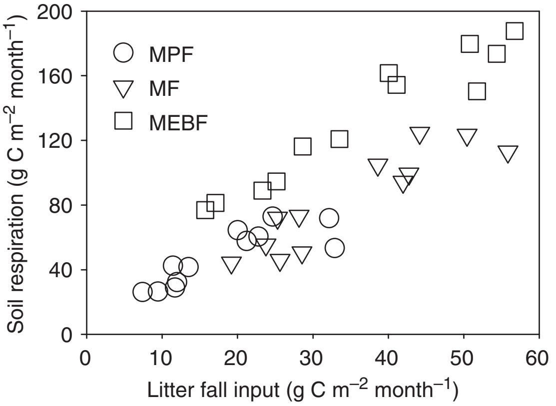

Fig. 6 Correlation between monthly soil respiration and litter fall of the previous month in three forest types. Values of $r^2$ are 0.71, 0.83 and 0.93 for Masson pine forest (MPF), mixed forest (MF) and monsoon evergreen broad-leaf forest (MEBF), respectively ($n = 12$).

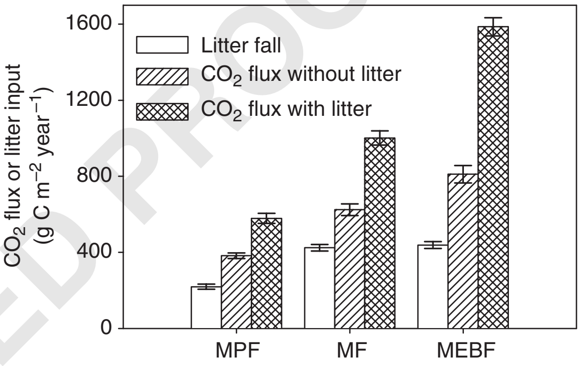

Fig. 7 Annual amount and one standard deviation of litter fall or soil respiration for the sites with or without surface litter cover in three forest types. Number of observations is 12.

Input to the Rothamsted soil carbon model includes both aboveground and belowground daily litter input and soil temperature at 5 cm depth. We used the measurements of soil temperature at 5 cm depth at sites adjacent to the chamber sites and measurements of monthly aboveground litter fall of leaves ($D_{\mathrm{leaf}}$) and branches ($D_{\mathrm{branch}}$). We assumed that litter fall rates of leaves and branches are constant within a month and vary from month to month. Changes in CWD ($\Delta D_{\mathrm{cwd}}$) are estimated from the forest inventory (Tang *et al*. 2005), and are 1.6, 135 and 205 g C m$^{-2}$ yr$^{-1}$ for MPF, MF and MEBF, respectively.

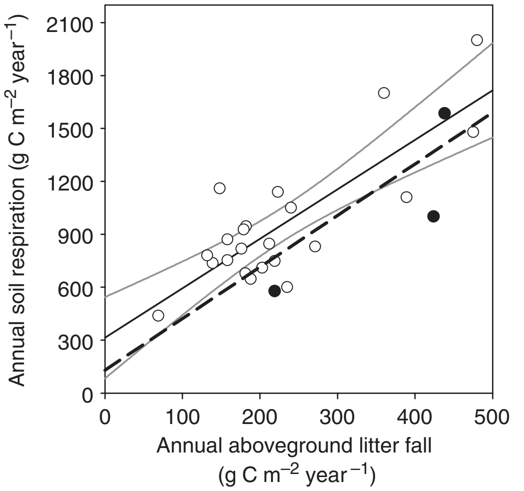

**Fig. 8** Relation between annual aboveground litter fall and annual soil respiration for mature forests. The open circles are for data as compiled by Davidson *et al*. (2002), and linear regression equation we fitted for their data $y = 313 + 2.80x$ ($n = 22$, $r^2 = 0.65$), is shown in solid line and the 95% confidence intervals are shown in dark gray lines. The dash line represents the linear regression obtained by Raich & Nadelhoffer (1989), $y = 130 + 2.92x$. The closed circles are for three forests from this study.

**Table 4** Estimates of some model parameters as used in the simulation

| Parameter | Estimate | Unit | Source |
|---|---|---|---|
| $\alpha_{root}$ | 0.1 | $^{\circ}C^{-1}$ | Yi *et al*. (2003) |
| $\alpha_{g}$ | 0.087 | $^{\circ}C^{-1}$ | This study |
| $\kappa_{r,25}$ | 0.3 | year$^{-1}$ | Jenkinson (1990) |
| $\kappa_{d,25}$ | 10 | year$^{-1}$ | Jenkinson (1990) |
| $\kappa_{b,25}$ | 0.66 | year$^{-1}$ | Jenkinson (1990) |
| $\kappa_{h,25}$ | 0.02 | year$^{-1}$ | Jenkinson (1990) |
| $f_{leaf}$ | 0.3 | dimensionless | Polglase & Wang (1992) |
| $f_{branch}$ | 0.05 | dimensionless | Polglase & Wang (1992) |
| $f_{cwd}$ | 0.05 | dimensionless | Polglase & Wang (1992) |
| $f_{root}$ | 0.3 | dimensionless | Polglase & Wang (1992) |
| $m_c$ | 1.84 | dimensionless | Polglase & Wang (1992) |
| $W_{root}$ (MPF) | 405 | g C m$^{-2}$ | Unpublished data |
| $W_{root}$ (MF) | 440 | g C m$^{-2}$ | Unpublished data |
| $W_{root}$ (MEBF) | 480 | g C m$^{-2}$ | Unpublished data |

Value of $m_c$ was calculated using the equation from Jenkinson (1990) using a value of 15 cmol kg$^{-1}$ soil for soil cation exchange capacity.
MPF, Masson pine forest; MF, mixed forest; MEBF, monsoon evergreen broad-leaf forest.

NPP of all three forests can then be calculated using Eqn (2) if $a_3$ is known. We estimated $a_3$ and other two parameters ($a_1$ and $a_2$) using nonlinear optimization. We ran the model as described by Eqns (3)–(12) for 1000 years by reusing daily measurements of soil temperature and aboveground litter fall carbon until all carbon pools reached steady state and ran another year for calculating $J$ (see Eqn (14)). Values of $\sigma_R$ and $\sigma_C$ used in the optimization were 0.1 μmol m$^{-2}$ s$^{-1}$ and $0.01C_{obs}$, respectively.

The optimal estimates of total soil organic carbon are 6510.7, 7442.1 and 9107.0 g C m$^{-2}$, as compared with measurements of 6510.6, 7442.4 and 9104.7 g C m$^{-2}$ in the top 60 cm depth of soil in the three respective forests. Figure 9 compares the modeled daily soil respiration rates with measurements for each of the three forest types. The model simulates the seasonal variation of soil respiration rates very well, but underestimates between day of year (DOY) 200 and 220 and overestimates between DOY 250 and 280 of the soil respiration rate as compared with the measurements for both MF and MEBF. Detailed analysis shows that the differ-

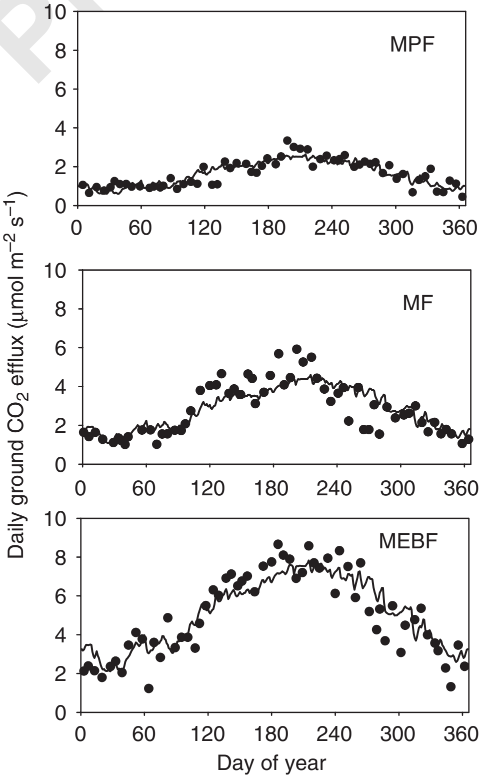

**Fig. 9** The simulated (curve) or observed (point) 24-hour mean soil respiration rate throughout the year 2003/2004 in three forest types. The 365 days of the year are arbitrarily made up of months of January to April of 2004 (day of year 1–121) and months of May to December of 2003 (day of year 122–365).

**Table 5** Estimates of three model parameters from nonlinear inversion

| | $a_1$ | $a_2$ | $a_3$ |
|---|---|---|---|
| MPF | 1.29 (0.08) | 0.40 (0.07) | 1.17 (0.12) |
| MF | 2.32 (0.26) | 0.86 (0.29) | 0.60 (0.22) |
| MEBF | 3.32 (0.38) | 1.82 (0.50) | 1.62 (0.36) |

Numbers with brackets represent one standard deviation of the mean.

MPF, Masson pine forest; MF, mixed forest; MEBF, monsoon evergreen broad-leaf forest.

ence in temperature between the soil in the chamber and site where continuous soil temperature measurements were taken and used for modeling annual soil respiration using the Rothamsted soil model can explain most of the differences in soil respiration rate at the two forest sites.

Optimal estimates of three parameters, $a_1$, $a_2$ and $a_3$, are shown in Table 5. As the decomposition rate of each soil carbon pool is $\kappa_{i,25} f_T C_i$, parameter $a_1$ represents the relative SOM turnover rate at 25$^{\mathrm{o}}$C. The higher the value of $a_1$, the faster the SOM decomposes at a given temperature. Estimates of $a_1$ increase from pioneering forest type (MPF) to transition forest (MP) to the mature forest (MEBF); therefore, the rate of soil carbon and other nutrients cycling also increases with maturity.

Parameter $a_2$ represents the specific respiration rate of belowground root biomass. As much of root respiration is related to fine-root production and maintenance (Nadelhoffer & Raich, 1992), the rate of fine-root turnover can be considered to be proportional to $a_2$. Our results show that the fine-root turnover rate in MEBF is twice as much as that in MF, and four times as fast as that in MPF. Some of the difference may result from the fast turnover rate of the root system of a very dense understory in MEBF, as compared with relatively sparse understory in MPF and MF.

Assuming net standing biomass accumulation over the year ($\Delta C_{\mathrm{plant}}$) is zero in all three forests, we can estimate the belowground and total NPP of all three forests. Parameter $a_3$ relates NPP belowground to that aboveground. The ratio of belowground to aboveground NPP varies from 0.6 for MF to 1.62 for MEBF, and is higher than the range of 0.2 to 1.2 reported by Clark *et al*. (2001) for tropical forests. Aboveground NPPs excluding change in standing biomass as measured were 219, 424 and 438 g C m$^{-2}$ yr$^{-1}$ for MPF, MF and MEBF, respectively. Our inversion estimates of belowground NPP were 256 ± 26, 254 ± 93 and 710 ± 158 g C m$^{-2}$ yr$^{-1}$.

Based on forestry inventories in 1994 and 1999 in all three forests, we estimated that the amount of CWD over the period increased in all three forests (Tang *et al*., 2005). Annual increases in CWD are 2, 135 and 204 g C m$^{-2}$ yr$^{-1}$ for MPF, MF and MEBF, respectively. Forest inventory data for MPF and MF have not been fully analyzed yet. Measurements from MEBF show that the total standing biomass including belowground roots decreased at a rate of 382 g C m$^{-2}$ yr$^{-1}$ from 1994 to 1999 (Zhang *et al*., 2003). Therefore, our estimate of total NPP of MEBF was 970 g C m$^{-2}$ yr$^{-1}$, which is slightly lower than the highest NPP (1085 g C m$^{-2}$ yr$^{-1}$) reported by Clark *et al*. (2001) for tropical forests.

Because no measurements are available for the standing biomass carbon changes for MPF and MF, our estimates of total NPP for these two forests may be biased, and the biases are expected to be probably less than 10%. Previous studies of these two forests in the 1990s suggested that increases in standing biomass carbon are positive in MPF and close to zero in MF (Zhou unpublished data).

Using inversion, we estimated that belowground NPP is 256, 254 and 710 g C m$^{-2}$ yr$^{-1}$ and annual totals of root respiration are 132, 250 and 544 g C m$^{-2}$ yr$^{-1}$ for MPF, MF and MEBF, respectively. Therefore, the total amount of carbon allocated belowground is 388, 504 and 1254 g C m$^{-2}$ yr$^{-1}$ for these three forest ecosystems. Our estimates of total belowground carbon allocation are much smaller than the estimates using the equations of either Raich & Nadelhoffer (1989) or Davidson *et al*. (2002) for MPF and MF, but slightly higher for MEBF. It is possible that the steady state assumption as used by Raich & Nadelhoffer (1989) and Davidson *et al*. (2002) does not hold for these two relatively younger forests (MPF and MF), but is reasonably good for MEBF. Another cause for the discrepancy may include a small sample size of soil respiration measurements in this study.

## Discussion

Raich & Schlesinger (1992) found that soil temperature can be used to explain much of the observed variation in soil respiration in different ecosystems. We also found that a single exponential function can be used to describe the responses of soil respiration rate to soil temperature quite well, and that the response of soil respiration rate to temperature, parameter $b$, is stronger in MPF than in the other two forests. It is possible that microbial communities adapt to temperature change in the more advanced succession forests (MF and MEBF) better than the pioneering forest (MPF), and can maintain relatively high activity throughout the year when soil temperature changes from a cool dry season to a warm wet season. The equivalent values of $Q_{10}$ for all three forests with surface litter vary from 2.4 to 2.3, similar to the median value of 2.4 as reported for soil respiration from different terrestrial ecosystems in the world by Raich & Schlesinger (1992). The $Q_{10}$ values in this paper included possible moisture limitations, and, therefore, represent the sensitivity of belowground biological activities to temperature and moisture in the field. As pointed out by Lloyd & Taylor (1994) and Kirschbaum (1995), the $Q_{10}$ value generally decreases from cold climate to warm climate, or the soil microbial activity in cold climate regions is more sensitive to temperature than in temperate and tropical regions. For example, a value of 4.8 was estimated for boreal forest soil (Moren & Lindroth, 2000), of 3.9 for a temperate mixed hardwood forest (Davidson *et al*., 1998) and of 2.4 for a subtropical forest in this study. Values of $Q_{10}$ less than 2 have also been reported for tropical forest soils (Tjoelker *et al*., 2001). However, it is important to distinguish the short-term response from the long-term response of soil respiration to temperature. For example, we do not find any seasonal change in $Q_{10}$ in this study in all three forests. For the mean annual temperature of 22 °C at DBR, the equation used by Kirschbaum (1995) gives a value of 2.3 for $Q_{10}$ ($Q_{10} = \exp[2.04(1-T_s/36.9)]$), which is very similar to our estimate of 2.4.

Litterfall and decomposition processes strongly influence primary production and regulate energy flow and nutrient cycling in the forest ecosystems (Waring & Schlesinger, 1985). We found that the total monthly soil respiration rate increases linearly with the aboveground litter of the previous month. Removal of surface litter significantly slowed down the decomposition of SOM or root respiration or both. This study also found that removal of surface litter significantly increased the sensitivity of soil respiration rate to temperature. All three forests we studied are relatively stable or the differences between two fluxes: annual NPP and annual soil respiration are much smaller than the fluxes themselves. Sudden removal of surface litter has a significant impact on the cycling of carbon, nitrogen and other nutrients in the ecosystem and possibly on the composition of soil microbial biomass. Further studies are needed for a better understanding of why removal of surface litter increases the temperature sensitivity of belowground biological activities.

Our inversion study shows that fractions of NPP allocated belowground are 54%, 37% and 62%, and that respiration from the decomposition of SOM accounts for 56%, 75% and 55% of total soil respiration for MPF, MF and MEBF, respectively. Our results confirm our hypothesis that belowground carbon allocation increases during forest succession because of increasing belowground competition, and are consistent with the results of previous studies (Zhou & Yan, 2000, 2001). We may have overestimated the belowground allocation for MPF and MF because a small increase (<10%) in standing biomass in 2003/4 in these two forests has not been accounted for in our estimate of NPP. During forest succession in subtropical China, needle-leaved species are dominant. Establishment of pioneering needle-leaf species from a severely disturbed ecosystem reduces soil erosion and increases soil fertility, which created a more suitable environment for the invasion of broad-leaf tree species. The fast-growing broad-leaf species have higher NPP and allocate more carbon belowground, and thus eventually succeeded in becoming the dominant species in the forests. When the canopy is closed during succession, competition for belowground nutrients intensifies, and, therefore, belowground carbon allocation will increase.

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